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Proceedings – Ecology and Management of Annual Rangelands

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Preface

Introduced weeds, both annuals and perennials, have become a problem in sustaining native plant communities. Within the Intermountain Region, no other weedy species has attained the widespread distribution and dominance of cheatgrass (*Bromus tectorum*). Other weeds possess undesirable features and may be difficult to eradicate or control, but few have occupied and disrupted the ecology of such vast areas as cheatgrass. Early workers and land stewards recognized the explosive nature of this annual grass as it caught fire and its ability to compete with native vegetation. Initially, some land managers were concerned about the loss or gain in seasonal forage as cheatgrass and other annual weeds appeared, but the ecological impact of this species was soon realized.

Although various efforts have been directed toward containing and restoring infested sites, cheatgrass and other related annual weeds continue to expand, presenting ever more serious management problems. The loss of native plant communities to less desirable introduced annuals damages various resources—including watershed and wildlife. The value of these resources has become increasingly important as weeds have continued to expand.

Cheatgrass presents an increasingly acute problem—fire. The conversion of diverse native communities to annual grasses has resulted in a dramatic increase in the frequency of fires. The cost of containing and restoring sites that frequently burn has become a major problem throughout the West. Site degradation results not only from the displacement of native vegetation by cheatgrass, but also from repeated burning.

Although considerable information has been developed concerning the ecology, competitive traits, management, and revegetation potential of cheatgrass communities, measures are needed to contain and restore weed-infested sites. Continued expansion of annual weeds must be corrected. This symposium was developed to better identify weed problems on range and wildland sites, and to address management and restoration measures that can be employed.

Papers in the proceedings are grouped in nine principal topics that range from introductory material to information on ecology and resources, various restoration subjects, and management.

Acknowledgments

The symposium was cooperatively developed by the U.S. Department of the Interior, Idaho Bureau of Land Management, the U.S. Department of Agriculture, Forest Service, Intermountain Research Station, and the University of Idaho. Appreciation is extended to Mike Pellant, Idaho Bureau of Land Management, Boise, who assumed a major role in developing the program. Other individuals contributed to the symposium, field tours, and publication of the proceedings. Their efforts are certainly appreciated, and they have provided considerable information and insight to the management of sites infested with weeds.

In addition, we appreciate the efforts of the following individuals who coordinated and hosted their symposium sections:

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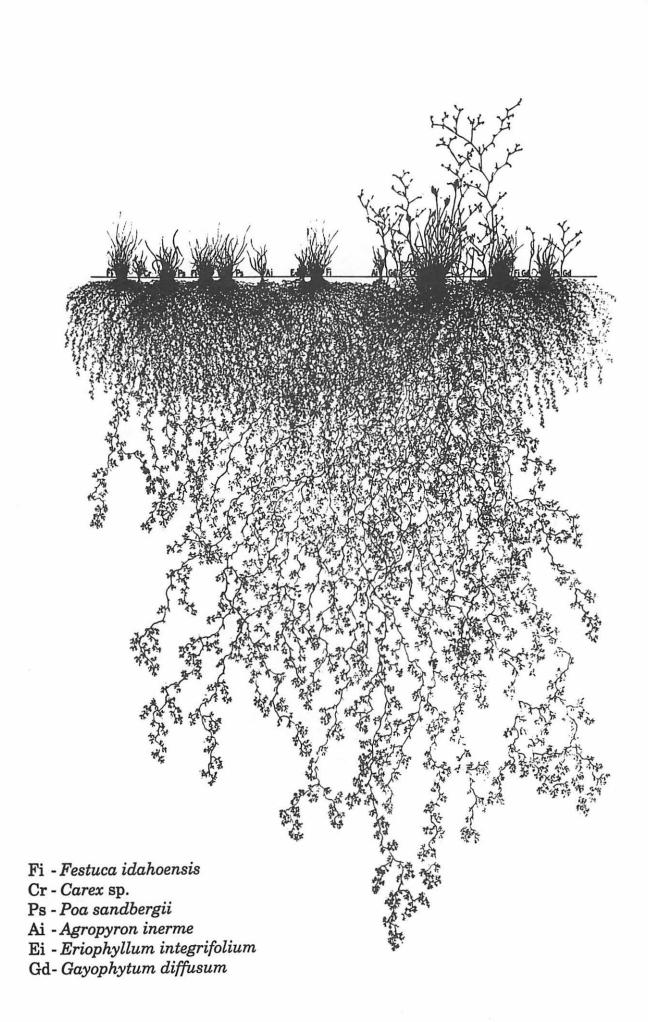
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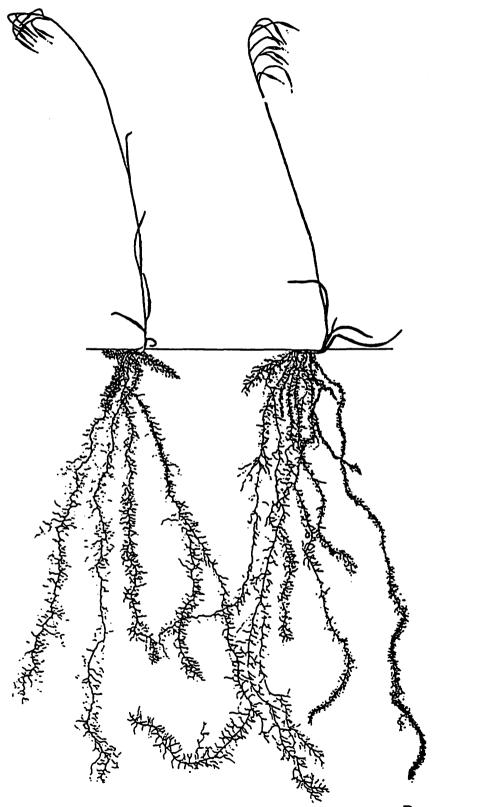
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Management

Introductory Papers



Bromus tectorum

SYMPOSIUM INTRODUCTION: MANAGEMENT OF SEMIARID RANGELANDS—IMPACTS OF ANNUAL WEEDS ON RESOURCE VALUES

Delmar Vail

Weeds may be the most serious natural resource threat ever seen in the Great Basin. Annual weeds have invaded and now dominate many of our plant communities. They greatly complicate management of rangelands under our land use plans. Our best information to date indicates that there are about 62 problem weed species in southern Idaho. That figure alone says we are dealing with a problem unprecedented in the history of public land management. It's going to take our best multi-State and multiagency efforts to deal effectively with the annual weed problem. Cooperation between Bureau of Land Management personnel and other agencies has been good, and we'll need to continue to work together. We've made tremendous progress in the last few years, but the challenge is still huge.

First, a little background concerning Idaho, the site of this symposium. The 12 million acres of public land in Idaho contain many resource values—wildlife, forage for livestock grazing, watershed values, recreation, threatened and endangered species. This list goes on and on. Management of all these resources depends on the kinds and proportions of vegetation that grow on public land. And that's what we're here to talk about.

Here's a closer look at some of the annual weed problems in Idaho and other Great Basin locations.

Halogeton...I can remember when I first started with BLM back in the mid-1950's, and halogeton was a key word. It brought BLM partial rehabilitation funding back in those days. Halogeton is an annual forb that is most poisonous to sheep but can also affect cattle in certain conditions. The Halogeton Control Act of 1952 authorized funding for BLM to seed crested wheatgrass on about 300,000 acres. These seedings, in the mid-1950's, combined with better livestock management, greatly reduced the halogeton problem.

Along with that, we had Russian thistle, another annual forb that thrives in disturbed environments. Russian thistle also presented us with a funding opportunity because it was a host to the beet leaf hopper that damaged irrigated crops. BLM seeded crested wheatgrass on thousands of acres around croplands in the 1950's and 1960's.

But with all this going on, it was cheatgrass, introduced to southern Idaho in the late 1890's, that became our main problem. Recent surveys in Idaho indicate that we have a cheatgrass monoculture of about 1.1 million acres and a cheatgrass understory of 1.8 million acres. And there is strong cheatgrass potential on another 1.3 million acres. Figures of the same magnitude have been found for Oregon, Nevada, and Utah.

Here are some of the impacts of cheatgrass in Idaho, and particularly on BLM land.

Cheatgrass has increased the size and intensity of wildfires. Rangeland burned in Idaho since 1980 is 1.8 million acres. Fire suppression costs average almost \$4 million annually. During the mid-1980's, our worst fire years, rehabilitation efforts cost about \$2 million annually.

The impacts of wildfires include loss of livestock forage immediately after the fire and during the rest-rehabilitation period. One of our biggest concerns, however, is the loss of plant diversity, especially shrubs, that are continually burned because of the presence of cheatgrass.

I'd like to talk about three specific areas. In the Snake River Birds of Prey Area, over 50 percent of the 480,000 acres have burned at least once in the last 10 years. Loss of this habitat may ultimately affect rodent—and therefore, raptor—productivity in this unique area that has North America's highest density of breeding raptors.

Near the Picabo Hills, in south-central Idaho, northeast of Twin Falls, extensive wildfires in the early 1980's caused extensive loss of important deer and antelope winter range. In the winter of 1985-1986, severe winter weather conditions caused large numbers of animals to migrate near the urban areas of the Treasure Valley. Many animals were killed by automobiles and trains, prompting formation of an ad hoc shrub restoration committee. Through this committee, shrub restoration and planting fire-resistant plants began, and we're still working on that.

We found that the Intermountain Research Station's Shrub Sciences Laboratory in Provo, UT, had been working for the previous 20 or 25 years on restoring disturbed rangelands infested with cheatgrass. When we began looking for plants for this restoration program, the lab was happy that an agency was coming to it with this need.

On the Squaw Butte Fire complex, to the northeast of Boise, ID, 30 wildfires were started by lightning in 1986, burning more than 218,000 acres of rangeland north of Emmett. Loss of more than 59,000 acres of critical deer winter range prompted officials at the Idaho Department of Fish and Game to label this the worst wildlife disaster in 20 years.

Again, we developed a coordinated rehabilitation plan that included shrubs to restore these burned rangelands.

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. Delmar Vail is the Idaho State Director of the Bureau of Land Management, U.S. Department of the Interior, Boise, ID.

Unfortunately, the extended drought of the late 1980's hampered shrub restoration success.

Another rangeland invader is medusahead wildrye, an annual grass that was introduced to Idaho in the 1930's. In some ways, I think it's a greater problem than cheatgrass. It's less desirable as forage than cheatgrass, and it's more flammable because its litter doesn't decompose as readily as cheatgrass. It can outcompete cheatgrass, and it now grows on new sites on the Snake River Plain.

And we can't talk about weeds without including the noxious weeds that are invading areas now dominated by cheatgrass-infested and medusa-infested rangelands. These include leafy spurge, knapweed, rush skeletonweed, and yellowstar thistle. Noxious weeds are more difficult to control and provide less forage and habitat than cheatgrass and medusahead.

Even though the problems posed by weeds are immense, they are not unsolvable. Some of the actions we've initiated in Idaho to help solve the problems are:

- Improved management of rangelands. We need to consider annuals in designing grazing systems in allotment management plans. Proper levels and timing of livestock grazing can reduce cheatgrass fuels.
- Aggressive fire suppression program using state-ofthe-art firefighting technology. Idaho has some of the most experienced and dedicated rangeland firefighters in the West. We are also lucky to have the fire professionals at the nearby National Interagency Fire Center at Boise.
- Innovative fire rehabilitation program. In addition to grasses and forbs, we are reseeding native shrubs on burned rangeland where wildlife habitat values are high. A good example of this approach is the Thorn Creek Fire Rehab Project in the Shoshone District. After a 60,000-acre wildfire in July 1990, seven seeding prescriptions were developed by an interdisciplinary team based on site potential and management objectives. Two seeding mixtures contained nine species and all mixtures contained at least one grass, forb, and shrub species. Native grasses, especially bluebunch wheatgrass, were extensively used. Big sagebrush was aerially seeded on 14,000 acres.

- Greenstripping program. Implemented in 1985, the goal of the greenstripping program is to plant fireresistant plant materials at strategic locations to reduce wildfire spread. Other objectives are to protect shrublands and private property at urban-wildland interfaces and to reduce fire suppression and rehabilitation costs. So far, 350 miles of greenstrips have been planted in Idaho. And they seem to be working. Two wildfires have burned into the greenstrips and were slowed or stopped. However, drought has slowed establishment of some greenstrips. Some herbicides are again available to control cheatgrass, providing us another control tool. A multi-State cooperative greenstrip program was initiated in October 1991. Greenstrip pilot projects were started in Oregon, Nevada, and Utah in 1992.
- A cooperative "Intermountain Greenstripping and Rehabilitation Research Project." Started in 1987, the six cooperators involved are the University of Idaho, the Forest Service's Intermountain Research Station, the Agricultural Research Service, the Soil Conservation Service, Boise State University, and the Idaho Department of Fish and Game. Project goals are to develop plant materials and seeding technology to improve greenstripping and range rehabilitation project success. In Oregon, BLM initiated a cooperative research unit with Oregon State University to develop management strategies and plant materials to enhance our ability to maintain and restore native plants. This "Plant Diversity Research Project" is compatible and complementary with the Intermountain Greenstripping and Rehabilitation Research Project in Idaho.

These steps are a start, but we need to continue finding new ways to fight the annual weed problem. Symposiums such as this offer excellent opportunities for coordination and exchange of new technology. Let's continue our efforts, and perhaps at a meeting like this in the next century, we can exchange success stories on management restoration projects.

HISTORY AND USE OF SEMIARID PLANT COMMUNITIES—CHANGES IN VEGETATION

James A. Young

ABSTRACT

The sudden introduction of concentrations of large herbivores to the sagebrush (Artemisia)/bunchgrass ranges of the Intermountain area dramatically changed the balance between herbaceous understory and woody overstory species. The near biological vacuum created by overutilization of understory species was rapidly filled by the introduction of a host of alien annual species. Cheatgrass (Bromus tectorum) dominates many of these alien communities and truncates succession. Seedling establishment of perennials, especially herbaceous perennials, is limited by cheatgrass competition for soil moisture.

INTRODUCTION

The last symposium held in the Intermountain area to discuss the ecology, management, and restoration of annual-dominated rangelands was the Cheatgrass Symposium held 27 years ago. During the introduction to my presentation at this symposium I asked how many of the audience had attended the previous meeting, and only one person responded.

This dramatically illustrates the importance of communicating historic perspectives concerning even the recent past to those currently interested in the management and restoration of rangelands. Toward establishing historical perspective for the ecology and management of Intermountain ranges this symposium provides both firstperson contact in the person of Dr. Dwight W. Billings who established research plots in the Great Basin in the 1930's (see Billings, these proceedings) and a glimpse at the future in the presentation of Dr. Ross Wight on the development of expert systems for transfer of knowledge across generations (see Wight, these proceedings).

HISTORIC CHANGES

The vegetation of the pristine sagebrush/grasslands was rather simple and extraordinarily susceptible to disturbance. The potential of the environment to support plant and animal life was limited by lack of moisture and often by accumulation of salt in the soil. The native vegetation lacked the resilience, depth, and plasticity to cope with concentrations of large herbivores. The plant communities did not bend to adapt; they shattered. This tends to make the review of grazing in the sagebrush/ grasslands a horror story, resplendent in examples of what should not have been done. In perspective, the development of ranching in the sagebrush/grasslands was a grand experiment initiated by men willing to venture beyond the limits of accepted environmental potential to settle the Great Sandy Desert between the Rocky, Sierra Nevada, and Cascade Mountains (Young and Sparks 1985).

There is a large amount of literature available with more or less direct bearing on the paragraph quoted above. The salient points in this historic perspective are: (1) the current vegetation of the Intermountain area originated during the wild climatic fluctuations of the Pleistocene as the western mountain barrier of the Sierra-Cascades arose and cast a rain shadow across the area; (2) in most of the area, native large herbivores withdrew their natural distribution from the bulk of the landscapes, except for periodic pulses of the American bison (Bison) across the Snake River Plains to eastern Oregon and the Columbia Basin; and (3) under post-Pleistocene conditions the concentration of large herbivores was sparse, especially in the Great Basin, and the dominant vertebrate herbivores were jackrabbits (Lepus spp.) (McAdoo and Young 1980).

Dr. Wayne Burkhardt of the University of Nevada strongly disagrees with most of the commonly accepted ideas concerning the evolution of the rangelands of the Intermountain area (Burkhardt 1992). He considers large herbivores to have been abundant in the Intermountain area at contact time. The classic study of the American bison by Hornaday (1887) strongly disputes this point as do the journals of such contact time travelers as Peter Skeen Ogden (Cline 1963). Burkhardt also suggests that the vegetation of the Great Basin has been stable since well into the Tertiary.

The classic study of the evolution of mid-latitude deserts conducted by Axelrod (1950) amply illustrates the relatively recent evolution of temperate desert vegetation. Perhaps the most interesting supportive evidence for Burkhardt's argument is the lack of preference domestic large herbivores exhibit for the herbage of most species of sagebrush. It well may be possible that the progenitors, North American members of the section Tridentate of *Artemisia*, did evolve under extreme browsing pressure. The evolution of secondary compounds by sagebrush species also may have been in response to nonvertebrate herbivores, by browsing pressure from jackrabbits, or they

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. James A. Young is a Range Scientist, U.S. Department of Agriculture, Agricultural Research Service, 920 Valley Road, Reno, NV 89512.

may be biochemical accidents that happened to influence preference and the rumen microflora of domestic livestock.

Of direct application to this symposium, Burkhardt uses his hypothesis of evolution of the native vegetation under intensive grazing in the Intermountain area to justify managing for cheatgrass rather than managing for the restoration of native herbaceous perennials. Apparently I am missing the point of this self-defeating reasoning (see Tipton, these proceedings, for managing with cheatgrass, but not for cheatgrass).

CLIMATIC CHANGE

One of the most significant advances in understanding the ecology of rangelands has been the widespread acceptance or realization that climatic change is a continuous process. The basis for measuring range condition and trend has been departure from the potential vegetation that often has been equated with the pristine vegetation. We now recognize that the dynamic equilibriums that existed in natural plant communities at contact times were transitory scenes on a time scale that has ecological significance to modern management.

The most significant aspect of climatic change is that anthropocentric influences, through the mechanism of changing concentrations of atmospheric gasses, may be inducing change (see Mayeux, these proceedings). Some scientists (for example, Burkhardt 1992) have used the climatic change issue as additional evidence that Intermountain rangelands should be managed for cheatgrass rather than attempting restoration of native plant communities. Essentially, the pristine plant communities of the sagebrush/grasslands were relics of former climates that were predetermined to change even if they were not grazed by domestic livestock (see Tausch, these proceedings). The relative importance of the grass genera Agropyron versus Stipa or Oryzopsis in the structure of the pristine vegetation is an interesting aspect of this argument.

RESTORING PLANT COMMUNITIES

The area of the greatest polarization of opinion concerning the management of Intermountain rangelands is centered on the use of exotic or native perennial grasses for the biological suppression of cheatgrass and the revegetation of rangelands. It has been generally accepted that restoration of rangeland plant communities using the native grasses—bluebunch wheatgrass (Agropyron spicatum), Thurber's needlegrass (Stipa thurberiana), needleand-thread (S. comata), or Indian ricegrass (Oryzopsis hymenoides) is quite difficult. During the panel discussion held at this symposium the question was raised if this was based on historic fact or was a perceived idea.

The need to seed Intermountain rangelands to restore productivity was perceived by portions of the general public as early as the 1880's (Young and Sparks 1985). P. B. Kennedy strongly advocated the use of **native** species to restore depleted ranges at the beginning of the 20th century (Kennedy and Doten 1901). As far as is known Kennedy never tried to seed native perennial herbaceous species. The earliest publications dealing with seeding depleted ranges (for example, Cotton 1908 or Griffiths 1907) dealt with exotic species for which there was a ready supply of seed. These were essentially the introduced forage species that had proven so successful in the humid East. The classic studies of A. W. Sampson (1913) also used, as the title of a bulletin reporting his research indicated, cultivated forage species. The early trials were extensive, consisting of some 500 experiments located on 86 National Forests in 11 Western States. Sampson considered most of these experiments, with notable exceptions, to be failures.

Forsling (1931) summarized the results of 2 decades of seeding trials on the rangeland of National Forests in 1931. It is important to note that the basic idea governing these seeding trials was that the greatest good could be accomplished by working with the most productive environments. This meant that seeding trials were concentrated on meadows, especially the margins of depleted meadows and depleted subalpine grasslands that formed critical watersheds.

Forsling reported establishment data for several species of native grasses, including slender (A. trachycaulum) and violet (Agropyron [?]) wheatgrass and mountain brome (Bromus marginatus). He admitted that the potential of native plant material for range seeding had hardly been touched. Forsling (1931) placed emphasis on the use of exotics: "Introduction of plants from foreign countries and the development of superior varieties by selective breeding both offer hope for the future."

In interpreting all of these early reports you must consider that they pertained to high-elevation meadows and conifer/aspen (*Populus tremuloides*) parklands. If artificial seedings were attempted in depleted big sagebrush (*Artemisia tridentata*)/ bunchgrass rangelands they were not reported. Interviews with scientists such as J. H. Robertson, whose career started as a scientist late in the 1930's, indicate that it was initially not considered possible to artificially seed in sagebrush environments with the plant material available.

RURAL RESETTLEMENT ADMINISTRATION

Seeding of sagebrush ranges in the Intermountain area was initiated in a rather unique manner. The agricultural economic conditions associated with the Great Depression coupled with a prolonged drought made it abundantly clear that many areas in Western North America were not suited for dryland farming. As part of the New Deal era, the Rural Resettlement Administration was established to purchase blocks of homesteads and return the property to public domain. In the Intermountain area, sites where this was carried out included the Crooked River area of eastern Oregon and Curlew and Black Pine Valleys in Oneida County, ID (Young and McKenzie 1982). Attempts were made to prevent accelerated wind erosion on these abandoned farms by seeding perennial grasses. The exfarmers and their largely horse-drawn equipment were hired to seed the former wheat fields.

These seedings were highly successful because of the recently introduced crested wheatgrass (Agropyron desertorum).

CRESTED WHEATGRASS

Crested wheatgrass was introduced to the northern Great Plains and was widely used to seed abandoned cropland (see Lorenz 1986 for history of introduction). It had been tried by the Forest Service, U.S. Department of Agriculture, for high-elevation seedings and was not considered a success (Forsling 1931). It had been tried in native hay meadows in the Great Basin and not considered successful because of lack of grazing animal preference when the herbage was mature.

During World War II as part of the war production effort, scientists with the Intermountain Station of the Forest Service established about 20,000 acres of experimental seedings designed to increase red meat and wool production from rangelands. This resulted in a series of publications under the general title, "How To Seed _____ Rangelands." There was one of these for southern Idaho (Hull and Pearse 1943), Nevada (Robertson and Pearse 1943), and Utah (Plummer 1943).

The "how to seed" bulletins contained nearly the same text. In comparing the native bluebunch wheatgrass and crested wheatgrass it was stated that: "Planting this species [bluebunch wheatgrass] alone is generally not recommended because of the risk involved in securing a stand. On adapted sites it is a good species to plant in combination with crested wheatgrass" (Robertson and Pearse 1943). For crested wheatgrass the bulletins state: "This hardy, long-lived, deep rooted bunchgrass is the most generally successful species for seeding the low valleys, foothills, and lower mountain slopes...."

One of the first publications that extensively dealt with native species for use in revegetation was Hoover (1939). One of the objections to the use of bluebunch wheatgrass was the awned seeds were difficult to meter from drill boxes and pass through seed tubes. This led to the popularity of the awnless form of bluebunch wheatgrass then known as beardless wheatgrass (Agrópyron inerme). There are few reports of experimentation with native grasses from the Stipa group. Schwendiman (1940) developed methods for removing awns from caryopses of native grasses including needle-and-thread. The inherent dormancy of many Stipa species may have limited experimentation with these species (for example, Rogler 1960 for S. viridula). The seeds of some of the Stipa species will germinate (Young and others 1990), but the dormancy of landscape-characterizing species such as Thurber's needlegrass has never been overcome.

I believe that a fair summary of the published and anecdotal information available concerning attempts to artificially seed big sagebrush potential ranges with native grasses through 1945 is that such attempts were generally unsuccessful. This is based on largely negative information rather than positive, published data. The introduction of crested wheatgrass made large-scale seeding of sagebrush ranges possible. Relative seedling vigor of crested wheatgrass coupled with an abundant, inexpensive supply of seed that was highly germinable may have been the major factors governing the success of crested wheatgrass. Subsequent forage production and resistance to grazing may also have been important considerations.

CHEATGRASS AND THE CLOSED COMMUNITY

During the period from 1945 until 1965, several million acres of sagebrush potential rangeland were seeded to crested wheatgrass in the Intermountain area. Much of this seeding was done to biologically suppress halogeton (Halogeton glomeratus). It is very important to recognize that a large percentage of these seedings could not be repeated today because of subsequent increases in the distribution and density of cheatgrass. The original crested wheatgrass seedings were established in seedbeds with limited cheatgrass. Cheatgrass was limited in the late 1940's and 1950's by the extreme grazing pressure that existed on many ranges (for example, Emmerich and others 1992). The dramatic increase in the forage base for Intermountain area sagebrush ranges that came about through establishment of crested wheatgrass partially permitted the establishment of universal grazing management systems that were designed to favor the establishment of native perennial grasses. The net result of these well-meaning applications of range science appears to have contributed to a gross increase in cheatgrass and new habitat for cheatgrass through associated wildfires. The biology of this process is quite simple. As predicted on the basis of research, deferment of grazing until after seed ripe or rest from grazing on a rotational basis favors the production of seeds by herbaceous perennials and the ultimate recruitment of new seedlings, provided (1) there are sufficient herbaceous perennials left to produce seeds, (2) woody plant competition permits herbaceous seedling recruitment, and (3) cheatgrass does not preempt the environmental potential. On millions of acres where rotational grazing management was applied, all of the above points were stacked against the native perennial grasses.

J. H. Robertson published the classic paper on cheatgrass competition with perennial seedlings in 1945 (Robertson and Pearse 1945). Since 1945, many scientists have established the competition mechanism of why cheatgrass communities are closed to perennial seedlings. If it was very risky to try to seed bluebunch wheatgrass in 1943 before cheatgrass became so dominant on Intermountain ranges, what are the chances for widespread range **restoration** using native species today?

The sad part of this whole scenario is that weed control revegetation systems employing herbicides that could control cheatgrass and allow range restoration have been eliminated by withdrawal of registration. Future registration of herbicides for use on rangelands to control cheatgrass competition in seedings is highly problematic (see Ogg, these proceedings).

The inherent variability in bluebunch wheatgrass and related native species is a vital part of the cheatgrassrange restoration picture. If the genotypes cannot be found in bluebunch wheatgrass populations, which can compete with cheatgrass, then range restoration is dependent on: (1) reestablishment of high-technology weed control systems, (2) hybridization of bluebunch wheatgrass with relatives such as quackgrass (A. repens) that are not native, followed by selection for competitive ecotypes, or (3) accept exotic hybrids that are competitive.

GENETICS OF CHEATGRASS

Perhaps the most important papers at this symposium are those dealing with the population genetics and evolution of cheatgrass (for example, see Novak, these proceedings). We need to remember that while we are trying to arrive at a policy and implementing procedures to biologically suppress cheatgrass so that ranges can be restored, cheatgrass is apparently evolving into a more competitive species.

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EVOLUTION OF WEEDY ANNUALS

Howard C. Stutz

ABSTRACT

In the evolution of annual plants, natural selection always reduces both phenotypic plasticity and genetic flexibility. All annuals derived by natural selection are therefore phenotypically uniform and self-fertilized. Some annuals have become weedy because they were fortuitously preadapted for successful occupation of new "weedy" habitats created by humans. Others became weedy because of novel adaptive plasticity displayed when introduced into new habitats. A few weedy annuals are genetically flexible and also phenotypically plastic. These are not the products of natural selection, but owe their plasticity and flexibility to their recent origin from an ancestry that included hybridization between a genetically uniform, phenotypically constant, annual species and a genetically flexible, phenotypically plastic, perennial species. Because of the resulting rich genetic heritage, these are sometimes phenomenally aggressive.

INTRODUCTION

Survival on planet Earth is an awesome challenge. Considering that no two spots on Earth are identical and that no spot on Earth remains unchanged, even for a moment, it is a marvel that living organisms can survive here at all. In a broad sense they do so because of two principal attributes: (1) phenotypic plasticity and (2) genetic flexibility.

Phenotypic Plasticity

Plasticity refers to the range of phenotypic expressions that may be expressed by one specific genotype. Since there is perpetual inconstancy everywhere on Earth, considerable plasticity is required of every living organism. As the environment changes, so must each organism. Death occurs when plasticity is insufficient to accommodate new conditions.

As pointed out by Waddington (1953), Stutz (1962), and others, plasticity is under genetic control and is thereby affected by natural selection. Where environmental changes are rampant and natural selection is consequently minimal, plasticity is high. Where environmental conditions are more constant and natural selection is therefore more intensive and effective, plasticity is low. Consequently natural selection always tends to reduce plasticity.

One of the most conspicuous avenues by which plasticity may be altered is by extending or reducing the length of life. Organisms with brief lifespans usually experience fewer environmental modifications than those with long lifespans. Consequently, since natural selection always tends to reduce plasticity, and hence lifespan, annual plants are the result of exposure of populations to long or intense directional selection. In many cases natural selection is so effective in reducing plasticity that the species produced are so genetically and phenotypically uniform that they are incapable of accommodating new challenges when they arise and therefore become extinct.

Genetic Flexibility

Reduction of lifespan by natural selection is always accompanied by, and accomplished by, a reduction in genetic flexibility. As a result, most annual plants are genetically uniform. During the long history of selection that results in annual growth habit, many genotypes are discarded. In contrast to many perennial species, each plant in populations of most annual species is almost identical to each of the others. Also, because annuals are low in both flexibility and plasticity, even plants in separate populations of annual species are nearly identical. Such high levels of integrity usually make annuals easy to describe taxonomically. High integrity also makes them highly susceptible to extinction.

The reduction in flexibility that results from intense selection can be accomplished in several ways, the most conspicuous of which is a reduction in effective sexuality. Many, and probably the vast majority, of annuals have "given up sex" in that most have perfect flowers and are therefore capable of self-fertilization. Some are monoecious, which also permits self-fertilization. Rarely are annual species dioecious. As shown in table 1, all annuals

Table 1—Sexuality of the annual species in the family Chenopodiaceae in North America (from Standley 1916)

	Number of species				
Genus	Bisexual	Monecious	Dioecious		
Aphanisma	1	0	0		
Atriplex	0	25	0		
Blitum	1	0	0		
Chenopodium	32	0	0		
Corispermum	2	0	0		
Cycoloma	1	0	0		
Endolepis	0	2	0		
Meiomeria	1	0	0		
Monolepis	3	0	0		
Salicornia	3	0	0		
Suaeda	10	0	0		
Suckleya	0	1	0		
Total	54	28	0		

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in the family Chenopodiaceae are hermaphroditic or monoecious and therefore capable of self-fertilization. Also among 101 species of grasses catalogued by Stebbins (1950), 27 of the 30 annual species were self-fertile, three were facultatively cross-fertilized, and none were obligately cross-fertilized.

The inbreeding that results from self-fertilization in annuals results in high levels of homozygosity. The principal source of variation to annuals is therefore from new mutations. Because of their short lifespan, new mutations can be more readily incorporated in annual species than in perennials, which is probably why the extinction rate in annuals is less than would otherwise be expected.

ANNUALS VS. PERENNIALS

In contrast to annuals, perennial species are less subject to strong selection for phenotypic plasticity. During the long lifespan of perennials, selection vacillates from moment to moment, day to day, year to year, and therefore permits the perpetuation of high levels of plasticity. The impact on genetic flexibility that accompanies intense selection for low plasticity in annuals is therefore reduced in perennials. Genetic flexibility in perennials may therefore be altered by natural selection independently of alterations in plasticity. Consequently, although selection for low plasticity is always accompanied by a concomitant reduction in genetic flexibility, strong selection for reduced genetic flexibility does not necessarily carry with it a corresponding reduction in phenotypic plasticity.

This is conspicuous in the modes of sexuality expressed in perennials as compared with those in annuals. As shown in tables 2 and 3, although all annual species of chenopods in both North America and Australia are either hermaphroditic or monoecious (and therefore have low genetic flexibility), perennials may be hermaphroditic, monoecious, or dioecious. The higher frequency of hermaphroditic perennials in Australia, compared to North America, reflects the much longer history of chenopod evolution in Australia. During the millions of years of comparatively more stable geology in Australia, genetic flexibility has been reduced in perennial chenopods by natural selection resulting in a high incidence of perfect

Table 2—Sexuality of the perennial species of the family Chenopodiaceae in North America (from Standley 1916)

	ł	Number of specie	s
Genus	Bisexual	Monecious	Dioecious
Allenrolfia	1	0	0
Atriplex	0	0	31
Ceratoides	0	1	0
Grayia	0	2	0
Kochia	1	0	0
Sarcobatus	0	2	0
Suaeda	1	0	0
Zuckia	0	1	0
Total	3	6	31

Table 3—Lifespan and sexuality of Australian chenopods (from Wilson 1984)

	Number of species			
Lifespan	Bisexual	Monecious		Total
Annual	16	13	0	29
Perennial	85	10	8	103

flowers. In contrast, because of the younger, less stable, geology of North America, genetic uniformity has been less severely selected, and most perennials are consequently dioecious and therefore rich in genetic flexibility.

Phenotypic plasticity and genetic flexibility of plants are thus reflections of the stability or instability of the landscapes they occupy. Tumultuous environmental changes translate to low predictability, and hence relaxed selection, the consequence of which is high plasticity and high flexibility. Repeated, predictable conditions such as those that occur diurnally, seasonally, or after a summer rainstorm, or in a plowed field, equate to effective selection, which always reduces both plasticity and flexibility.

As shown in table 4, high flexibility and high plasticity characterize perennials that occupy fluctuating, unpredictable sites. They are typically dioecious. Monoecious or bisexual perennials that occupy rythmically predictable, but restricted, sites have sufficient plasticity to permit their long lifespan but, because of inbreeding, are low in genetic flexibility. Highly predictable, narrow ecological sites are occupied by self-fertilized annuals that are low in both flexibility and plasticity. There are no dioecious annuals, because they would require low plasticity and high flexibility, an impossible situation because selection for low plasticity is always accompanied by selection for low flexibility. Exceptions are in cases like cereal rye that have a cross-fertilized perennial in their recent ancestry from which they attained both high flexibility and high plasticity.

WEEDY VS. NONWEEDY ANNUALS

Weedy annuals are usually subject to novel environments not experienced by nonweedy annuals and therefore have some unique attributes. Because they usually occupy habitats that have been only recently disturbed by humans, their uniqueness is new. In some cases, annuals have become weedy because their genetic uniformity and low plasticity fortuitously favor some particular uniform, extant habitat created by human activity. Such appears to be the case with weeds such as "lambsquarter" (*Chenopodium album*) and "purslane" (*Portulaca oleracea*) that have found a favorable habitat in our gardens. They both show little genetic flexibility and low phenotypic plasticity. Their success as weedy annuals appears, therefore, to result mostly from a fortuitous abundance of a uniform habitat to which they happened to be suitably adapted.

Some weedy annuals appear to have become successful because of residual phenotypic plasticity that became Table 4—Interactions of genetic flexibility and phenotypic plasticity in relation to lifespans and sexual strategies in chenopods

Flexibility	Sexual strategy	Plasticity	Lifespan	Ecological niche	Examples (genera)
High	Dioecious	High	Perennial	Wide, unpredictable	Atriplex
High	Dioecious	Low	Annual	_	
Low	Monoecious or bisexual	High	Perennial	Restricted, rhythmically predictable	Ceratoides Sarcobatus Maireana Sclerolaena
Low	Monocecious or bisexual	Low	Annuai	Narrow, highly predictable	Chenopodium Atriplex

released in their new environments, without significant increase in genetic flexibility. This appears to be true of *Bromus tectorum, Salsola australis, Halogeton glomerata,* and several other species that became weedy upon introduction into new environments.

Other weedy annuals owe their success to their evolutionary ancestry. This is true of the annual species Secale cereale (cultivated rye), which only recently became weedy in the Western United States. In contrast to most annuals, Secale cereale is cross-fertilized and is therefore rich in genetic flexibility. It also differs from most annuals in being phenotypically highly plastic. S. cereale obtained these striking attributes from its ancestors, not from relaxed selection. One ancestor of Secale cereale (Secale silvestre) is a highly uniform, self-fertilized annual species. As with most annuals, it is extremely site specific, growing only in the sandy steppes of southwestern Russia and southeastern Europe. It is low in both genetic flexibility and phenotypic plasticity. The other ancestor of cultivated rye, S. montanum, is a cross-fertilized, highly variable, perennial species. It has a widespread distribution throughout the Mediterranean and Middle East countries from Spain and Morocco to Iran and Iraq. It is rich in both genetic flexibility and phenotypic plasticity. Hybrids are common between S. montanum and S. silvestre (and S. vavilovii, a derivative of S. silvestre) in northeastern Turkey and northwestern Iran. Hybrid swarms resulting from these hybrids have produced several new

species, one of which is cereal rye (*Secale cereale*). The annual habit, rich genetic flexibility, and extensive phenotypic plasticity of cereal rye preadapted it for its rapid invasion of disturbed habitats both in the Middle East and in western North America.

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CHEATGRASS DEMOGRAPHY— ESTABLISHMENT ATTRIBUTES, RECRUITMENT, ECOTYPES, AND GENETIC VARIABILITY

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ABSTRACT

The ability of cheatgrass (Bromus tectorum) to establish and survive in variable environments is critical to its success. In locations with adequate autumn moisture cheatgrass behaves as a winter annual, but can germinate and produce viable seeds even when it germinates in late spring. Survivorship is high and appears to be independent of density. Genetic variation among North American populations is low, yet considerable phenotypic plasticity in seed production maintains populations in highly variable environments.

INTRODUCTION

As humans migrate to new areas they may intentionally or accidentally bring plants and animals from their former homeland. Most of these introduced species are not adapted for their new environments and eventually become extinct. Occasionally, introduced organisms are preadapted to their new environments, become established, and eventually dominate portions of their new ecosystem. Darwin observed this phenomenon while exploring the South American Pampas where European plants were notable in overgrazed areas (Darwin 1968).

One hundred years ago, several botanists were expressing their concerns over the introduction and spread of exotic annual plants into the Intermountain West (see Mack 1986). Little did these prophets of impending doom know that one of the greatest threats to native plant communities was just being introduced into the region. Bromus tectorum L., known commonly as cheatgrass, downy brome, downychess, and cheat, is thought to have been originally introduced into this region through contaminated grain sown in areas of deep soils (Mack 1981). Through a combination of events associated with poor agricultural practices such as continued problems with impure grain seeds and with overgrazing of semiarid rangelands, cheatgrass quickly expanded its range so that by 1930 it was found in areas of its current distribution. Through this paper, we will review the demographic attributes that have led to the successful introduction and establishment of cheatgrass. Then we will discuss the phenotypic and genetic variability within the species that may have led to its successful expansion across the Intermountain West.

SEED SURVIVAL

The survival of a population of semiarid seeds after they are dispersed from their parents is a dynamic process. There is a considerable amount of spatial and temporal variability in seed populations of semiarid plants (Coffin and Lauenroth 1989). Spatial patterns largely reflect dispersal patterns of the seeds, while temporal patterns reflect probabilities of predation, dormancy, mortality, and germination.

Primary dispersal of cheatgrass seeds occurs in late May on xeric sites, but can be delayed until late June on cooler, mesic sites (Mack and Pyke 1983; Pierson and Mack 1990). The majority of seeds are dispersed short distances from the parent plant by wind. Most seeds drop near the parent and are secondarily dispersed along the soil surface by wind until they contact an obstruction, for example litter or a crack in the soil (Hulbert 1955). On a semiarid site near Richland, WA, about 90 percent of marked seeds were recovered within 1 m of their release point after 1 month during the summer (Mack and Pyke, unpublished data).

Long-distance dispersal is enhanced by seeds attached to animal fur or human clothing. Attachment is aided by the presence of short, stiff hairs on the lemma and awn. Other suspected means of long-distance dispersal are contaminated grain seed, ballast of sailing ships, and packing materials with contaminated straw (Mack 1981; Morrow and Stahlman 1984). Seed-caching rodents can disperse seeds intermediate distances through their caching activity (La Tourette and others 1971).

Seed predation by animals is not a significant factor in reducing or controlling populations of cheatgrass seeds. Rodents, birds, and harvester ants have low preferences for cheatgrass when other species are available (Goebel and Berry 1976; Kelrick and others 1986; La Tourette and others 1971; Young 1981). Therefore, granivores may selectively avoid cheatgrass thereby enhancing its increase relative to native perennials.

As seeds lie dormant in the soil they are at risk of attack from soil-borne pathogens. Few studies have noted any microbial attack of healthy seeds. Young and others (1969)

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noted that when fungal synemata similar to *Podosporielli* verticillata were present survival of cheatgrass seedlings was less than 1 percent. Although this fungus associates with cheatgrass (Kreitlow and Bleak 1964), it is not known if it kills the plant before or after germination.

Cheatgrass seeds are capable of remaining dormant in the soil for more than 1 year; however, most seeds germinate if given adequate conditions (Hulbert 1955; Pyke, these proceedings). Of the three major types of seed dormancy, innate, enforced, and induced (after Harper 1977), cheatgrass shows clear evidence for enforced dormancy when seeds located in litter above the soil surface never gain adequate moisture conditions for germination (Young and others 1969). Evidence for another form of dormancy has been reported twice. Combinations of freezing temperatures and of desiccation while seeds were at least partially imbibed induces a dormancy that requires a flush of nitrate to break dormancy (Kelrick 1989; Young and Evans 1975). This form of dormancy is likely to result in a cheatgrass seed bank persisting into the next growing season, especially if dormancy is induced during spring (for example by a hard spring frost) after soil and temperature conditions have allowed a peak in nitrogen turnover to occur (Burke 1989).

GERMINATION

Cheatgrass germination occurs under a normal range of soil moisture conditions. Germination is uninhibited to a soil moisture of -1.5 MPa. Time to germination may increase as soil water potentials become more negative (Evans 1961; Evans and Young 1972). A series of successive days of >1 mm of precipitation during autumn appears adequate for germination (Mack and Pyke 1984).

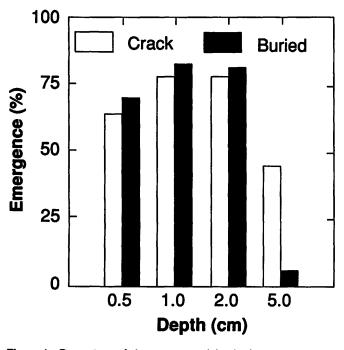


Figure 1—Percentage of cheatgrass seed that had seedlings emerge from cracks or from being buried at four depths (from Bookman 1983).

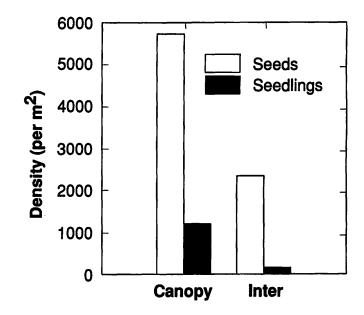


Figure 2—Density of cheatgrass seeds and seedlings found under the canopy of big sagebrush and in the interspaces (INTER) between sagebrush (from Young and Evans 1975).

Cheatgrass is adapted to a wide range of temperatures in which germination approaches 100 percent in 4 weeks (20-30 °C day; 5-20 °C night). At least some germination is possible with temperatures as low as 0 °C and as high as 40 °C (Young and Evans 1985). This range in germination temperatures allows cheatgrass to germinate earlier in autumn than most natives and during winter when temperatures are too cold for native species to germinate (Martens and others, these proceedings).

Safe sites for germination are microsites that provide the appropriate physiological conditions for germination. Safe sites for germination provide adequate contact with the soil for seeds to imbibe. At depths of 2 cm or less, germination is slightly enhanced if seeds are buried in soil rather than located in a crack in the soil. However, burial at 5 cm does not allow the plant to emerge and become autotrophic. Seeds located in 5-cm deep cracks are more capable of germinating and surviving (fig. 1).

The direction of exposure of a seed on a soil mound may impact the temperature and moisture conditions sufficiently to affect germination. Spring-emerging cheatgrass seeds had higher germination on the northern side of mounds than on the southern side (Bookman 1983). The southern exposure may increase the evaporation from the soil in spring, resulting in the reduced germination.

Shrubs may also provide environmental conditions more conducive to germination and survival than interspaces between shrubs. In Nevada, Young and Evans (1975) demonstrated that the litter accumulation under shrub canopies enhances the capture of dispersing cheatgrass seed and also enhances the successful establishment of seedlings (fig. 2). They found that 21 percent of the seeds under shrub canopies established, while only 9 percent of the seeds in the interspaces survived. Similar results have been shown for populations in western Wyoming (Kelrick 1991).

GROWTH, SURVIVAL, AND REPRODUCTION

Cheatgrass is a C_3 plant (Waller and Lewis 1979) that normally grows as a winter annual monocarpic, germinating during the autumn, remaining dormant aboveground during the winter months, and then resuming growth during the spring. It is also capable of two more-abbreviated fecundity schedules, an annual monocarpic or an ephemeral monocarpic, allowing it to persist in unpredictable environments by distributing its emergence from late summer through to May while still producing viable seed (Mack and Pyke 1983). Vernalization or short days followed by long days may induce flowering in cheatgrass (Finnerty and Klingman 1961; Hulbert 1955). However, Mack and Pyke (1983) mapped individuals that emerged in May and produced at least one viable seed by June.

After germination in autumn, the number of leaves, tillers, and plant height remains small through winter. The majority of aboveground growth occurs during spring; however, cheatgrass is highly plastic for these characteristics (fig. 3). Autumn growth is allocated mainly to roots. During the first 45 days of growth, cheatgrass is capable of producing twice as many roots as bluebunch wheatgrass (*Pseudoreognaria spicata*), the dominant native grass throughout much of the Great Basin (fig. 4) (Aguirre and Johnson 1991). Root growth continues throughout the winter extending to depths of 75 cm by January in Pullman, WA; bluebunch wheatgrass root growth stopped in November at 10 cm and resumed growth in March as soils warmed (Harris 1967). Hulbert (1955) reported maximum root growths of 150 cm.

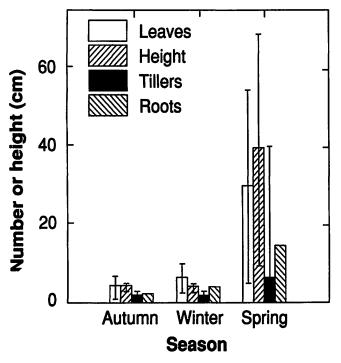


Figure 3—Number of leaves, tillers, and roots, and height of tallest leaf per cheatgrass plant in the three seasons of growth (from Harris 1967).

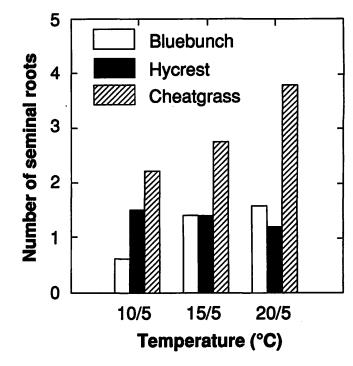


Figure 4—Number of seminal roots of bluebunch wheatgrass, 'Hycrest' crested wheatgrass, and cheatgrass grown for 45 days at three day/night temperature regimes (from Aguirre and Johnson 1991).

As cheatgrass roots grow, they appear to seek and proliferate in soil spaces not occupied by roots of perennial plants (Bookman and Mack 1982). These root characteristics are thought to be closely linked with the enhanced competitive nature of the plant.

Intra- and interspecific competition may reduce the growth of cheatgrass. Biomass and seed production correlate positively with time of growth and negatively with grazing frequency, grazing severity, and density of neighboring plants (Mack and Pyke 1983; Pyke 1986, 1987). Biomass and seed production are also negatively related to density of neighboring conspecifics or of competing species (Francis and Pyke 1992; Harris 1967). However, some species may have no effect on the production of cheatgrass. Francis and Pyke (1992) have shown that first-year seedlings of Nordan' crested wheatgrass (Agropyron desertorum) had no significant effect on the production of competing cheatgrass; 'Hycrest' crested wheatgrass (Agropyron desertorum x cristatum) grown in the same densities showed a significant negative effect on cheatgrass.

Eliminating early root competition from mature native and introduced perennials by using root exclusion tubes had no significant impact on the survival of cheatgrass seedlings. However, the species of the mature perennial did significantly influence cheatgrass survival. Big sagebrush (*Artemisia tridentata*) reduced cheatgrass survival more than crested wheatgrass and bluebunch wheatgrass (fig. 5a). Early root competition with mature perennials reduced the seed production of cheatgrass by nearly 50 percent (fig. 5b) (Reichenberger and Pyke 1990).

In general, survival for cheatgrass populations tends to remain high, but cohorts may vary in their specific shape

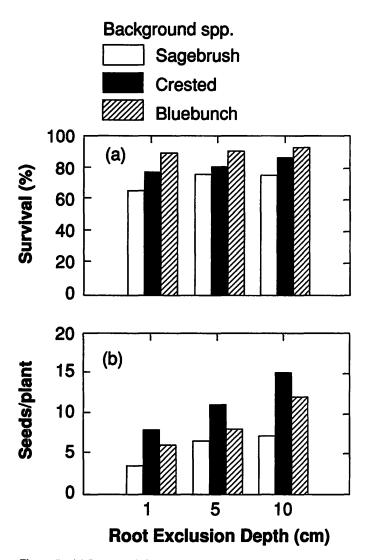


Figure 5—(a) Percent of cheatgrass seedlings that survive; and (b) the number of seeds per cheatgrass plant when grown in a background of three mature perennial plants (big sagebrush, crested wheatgrass, and bluebunch wheatgrass) and with three depths of root exclusion (from Reichenberger and Pyke 1990).

of survivorship curves from high mortality risk early in life to a high risk late in life (Mack and Pyke 1983). The major sources of mortality changed depending on the season of emergence. Autumn cohorts tend to be susceptible to desiccation during periods of unpredictable temporary drought after emergence. Winter-emerging cohorts on heavy soils may succumb to frost-heaving; spring-emerging cohorts are susceptible to a smut fungus (Ustilago bullata) (Mack and Pyke 1984).

GENETIC VARIABILITY

In this section, we will: (1) describe the amount and distribution of genetic variability for North American populations of cheatgrass as measured by enzyme electrophoresis; (2) describe the level of genetic variation in cheatgrass populations from Eurasia; (3) use the presence of novel alleles to demonstrate multiple introductions of cheatgrass in western North America; and (4) briefly present results obtained from a study of phenotypic variation in cheatgrass.

Almost all plant invasions occur following the accidental arrival of a few individuals. These founders usually possess little of the genetic variability found within and among populations across the entire home range of the species (Brown and Marshall 1981; Gray 1986). A reduction in the genetic variability (a reduction in the number of alleles and average heterozygosity) for the descendants of such immigrants is predicted from theory (Nei and others 1975). In addition, loss in genetic variation within populations and an increase in differentiation among populations in the new range would be expected to be greater in a selfing species (Barrett and Richardson 1986; Brown and Marshall 1981). Data on the genetic variation of introduced species provide information on the basic biology of weedy species and have been used to predict the success of biological control efforts directed at such species (Burdon 1987; Burdon and Brown 1986; Burdon and others 1980).

Introduced species that have a selfing mating system typically possess low levels of genetic variation; however, this mating system does impart several advantages to these species. Selfing frees a plant from dependence on the proximity of mates (Baker 1955), confers reproductive success during unfavorable environmental conditions (Stebbins 1957), and ensures the maintenance of adaptive gene complexes within the population (Antonovics 1968; Brown 1979). The genetic structure within populations of highly selfing species is often quite uniform, composed of one or a few homozygous lines (Barrett and Shore 1989). Also, the level of interpopulation genetic differentiation would be high in a widely distributed selfer (Brown 1979; Hamrick 1983; Hamrick and Godt 1990; Loveless and Hamrick 1984).

Twenty-five Eurasian and 60 North American populations of cheatgrass were sampled for genetic variation using enzyme electrophoresis (Novak and Mack in preparation; Novak and others 1991). These populations were ultimately assigned to six regions: (1) Europe, (2) Southwest (S.W.) Asia, (3) the United States east of the Rocky Mountains, (4) Nevada-California, (5) the Intermountain West, and (6) British Columbia (BC). Collection data and habitat descriptions of these populations are given in Novak (1990). Cheatgrass seeds from each population were randomly selected and placed on moistened filter paper in a petri dish. No additional treatment, such as scarification, is required for germination of cheatgrass seeds (Hulbert 1955). Seedlings were harvested approximately 7 days after germination; this time span maximized staining intensity for the enzymes used here. Starch gel electrophoresis and enzyme staining schedules followed the methods of Soltis and others (1983).

Genetic variability for cheatgrass was assessed using the number of alleles per locus (A), the percent polymorphic loci per population (%P), and the observed and expected mean heterozygosity [H(obs) and H(exp)]. Wright's fixation index (F) (Wright 1965) was calculated at each polymorphic locus as the ratio of the number of observed to expected heterozygotes: F = 1-[H(obs)/H(exp)]. The gene diversity statistics of Nei (1973, 1977) were used to partition the total gene (allelic) diversity within these

Table 1Number of alleles at each locus surveyed among native
and introduced populations of cheatgrass. The total
number of populations sampled in each region is in
parentheses

	Numb	er of alleles
Locus	Native range (25)	Introduced range (60)
Adh	2	1
Ald	1	1
G6pdh-1	1	1
G6pdh-2	1	1
Gdh	1	1
Got-1	2	1
Got-2	1	1
Got-3	2	1
Got-4	3	3
ldh	2	1
Lap	2	1
Mdh-1	1	1
Mdh-2	2	2
Mdh-3	2	2
Мө	1	1
Pgi-1	1	1
Pgi-2	3	2
Pgm-1	2	2
Pgm-2	2	2
6Pgd-1	- 1	1
6Pgd-2	1	i
Skdh	3	i
Sod	1	1
Tpi-1	2	2
Tpi-2	- 1	- 1

populations. At each polymorphic locus, the total allelic diversity is represented by H_T , which is partitioned into the mean allelic diversity within populations, H_S , and the allelic diversity among populations, D_{ST} . These quantities are related by the expression, $H_T = H_S + D_{ST}$. The proportion of the total allelic diversity found among populations, G_{ST} , is calculated as the ratio D_{ST}/H_T . The unbiased genetic identity (I) coefficient of Nei (1978) was calculated for all possible pairwise comparisons among the 85 populations. These values were averaged within and between all populations across the six regions.

A total of 1,014 individuals from Eurasia, and 2,141 individuals from throughout the introduced range of cheatgrass in North America, were analyzed in these studies. The 15 enzymes used in this study were encoded by 25 putative genetic loci. Across all Eurasian populations 13 loci (52 percent) were polymorphic; seven loci (28 percent) were polymorphic across all North American populations (table 1). Forty-one alleles were observed for Eurasian populations, while 33 alleles were observed for the North American populations (table 1). These data indicate that the level of genetic variation (number of polymorphic loci and number of alleles) across Eurasian populations is higher than that detected across North American populations. The theoretical models of Nei and others (1975) predict a decrease in the number of alleles per locus, following an introduction event, through the loss of low-frequency alleles found in native populations.

Averaged across all 85 populations, A is 1.04 and %P is 4.05 (table 2). Genetic variability statistics [A, %P, H(obs) and H(exp)] reveal both large regional differences and a consistent pattern. Populations from British Columbia have the highest values for these parameters, while populations east of the Rocky Mountains possess the lowest values. British Columbia populations display a sevenfold greater %P (8.40) and H(exp) (0.021) compared to populations east of the Rocky Mountains (1.14 percent and 0.003, respectively) (table 2). Values for Southwest Asia, Intermountain West, and Nevada-California are somewhat similar to each other and intermediate between values from two regions discussed above. Genetic variability statistics for populations from Europe and east of the Rocky Mountains are very similar (table 2).

The low electrophoretic variability in cheatgrass in North America and Eurasia is similar to that reported for other selfing plant species. In a summary of electrophoretic studies, Hamrick and Godt (1990) observed that the average A and %P are much greater in outcrossing species (1.64 and 41.2 percent, respectively) than the values reported for selfing species (1.31 and 20.0 percent). Cheatgrass represents an extreme example of this difference: the average %P reported for selfing plants by Hamrick and Godt (1990) is approximately fourfold larger than the value observed for cheatgrass (4.60 percent). Equally low levels of genetic variation have been observed for other introduced plants with selfing mating systems such as Noogoora burr (Xanthium strumarium) (Moran and Marshall 1978), skeleton weed (Chondrilla juncea) (Burdon and others 1980), little jack (Emex spinosa) (Marshall and Weiss 1982), witchweed

Table 2—Genetic variability for cheatgrass summarized for the six regions of the native and introduced ranges. S.E. appear in parentheses. See text for description of the statistics

					Mean heterozygosity		
Regions	Populations	<u> </u>	A	%P	Observed	Expected	F
Europe	13	530	1.02	1.85	0.0001	0.007	0.999
Southwest Asia	12	484	1.03	3.67	.0002	.005	.993
East of Rocky Mountains	14	441	1.01	1.14	.0000	.003	1.000
Nevada and California	14	546	1.05	5.14	.0000	.014	1.000
Intermountain West	22	825	1.05	4.73	.0000	.012	1.000
British Columbia	10	329	1.08	8.40	.0000	.021	1.000
For all populations analyzed	85	3,155	1.04	4.05	.0000	.010	.999
		•	(.005)	(.527)	(.0000)	(.001)	(.001)

Table 3—Comparison of Nei's gene diversity statistic	s for native
and introduced populations of cheatgrass.	See text for
description of statistics	

Range	H _P	H _s	D _{ST}	G _{ST} (D _{ST} /H _T)	Within populations (H _s /H _T)
Native	0.136	0.012	0.124	0.753	0.251
Introduced	.115	.046	.069	.478	.522

(Striga asiatica) (Werth and others 1984), and Johnson grass (Sorghum halepense) (Warwick and others 1984).

MATING SYSTEM

Because no heterozygous individuals were detected in our analysis of North American cheatgrass populations, the outcrossing rate among these populations was 0.0 percent. Two heterozygous individuals were detected in our Eurasian sample; therefore, the outcrossing rate for these populations was slightly higher (0.17 percent). The expected mean heterozygosity averaged across all populations was 0.010, indicating that the level of heterozygosity expected is very low. The mean value for Wright's fixation index (F) calculated across loci for each population was 0.999 (table 2). This value for the fixation index indicates a massive deviation from Hardy-Weinberg equilibrium through almost a complete lack of heterozygous individuals. Data from enzyme electrophoresis are in agreement with the results of seed set in bagging experiments and male and female reproductive allocation in cheatgrass, which indicates that this species is exclusively selfing (McKone 1985, 1987, 1989).

POPULATION DIFFERENTIATION

Nei's gene diversity statistics were used to describe the distribution of the total allelic diversity within and among populations (table 3). The values for total gene diversity (H_T) for native and introduced populations were similar (0.136 and 0.115, respectively). However, the value for the

among-population component (D_{ST}) was much higher for native range populations. The value for G_{ST} , therefore, was much higher in the native populations (0.753) compared to the value for the introduced populations (0.478). This value (0.753) indicates a higher level of population differentiation among native populations. Conversely, the withinpopulation component (H_S/H_T) for introduced populations (0.522) was twofold larger than that calculated for native populations (0.251). Apparently, genetic variability in the native populations is partitioned among populations, but the total gene diversity in the introduced populations is evenly partitioned among and within populations.

The unbiased genetic identity (I) coefficient of Nei (1978) ranges from 0.0 to 1.0, where a genetic similarity value of 1.0 indicates that a population pair is genetically identical. Genetic identity values were averaged within and between each region in the native and introduced ranges (table 4). Mean values of I for native and introduced populations were 0.932 and 0.980, respectively. The value of I for all comparisons between native and introduced populations was 0.951; the mean for all populations was 0.967. The lowest mean genetic identity value occurred for the within-region comparison of Southwest Asia populations (table 4). The interregional comparisons between the Southwest Asia populations and populations from all other regions were consistently lower than all other comparisons. These data indicate that the genetic similarity for all cheatgrass populations is quite high; however, the populations from Southwest Asia do appear to be genetically distinct.

MULTIPLE INTRODUCTIONS

Cheatgrass was first collected within the Intermountain region of western North America in 1889 (Mack 1981). This first collection was made at Spences Bridge, BC; however, cheatgrass was found repeatedly over the next decade at several locations. This early collection history suggests that cheatgrass was introduced almost simultaneously into several widely separated areas in this region (table 5), and that range expansion occurred rapidly through a coalescing of isolated foci (Mack 1981). We used the presence of

Table 4—Nei's genetic identity for populations of cheatgrass within and between regions of Eurasia and North America. N is the number of populations in each region. The mean of all intra-regional pair-wise population comparisons appears along the diagonal, and the mean of inter-regional comparisons appears below the diagonal. The range of values for population pairs for each comparison is given in parentheses

Region	N	Europe	Southwest Asia	East of Rocky Mountains	Nevada and California	Intermountain West	British Columbia
Europe	1	0.970					
•	3	(0.920 - 1.000)					
Southwest Asia	1	0.927	0.899				
	2	(0.720 - 1.000)	(0.680 - 1.000)				
East of Rocky	1	0.972	0.928	0.975			
Mountains	4	(0.880 - 1.000)	(0.760 - 1.000)	(0.890 - 1.000)			
Nevada and	1	0.974	0.927	0.975	0.983		
California	4	(0.920 - 1.000)	(0.738 - 1.000)	(0.880 - 1.000)	(0.951 - 1.000)		
Intermountain	2	0.973	0.927	0.975 ⁽	0.986	0.989	
West	2	(0.920 - 1.000)	(0.758 - 1.000)	(0.880 - 1.000)	(0.951 – 1.000)	(0.960 - 1.000)	
British	1	0.971	0.927	0.976	Ò.980	0.983	0.979
Columbia	0	(0.908 – 0.999)	(0.765 – 0.999)	(0.898 – 1.000)	(0.908 – 1.000)	(0.908 – 1.000)	(0.924 - 1.000

Table 5-Earliest k	nown localities	for cheatgrass	in west-
ern North	America (from	Mack 1981)	

Locality	Collection date
Spences Bridge, BC	1889
Ritzville, WA	1893
Provo, UT	1894
Pullman, WA	1897
Eastern Colorado	1897
Klamath Falls, OR	1902

Table 6—Localities in western North America that possess novel alleles. N is the number of populations possessing the novel alleles in each locality

Locality	N	Locus/allele
British Columbia	7	Pgm-1a; Pgm-2a
Eastern Washington	4	Mdh-2b; Mdh-3b
Vicinity of Reno, NV	4	Pgi-1b
Eastern Nevada	2	Mdh-2b; Mdh-3b
Eastern Idaho	1	Got-4d
Utah	1	Got-4d

novel alleles to determine whether cheatgrass populations at these locations may be the product of multiple introduction events (Novak and others, submitted).

Novel alleles were detected in populations from British Columbia, eastern Washington, western Nevada (near Reno), eastern Nevada, eastern Idaho, and Utah (table 6). These novel alleles were at their highest frequency at or near the early collection sites, a likely consequence of multiple introductions. In addition, enzyme markers were also present in populations near these putative points of introduction. The spread of these genotypes indicates that gene flow, probably through seed dispersal rather than pollen movement, has occurred. The introduction and spread of different allelic variants in these populations has led to a mosaic of genotypes over the new range of cheatgrass, especially among populations in the Intermountain West.

A detailed example of multiple introductions of cheatgrass is provided by the discovery of novel allelic variants in several populations from Washington and British Columbia (fig. 6). The Ritzville, WA, population possesses two unique allelic variants (frequency = 0.250) for the enzyme malate dehydrogenase (MDH). These alleles were also found at Rattlesnake Springs (0.080), Hodges Ranch (0.040), and Tonasket (0.029), although at lower frequency. Six populations near Spences Bridge, BC, possess two novel alleles for

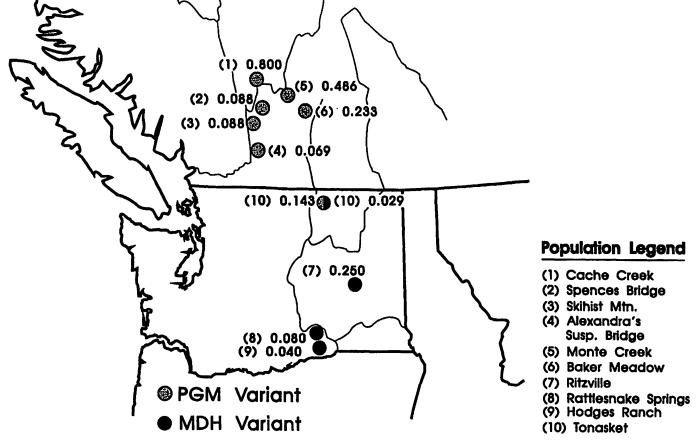


Figure 6—Distribution of novel allelic variation (frequencies of variants are numbers by each population) for the enzymes MDH and PGM in Washington and British Columbia populations of cheatgrass (from Novak and others, submitted).

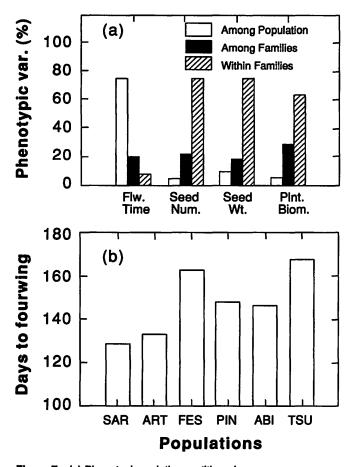


Figure 7—(a) Phenotypic variation partitioned among the sources of variation for four growth characters of cheatgrass; and (b) the time from germination to flowering for six populations found in communities dominated by Sarcobatus vermiculatus (SAR), Artemisia tridentata (ART), Festuca idahoensis (FES), Pinus ponderosa (PIN), Abies grandis (ABI), and Tsuga heterophylla (TSU) in eastern Washington and northern Idaho (from Rice and Mack 1991).

the enzyme phosphoglucomutase (PGM). The highest frequencies of the PGM variants occur in the Cache Creek, BC, population (0.800). Other populations nearby exhibit sharply lower frequencies of these alleles. It is important to note that the Tonasket population, in north-central Washington, possesses the PGM variants from British Columbia and the MDH variants found in eastern Washington. The Tonasket population has a high level of genetic polymorphism and suggests the importance of multiple introductions, followed by gene flow, in off-setting the reduction in genetic variation often associated with biological invasions.

PHENOTYPIC VARIATION

In a study of six cheatgrass populations from eastern Washington and northern Idaho, Rice and Mack (1991) examined the hierarchical distribution of phenotypic variation for five morphological and life history characters. Percentages of total phenotypic variance for flowering time, seed number per plant, individual seed weight, total seed weight, and plant dry weight were partitioned among populations, among families, and within families (fig. 7). Most of the variation in flowering time was explained by differences among populations, suggesting genetic differentiation among these populations for time to flowering. In contrast, for the other four traits within-family variance contributed most to the total phenotypic variance. These results indicate that for four of five traits most of the variation is due to phenotypic plasticity and not due to genetic differentiation among populations. It appears that the success of cheatgrass throughout many areas in western North America is not due to genetic variation but perhaps due to phenotypic plasticity.

CONCLUSIONS

The combination of an extremely plastic growth form and life history strategy coupled with multiple introductions into a region of the Country that was poorly managed has led to the spread and dominance of cheatgrass in much of the Intermountain West. We probably know more about this exotic than any other semiarid weedy species. There are a host of other species for which we know comparatively little. These include medusahead, knapweeds, yellow starthistle, and leafy spurge.

The challenge before researchers and land managers is threefold. First is to better understand these exotic species that are spreading at enormous rates across the Intermountain West. Second is to simultaneously take our current knowledge and translate it into prescriptions for restoration of these rangelands. Third is to apply management strategies that will maintain healthy native communities.

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ECOLOGICAL IMPACTS OF CHEATGRASS AND RESULTANT FIRE ON ECOSYSTEMS IN THE WESTERN GREAT BASIN

W. D. Billings

ABSTRACT

All catastrophic ecosystemic change is not due to physical environmental forces, climatic change, or urban development. Certain plants can trigger drastic changes in an ecosystem. Cheatgrass (Bromus tectorum) in the Great Basin area has become abundant enough to provide fuel for extensive and disastrous range fires.

THE ORIGINAL VEGETATION OF THE WESTERN GREAT BASIN

No written historical records exist of the appearance and floristic composition of the semi-arid vegetation east of the Sierra Nevada in the 18th century. A knowledge of the plant life there at that time must be derived from a few scattered observations. For example, the first crossing of the Sierra, except for those by the native Paiutes, did not come until 1827 when the American trapper Jedediah Smith crossed from west to east in May of that year. Smith continued across what is now central Nevada to the Great Salt Lake (Morgan 1953); his vegetational descriptions are scanty and generalized.

The first expedition with scientific observers was that of John C. Fremont in January 1844 (Fremont 1845). He came into what is now western Nevada from the north by way of the Hot Springs near the present little town of Gerlach, NV, at the junction of the Smoke Creek and Black Rock Deserts. Proceeding southwest, Fremont and Fitzpatrick found "excellent grass in the hills" for the expedition's horses. Such grass had to be native bunchgrasses such as Agropyron, Festuca, and Elymus. The next day, January 10, he found "an abundance of good bunchgrass in a hollow several miles long." That same day, the expedition discovered Pyramid Lake which Fremont named for the high conical island near the eastern shore. Fremont had thought that he was approaching San Francisco Bay but realized that with a river flowing into the lake from the southwest that the Sierra Nevada blocked his way and that the expedition was still in an interior drainage. On his 1845 map, Fremont designated this large Intermountain region as the "Great Basin" and "almost unknown." To get to California, Fremont, aided by one of his scouts, Kit (Christopher) Carson, led his expedition in deep midwinter snows across the Sierra

through Carson Pass south of Lake Tahoe. In so doing, they discovered both the pass and the lake.

In Fremont's path came the great migrations to California from the Midwest and the East. Beckwith, after the death of Gunnison, lead the remnants of that expedition across the northern Great Basin down the Humboldt River and thence across by way of the Smoke Creek Desert to California. He reported an abundance of nutritious grasses in the hills above the California Trail along the lower Humboldt River that supported the horses of his Army detachment. This grass was also being used by the bands of livestock being driven to California. In Beckwith's report, there is no mention of wildfires in this sagebrush-bunchgrass ecosystem during those middle years of the 19th century.

After the Civil War, the large and diverse King Expedition explored the Great Basin from California to Utah. The botanical part was led and reported by Sereno Watson (1871), a trained botanist. He listed the principal bunchgrasses (primarily tussocks) in the sagebrush ecosystem: Festuca idahoensis, Poa canbyi, Poa sandbergii, Leucopoa kingii, Agropyron spicatum, Elymus cinereus, Sitanion hystrix, Oryzopsis hymenoides, Stipa comata, and Stipa occidentalis. These were the grass dominants before the advent of heavy grazing.

To integrate knowledge of the zonal distribution of vegetation in the western Great Basin both latitudinally and vertically, Billings (1951) described three latitudinal zones from south to north: A. the Creosote Bush Zone, B. the Shadscale Zone, and C. the Sagebrush-Grass Zone. Superimposed on these were three montane zonal series: A. the Sierran Series, B. the Basin Range Series, and C. the Wasatch Series. Only the first two of the montane series-the Sierran and the Great Basin-are pertinent to this paper (fig. 1). The area of vegetation concerned in the present paper lies between latitudes 38 and 41 degrees north and longitudes 117 and 120 degrees west. The total area is 29,766 square miles or 77,392 square km. The vegetation zones of this large region were mapped by Billings (1954) and their respective areas determined (table 1).

About 34 percent of this land area was originally characterized by a cold desert of relatively barren land with scattered dwarf shrubs of *Atriplex confertifolia* (shadscale), *Sarcobatus baileyi* (little greasewood), *Artemisia spinescens* (bud sage), *Lycium cooperi*, and a few perennial herbaceous plants occupying dry hillsides both above and below the highest water line (about 1,341 m elevation above sea level) of Pleistocene Lake Lahontan. Embedded in this

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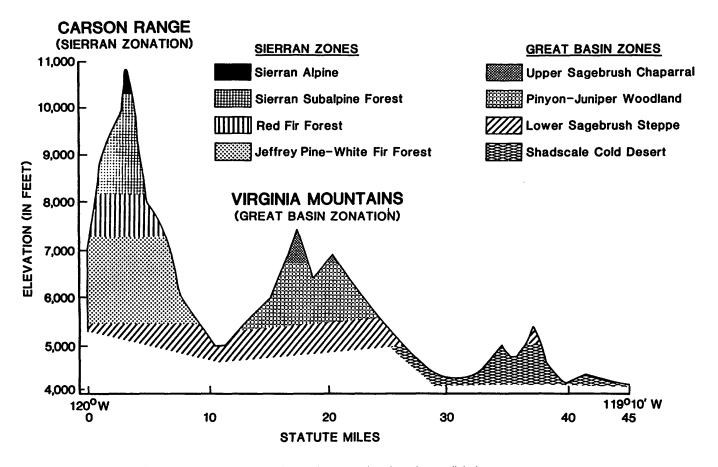


Figure 1—Cross-section diagram of vegetational zonation on the mountains along the parallel of 39° 20' N latitude. The diagram shows the sharp boundary between the Sierran vegetation and that of the Great Basin across Washoe Valley about 15 miles south of Reno, Nevada. Vertical scale is exaggerated.

dwarf shrub matrix are extensive wet, saline playas with widely separated large shrubs of Sarcobatus vermiculatus. Here and there are shelves of wind-blown sands occupied by deep-rooted shrubs of Tetradymia comosa, Atriplex canescens, and Psorothamnus polydenius, and the perennial Oryzopsis hymenoides (Indian rice grass), and numerous small annual Dicot herbs. Galeria riverine woodlands of cottonwoods (Populus fremontii) exist within these deserts along the principal rivers (Truckee, Carson, and Walker) that originate on the eastern escarpment of the Sierra Nevada. For details of the above ecosystems, see Billings (1945, 1949, 1980).

Before settlement, another third of the land area (over 38 percent) was sagebrush (*Artemisia tridentata*-bitterbrush; *Purshia tridentata-Ephedra viridis*) and bunchgrass steppe forming a vegetational zone above the cold desert in elevation. The principal perennial bunchgrasses are the same ones noted by Watson (1871) and listed above.

South of the Humboldt and Truckee Rivers a wide band of conifer woodland on the sides of the mountains divides the sagebrush-bunchgrass ecosystem into a large lower zone and a smaller upper zone of sagebrush-bunchgrass.

Table 1—Areas and	percentages of the principal ecosystems in
Western N	levada between latitudes 38° and 41° N and
longitudes	117° and 120° W

Ecosystem type	Area	Area	Total area	
	Miles ²	km²	Percent	
Alpine fell-fields	9.7	25.2	0.03	
Cottonwood forest	101.6	264.2	0.34	
Greasewood salt desert	1,403.6	3,649.4	4.72	
Jeffrey pine-white fir forest	222.6	578.8	0.75	
Juniper-sagebrush	701.8	1,824.7	2.36	
Limber pine forest	135.5	352.3	0.46	
Open water	411.4	1,069.6	1.38	
Pinyon-juniper woodland	3,605.8	9,375.1	12.11	
Red fir forest	96.8	251.7	0.33	
Sagebrush, lower	10,890.0	28,314.0	36.59	
Sagebrush, upper	532.4	1,384.2	1.79	
Saline playas (bare)	1,069.6	2,781.0	3.59	
Shadscale desert ¹	10,251.1	26,652.9	34.44	
Sierran subalpine forest	19.4	50.4	0.07	
Tule marsh	203.3	528.6	0.68	
Willow meadow	111.3	289.4	0.37	
Total	29,765.9	77,391.5	100.01	

Including dune vegetation and unstabilized dunes.

The upper subzone is floristically richer and more productive of forage than the lower drier subzone. This upper subzone is colder and snowier, and in places resembles a montane chaparral with Ceanothus velutinus, Amelanchier, and Arctostaphylos. When one combines the area of the sagebrush-bunchgrass ecosystem with that of the conifer woodland of pinyon and juniper (Pinus monophylla and Juniperus osteosperma), the total area of this sagebrushconifer woodland complex occupied about 50 percent of the land in the western Great Basin two centuries ago. At that time, fires were rare in these ecosystems and there was little dry herbaceous vegetation to carry fire any distance (Billings 1990). Lightning strikes could start small fires in dense stands of pinyon-juniper (as reported by Tausch and West 1988, in southwestern Utah). Such fires were probably rare in western Nevada during the 19th century due partly to a lower incidence of lightning storms in the lee of the Sierra than in southern Utah.

EFFECTS OF 19TH CENTURY LIVESTOCK GRAZING

The best measure of the effects of grazing during the 19th century in the sagebrush-bunchgrass ecosystem is that of P. B. Kennedy's pioneer study done in 1902 along a 55-mile survey transect across the Tuscarora Mountains in Elko County, NV (Kennedy 1903). In this early work in range ecology, Kennedy mapped the state of vegetation and soil conditions at the turn of the century. In the years prior to his study, it had been heavily grazed by sheep and cattle. At that time, Kennedy did note perennial grasses and some range deterioration, but no fire scars, and no *Bromus tectorum*. It was 7 years before Mrs. J. S. Thompson would find and collect this *Bromus* near the village of Tuscarora northwest of Kennedy's transect, and 4 years before Kennedy himself would note its presence along the railroad at Reno more than 250 miles to the west.

In 1952, Robertson (1954) re-surveyed Kennedy's same route exactly 50 years later. Robertson found five principal changes to this rangeland since Kennedy's time:

1. Desirable shrub livestock browse had decreased.

2. Agropyron spicatum described as "abundant" by Kennedy had decreased to "generally absent" or "less than 5 percent density" the time of Robertson's re-survey.

3. Annuals had "increased to an extreme degree"; much of this was *Bromus tectorum*.

4. Burn scars, absent in 1902, now covered much of the route and were covered with cheatgrass everywhere along the way.

5. The stream channels had eroded deeper and wider.

CHEATGRASS AND FIRE

Cheatgrass (Bromus tectorum L.)—"bromegrass of the thatched roofs"—is an annual grass native to western Europe whose natural range extends eastward to the TransCaspian cold deserts, and thence southward into Asia Minor. It was adventive into the cooler regions of eastern North America from ships bringing the early settlers of the 17th and 18th centuries. It has not assumed dominance in the native vegetation of the eastern states and provinces. Most likely this is because of shading, abundant moisture, and competition from taller plants and trees. The warmer winter climates of the southeastern states have made it rare or even absent south of Tennessee or North Carolina.

Mack (1981) has documented the history of the introduction of cheatgrass into western North America. He reports that plants of this species were collected by J. Macoun in 1890 at Spence's Bridge, interior British Columbia, where it was present "in meadows and cultivated fields." It was not present there when Macoun made his earlier collections in 1877 in the same region. In 1893, near Ritzville, WA, this grass was collected along the Great Northern Railroad by Sandburg and Leiburg. A year later, it was collected near Provo, UT, by M. E. Jones. All these places were interior wheat-growing areas. Mack (1981) suggests that the *Bromus* seeds entered the the drier regions east of the Cascades and Sierra Nevada as a contaminant in grain seed.

The first collection of this species in western Nevada was by A. A. Heller, #10488 in 1912 from Reno. This specimen is in the Herbarium of the University of Nevada Reno. However, *Bromus tectorum* was present in Reno as early as 1906. P. B. Kennedy had reported it, with *B. rubens* and other *Bromus* species, as occupying "considerable areas along embankments, but always near the railroad or highways" (Kennedy 1907). No voucher specimen is known to exist of this observation, but Kennedy did know the species. From the railroad and Reno, this cheatgrass species spread rapidly and widely into the overgrazed sagebrush rangeland during the first three decades of this century.

The spread of *Bromus tectorum*, which dries out in late May and June in this summer-dry region, brought a new and explosive factor to the summer environment of the sagebrush zone: *fire*. When the herbaceous stratum in the sagebrush-bitterbrush ecosystem was occupied mainly by widely scattered bunchgrasses, there was little tinder to carry fire through the community. Cheatgrass invaded this overgrazed ecosystem easily and filled an open environmental niche due to available soil moisture and low temperatures favorable to this winter annual. Once present, it readily occupied much of the open space between the shrubs.

During those spring seasons following wet, snowy winters, this grass grows rapidly in April and May reaching heights of 20 to 30 cm. It dries rapidly in late May and early June. From then to October, it provides abundant fuel for the start and spread of extensive range fires, often in terrain where such fires are difficult to control.

I do not know exactly when cheatgrass in the sagebrush ecosystem became abundant enough to provide fuel for extensive and disastrous range fires in the western Great Basin. But such fires were common in the mid-1930's. Pickford (1932) reported that on burned areas in the Great Salt Lake District, UT, *Bromus tectorum* had replaced sagebrush as a dominant, and often covered burned sites in dense stands. It was still spreading into

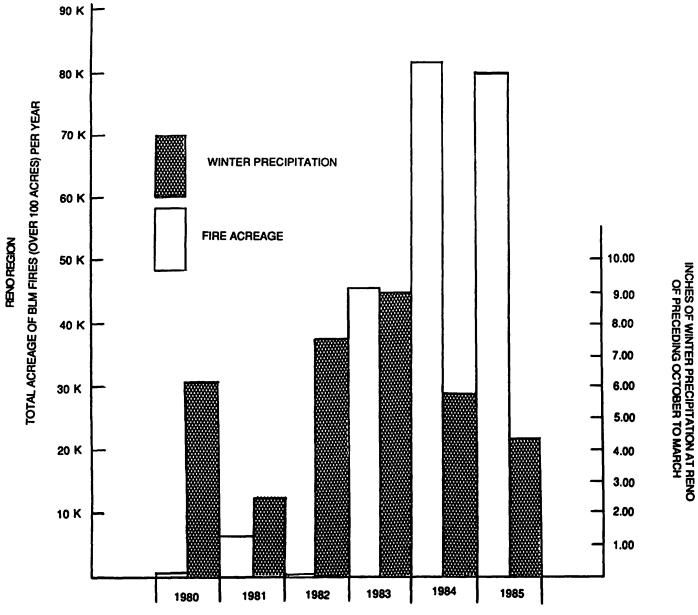


Figure 2—Quantitative relationship between winter precipitation at Reno, Nevada, and wildfire acreage in the Reno Region of the Bureau of Land Management during the following summer.

new areas of the sagebrush biome. As Aldo Leopold (1941) expressed it: "One simply woke up one fine spring to find the range dominated by a new weed...cheat grass (*Bromus tectorum*)". Fires accelerated during the 1940's and much acreage was devastated in western Nevada.

In an effort to quantify the relationship between wet winters and subsequent cheatgrass-caused fires, I used BLM Reno Region fire data and winter precipitation (October through March) totals from the Reno National Weather Service Station for the 6 years from 1980 to 1985. The results shown in graphic form appear in figure 2. An apparent positive relationship exists between precipitation for the preceding winter months and the total fire acreage of those fires larger than 100 acres during the following summers. Other factors aside from winter precipitation also govern fire acreage during the following summer, so this relationship is only approximate but suggests that further research might be helpful.

The effects of higher winter precipitation appear to be cumulative through time since fire acreage also tends to increase. In part, this may be due to increasing seed production of cheatgrass as a result of soil moisture during the subsequent spring seasons. The seeds of this species remain alive in the upper soil for some time, especially under dry, cold seasons and can germinate as wet winters re-occur. Hulbert (1955) found that 1-year-old seeds of *Bromus tectorum* stored in the laboratory germinated at 96 percent within 34 days. In another experiment, Hulbert found that seeds of the same species that had been stored for 7.5 years germinated at about 96 percent also, after 18 days in moist petri dishes. In field tests, in moist soil, *Bromus* seeds buried in small cloth sacks at depths to 100 cm for 9 months germinated less well. This apparently was due to the seeds taking up some moisture followed by periods of dry soil after roots had developed and subsequent death of the roots and young seedlings. Hulbert also used germination tests in the laboratory on cheatgrass seeds collected in western Montana by Joseph Kramer and stored in paper sacks in the laboratory for 5.5, 7.5, 10.5, and 11.5 years. These all germinated at 95 to 100 percent in petri dish tests. Soil drought in midgermination appears to be lethal to seeds of cheatgrass.

In September 1985, I collected a large quantity of top soil to a depth of 15 cm from an unburned sagebrush ecosystem on the southeast slopes of Peavine Mt., at an elevation of 1,740 m, about 10 km northwest of Reno, NV. The parent material at the site is unaltered andesite of the Alta Formation (Gianella 1936). These brownish semidesert soils have been described and designated as Xerollic Haplargids by DeLucia and others (1989). The collected soils were allowed to air-dry until March 1986. At that time, we set up an experiment under greenhouse conditions at 20 to 25 °C. By watering 291 pots of the sagebrush soil, each containing 237 cc of soil with a surface area of 38.5 cm square, the experiment was designed to determine the seed bank of viable seeds of cheatgrass in the upper 15 cm of soil in this unburned sagebrush ecosystem. The pots were watered daily for 3 weeks and the resulting seedlings of Bromus were counted. At the same time, 216 pots were filled with the acid soil from a nearby outcrop of hydrothermally altered andesitic rock from the same geologic Alta Formation (Billings 1950, 1992). This outcrop is occupied by a very open stand of Pinus ponderosa with no shrubs and very few small herbaceous plants.

The total number of cheatgrass seedlings produced in the 291 pots of sagebrush brown soil was 1,318. The mean number of seedlings per pot was 4.53. Therefore, the seed bank of Bromus tectorum in the upper 15 cm of soil of the sagebrush ecosystem at this site in the early autumn of 1985 was about 1,177 seeds per meter square as a minimum. Due to the possibility of viable ungerminated seeds, it could have been a bit more. In contrast to the seed bank of Bromus in the sagebrush community, that of the same species in the 216 pots of soil from the hydrothermally altered rock soil totaled only 5 seedlings for a mean of 0.023 per pot or about 6 seeds per meter square. Bromus tectorum is not tolerant of the acid, nutrient-poor soils over the hydrothermally altered andesites and cannot invade such ecosystems. What is indicated here is that after a winter of very heavy precipitation and resultant high soil moisture during the following spring, there could be a large standing crop of dry cheatgrass in the as-yet-unburned sagebrush community ready to burn and carry a fire. In contrast, a ground fire in the open ponderosa pine groves on hydrothermally altered rock would be impossible because there are so few dry herbaceous plants, including cheatgrass, to carry the fire. Actually, these pine stands seldom burn except by crown fires on very steep slopes where the trees are close together.

VEGETATIONAL SUCCESSION FOLLOWING FIRE

In 1941, I established permanent plots in unburned north-facing and south-facing sagebrush vegetation at an elevation of about 1,525 m approxiately 5 km northwest of Reno. These were re-sampled and re-photographed from time to time for the next 47 years. In 1941, *Bromus tectorum* had already invaded these unburned communities but was much more abundant on the south-facing slope in which shrub cover was more open. The principal shrubs were Artemisia tridentata, Purshia tridentata, Ephedra viridis, and Tetradymia glabrata.

On July 15, 1947, a large wildfire of some 360 ha swept across the plots and the surrounding, previously unburned shrubland. The vegetation of the plots was completely burned and little aboveground vegetation remained. Repeat photographs, from the same spot as those of 1941, were made in 1953 (6 years after the fire) and in 1988 (41 years after the fire). The 1941, 1953, and 1988 photographs showing both slopes appear in figure 3. Shrub succession has been slow, and Artemisia tridentata scarcely returned at all even after 45 years. However, the sprouting shrubs (Ephedra viridis, Prunus andersonii, Tetradymia glabrata, and Tetradymia canescens) have been aided in their return by their sprouting ability as well as seed production. The nonsprouting Purshia tridentata, which relies only on seeds for re-establishment in western Nevada, surprisingly came back fairly well compared to Artemisia, which also reproduces only by seeds. Purshia came back in greater abundance on the north-facing slope. But none of the shrub species had the speed of return in reproduction that was shown by Bromus tectorum. This annual cheatgrass was the most abundant plant species in 1948, the year following the fire. Forty years later, in 1988, Bromus tectorum had increased its density per meter square on both south-facing and north-facing plots by an order of magnitude. After wet winters, the cheatgrass fuel value per unit area is great indeed, as can be seen in a photograph of the south-facing slope in the summer of 1986 (fig. 4).

Young and his co-workers (1972, 1976, 1978, 1985, 1987, and this volume) have carried on intensive research throughout Nevada in regard to succession and competition between species following wildfires in which *Bromus tectorum* has been involved. Their work has been specific and definitive with data from a number of sites. Neil West and his co-authors (for example, West and Hassan 1985) have followed succession after similar fires in the sagebrush communities of central Utah.

Also, in the Reno region, the laboratory of Nowak and Tausch at the University of Nevada has done excellent pioneer research on the physiological ecology of *Bromus tectorum* in competition with a native shrub species, *Chrysothamnus viscidiflorus*, and a native perennial grass, *Stipa comata*, after fires in the sagebrush ecosystem (Melgoza and others 1990). It is not my purpose to review the above-mentioned research here since all of these authors are well-represented in this volume with more recent research.

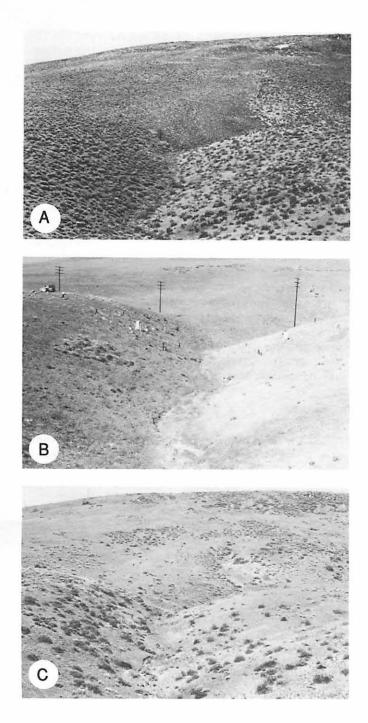


Figure 3—(A) The original unburned sagebrush vegetation at Ecology Canyon northwest of Reno, NV, in summer 1941. The north-facing slope is on the left; the south-facing slope is on right. The light color on the South-facing slope is a complete cover of *Bromus tectorum*. (B) The same view photographed in 1953, 6 years after the wildfire of July 15, 1947. The south-facing slope is covered almost entirely with *Bromus tectorum*. There are a few small sprouting shrubs. (C) The same view in 1988, 41 years after the fire. *Bromus tectorum* still is abundant on the south-facing slope. The darker shrubs are mostly bitterbrush, *Purshia tridentata*.



Figure 4—The south-facing slope and plot in 1986, 39 years after the wildfire burn. The slope is covered with tall, light-colored dry *Bromus tectorum. Purshia tridentata* and *Ephedra viridis* are the principal shrubs. There has been little recruitment of shrubs since 1953, and there is still little if any *Artemisia tridentata*.



Figure 5—Large area where pinyon-juniper woodland has been burned and destroyed by a wildfire of the late 1970's in the Virginia Range between Reno and Virginia City. A few remnants of the original woodland are on the distant ridge. The original unburned pinyon-juniper was a dense stand. The light-colored vegetation is *Bromus tectorum*; it is not snow. Elevation is about 1,900 m.

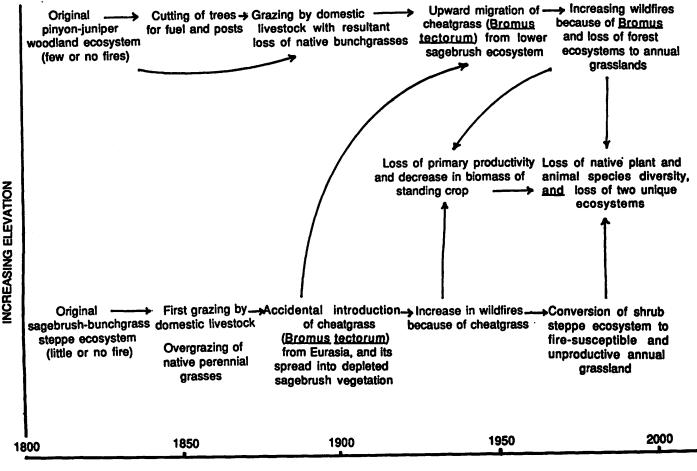
EFFECTS OF CHEATGRASS ON THE PINYON-JUNIPER WOODLAND

Billings (1951) described the elevational mountain vegetation zones of the Great Basin as a distinct series from the Sierran series. The boundary between these two series is quite sharp and lies in the valleys of western Nevada and eastern California in a line running approximately northwest to southeast between Reno and Bishop. The boundary and the vertical zonation of these two series can be seen in figure 1.

Lying just above the lower sagebrush zone in the Great Basin series is the pinyon-juniper woodland zone characterized by *Pinus monophylla* and *Juniperus osteosperma*. Tueller and others (1979) have mapped the areal distribution of this Great Basin pinyon-juniper vegetation zone, its flora, and vegetational cover in detail. In the strictest sense, the pinyon-juniper woodland in the western Great Basin is a mountainside zone lying almost entirely south of the Truckee and Humboldt Rivers from northeastern Elko County to Winnemucca to Reno (also, see the Billings 1954 map). There are a few outlier populations of pinyon in the Pah-Rah Mountains south of Pyramid Lake and on the sides of the Eugene Mts. southwest of Winnemucca but north of the Humboldt River.

Until about the 1950's, *Bromus tectorum* had not invaded the pinyon-juniper woodland to any serious extent. Since then, it has invaded upward into this coniferous zone. In the last 30 years, fires have become much more common in this woodland ecosystem fueled not only by the dry cheatgrass but, once started, by the resins of the trees themselves. This is particularly true in the Virginia Range between the Truckee and Carson Rivers, and also in the Pine Nut Range south of the Carson River. The result is the destruction of thousands of acres of this unique woodland ecosystem with its characteristic conifers, its birds, and mammals. This woodland is being replaced after fire by great expanses of annual grassland dominated by even more *Bromus tectorum* as shown in figure 5 of the destruction of pinyon-juniper woodland in the Virginia Range and its replacement by the light-colored, dry cheatgrass.

Koniak (1985) studied succession following such fires of the last 30 to 40 years in central and western Nevada. She also found that cheatgrass returns early in succession. In some of the older burns, the two tree species began to re-establish in 20 to 30 years but the tree cover was minimal even 60 years after the fire. I would suggest that return of the tree species would be much slower on those burns of greater extent where the seed source and the animal and bird vectors are far away. The oldest burn in pinyon-juniper that has been studied (Tausch and West 1988) dates from the mid-19th century in southwestern Utah long before the advent of *Bromus tectorum*. It is notable that this was a small fire (only 3 ha) compared to the large areas now being burned. Tausch and West found that pinyon density exceeded that of juniper for the



APPROXIMATE DATES

Figure 6—A flow diagram of changes in the sagebrush-bunchgrass and the pinyon-juniper ecosystems through the 19th and 20th centuries as postulated by the author.

first 60 years after the fire. And, pinyon had nearly six times the density of juniper 145 years after the fire. In contrast, the surrounding unburned woodland consists only of about 50 percent pinyon (*Pinus monophylla*), about the same as the juniper (*Juniperus osteosperma*).

LONG-TERM IMPLICATIONS

The invasion of cheatgrass into the vegetation of the Great Basin and its effects in relation to fires with their cumulative and repetitive impacts on the native ecosystems are products of the 20th century. As we approach the 21st century, what can we do in attempting to predict the structure and operation of semi-arid ecosystems in the Intermountain region during the next 100 years? Our crystal ball is somewhat clouded and filled with surprises.

I shall let the flow diagram in figure 6 speak for my best guesses, which are:

1. Some of the native plant and animal species in those ecosystems that are now prone to widespread wildfires are at considerable risk of going extinct at the population level locally or even regionally. The result will be loss of biological and genetic diversity, and also operational efficiency of the ecosystem.

2. There could be a genuine threat to the existence of large integrated ecosystems that have existed since the Pleistocene in the relatively arid lands between the Rocky Mountains and Sierra Nevada. These operational ecosystems could disappear over large areas of thousands of square kilometers. This is primarily because of one innocuous-appearing annual species of grass, Bromus tectorum, an invader, and probably other invaders of the same life form such as Taeniatherum asperum, medusahead, another non-native from the Old World. The results could be conversion of these native ecosystems to unproductive and simplistic annual grasslands lacking not only the native vertebrates but also those invertebrates and cryptogams that are involved in the operation of the system including energy flow, water cycling, and nutrient balance. This kind of ecosystemic conversion has taken place before, with different species, on the barren hills surrounding the Central Valleys of California that were once covered with complex native bunchgrass ecosystems supporting unique floras and animal life.

3. The cheatgrass-fire situation demonstrates that not all global ecosystemic change is due to climatic change in which prediction is somewhat easier. Ecological surprises can come quickly and often with such speed that there is always the possibility that ecosystemic destruction could be irreversible.

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FIRE CONDITIONS PRE- AND POSTOCCURRENCE OF ANNUAL GRASSES ON THE SNAKE RIVER PLAIN

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ABSTRACT

Fire has been an important factor in the development of the vegetation of the Snake River Plain. Prior to Euro-American influence, fire helped determine the physiognomy and species composition of many communities. The occurrence of fire varied widely depending on the vegetation present, topography, and other factors. This impact can be detected in many historical documents and inferred from species response to fire. On the upper Snake River Plain, fire was frequently reported and was an important factor in vegetation development. On the lower plain, fire appears to have been less common. Low amounts of fine fuel probably limited the extent. During the postsettlement period, the occurrence of fire has increased throughout much of the Snake River Plain. The introduction of annual grasses, particularly cheatgrass (Bromus tectorum L.), has altered fuel loads and fuel distribution, which in turn has changed fire intensity and extent. Increased human activity has resulted in greater numbers of ignition sources. The decreased fire-free interval (FFI) has greatly modified the presettlement role of fire and the distribution of many species.

INTRODUCTION

The introduction of exotic annual grasses, particularly cheatgrass (*Bromus tectorum* L.) and medusahead (*Taeniatherum caput-medusae* Nevski) into the Snake River Plain may have been the most important event in the natural history of that region since the last glacial period. The associated changes in plant recruitment and fire history, as well as domestic livestock grazing, have completely changed the species composition, physiognomy, and functioning of many vegetation types within the region. The adjustments in biotic community structure following the introduction of the species are continuing to be reflected in the vegetation. Throughout much of the more arid portion of this region, the development of vegetations dominated by one or more annual grasses with frequent fire occurrence is taking place. In this paper we will discuss the occurrence of fire prior to and following the introduction of annual grasses and the subsequent effects on the vegetation. Changes on the Snake River Plain will be emphasized, but information is applicable to adjacent areas of the Great Basin.

In recent years authors have discussed the nature of pristine vegetation on the Snake River Plains and Great Basin based on anecdotal information (Christensen and Johnson 1964; Hull and Hull 1974; Johnson 1986; Vale 1975). These studies have placed primary emphasis on the existing diaries and journals of people entering the region in the early to mid 19th century. The interpretations based on these accounts are highly variable. This is probably expected given the wide variety of vegetation types involved, the long timeframe, and variety of perspectives included in the descriptions and narrations. Most of the observers were from more humid areas of eastern North America, and the arid stark conditions, long distances, lack of water, and strange plants must have made many travelers uneasy. This may have certainly colored many narratives. Most west-bound travelers, leaving Missouri in the spring, did not reach the Snake River Plains until late summer when most of the forage was dormant. Perhaps the first scientist to observe and write about the Snake River Plain in the spring was C. H. Merriam (1890). Also included in these observations are those of the "professional" travelers such as Peter Skeene Ogden, John C. Fremont, Osborne Russell, and John Work who were well equipped and trained for surviving in the region. Due to the amount of time the writers spent in the region and their continual need for water, forage, game, and fuel, these accounts may be our most valuable for the purpose of reconstructing the role of fire in the pristine conditions.

These accounts, supported by old photographs, have also been used to assess the role that fire may have had in the development of vegetation prior to the settlement of the region by Euro-Americans (Gruell 1983; Gruell 1985; Gruell 1986; Gruell and others 1985). In addition, more quantitative approaches to documenting the occurrence of fire have been done for areas that have a tree species that firescars and retains a long-term history (Burkhardt and Tisdale 1969; Burkhardt and Tisdale 1976; Gruell and others 1985; Houston 1973). Because of the reliance on trees to record fire occurrence, these quantitative studies have been done at elevational and precipitation zones that are greater than the area most greatly impacted by the introduced annual grasses. Generally these studies have documented a decrease in fire occurrence and a subsequent increase in the

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woody component of the associated plant community. However, most of the studies did not include the region specifically dominated by cheatgrass and medusahead today. Rather more attention has been given to those areas of the sagebrush-grassland that are on or near the ecotone between sagebrush and woodland or forested vegetation such as western juniper (*Juniperus occidentalis* Hook.), mountain-mahogany (*Cercocarpus ledifolius* Nutt.), ponderosa pine (*Pinus ponderosa* Dougl.), and Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco).

PREOCCURRENCE OF ANNUAL GRASSES

The impression given by the anecdotal accounts for the lower Snake River Plain is that big sagebrush (Artemisia tridentata Nutt.) was an overwhelming dominant in the region. We will define the lower Snake River Plain as that portion west of a line from Arco to American Falls, ID. Many individuals describe the appearance, often unfavorably, that sagebrush gave to the landscape. In 1843 near the mouth of Goose Creek, John C. Fremont noted that "the country has a barren appearance, sandy, and densely covered with the artemisias from the banks of the river to the foot of the mountains." Several days later near the present site of Twin Falls he added that "there was no grass here, the soil among the sage being entirely naked" (Fremont 1988). In 1812 describing the area near the present town of Burley, Stuart noted that "the whole face of the country appears level before us, ..., the sage wormwood and saltwood cover a parched soil of sand, dust and gravel" (Spaulding 1953). Townsend (1839) described the area between Blackfoot and Arco as a "wide sandy plain, thickly covered with wormwood."

In 1830, Wislizenus (1912) described the area along the Portneuf River near its confluence with the Snake. "On the east side of the river the plain is barren sandy, and level, and produces only prickleypear, sage and occasional scanty tufts of dry grass. On the west side, the plain is much more extensive stretching often away to 50 and even 60 miles...like the other, barren of vegetation except prickleypear and sage."

Forage for stock was also a concern for most travelers. Many accounts indicate concerns of being able to locate adequate forage for animals. The Oregon and California migration began in 1841. By 1843 tens of thousands of people journeyed along the Oregon Trail annually, and most had stock of some type. The Oregon Trail was not a single track but rather a series of routes. Forage utilization along the trail was undoubtedly high during the years of high migration. Many immigrants were forced to range up to several miles from the trail in order to find adequate feed (Hill 1987). The high utilization makes interpretation of Oregon Trail diaries after 1843 questionable when the authors are discussing vegetation. It was probably very impacted by the mid-1840's. In some locations the evidence of this intense use is still visible on the landscape. However, many accounts that predate the high migration period also express concern for the availability of forage. Near Shoshone Falls, Cross (1851) stated, "They (the mules) were therefore turned out to graze among the sandhills and artemisia, there being scarcely a particle of

grass either on the bluff or in the canyon." Stuart in 1812 indicated at Three Island Crossing near present Glenns Ferry, ID, that "scarce and bad indeed is the fodder for our horses" (Spaulding 1953). Limited forage was particularly a concern for those forced to take the route that followed the south bank of the Snake River when high water at Three Island Crossing did not permit fording the river. Forage and water availability were apparently greater along the northern route that followed the lower Boise River. Cross (1851) wrote of the route from Rock Creek to Fort Boise that "the condition of our mules did not justify such long marches; but we were driven to it by compulsion, as neither water nor grass was to be had at any intermediate point." He later stated that the grazing near the mouth of the Malheur River was the best they had seen for some time.

Those able to ford the Snake River at Three Island Crossing found forage conditions more favorable. This was particularly true once the Boise River was reached. Many accounts describe the beauty and lush pasture conditions of the Boise River Valley (Fremont 1988; Haines 1971; Townsend 1839). Bonneville describes the Boise River Valley as the most enchanting he had seen in the far West, presenting the mingled grandeur and beauty of mountain and plain, bright running streams, and vast grassy meadows (Irving 1986). The combination of plentiful forage, water, cottonwood groves, and abundant game and salmon made this area a frequently used rest stop to recover from the hardships of travel across the plain.

Observations on wildfires were uncommon on the lower Snake River Plain. Gruell (1985) documented only five observations of fire in his survey of the historic literature during the 1800-46 period. However, fires did occur. On September 14, 1830, John Work made the following notes on a fire that had occurred 30 km southeast of the present site of Boise: "The country has recently been overrun by fire. Scarcely a spot of grass left for the horses to feed." He continued to cross this burned area for part of the next day (Haines 1971), so it must have been relatively large in size.

The lack of observations of fire on the lower Snake River Plain can probably be explained by the low forage (fine fuels) produced by the vegetation. The region is comprised of several habitat types dominated by an overstory of Wyoming big sagebrush (Artemisia tridentata Nutt. ssp. wyomingensis Beetle and Young) (Hironaka and others 1983). During most years, perennial grass (fine fuel) production in these habitat types was probably less than 400 kg/ha (personal communication, M. Hironaka, 1992). While wildfires could occur, even extensive fires under extreme conditions, fires were generally limited by low fuel loading. Fire behavior and fire spread become very erratic when less than 650 kg/ha of fine fuels are present (Beardall and Sylvester 1976; Bunting and others 1987). Once burned, an area was probably unable to sustain a large fire until a new stand of Wyoming big sagebrush became established and contributed to the fuel loading on the site. Prior to the establishment of sagebrush the perennial grasses were too low in density to provide for fire spread under most environmental conditions. Consequently the possibility of frequent reburns was self limiting. Much of the area south of the river is comprised of

Wyoming big sagebrush habitat types as well as one of several salt-desert shrub communities dominated by winterfat (*Ceratoides lanata* [Pursh.] J.T. Howell), saltsage (*Atriplex nuttallii* Wats.), shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.), or greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.). These salt-desert communities produce even less fine fuels than the Wyoming big sagebrush communities and rarely burned under pristine conditions.

A recent hypothesis explaining the scarcity of bison (Bison bison) west of the Rocky Mountains supports the low finefuel concept for the lower Snake River Plain. Van Vuren (1987) has suggested that the distribution of bison was limited by low overall forage conditions. Frequent observations of large numbers of bison prior to 1830 were reported for the upper Snake River Plain and adjacent valleys (Ferris 1983; Haines 1965; Haines 1971; Irving 1986; Ogden 1910; Townsend 1839; Wislizenus 1912). The only location farther west where they were consistently found was in the Raft River Valley. This area was frequently used as a supply point for trapper brigade expeditions into the northern Great Basin (Haines 1971). The great areas once dominated by Wyoming big sagebrush on the lower plain were seldom reported as having large numbers of bison. However, occasional observations were made on the eastern portion of the lower plain. The long severe winter of 1830-31 is generally credited for destroying the Snake River bison herd (Haines 1971). The high winter mortality combined with more efficient hunting methods by Indians, who had acguired the horse and the firearm, and increased hunting pressure from the trapper brigades during the 1810-40 period, probably never allowed the bison to recover. The herd was most likely extinct by 1840, as no references to bison on the Snake River Plain appear in the Oregon Trail diaries.

The upper Snake River Plain and adjacent valleys were distinctly different from the lower plain in characteristics other than the presence of bison. While variable, more grass was consistently reported for this region (Haines 1965; Haines 1971; Irving 1986; Mullan 1855). Ferris (1983) indicated that as one traveled up the Snake River from the mouth of the Portneuf River you crossed "a rich and continuous bottom of excellent grass." Townsend (1839) described the Big Lost River Valley as being "about a mile in width, and covered with excellent grass." The Lemhi Valley, Teton Basin, and south of Monida Pass were also frequently described as having good grazing. Reports of fires prior to 1846 are much more common in the historic literature for the upper Snake River Plain and adjacent valleys (Gruell 1985).

Another area frequently described for its lush valleys was the Camas and Little Camas Prairies 35 km north of Three Island Crossing (Haines 1971; Irving 1986). Fremont (1988) stated, "There is no dispute about the grass, which is almost universal on the hills and mountains, and always nutritious, even in its dry state." He also stated, "Here the vegetation was very much changed, the artemisia disappeared almost completely,...and was replaced by purshia tridentata. These (the hills) were everywhere covered with a fresh and green short grass, like that of early spring. This is the fall or second growth, the dried grass having been burnt off by the Indians; and wherever the fire has passed, the bright-green color is universal." Fires were also reported a number of times in other accounts from this area (Haines 1971). These prairies are higher in elevation and receive greater precipitation, and the uplands are dominated by mountain big sagebrush (*Artemisia tridentata* Nutt. ssp. vaseyana [Rydb.] Beetle), not Wyoming big sagebrush. A number of references to wildfires on these prairies can be found in the historic literature. Fires, both wild and prescribed, are common today, and cheatgrass is present but does not dominate.

POSTOCCURRENCE OF ANNUAL GRASSES

Prior to the 1890's, only a few native grass species occupied the early seral position in disturbed landscapes of the Snake River Plains. Of these, the annual fescues (Festuca octoflora Walt. and F. megalura Nutt.) were the primary annual grasses. These species would increase for a few years following disturbance, and then be suppressed by perennial species, such as squirreltail (Sitanion hystrix [Nutt.] J. G. Smith), Idaho fescue (Festuca idahoensis Elmer), bluebunch wheatgrass (Agropyron spicatum [Pursh] Scribn. and Smith), rabbitbrush (Chrysothamnus spp. Nutt.), and sagebrush. Fire historically occurred in these communities at intervals of 20 to 100 years (Houston 1973; Wright and Bailey 1982; Wright and others 1979), and a successional cycle of early seral perennial to lateseral perennial (sagebrush-bunchgrass) dominance was thought to have occurred. The introduction of cheatgrass and medusahead, both Eurasian winter annuals, has significantly altered the dynamics of these rangeland ecosystems by changing the fire regime and successional patterns.

Cheatgrass, introduced into the Intermountain West in the 1890's, began to appear on the Snake River Plains in the years between 1915 and 1920 (Mack 1981). The primary route of introduction is believed to have been in seed grain, and shipment via railways offered widespread dispersal (Mack 1981). Animals, especially sheep, may have also been important contributors to cheatgrass spread (Yensen 1981). According to accounts, cheatgrass flourished in disturbed areas, such as abandoned farmlands (Piemeisel 1938; Piemeisel 1951), roadsides, and overgrazed range (Mack 1981), and was rapidly distributed across diverse habitats over much of the United States. Cheatgrass was found to provide good forage in the early spring (Harris 1967; Hull and Pechanec 1947), and many ranchers intentionally burned sagebrush rangeland to increase this forage source. However, by maturity its forage value is lowered, and annual yield variation is much greater than for perennial grasses (Hull and Pechanec 1947; Tisdale and others 1969).

Medusahead was introduced into the Western United States in the 1930's and first collected in Idaho in 1946 (Torell and others 1961). It was also probably introduced in seed grain and dispersed via animals. The range of occupation by medusahead is less than that occupied by cheatgrass, as it appears to require more well-developed, finer textured soils (Dahl and Tisdale 1974). Despite the soil limitations, it appears to be moving eastward (Dahl and Tisdale 1974). Throughout the entire plant, medusahead has high silica content (Bovey and others 1961), and thus has low forage quality. Both cheatgrass and medusahead germinate in the fall after the commencement of the fall rains and are capable of root growth throughout the winter (Hironaka 1961). The amount of growth or tillering by these species depends on the amount of moisture received, but even in low precipitation years both species are capable of forming dense stands and producing viable seed (Tisdale and Hironaka 1981). Upon maturity, medusahead and cheatgrass produce a very fine fuel source, and both may lodge, thus forming a continuous fuel source (Turner and others 1963). The high silica content of medusahead also slows decomposition and thus, over several years, medusahead is capable of forming a dense mat of highly flammable material (Turner and others 1963).

The following two situations are given as examples of the effect that exotic annual grasses have had on communities within the sagebrush-grassland region of the lower Snake River Plains. The upper Snake River Plains receive higher amounts of precipitation and thus do not have the problem with annual grasses, as on the lower Snake River Plains (Bunting and others 1987).

In the first scenario the dominant perennial grasses and forbs have been reduced by overgrazing, while sagebrush and rabbitbrush have increased. Within these communities, the shrub component has formed a dense canopy, and there is little understory vegetation. The closed canopy of these communities is very susceptible to fire. Fire is carried through the community within the canopy, and the overstory species are greatly reduced. If a seed source for annual grasses is present, they will increase following fire. Perennial grass and forb species may maintain prefire population numbers, but more likely will decrease. As annual grass dominance increases, these communities become more susceptible to fire. Within 3 to 6 years following the initial fire, the dried annual grass culms will develop sufficient continuity of fuels to readily support a second fire. Successive fires become common, and each fire reduces the surviving sagebrush and rabbitbrush further. Although resprouting species, such as rabbitbrush, increase with fire, these resprouting species are also lost when the fire-free interval (FFI) is decreased to 5 or less vears (Whisenant 1990). In addition, repeated fires with short FFI's deplete the soil seed reserves of sagebrush and other fire-sensitive species.

The second situation occurs in areas where the shrub component has been removed, and annuals and perennial grasses are present. As a fire burns these communities, the perennial species will respond differentially to the fire. Species such as squirreltail are more fire tolerant than the fescues or wheatgrasses (Wright 1971; Wright and Klemmedson 1965; Young and Miller 1985). Perennial forbs are more tolerant of fire in the late summer (Wright and Bailey 1982). Although a reduction in annual grass density occurs after fire, there is a flush of nutrients that the annuals take advantage of, and if adequate moisture is present, they will produce an ample seed crop (Young and Evans 1978). Competition from the cheatgrass and medusahead limits recruitment of perennial grasses, due to the earlier initiation of spring growth of the annual grass seedlings. Thus, over a few years, the annuals will again dominate, litter will accumulate, perennial grasses

will be those more tolerant of fire, and the community will be capable of supporting another fire. Throughout this time, the perennial seed bank diminishes. If there are no adult perennial species to produce more seed, the burned community would rely on dispersal from adjoining nonburned communities to provide the seed source necessary for perennial recruitment. But with each fire the area of annual dominance increases, and exogenous seed sources become more dispersed. Also, recent research (Melgoza and Nowak 1991; Melgoza and others 1990) has demonstrated that cheatgrass negatively affects the growth and productivity of established perennial species. Thus, regeneration of the perennial species is limited.

These two examples are likely to occur in years of belowaverage precipitation ("dry") or above-average precipitation ("wet"). Perennial seedlings are more able to become established in wet years, in spite of increased annual seedlings. Also, during wet years, spread of the annual grasses into the salt-desert shrub communities occurs. Thus, in wet years, these communities, too, become more susceptible to fire.

Although wet years are good for perennial plant establishment, the increased production of the annual grasses results in increased fuel continuity and fine fuel. The annuals become dormant in late summer, and therefore the community has a greater chance for fire. This is reflected in the statistics of the acreage burned within Idaho. Within a 10-year period, 2,412,890 acres (976,879 ha) burned primarily on the Snake River Plains, and until the drought years of 1987 and 1988, the amount of land burned annually had steadily increased in the previous 5 years (Pellant 1990). Production of annual grasses is reduced during drought years, litter accumulation rates are reduced, and the community will become less susceptible to fire. Within annual-dominated rangelands, an FFI of 10 to 12 years, or less, is likely. For these communities to become more resilient to fire, FFI's probably need to be greater than 20 to 50 years, to allow establishment of the sagebrush species occupying the various habitat types on the burned area.

SUMMARY

The vegetation within the Snake River Plains was historically shrub-bunchgrass communities, with bunchgrasses occupying the interspaces between the shrubs. Fire occurred in the more arid communities only if the sagebrush was sufficiently dense to carry a fire, as the bunchgrasses did not provide adequate continuous fuel. As a result of the introduction of exotic annuals into the Snake River Plains, the historical successional patterns after disturbance were altered. Grazing and agricultural practices have disturbed many habitats, but the primary disturbance in the lower Snake River Plains is fire. Each year more sagebrush rangeland is converted to annual grass rangeland due to wildfires. With each successive fire, annual grass dominance is enhanced, and the FFI is decreased. The landscape has become more homogenous, species diversity has decreased, and burns are larger and more continuous.

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POTENTIAL FOR REPLACING NATURALIZED WEEDS IN CALIFORNIA'S ANNUAL GRASSLANDS WITH SELECTED MEDITERRANEAN SPECIES: PLANT EXPLORATION AND MANAGEMENT CONSIDERATIONS

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ABSTRACT

California's annual grasslands developed under a Mediterranean climate with variable winter rainfall and long, dry, warm summers. These grassland associations are now dominated by aggressive, adventive, low-quality forage annuals introduced from the Western Mediterranean region. A program was initiated to introduce and select desirable Mediterranean forage legumes adapted to California and to develop management strategies appropriate for their use. The important factors are introduction and evaluation of a large number of accessions, matching the legume host with a specific and efficient Rhizobium strain, adequate soil phosphate and sulfur levels, appropriate and timely grazing management, and minimum tillage and selective herbicides if used in pasture rotations with dryland cereals.

INTRODUCTION

California's grasslands have evolved under a Mediterranean climate with a highly variable winter rainfall and long, dry, warm summers (Burcham 1982; Woods 1976). Aggressive exotic annual species began to replace the native plants in these grasslands and associated vegetation types following the introduction of livestock and crops from Western Europe and North Africa (Baker 1989; Burcham 1982). These grassland associations are now dominated by the introduced annuals. Although the alien species are opportunistic and produce quality forage during very short late-winter to spring periods when moisture and temperature conditions are optimal for growth, their mature forage is of poor quality (Murphy and others 1973). Grasslands and associated grassland vegetation types (Hardwood/Savannah, Shrub/Chaparral) represent 15 million ha (37 million acres); more than one-third of California's total land area of 41 million ha (100 million acres). Improvement of this vegetation plant cover would minimize soil erosion, restore depleted soil organic matter, and help sustain the multiple use of this natural resource.

Soils in California's annual grasslands usually are deficient in nitrogen and thus limit plant use of available moisture. Nitrogen fertilizers were used to correct this deficiency, but this practice became unprofitable in the late 1960's. Nitrogen fertilizer is manufactured from natural gas, a fossil fuel. Following the energy crisis of 1973 and the Middle East situation of 1990, application of nitrogenous fertilizers to grasslands became impractical (Green 1978).

Another approach to improving nitrogen levels in these soils is the establishment of nitrogen-fixing legumes. Annual legume adaptation and management research has been carried out in the California annual grasslands since the 1940's. Early work by Williams and others (1956) and Jones and Evans (1960) established the need for adequate levels of soil phosphorus and sulfur and timely grazing to establish and maintain annual subclover (*Trifolium subterraneum* L.) and rose clovers (*Trifolium hirtum* All.). This work was further fine-tuned in the 1960's to develop competitive and effective *Rhizobium* strains needed for subclover establishment and persistence in many of California's annual grassland soils (Jones and others 1978).

The 1960's also saw the development of herbicide technology to control weed competition and aid annual legume establishment in grasslands (Kay 1964; Kay and McKell 1963; Murphy and others 1962).

Murphy and others (1973) summarized the state-of-theart of establishment and management of annual legumes on California's annual rangelands in the early 1970's. In recent years, research emphasis on improving annual rangeland productivity with annual legumes has concentrated on intensive animal management schemes and adjustment of P and S fertilizer inputs (Demment and others 1987; Jones and others 1990; Phillips and others 1987; Raguse and others 1988).

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While the introduction of annual legumes adapted to a Mediterranean climate and capable of biologically fixing significant amounts of nitrogen is promising, they are not being used on a large scale in the lower and less dependable rainfall regions of central and southern California. The establishment success of imported Australian cultivars, particularly subclovers, has been erratic. California's rainfall amounts and distribution are less dependable than in Mediterranean climate areas of Australia where annual legumes are commonly used (Graves and others 1991).

The naturalized annual legume, bur medic (Medicago polymorpha L.), became an alternative host for the alfalfa weevil (Hyperia brunneipennis) following its introduction as a pest on irrigated alfalfa (M. sativa) in the Central Valley. This weevil caused the decimation of bur medic in much of the pasture area of the dryland grain-pasture rotation system on the west side of the Sacramento Valley. After the elimination of bur medic, the soils of this system also became nitrogen deficient and regular applications of expensive nitrogen fertilizer are now needed to make this dryland grain-nonlegume annual grassland pasture rotation system productive (Graves and others 1987).

Australian scientists and land managers developed techniques to displace introduced annual plants of poor forage quality with more desirable forage legumes, primarily subclover and annual medics (*Medicago* sp.) (Crawford and others 1989; Reed and others 1989).

The Australian use of annual legumes in pastures in rotations with cereals, called "Ley Farming" in Australia, has been extensively reviewed by Puckridge and French (1983). An excellent review of subclover-based pasture establishment and management in Western Australia also is found in the 1983 issue of the *Journal of Agriculture of Western Australia* (Gillespie and others 1983).

Since the widespread sowing of subclovers in the 1920's and annual medics in the 1930's, the Australian experience in establishing and managing some 40 million ha (99 million acres) of annual legumes emphasizes the importance of the correct legume-*Rhizobium* association, cultivar screening and selection, macro and micro soil nutrients availability, grazing management to control undesirable weedy species, and the use of selective herbicides and shallow tillage in pasture-dryland cereal rotations (Carter 1987; Crawford and others 1989; Reed and others 1989). In recent years, factors affecting legume seed bank ecology have received considerable attention. Maintaining optimum levels of seed reserves of target legume species is important for long-term persistence and productivity (Carter 1989).

The Australian pasture legume researchers make a strong case for the value of the accidental introductions into Australia, in the 19th century, of annual legumes from countries bordering the Mediterranean Sea (Cocks and others 1979; Gladstones 1966, 1967).

They continue to emphasize Mediterranean region plant exploration programs to search for better adapted and more persistent legume germplasm (Crawford 1983; Crawford and others 1989; Francis and Gladstones 1983).

Although Australian and California annual legume establishment and management technology have similar historical development patterns and common principles and practices, we do have one important difference—California was not blessed with opportune accidental introductions of annual legumes other than the weevil-susceptible bur medic. Until recently, we had not thought it necessary to conduct plant explorations to the Mediterranean regions to improve our annual legume germplasm base. Instead, we depended heavily on the Australian cultivar development and seed production program to meet our annual legume introduction needs.

The USDA National Plant Introduction Program was initiated in 1898. However, by 1979 only a very limited number of annual legume introductions that performed well in California's annual grasslands had been acquired (White and Oakes 1979). Although preliminary annual legume testing and evaluations by Graves and others (1980) in southern California in the 1970's demonstrated that there was a potential for more extensive annual legume use in this area, the cultivars available to us at that time did not seem to possess persistence characteristics suited to our highly variable annual rainfall pattern. While the Australian cultivars were not adapted to our environment, the principles used in the Australian plant exploration and selection programs seemed to be worthy of consideration. We needed to develop our own plant exploration program to target climatic analogs and search for annual legume ecotypes that had evolved and persisted under similarly harsh conditions. The 1980's saw this goal achieved and our hypothesis tested. This plant exploration program is covered in more detail in Graves and others (1987 and 1991) and Rumbaugh and Graves (1985).

It is the objective of this paper to report on the field testing of these annual legume introductions from our plant exploration and exchange program with Mediterranean collaborators and the adaptation of this plant material to the annual grasslands of southern California.

FIELD TRIALS

Oak-Annual Grassland (Savannah) Middle-Elevation Site-This evaluation of annual legume introductions from our 1983 plant exploration program in Morocco (Rumbaugh and Graves 1985) was initiated in the fall of 1984. It included accessions that we had targeted as originating in zones of similar climate pattern. The trial consisted of 20 entries of 11 wild subclover accessions native to Morocco, four Australian subclover cultivars, three naturalized rose clovers from northern California, and two Australian rose clover cultivars. The test site is located in San Diego County at 975 m (3,200 ft) in a 600-mm (23.6-inch) September 1 through May 31 effective seasonal rainfall zone. Details of the materials and methods and site characteristics have been reported and the evaluations for the first 4 years of testing summarized (Graves and others 1991).

The significance of persistence evaluation in this zone is the lack of success of annual legume establishment and the fact that a somewhat long drought and poor rainfall distribution period occurred over a 5-year span from the 1986/87 season through the 1990/91 season. Plots were located in an open range pasture and were not fenced to exclude grazing. The pasture with the test plots received continuous moderate grazing by cattle during the late winter and spring growing seasons in the establishment year and throughout the duration of the 8-year evaluation period. Stand cover evaluations were made each spring near the end of the growing season by visually rating plot cover on a 0-10 scale (0 = no plants, 10 = complete ground cover of the seeded plot). Stand regeneration was defined as the annual clover's ability to regenerate its cover within the planted plot of 1.45 m^2 (16 ft²). The most recent stand persistence evaluations were made on April 24, 1992. Flowering also was recorded on the date of the 1988 stand ratings. Stand regeneration data were analyzed statistically for strain differences.

Annual Grasslands-Lower Elevation Site—It is believed that hardseededness may be the most important characteristic that an annual legume may possess in order to persist in a highly variable rainfall region such as that found in southern California. Smith (1988) pointed out the importance of hardseededness as an adaptation and survival mechanism in the highly variable rainfall patterns characteristic of Mediterranean climates. The need to screen and breed for hardseededness in subclover was recognized in Australia (Francis and Gladstones 1983) and in Spain (Gomez Pitera and Ramos Monreal 1980) as an important component of persistence in areas of 375 mm (15 inches) or less rainfall and for successful stand regeneration after cereal cropping.

Gomez Pitera and Ramos Monreal (1980) screened more than 2,000 subclover lines from southern Spain for hardseededness, estrogen levels, and seed production, and a small number of the superior lines from this research were sent in the fall of 1979 to the University of California, Davis, for seed increase and field evaluations. Seven of these subclover lines of Spanish origin (Spanish Forage and Pasture Research Institute, Badajoz numbers: 1142, 59, 245, 92, 312-A, 704 and 393) of high hardseededness were increased by Burgess Kay, wildlands reseeding specialist, at the Department of Agronomy and Range Science, University of California, Davis, during the spring of 1980 and distributed for field trials during the fall of 1980. During the 1980 to 1982 period these Spanish lines were established in annual grassland locations in San Diego and San Luis Obispo Counties. Medium-term evaluations were made on five lines in the spring of 1987 (Graves and others 1991).

An additional trial with the seven Spanish lines was initiated near the town of Alpine in San Diego County in the fall of 1982, with the objective of evaluating long-term persistence. This test site is located at 714 m (2,345 ft), some 53 km (33 mi) inland to the east of the San Diego coast. The location is in the inland foothill climate zone with a mean annual rainfall of 450 mm (18 inches). The soil is a Wyman (fine-loamy, mixed, thermic, Typic Haploxeralfs) soil with neutral to slightly acid pH, loam to clay loam texture, 2-5 percent slope, and with low nitrogen, phosphorus, and organic matter levels. The site is classed as annual grassland and has been used for livestock grazing since the late 1800's. The site is dominated by filaree species (Erodium sp.), annual bromes (Bromus sp.), and foxtail fescue (Vulpia myros [L.] K.C. Gmelin var. hirsuta Hack).

The seven Spanish lines and three early maturing hardseeded Australian subclover cultivars (Nungarin, Geraldton, and Daliak) were seeded on November 24, 1982. Single superphosphate (0-18-0-12) was applied by broadcasting at the rate of 300 kg/ha (277 lb/acre) prior to seeding. One hundred seeds of each of the entries were planted 8 mm (0.33 inch) deep in 1.20-m (4-ft) single-row plots (no-till) arranged in a randomized block design, replicated four times. All seeds were freshly pellet-inoculated at the rate of 5 kg of inoculant per 100 kg of seed (Pelinoc inoculating system, Milwaukee, WI).

The pasture containing the trial received continuous, moderate-to-heavy grazing by cattle during the winterspring growing season for the 10-year evaluation period. Plant stand evaluations were made April 6, 1983, to verify first-season establishment (by visually rating row cover on a 0 to 10 score (0 = no plants, 10 = complete coverage of the row). Stand persistence evaluations were made at the end of the tenth growing season, (April 24, 1992) to measure the subclover lines' long-term ability to regenerate following low rainfall (drought) years stress. Initial plant and 1992 plant stand persistence evaluations were analyzed statistically for strain differences.

OAK-GRASSLAND RESULTS

The results from this trial are most encouraging (table 1). Following the long 5-year drought from 1987 through 1991, three of the Moroccan subclovers regenerated and one experimental accession, GR 508 (PI 517171), was significantly (P < 0.05) superior to all other entries including the rose clover cultivars and the northern California naturalized lines. None of the Australian subclover cultivars, Seaton Park, Northam, Geraldton, or Nungarin, persisted. These results confirm the difficulty that we have had with the establishment and persistence of Australian subclover cultivars in this southern California zone.

The Australian rose clover cultivars, Hykon and Kondinin, continue to show some degree of persistence, as did the naturalized collections from Mendocino, Shasta, and Siskiyou Counties. These three naturalized rose clover accessions are much later in maturity than the superior subclover accessions and the two rose clover cultivars, and we would expect these naturalized northern California lines to be at a disadvantage in this zone due to its short rainfall season. Thus, we would not expect the accessions to persist or, at best, to regenerate only during years of above-average rainfall.

Considering that rainfall was 25 to 40 percent below average during this 5-year-long drought period (1987 to 1991), the test results are indicative of adaptation to the extreme stress conditions of this zone. At least one of the three persistent Moroccan accessions, GR 508 (PI 517171), has demonstrated the potential for long-term regeneration and adaptation to this annual grassland type of southern California.

ANNUAL GRASSLAND RESULTS

After 10 seasons, including 5 drought years from 1987 through 1991, Spanish experimental accession 1142 was significantly (P < 0.05) superior in stand persistence to all the other accessions, including the Australian cultivars (table 2). These results follow the pattern and confirm the findings as reported by Graves and others (1991) who used

Variety/	Ranking/plot coverage ¹		Flowering on	
accession	Fourth season	Eighth season ²	3/29/88 ³	
GR 508 Sub (PI 517171)	8.8	6.2	+	
GR 565 Sub (PI 517173)	7.2	3.0	+	
GR 567 Sub (PI 517174)	6.2	2.2	+	
Shasta 4300' Rose	5.8	3.0	-	
Kondinin Rose	5.0	2.0	+	
Siskiyou Rose	5.0	2.8	-	
Mendocino Rose	5.0	2.5	-	
Hykon Rose	4.5	2.0	+	
Seaton Park Sub	4.2	0	+	
Northam Sub	3.5	0	+	
GR 435 Sub (PI 517164)	3.2	0	+	
Geraldton Sub	2.2	0	+	
GR 448 Sub (PI 517167)	2.0	0	_	
GR 450 Sub (PI 517168)	1.8	0	-	
GR 316 Sub (PI 517155)	1.8	0	+	
GR 436 Sub (PI 517165)	1.8	0	-	
GR 494 Sub (PI 517170)	1.2	0	+	
GR 519 Sub (PI 517172)	1.2	0	-	
Nungarin Sub	1.2	Ō	+	
GR 301 Sub (PI 517154)	1.0	0	+	
LSD (0.05)	1.5	²1.3		

Table 1—Subclover (sub) and rose clover entries regeneration and flowering evaluations at the Alford Ranch, Mesa Grande, San Diego County, at the end of fourth and eighth growing seasons

¹Average of four repetitions (0 = no plants, 10 = complete coverage of plot).

²Analysis of variance calculation did not include entries that did not persist; "0" (zero) ratings. ³(+ = flowers; - = no flowers).

Strain/cultivar	Stand establishment on 4/6/831	Stand persistence 10th yr, 4/24/92 ¹	Flowering maturity ² +3	
59	7.5	1.8		
312-A	7.5	0	+6	
245	7.2	0	+3	
393	7.0	2.0	+3	
92	6.8	0	+3	
704	6.8	1.8	+2	
1142	6.0	5.5	+3	
Geraldton	7.0	2.8	+3	
Daliak	7.0	0	+3	
Nungarin	7.0	3.0	0	
LSD (0.05)	0.8	³ 2.1	(4)	

 Table 2—Spanish and Australian subclover stand establishment, 10th-yr persistence, and flowering maturity date at the Alpine, San Diego County, site

¹Average of four repetitions (0 = no plants, 10 = complete coverage of the plot row).

²(Weeks after Nungarin) Nungarin is considered earliest of trial entries.

³Analysis of variance calculations did not include entries that did not persist; "0" (zero) ratings.
⁴Average of observations, no statistics completed.

these same lines in other localities. The lack of persistence of the Australian cultivar Daliak confirmed the inability of this cultivar to adapt to the harsh conditions of southern California.

The stand establishment ratings showed that most of the trial entries were similar in ability to establish the first year from the initial seeding. However, Spanish line 1142 showed a significantly lower plant stand ($P \le 0.05$) than any of the other experimental lines or Australian cultivars. Yet, by the end of the 10th season, this line was the only trial entry that was regenerating at a desirable level of greater than 40 percent cover. The point to be made here is that under unfavorable and stressful climatic conditions there is a need for long-term evaluation trials to allow adaptability characteristics to express themselves. We assume that early flowering gives the annual legumes an added adaptability advantage in escaping drought stress in low rainfall years; however, we can see from the poor showing of the Nungarin cultivar, the earliest flowering entry, this extreme early flowering characteristic is not the most important factor in helping the plant to persist in these conditions.

While our results did not allow us to choose between Spanish lines 1142 and 59 on the basis of other agronomic traits, this long-term trial does allow us to select line 1142 as the most persistent in the annual grassland zone of southern California.

SUMMARY

These long-term persistence evaluations provide a very exciting example of the successful collection and introduction of wild-type annual legumes from native habitats in the Mediterranean region. We believe that our hypothesis of expecting to find wild types of annual legumes in analogous climatic zones in the Mediterranean region that offer a potential for adaptation under a number of varied and variable California environments has been confirmed.

Several principles, practices, and techniques have been proven to be important for successfully displacing introduced annual Mediterranean plants of poor forage quality with more desirable forage annual legumes. These factors are plant exploration, plant introduction, evaluation of a large number of collections, and matching the legume host with an effective and competitive Rhizobium strain. Once the array of adapted annual legume types is found, their use will be optimized and sustained by providing them with adequate levels of soil-deficient nutrients, such as phosphorus and sulfur for the California annual grasslands. Timely and early-season animal grazing management will help to reduce poor-quality annual species, optimize seed production, and increase nitrogen cycling. Where these legumes can be used in pasture rotations with dryland cereal farming systems, one can use minimum tillage and selective herbicides to enhance the annual legume component and its regeneration.

Our results point out the need to maintain a testing and evaluation program of present and future cultivar introductions to assess their adaptations to California conditions. Through continued exploration for better adapted and persistent annual legume plant materials, the annual grasslands and associated vegetation types of California can be restored and this natural resource sustained for multipleuse management needs.

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THE COMPETITIVE INFLUENCES OF CHEATGRASS (BROMUS TECTORUM) ON SITE RESTORATION

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ABSTRACT

Cheatgrass (Bromus tectorum) continues to expand its area of occupation and dominance. The plant now exists amid the salt desert shrublands and upper pinyon-juniper and ponderosa pine communities. Significant increases have been reported within the past 20 to 40 years. The competitive features of this weedy annual prevents natural recovery of native species and requires extensive control measures to assure other species become established after seeding. Some progress has been made using selected native species to restore cheatgrass-infested sites. Properly planned seedings in the sagebrush benchlands and pinyonjuniper woodlands usually can restore the native understory and prevent further spread of this weed. Remedial treatments conducted in areas receiving less than 10 inches of annual rainfall is hazardous, consequently restoration is still quite limited.

INTRODUCTION

Cheatgrass (Bromus tectorum) has invaded and disrupted many plant communities throughout the Intermountain and Columbia Basin Regions (Hulbert 1955). In many situations, cheatgrass has gained dominance and exists as nearly pure stands devoid of any native species (Morrow and Stahlman 1984). The presence of cheatgrass has resulted in the loss of plant diversity and associated resource values (Harniss and Murray 1973; Young and Evans 1978). The conversion of native communities to annual grasslands has occurred over an extended period, having a cumulative effect on existing resources (Pickford 1932). Many sites initially occupied with scattered cheatgrass plants have been converted to nearly pure stands of annual grass (Whisenant 1990). The stands have been converted to annual grass by the intense competition of cheatgrass and the sequence of fires attributed to its flammability (Young and Evans 1973). As cheatgrass gains dominance, the incidence of wildfires increases significantly. Sites are likely to burn at more frequent intervals, resulting in the perpetuation of the annual weed, coupled with the loss of many native species (Whisenant 1990).

Measures to prevent the spread of cheatgrass or to restore infested ranges with native species or more acceptable introductions have been investigated. The plant is unusually competitive and difficult to displace without extensive remedial treatments (Stewart and Hull 1949). Stands of cheatgrass must be thinned to permit seeded plants to become established (Hull and Pearse 1943; Platt and Jackman 1946; Robertson and Pearse 1945). Although treatments have been developed to restore or revegetate areas occupied by cheatgrass, costs of site preparation and seeding often limit treatment projects. In addition, many sites are not accessible, limiting restoration practices. Efforts to restore cheatgrass ranges to perennial plant cover by natural revegetation have had limited success and have required a long time before appreciable changes have occurred (Hironaka and Tisdale 1963). Cheatgrass continues to spread and now exists in drier environments than it did previously. These sites are more difficult to restore.

Some progress has been made in developing techniques and practices to control this weed and to develop plants that are better suited for seeding. This paper discusses some of the competitive attributes of cheatgrass and presents some advances in restoration.

DISTRIBUTION AND AREAS OF OCCUPATION

Cheatgrass is most abundant in the Great Basin and Columbia Basin of the Western United States, but it is also encountered throughout the continental United States and portions of Canada and Mexico (Morrow and Stahlman 1984). Warg (1938) states cheatgrass was probably introduced into the eastern Coastal States prior to its entry into the West. It may have migrated across the country or have been introduced directly from the Mediterranean region (Novak and Mack 1993; Novak and others 1993). The earliest reported collection in the West was made in Washington by Sandberg and Lieberg in 1883 (Warg 1938). Mack (1981) postulated that seeds arrived in contaminated grain, which may explain its rapid spread. It was widely scattered throughout the West prior to 1900 as successive collections were reported from central Utah in 1894, Colorado in 1895, and Wyoming in 1900 (Hulbert 1955). The grass expanded rapidly, and by 1928 it was reported to have reached its present distribution (USDA 1970). Mack (1981) reported that the grass had become the dominant species in most disturbed steppe communities by 1930. Platt and Jackman (1946), reporting on earlier studies, concluded that cheatgrass was present in Oregon for at least 50 years (1880), but had abandoned its role as an ally to become an aggressor within the last 30 years (1916 to 1946). The authors report the plant was found mostly in areas receiving between

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6 and 16 inches of annual rainfall. By 1946 it occupied at least 10 million acres in eastern Oregon.

Hull and Pechanec (1947) reported that cheatgrass infestations occurred from the salt desert shrub community through the big sagebrush (Artemisia tridentata) zone and into the ponderosa pine (Pinus ponderosa) and Douglas-fir (Pseudotsuga menziesii) zones. Stewart and Hull (1949) described the distribution of cheatgrass in Idaho, concluding that the plant existed as the dominant species on approximately 4 million acres. It existed with sagebrush on another 2 million acres as the principal understory plant. It occurred on another 10 to 15 million acres as a component of the herbaceous vegetation. Cheatgrass was first observed to occupy abandoned croplands, roadways, and thin or weak fields and orchards (USDA Forest Service 1914). It spread to occupy dry farms and areas that were not properly tilled. By 1915 to 1920 it had spread onto disturbed range and wildlands. After the recession of 1920, numerous dry farms and marginal, irrigated farmlands were abandoned. The sites were quickly occupied with the annual grass. Stewart and Hull (1949) estimated 2 million acres of abandoned farmland were converted to cheatgrass in Idaho.

Although cheatgrass invaded and quickly occupied areas throughout the West, its range and its dominance at various sites has changed within the past 20 to 30 years. Most noticeable has been a dramatic increase of cheatgrass density, coupled with a loss of native species. Many sites initially invaded by cheatgrass have been burned by wildfires or indiscriminate burning. As sites have burned, cheatgrass, in contrast with most native species, has recovered and gained dominance. Billings (1990) reports that without fire, cheatgrass invades overgrazed communities. As the community is burned, most shrubs and some herbaceous species are killed, but cheatgrass seeds are able to survive and recolonize the site. Cheatgrass increases in plant density as subsequent burns occur. The fuel created by the annual grass provides highly flammable tinder that results in more frequent fires (Billings 1948; Young and Evans 1978). The result has been a replacement of sagebrush with cheatgrass in many sites (Mack 1986; Pickford 1932; Piemeisel 1951; Young and Evans 1978). This cycle increases cheatgrass density and allows it to significantly expand its area of occupation. The conversion process has been going on since cheatgrass was introduced. The accumulated effects becomes increasingly prevalent.

Billings (1990) reported that native bunchgrasses did not carry fire very well, and that range fires were rare or absent in the sagebrush-bunchgrass steppe during the entire nineteenth century. In 1952 Robertson (1954) retraced the route and reevaluated the range-condition surveys made in northern Nevada in 1902 by P. B. Kennedy (1903). Robertson found that bluebunch wheatgrass (Agropyron spicatum) decreased from abundant to generally absent or less than 5 percent cover within the 52-year period. In addition, cheatgrass was not present in 1902, but had increased dramatically by the time of Robertson's survey. Burn scars were absent or unimportant in 1902, but by 1952 the entire route was bordered or crossed by burned ranges that were covered by cheatgrass. According to Robertson, the changes were a result of heavy grazing coupled with the invasion of cheatgrass and the occurrence of fires.

Changes in cheatgrass distribution can be determined, in part, by comparing previously reported studies with current surveys. Through a review of ecological studies by other authors, Klemmedson and Smith (1964) described the principal areas of occurrence or habitats in which cheatgrass was most prevalent about 30 years ago. Reports summarized in the publication concluded that cheatgrass did not tolerate saline soils well. These reports included Fleming and others 1942 and Piemeisel 1932. Few cheatgrass plants were reported to be found in greasewoodshadscale (Sarcobatus vermiculatus/Atriplex canescens) communities (Kearney and others 1914) and salt-desert shrub associations (Billings 1949; Stewart and Hull 1949). Robocker (1961) reported that cheatgrass was absent from stands of winterfat (Ceratiodes lanata) and Nuttall's saltbush (Atriplex spp.) communities and occurred in only small amounts in stands of shadscale. This situation has changed significantly as cheatgrass has expanded to occupy extensive areas once dominated by shadscale, winterfat, Nuttall's saltbush, and other woody species associated with salt desert communities. Studies by Harper (1959) reported little or no cheatgrass throughout the salt desert, black sagebrush (Artemisia nova), and Wyoming sagebrush (Artemisia tridentata wyomingensis) communities at the Desert Experimental Range in western Utah in 1959. However, Sparks and others (1990) found that former sagebrush- and shadscale-dominated sites in this same area had been converted to cheatgrass and other annual weeds on a massive scale.

Previous studies document the widespread occurrence of cheatgrass at elevations up to 6,000 feet (Klemmedson and Smith 1964), with plants common in the ponderosa pine zone throughout the West (Daubenmire 1952; Hulbert 1955). Cheatgrass density and distribution throughout the antelope bitterbrush (Purshia tridentata), mountain brush, pinyon-juniper (Pinus/Juniperus) and ponderosa pine communities has increased significantly in many situations. Fire frequency has increased in these sites as cheatgrass has gained dominance. Although the fire frequency and spread of cheatgrass has not been as evident as that within the big sagebrush communities, the fire cycle and changes in species composition of upland woody communities follows the same pattern of degradation reported at lower elevations. Wildfires that ignite or originate in the lower big sagebrush-cheatgrass disturbed communities now extend to upper elevation communities, reducing the composition of less fire-tolerant species and creating openings for the spread of the annual grass.

The fire cycle generated by cheatgrass has eliminated extensive stands of antelope bitterbrush in south central Idaho, central Utah, Oregon, and southern California. Monsen and Shaw (1994), reporting on the status and health of stands of antelope bitterbrush within the Western United States, indicated that many principal stands have been lost to cheatgrass-related fires and competition. Losses have been so critical that seed of many distinct ecotypes can no longer be collected commercially; protective measures are recommended to retain remaining stands. Cheatgrass has occupied many sites for nearly 100 years. During this time, different populations have evolved that appear site-adapted. Beckstead and others (1993) reported differences in seed dormancy and afterripening among collections of cheatgrass harvested from desert and mountain populations. Differences in these attributes affect timing of germination and the ability of cheatgrass to compete with native bunchgrasses. Cheatgrass populations differ genetically (Novak and Mack 1993; Novak and others 1993), which contributes to the evolvement of adapted ecotypes. The adaptability among different populations of cheatgrass is a significant problem in developing restoration measures.

COMPETITIVE ATTRIBUTES AND FEATURES OF CHEATGRASS

Cheatgrass possesses a number of distinct features that contribute to its competitive ability. Like other obnoxious weeds, this species is persistent and difficult to control. It not only competes well with a series of native species, but is difficult to remove from most infested areas without significantly disrupting the plant community and soil conditions. Harris (1967) described the competitive features of this plant. The array of characteristics is impressive, contributing to its highly competitive nature. Any attempt to remove and replace this grass with other species, either by artificial seeding or by management to encourage natural recovery, must consider the competitive factors controlling the ecological system. A list of principal factors or traits that contribute to the competitive nature of cheatgrass follows. Most features are interrelated, but each is vital and must be addressed in any remedial treatment program.

Broad Range of Geographic Distribution and Dominance

Cheatgrass exists as a dominant species over a broad range of sites in the semiarid grasslands and shrublands of the Intermountain and Columbia Basins. Within these two broad regions, considerable variation exists in soil features, topography, and the amount and distribution of precipitation, yet cheatgrass maintains dominance at all sites (Harris 1967). Few situations occur where native species suppress cheatgrass, even in small microsites. Few other weedy species exhibit adaptation to such a wide range of conditions. Within these two regions, cheatgrass occurs in quite arid environments. These sites are the most precarious areas to artificially seed, as climatic conditions are unpredictable and moisture is often insufficient to promote seed germination and sustain seedling establishment.

Cheatgrass is so universally abundant that it tends to saturate almost all sites. Attempts to seed or treat cheatgrass areas are often thwarted by rapid reoccupation of cheatgrass plants from adjacent untreated sites. Control measures must address the weed problem of adjacent areas, particularly when small or narrow tracts are treated. Interseeding selected sites and managing to encourage natural spread of the seeded species is usually not effective. Almost complete site renovation is required to control the weed and allow other plants to become established.

Lack of Competition From Native Species

No native species or more desirable introduced species has been found that can compete directly with cheatgrass throughout a broad range of sites. Most native species that dominate bunchgrass/shrubland associations are unable to compete with cheatgrass (McKell and others 1962). Billings (1990) found cheatgrass quickly invaded a sagebrush shrubland near Reno, NV, after a wildfire in 1947. Forty-one years after the burn, cheatgrass and other annual weeds dominated the south and north slopes, although some native species had returned on the north aspects. Fire-tolerant woody species, primarily antelope bitterbrush, had recovered to occupy 17 percent of the cover on the north-facing slopes. The fire removed both woody and herbaceous species that were not able to recover due to cheatgrass competition. Hironaka and Sindelar (1973) reported that squirreltail (Sitanion hystrix) is capable of reestablishing naturally within some sites occupied by cheatgrass and medusahead (Taeniatherium caput-medusae). Sandburg bluegrass (Poa secunda) has also been observed to invade cheatgrass stands in some situations, converting areas to perennial grass cover. Although natural changes have occurred, no program has been developed for extensive conversion projects.

Robertson and Pearse (1945) concluded that cheatgrass forms "closed communities," preventing the establishment of seeded species unless the cheatgrass competition is eliminated first. Similar results have been reported by Harris (1967). Considerable success has been achieved by planting either native or introduced species after cheatgrass has been eliminated or controlled by mechanical tillage or selected herbicides.

Various introductions have been investigated to control and convert cheatgrass ranges to a more acceptable cover, since few native species have demonstrated the ability to suppress cheatgrass over extensive areas. Some progress has been achieved in improving seedling establishment and planting practices that increased the use of certain introduced species, particularly crested wheatgrass (Agropyron cristatum) (Asay and others 1986) and forage kochia (Kochia prostrata) (Monsen and Turnipseed 1990). Although various grass introductions compete well with cheatgrass when the grasses are mature, the seedlings of few species can compete with cheatgrass.

Plant communities and sites differ in their ability to recover following occupation by cheatgrass. In general, low elevation communities and sites receiving less than 9 inches annual precipitation are less likely to recover to a native species complex through protection or management practices (Stewart and Hull 1949). However, during recent periods of drought from 1990 to 1994, cheatgrass has been observed to disappear from extensive arid sagebrush ranges in Nevada, Idaho, and Utah. In some situations, perennial bunchgrasses have replaced the annual. Klemmedson and Smith (1964) presented some preliminary

data summarized by Pearse that native species within the sagebrush/antelope bitterbrush/bunchgrass communities of south-central Idaho were capable of replacing cheatgrass if sites were protected from grazing. The conclusions provided by Pearse were based on the response of vegetation following 3 years of protection, 1931 to 1934. Voth (1979) reexamined the long-term ecological exclosures that Pearse had studied, and provided much different conclusions. Cheatgrass remained the dominant species on most south and west exposures after 58 years of protection. Although native species increased in density and cover on north exposures, cheatgrass had not been eliminated and remained an important component of the vegetation. Klemmedson and Smith (1964) summarized the results of several investigators, concluding that cheatgrass could be replaced by competitive natives, and that grazing and other management practices were detrimental to stands of cheatgrass (Hull and Pechanec 1947; Piemeisel 1938, 1945). Within the sagebrush communities, native species have not demonstrated the ability to reoccupy cheatgrassdominated sites. Extensive areas exist today as evidence of this problem. Billings (1990) concluded that little can be done to replace cheatgrass in the sagebrush ecosystem, to remove or to control the plant, and the only viable alternative would be to prevent it from expanding.

Seed Germination and Establishment

Cheatgrass is regarded as a winter annual. Some initial germination begins in late August coinciding with the occurrence of fall rains, followed by a major period of germination in September and October (Mack and Pyke 1983). Germination may occur thoughout the winter particularly in desert conditions following winter rain (Beatley 1966). Mack and Pyke (1983) reported cheatgrass recruitment continued throughout the winter months, contributing 30 percent of all individuals that appear. Spring recruitment occurs quite regularly and may be substantial, occurring as late as mid-May (Hull and Hansen 1974). Plants that germinate during the spring can produce a viable seed crop. Although plants may be grazed in the spring before seeds mature, seeds may still develop and germinate during the fall (Hulbert 1955).

Seed germination and growth of cheatgrass favor its establishment over most native herbs. Harris (1967) reports that at moderately low temperatures with moist soils, conditions often found in the fall at field sites, cheatgrass has a small advantage over bluebunch wheatgrass in the rate of germination, but the abundance of cheatgrass seeds provides a distinct advantage. Beckstead and others (1993) evaluated different ecotypes of cheatgrass and found that seeds of the annual grass consistently germinated earlier than squirreltail. Buman and others (1988) found cheatgrass seeds germinated at lower temperatures than perennial grasses, which was an important factor contributing to its successful establishment.

Cheatgrass plants produce an abundance of seeds almost every year regardless of weather conditions. Although the amount of seed produced depends on climatic conditions, sufficient seed is normally developed to repopulate a site. Hulbert (1955) reported counts of between 200 and 600 seeds per square decimeter from plots located near Lewiston, ID. Beckstead and others (1993) found cheatgrass seeds afterripen in dry storage, thus permitting fall germination. These authors also found betweenpopulation differences in afterripening patterns were habitat correlated. These factors were ecologically relevant and important to the survival of the species.

Seed germination features have apparently evolved to favor establishment of cheatgrass plants under different site or climatic conditions. Seed banking and afterripening provides sufficient seed for fall and spring germination. Although few seeds may carry over to germinate in succeeding years, yearly renewal of the seedbank is sufficient to maintain a competitive advantage.

As cheatgrass plants invade new openings, an abundant seed crop is quickly produced to perpetuate the plants. First-year plants produce sufficient seeds to create highly competitive problems. Weed seeds also spread quickly to occupy adjacent areas and serve as a reservoir of seed for further advancement.

Phenological Growth Attributes of Cheatgrass

Harris (1967) described the phenological growth characteristics of cheatgrass, which contribute to its competitive abilities. He found that once cheatgrass has germinated, it has a distinct advantage in the rate of root elongation over bluebunch wheatgrass. This advantage apparently exists for other native species. Roots of cheatgrass developed about 50 percent faster than roots of the perennial bluebunch wheatgrass. In addition, where soil conditions remained at or near freezing throughout the winter months. fall-emerging and over-wintering seedlings of cheatgrass have an additional advantage. Roots of cheatgrass were able to grow at temperatures as low as 3 °C, but the minimum temperature for bluebunch root growth is 8 to 10 °C. Harris reported the inherent greater root elongation rate of cheatgrass accounted for its dominance over bluebunch wheatgrass. Since cheatgrass seedlings develop much earlier than other species, the plants grow during a period of abundant moisture. Cheatgrass effectively extracts soil moisture regardless of plant density. Dense stands develop both primary and secondary root systems that deplete soil moisture as the root system advances. Sparse stands produce tillers and adventitious roots that grow faster than roots of other plants, thereby depleting soil moisture. Harris concluded that as growing conditions change to favor growth of bluebunch wheatgrass, cheatgrass has already dominated the site. The competitive advantage cheatgrass demonstrates over bluebunch wheatgrass is sufficient to overcome environmental differences throughout the semiarid grasslands and sagebrush sites of the Intermountain and Columbia Basin regions.

REMEDIAL TREATMENTS

Controlling Competition

Most weedy plants are difficult to control, and cheatgrass is no exception. Attempts to control cheatgrass under wildland conditions are extremely difficult. Failure to control cheatgrass competition is a primary factor preventing establishment of seeded species. Unlike some annual weeds, cheatgrass presents some unusual problems. To be effective, control measures must be capable of:

- Eliminating live plants
- Preventing seed formation
- Controlling seed germination and emerging seedlings.

Controlling live plants and the existing seedbank requires a combination of treatments conducted over a 1- to 2-year period. In addition, cheatgrass competition is the major deterrent preventing natural recruitment of new seedlings of native species. Generally cheatgrass can be controlled by spring tillage or by burning mature plants before seed dispersal. Both practices reduce recruitment of a seed crop. Fall tillage or application of a herbicide is employed as a followup treatment to eliminate seedlings that emerge in the fall. Artificial seeding is conducted in the late fall or early winter.

Site Conditions

Weed control measures and seeding practices that are used to restore cheatgrass-infested sites should be carefully designed. Techniques and methods that are used must be functional and effective. Seeding practices must include some means of weed control, proper seedbed preparation, and seeding. Plantings should also be conducted at the appropriate season for the planting site.

Restoration or control measures must address the inherent growth characteristics of the plant and must be functional within the climatic and environmental conditions of the existing communities where the plant occurs. Recognition of climatic and environmental conditons is critical in developing control measures. Since cheatgrass occurs in some semiarid and arid communities, practical control measures are frequently quite limited, as precipitation is not always adequate to assure seedling establishment. Thus, the sites in which cheatgrass occurs directly affect the chances for restoration or site enhancement.

Sites in the salt desert and lower big sagebrush communities normally are often the most arid and difficult to restore. Areas throughout the sagebrush benchlands, pinyonjuniper, and ponderosa pine communities can be planted without much difficulty. Once disturbances occur within these communities, openings should be seeded if an adequate understory does not exist and weed invasion is imminent. In many situations, the herbaceous understory has been removed from sites occupied by these woody species. Cheatgrass invasion can be expected as the overstory is removed or weakened. Measures to reestablish the native understory are recommended in these sites before natural disturbances such as fire or disease may weaken the overstory. Managers may be reluctant to recommend large-scale chaining and seeding of some communities, yet seeding can reduce the potential spread of cheatgrass. Areas surrounding large, dense stands of cheatgrass are prime areas for fires and invasion of cheatgrass. In many situations cheatgrass has invaded low valley bottoms and with the assistance of fire is spreading to dominate more upland communities. Proper management of

the upland sites, coupled with well designed seedings, can lessen the incidence of fire and restrict and limit encroachment of the annual weed.

Proactive seedings can also contain the spread of fires from areas that frequently reburn. Greenstrip seedings are commonly used throughout the Snake River Plain and other large topographic regions where nearly contiguous stands of cheatgrass occur. In these situations, broad areas are subdivided into small units by seeding less fireprone species in strips around the border of each subunit. This approach may not be appropriate in all situations, but the practice can reduce the number of large fires. In addition, the spread of fires into undisturbed areas surrounding areas dominated by cheatgrass can be prevented. An additional advantage is the concentrated attention given to seeding small areas. Considerably more attention and funds can be directed to seeding small strips than is normally given to large acreages. Fire barriers or greenstrips can normally be disked or treated to control weed competition, increasing the assurance of attaining a desirable stand after seeding. In addition, plantings can normally be more easily scheduled to take advantage of climatic conditions.

Cheatgrass can not be easily removed from all areas of current occupation. Artificial restoration of arid regions is extremely hazardous, but restoration of designated areas through proper management and seeding can aid weed control.

Development of Adapted Species

In many situations weeds have been controled by planting a more competitive and desirable species capable of containing or preventing the spread of the target weedy plant. Cheatgrass occupies a number of native communities, and the primary goal in site restoration is to reestablish the native composition. Planting a single species to control cheatgrass rarely results in the recovery of the native community. Plantings of various wheatgrasses, particularly crested and desert wheatgrass (Agropyron desertorum) have been effective in controlling annual weeds (Asay and Johnson 1983). In addition, some selections are able to compete directly with cheatgrass and can be planted with little site preparation. Established stands of these perennial grasses provide adequate ground cover, reduce the incidence of fires, and prevent cheatgrass from becoming more than a minor part of the community. However, the introduced perennials are not compatible with most native species and do not facilitate or allow recovery of the natives (Monsen and Shaw 1983; Walker and others 1993). The perennial grasses are very useful in controlling annual weeds and can be used where recovery of the native community is not a primary goal.

Ecologists have recognized that cheatgrass seedlings are able to suppress seedling growth of most native species. Although cheatgrass is able to invade some climax communities (Daubenmire 1942; Poulton 1955), the plant is unable to gain dominance of mature, established plants (Daubenmire 1942; Young 1943). If the native composition has been destroyed, cheatgrass can restrict natural recruitment of new seedlings required to reestablish the native vegetation. Consequently, most native species have not been considered potentially capable of competing initially with weeds unless they demonstrate unusual seedling vigor. Some attention has been given to the use of native pioneering species to compete directly with cheatgrass. Hironaka and Sindelar (1973) reported that squirreltail competed well with cheatgrass, and suggested the plant be used as a pioneer species to convert weedy sites to a perennial cover. Harris (1967) suggested selecting ecotypes of native grasses that have the ability to grow rapidly at low temperatures, thus providing plants that are capable of competing with rapidly growing cheatgrass seedlings. Kitchen and Monsen (1994) found that germination and establishment of bluebunch wheatgrass could be enhanced through selection, allowing more aggressive and competitive materials to be developed. Hardegree (1994) found that native seeds could be primed to initiate early germination, increasing the competitive ability of young seedlings.

Little attention has been given to the selection and use of some key native species for initial weed control and secondary successional recovery. Natural recovery of some cheatgrass sites by native species has been observed. Sandburg bluegrass, squirreltail, Thurber needlegrass, (*Stipa thurberiana*), western wheatgrass (*Agropyron smithii*), and streambank wheatgrass (*Agropyron riparian*) have been observed to invade and gain dominance of sites once infested by cheatgrass (personal observations). The recovery process has been evident throughout the Intermountain Region during recent periods of drought. The natural recovery process certainly suggests that these same species can be effectively used in artificial seedings if seed were available and planting requirements were better understood.

CONCLUSIONS

Cheatgrass is an extremely tenacious and competitive weed. Since being introduced into the Western United States over 100 years ago, it has spread to occupy extensive areas. It is particularly well suited to semiarid environments. It continues to spread and colonize additional plant communities. This species is able to encroach onto new sites as openings are created. Once established, it may persist as a minor component of the community for a considerable period of time. Its presence can restrict natural seedling establishment of most native species. If sites are burned or native plants are otherwise weakened, cheatgrass can flourish and may eventually gain dominance. Semiarid shrublands and associated plant communities that are naturally slow to recolonize following a disturbance are the primary sites where cheatgrass has increased. Once cheatgrass is in place, wildfires become more common as the plant produces highly flammable foliage. Less fire tolerant species are further weakened or eliminated by successive fires.

Cheatgrass provides such intense competition to new emerging seedlings that few native plants are able to become established. Natural succession is slow under these circumstances. Although some native species can reoccupy sites that were dominated by cheatgrass, the process requires a long time and is not a common occurrence. Consequently, artificial seeding is required to reestablish most plant communities. Cheatgrass competition can be controlled sufficiently by mechanical tillage, application of herbicides, and fires to allow seeded species a chance to establish. Seeding of native and introduced species can be successful once cheatgrass competition is diminished. Although cheatgrass has become a serious problem, control and restoration measures are not entirely adequate to treat all sites. In addition, the cost and resources required to restore large areas are not currently available. As additional resources are lost and fire-related costs continue to escalate, the need for cheatgrass control and restoration measures will become more critical.

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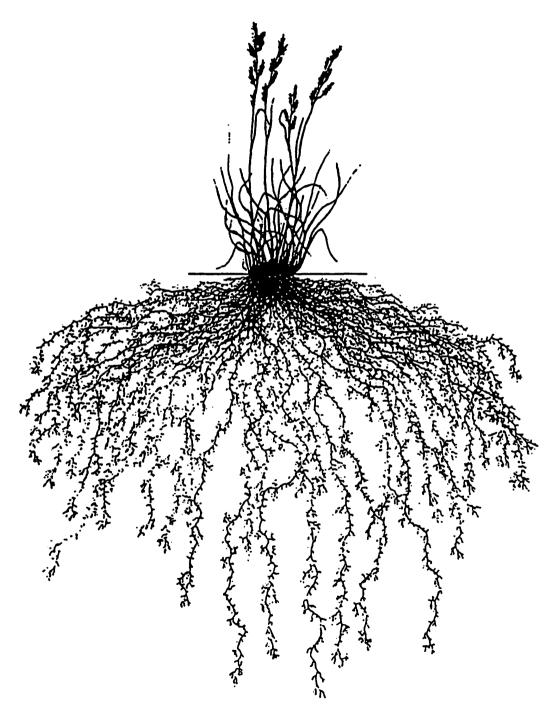
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Fire Ecology and Management





Festuca idahoensis

EFFECTS OF FIRE ON JUNIPER WOODLAND ECOSYSTEMS IN THE GREAT BASIN

Stephen C. Bunting

ABSTRACT

Juniper has invaded adjacent vegetation types throughout much of its worldwide range and is characteristic of these woodlands. In the Western United States this vegetation change has affected millions of hectares. Fire history studies for juniper-dominated areas indicate that firefree intervals of 50 years or less would probably have checked this advance during the pristine period. However, the number of fire ignitions we currently receive does not seem adequate given the dissected nature of the topography and the discontinuous fuels of these areas. Alternative scenarios are suggested to explain this inconsistency.

INTRODUCTION

Juniper woodlands are a major vegetation type found in most of the Western States. The term "pinyon-juniper" is commonly used for the woodlands in aggregate, although junipers (Juniperus spp.) are more common and significant portions exist that do not have a pinyon (Pinus spp.) codominant. Common juniper species included are oneseed (J. monosperma [Engelm.] Sarg.), Utah (J. osteosperma [Torr.] Little), redberry (J. pinchoti Sudw.), and alligator juniper (J. deppeana Steud.). The western juniper (J. occidentalis Hook.) woodland is located primarily in the northwestern Great Basin and Columbia Basin and has no pinyon associate. Additional juniper woodlands occur in North America on the northern Great Plains, southern mixed and tall grass prairies (Wright and Bailey 1982); and in southern Europe (di Castri and others 1981; Polunin and Walters 1985), Asia (Walter and Breckle 1986), and northern Africa (di Castri and others 1981).

During pristine times dense juniper stands composed of large trees were often restricted to rocky areas or areas with dissected topography (Burkhardt and Tisdale 1976; O'Rourke and Ogden 1969). Large trees may have also occurred in adjacent sites but in open savannahlike stands. The reduction of fire occurrence, in most juniper woodlands, resulted in increased density of juniper, an advance of juniper into adjacent vegetation types, and the concomitant reduction in the productivity and species diversity of herbaceous and shrub species. This has been noted for southwestern pinyon-juniper (Arnold and others 1964;

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Schott and Pieper 1987; Tress and Klopatek 1987), western juniper (Burkhardt and Tisdale 1969; Johnson and Smathers 1976; Martin 1978; Miller and others 1992; Young and Evans 1981), eastern redcedar (*Juniperus virginiana* L.) (Owensby and others 1973), Ashe juniper (*J. ashei* Buchholz) (Wright and Bailey 1982), and others. In the West, juniper has been noted to invade into sagebrush-grass, dry mountain meadow, curlleaf mountain-mahogany (*Cercocarpus ledifolius* Nutt.), and aspen (*Populus tremuloides* Michx.) vegetation.

ACCEPTED CAUSES

The causes for the invasion of juniper into adjacent communities have generally been credited to: (1) change in climate, (2) effects of livestock grazing on plant competition and fire potential, and (3) wildfire suppression (Blackburn and Tueller 1970; Burkhardt and Tisdale 1976; Gruell 1986; Wright and Bailey 1982; Young and Evans 1981). The latter two are usually given as the most likely causes. Livestock grazing reduces abundance of fine fuel and therefore the fire potential. Livestock grazing may affect the rate of invasion, but the eventual outcome for both grazed and ungrazed sites will be the same in the absence of fire.

Reintroduction of fire onto the juniper-dominated site has often resulted in increases in herbaceous productivity (Aro 1971; Despain 1987; Wink and Wright 1973) and species diversity (Tress and Klopatek 1987). Recent reviews of the effects of fire in the juniper woodlands on specific plant species and postfire succession have been written by Bunting and others (1987), Everett (1987), Koniak (1985), Martin (1978), and Wright and Bailey (1982).

Few detailed fire history studies have been completed for areas with juniper- or pinyon-juniper-dominated vegetation. The most complete study is that in western juniper in southwestern Idaho by Burkhardt and Tisdale (1969, 1976). Their data indicate that mean fire-free intervals (FFI) for old stands of juniper between the years 1650 and 1900 were 25 to 30 years. However, one site had an FFI of 13 years. There were a number of years that several sites burned during the same year even though the sites were a considerable distance apart. Few fires were documented for the stands of juniper that were invading sagebrush-grass communities. Young and Evans (1981) evaluated the fire history of a western juniper-dominated site in northern California. They found evidence of three large fires during the 1650-1900 interval. They concluded that FFI's less than 50 years

Table 2—Influence of fall-applied glyphosate + 2,4-D ¹ on forage
production of wheatgrasses at Fargo, ND

Species	Cultivar	Forage production Percent of nontreated	
Crested	Nordan	76	
	Fairway	129	
	Parkway	91	
	Ruff	127	
	Hycrest	93	
Western	Walsh	90	
	Rodan	68	
Intermediate	Mandan 759R	103	
	Slate	46	
Thickspike	Sodar	135	
•	Critana	68	

'Glyphosate + 2,4-D applied at 0.4 + 0.7 kg/ha on September 19, 1989, at Fargo, ND.

brome control in wheat is based on positional selectively. This herbicide must be incorporated mechanically, as it does not leach into soil. Wheat must be planted with drills that place the wheat seed below the treated zone.

The soil-persistent sulfonylurea herbicides such as chlorsulfuron and metsulfuron applied preemergence to downy brome have suppressed downy brome 30 to 40 percent in winter wheat, but rates used are generally too low to control this weed consistently.

In no-till winter wheat, a granular formulation of triallate plus trifluralin (BuckleTM) applied to the soil surface before planting wheat has controlled downy brome. The granules are not absorbed by surface litter in no-till fields and thus are more effective than liquid formulations of these herbicides. Selective use of this treatment is dependent on some movement of the herbicide away from the wheat row during the planting operation and on placement of the wheat seed at least 3 to 4 cm deep. Diclofop applied to the soil surface after planting wheat no-till has controlled downy brome selectively but can be absorbed by excessive surface residues and requires rain soon after application for activation. Under ideal conditions, weed control and crop yield response to the use of diclofop in no-till systems can be dramatic.

Pronamide applied in late fall will control downy brome selectively in established (1 year or older) slender wheatgrass (Elymus trachycaulus ssp. trachycaulus), tall wheatgrass (Elytrigia elongata), western wheatgrass (Pascopyrum smithii), crested wheatgrass (Agropyron desertorum), intermediate wheatgrass (Elytrigia intermedia), creeping foxtail (Alopecurus arundinaceus), and orchardgrass (Dactylis glomerata) grown in Conservation Reserve Program (CRP) lands. The current label for pronamide use on CRP lands prohibits the grazing of treated grasses. However, this herbicide may be useful in an integrated rangeland renovation program to prevent downy brome seed production and thus reduce the soil weed seed bank.

Downy brome is very competitive in new seedings of perennial rangegrasses and as few as 40 plants per m^2 will reduce shoot biomass of crested wheatgrass by 62 percent (Evans 1961). In the 1970's an atrazine-based chemical

fallow technique was developed to control downy brome during the renovation of rangelands in Nevada (Eckert and others 1974). Atrazine applied at 1.1 kg/ha in late fall controlled downy brome and most other vegetation for 1 year. A significant advantage of this technique was the accumulation of soil moisture that was available for germination and growth of perennial range grasses seeded 1 year after the atrazine was applied. This technique required the use of deep-furrow drills to move the treated soil away from the seeded grasses. The furrows had an added benefit of protecting the new seedlings from drought and coldtemperature stress. Broadleaf weeds such as Russian thistle (Salsola iberica) and mustards (Sisymbrium and Descurainia spp.) were controlled during the year of grass establishment with 2,4-D. Unfortunately, the use of this technique was limited, and atrazine is no longer registered for use on rangelands. Since the early 1970's, several new, highly active herbicides such as hexazinone and sulfonylureas have become available that may be adaptable to the chemical-fallow technique of renovating rangelands.

Glyphosate is a foliage-active herbicide that will control small downy brome at rates as low as 0.3 kg/ha. Research in Wyoming has shown that glyphosate and paraguat applied in May at low rates controlled downy brome with minimum injury to established range grasses (Whitson and others 1991). To be effective, treatments had to be applied after downy brome emergence was complete. In North Dakota, glyphosate applied at 0.2 kg/ha in the spring did not reduce forage production of western wheatgrass, blue grama (Bouteloua gracilis), and Stipa spp., whereas glyphosate applied in the fall reduced forage production of western wheatgrass (Lym and Kirby 1991). Cutlivars of crested, western, intermediate, and thickspike wheatgrasses (Elymus lancerolatus ssp. lanceolatus) differed greatly in response to applications of glyphosate plus 2,4-D (table 2). Therefore, any research on the tolerance of perennial grasses to herbicides such as glyphosate needs to include cultivars with germplasm diversity. Glyphosate may be useful for reducing the downy brome seed bank in rangelands and should be evaluated extensively.

As mentioned earlier, chlorsulfuron and metsulfuron will suppress downy brome in winter wheat. Comes (1985-87), conducting research in the low-rainfall area of Washington, has shown that new seedings of Nordan crested wheatgrass

Table 3—Control of downy brome and Russian thistle in new seedlings of Covar sheep fescue at Lind, WA

Herbicide	Rate	Downy brome	Russian thistle	Cov sheep f	
	kg/ha	Percent control		No./m²	Vigor
Nontreated	0.0	0	0	227	2.5
Bromoxynil + COC ²	.28	0	93	235	2.8
Quizalofop + COC	.11	97	0	323	3.5
Quizalofop +bromoxynil + COC	.11 +.28	99	86	253	3.0

1COC = Crop oil concentrate (1 percent v/v).

²Vigor rating: 0 = plants dead; 5 = plants normal and vigorous.

will tolerate preemergence applications of chlorsulfuron applied at up to 0.05 kg/ha. Forage dry weight of crested wheatgrass was similar to the hand-weeded controls during the year of establishment and was increased up to 200 percent during the second year when the controls were not hand weeded. Similar results were achieved with a number of other range grasses. Davison and others (1984) reported that Nordan crested wheatgrass grown in the greenhouse would tolerate 0.16 kg/ha of chlorsulfuron applied either preemergence or postemergence. Additional research on the use of chlorsulfuron in rangelands is needed to determine the full potential of this and related herbicides.

RECENT DEVELOPMENTS

In recent years, a new group of herbicides has been developed that will control most annual grass weeds, including downy brome, in fine-leaved fescues. Quizalofop applied postemergence (1990-91) at 0.1 kg/ha plus crop oil concentrate controlled downy brome selectively in seedling Covar sheep fescue (*Festuca ovina*) (Ogg, unpublished). Similar results were obtained with fluazifop for barnyardgrass (*Echinochloa crus-galli*) control in Durar hard fescue (*Festuca trachyphylla*). When these herbicides were tankmixed with bromoxynil, most seedling broadleaf weeds were controlled also (table 3). The use of these and related herbicides needs to be investigated more fully under rangeland conditions.

Herbicide cost and sprayer efficiency are major economic considerations in most croplands and are important especially in rangeland. Recently, a new sprayer has been developed that uses 2 to 5 L of total volume per ha (0.25 to 0.50 gallons per acre) and may enhance herbicide activity (Hanks and McWhorter 1991). Referred to as air-assist sprayers, these sprayers use compressed air delivered to each nozzle at 28 to 55 k Pa (4 to 9 psi) to propel the spray solution. Herbicides are dissolved in oil instead of water and micro-metering pumps deliver the herbicide-oil mixture to the nozzles. Spray droplet size is maintained at about 250 microns with this system. Because herbicides are dissolved in oil, coverage of leaf surfaces is improved and spray solutions do not dry as rapidly as water-based sprays (McWhorter and Barrentine 1988). These conditions have enhanced the activity of some herbicides. The air-assist sprayer would appear to have excellent applicability to rangeland conditions and should be evaluated thoroughly.

The most significant problems that need to be addressed in the use of herbicides on rangelands include:

- Cost of herbicides.
- Selectivity in mixed species.
- Inactivation of herbicides by surface litter.
- Weed seed longevity.
- Environmental concerns.

It should be emphasized that total reliance on one method of control, for example herbicides, is rarely successful and is never sustainable. An approach that integrates all available methods (cultural, mechanical, biological, and chemical) is much more likely to produce effective weed control. In addition, the weed management system developed must be integrated into a total rangeland system that recognizes biological, economical, and environmental concerns.

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CHEATGRASS DYNAMICS FOLLOWING WILDFIRE ON A SAGEBRUSH SEMIDESERT SITE IN CENTRAL UTAH

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ABSTRACT

Most vegetation studies tend to be short term and determine the status of communities at a single instance in time. Year-to-year and longer term environmental fluctuations, together with internally driven changes in vegetation, require studies conducted over periods of decades for a full understanding of the vegetation dynamics. This study considers 11 years of data from plots with burnt/ungrazed, burnt/grazed, and unburnt/grazed histories at an initially relict sagebrush steppe site near Mills in central Utah. Cover data were collected near the end of each growing season using a gimbeled point technique.

All burnt plots showed a complete reduction in sagebrush cover, and increased cover by native perennial bunchgrasses (on a percentage basis). All monitored plots showed considerable increase in cheatgrass (Bromus tectorum) during the initial 2 years, followed by a 2-year period of rapid reduction in cover. The ensuing 3 years show considerable yearto-year fluctuation in cover by cheatgrass. The final years of monitoring show a negligible presence of cheatgrass. These results deviate from commonly held notions that the presence of cheatgrass dictates irreversible change resulting in continued cheatgrass dominance. All treatment combinations involving burning showed similar, higher magnitudes of cheatgrass cover regardless of livestock grazing or not, negating conclusions derived from other, shorter term studies.

INTRODUCTION

Numerous papers have recorded the preponderance of cheatgrass (*Bromus tectorum*) in the Great Basin over the past decades (Billings 1990; Klemmedson and Smith 1964; Mack 1981; Morrow and Stahlman 1984; Tisdale and Hironaka 1981). The spread of cheatgrass has been associated with livestock disturbance, although studies of relict areas indicate *Bromus* spp. presence (and sometimes dominance) within undisturbed areas (Hunter 1991; Passey and others 1982; Svejcar and Tausch 1991; Tisdale and others 1965). Similar trends are observed within rangelands that have been rested for a long time (Anderson and Inouye 1989; Daubenmire 1940; Harris 1967).

It has become accepted that fire plays an important role in conversion of sagebrush-steppe to annual grasslands. Livestock grazing may be an important management tool for the maintenance of bunch grasses by preventing the accumulation of fire loads (Young and Evans 1978), thus preventing earlier and more frequent fires that are so detrimental to the native perennials (Hunter 1991; Whisenant 1990).

It is also generally assumed that cheatgrass invasion results in the degradation of sagebrush-steppe to a new stable state, and that only direct intervention is capable of returning this degraded system to a semblance of its former self (Miller and others, in press; Young and Evans 1978). This may be the case, but few long-term studies provide data to validate these notions.

One such long-term study is ongoing at the Idaho National Engineering Laboratory research sites in southcentral Idaho. Anderson and Inouye (1989) discuss the establishment of dense stands of cheatgrass since the initial appearance of cheatgrass in 1975. The authors note that cheatgrass establishment occurred in the absence of fire and grazing, and during a period of higher rainfall (1966-75). A subsequent decrease during drier years implies a dependence on rainfall trends.

Secondary succession within abandoned fields first examined by Piemeisel (1951) and Hironaka and Tisdale (1963) showed several stages of development. Cheatgrass dominated sites after a few years, but was followed by dominance by bottlebrush squirreltail (*Sitanian hystrix*), and the gradual spread of perennial herbs and Wyoming big sagebrush (*Artemisia tridentata* ssp. wyomingensis) (Hunter 1991).

One of the few studies examining postfire community dynamics within Wyoming big sagebrush-dominated vegetation was conducted in southeastern Idaho (Humphrey 1984). Eight environmentally similar sites were burned at different times over a period of 36 years, resulting in a series of communities representative of vegetation development following fire (Humphrey 1984). Data were collected at one instance in time. Initial establishment after disturbance favored perennial grasses and forbs able to resprout following fire. Cheatgrass showed a peak of approximately 11 percent relative cover 3 years after the fire event. This declined to 1-2 percent by the sixth year following the burn. Shrubs able to resprout became prevalent after 6 years, whereas shrubs establishing from seed required longer intervals.

Few long-term studies have been conducted examining community changes at a single site following fire or the advent of grazing, let alone their interaction. More needs to be known of the community changes occurring following

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these disturbances if we are to ably manage our rangelands. This study is aimed at increasing our understanding of community dynamics within burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments.

STUDY SITE

The study site is located near Mills in central Utah (Section 30, R2W, T15S, Salt Lake Meridian), Juab County, on a pediment remnant. Slopes are 1-2 percent east facing, and elevation ranges from 1,617 to 1,622 m (5,305-5,320 ft). For further details see West and Hassan (1985).

METHODS AND MATERIALS

A wildfire swept through the study site shortly after collection of the "pretreatment" data in 1981. Patchy burning of the site resulted in a natural experiment allowing the investigation of changes in burnt and unburnt patches under grazed and ungrazed conditions. Figure 1 summarizes the history of this study. Pretreatment data were collected on four macroplots (20 by 50 m) in 1981. The plots were fenced after the burn, but prior to the second season of data collection. Additional plots (three per treatment) were selected to represent the burnt-grazed and unburnt-grazed treatments. Livestock grazing was initiated after the establishment of watering points prior to the 1982 data collection season. The site may have supported light winter grazing by sheep before the start of the study. A second light wildfire occurred during 1987. One replicate of the burnt-grazed treatment was inadvertently lost due to chaining prior to the 1988 data collection season.

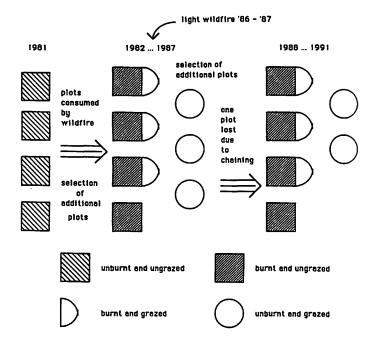


Figure 1—Graphical representation of the experimental design.

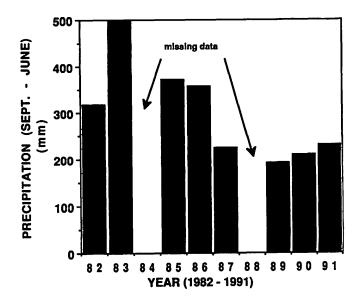


Figure 2—Precipitation records for the Mills study site (September-June; 1981-92).

Data were collected using a gimbeled point technique (Winkworth and Goodall 1962). One hundred points were sampled per macroplot, and interpreted as percentage cover. Data are presented as means with vertical bars representing the range of values for the treatments.

PRECIPITATON

Figure 2 indicates that the years 1987 to 1991 were considerably drier than the preceding years. Nineteen eightythree appears to have been the wettest year according to existing data.

PERCENTAGE LIVE PLANT COVER

No clear differences in total percentage live plant cover occurred between treatments (fig. 3), although the burnt and ungrazed (BU) treatment generally shows a higher percentage live plant cover than the burnt and grazed (BG) and unburnt and grazed (UG) treatments.

GROWTH FORMS

Four growth forms are considered in this section. Two natural groups are shrubs and perennial grasses. Halfshrubs represent a less distinct group. Since forbs comprised a small proportion of the plant community in this study, perennial and annual forbs are considered as a whole within the forb class. Cheatgrass represents an annual grass functional group, but is considered as an individual species.

Figure 4 (tree and shrub cover) shows only slight fluctuations in shrub cover within the UG treatment. Shrubs show no recovery in either the BU or BG treatments following the 1981 wildfire.

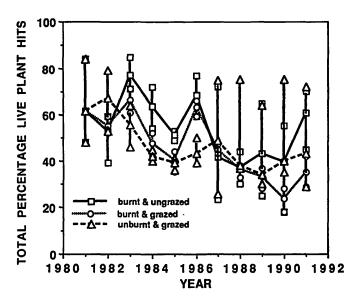


Figure 3—Total percentage live plant hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

Percentage cover by perennial grasses (fig. 5) shows considerable covariation. A large difference in mean percentage cover by perennial grasses between the BU and the BG and UG treatments developed from 1989 to present.

Percentage cover by forbs (fig. 6) fluctuates considerably on an annual basis within its range (approximately 0-8 percent live plant hits). No single treatment appears

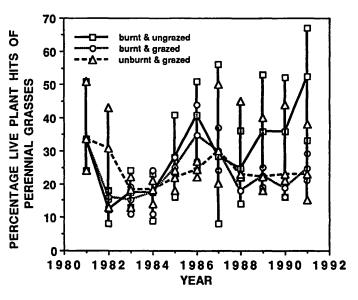


Figure 5—Percentage live perennial grass hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

to have a significantly different percentage cover by forbs. During 1982 the UG treatment showed the highest percentage live plant cover. During the final 2 years of study, the BG treatment showed relatively higher percentage forb cover than the BU and UG treatments.

Of note is the complete absence from all treatments of half-shrubs (fig. 7) during the initial years of the study. During the final 7 years, half-shrubs show considerable

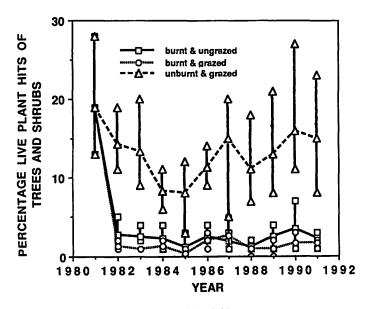


Figure 4—Percentage live tree and shrub hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

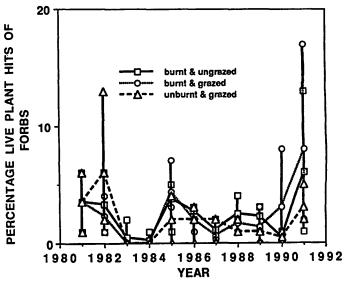


Figure 6—Percentage live forb hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

annual variation within the range of occurrence (approximately 0-3 percent live plant hits) in percentage cover for all treatments. The UG treatment shows higher abundance of half-shrubs during 1990 and 1991 than the other treatment combinations.

INDIVIDUAL SPECIES

Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) (fig. 8) is the predominant shrub within the study site, and thus follows the interpretation for the shrub functional group closely. Sagebrush cover is maintained within the UG treatment (approximately 4-9 percent live plant hits), but completely absent within the BG and BU treatments.

Bearded bluebunch wheatgrass (Agropyron spicatum) (fig. 9) is the dominant perennial grass, and thus follows the interpretation for the perennial grass functional group most closely. The only distinct difference between the long-term trends for the different treatments occurs during the latter 3 years of this study. The percentage cover of bearded bluebunch wheatgrass for the BU treatment increases to a peak (approximately 30 percent live plant hits) in 1991, whereas cover for the BG and UG treatments remains constant (approximately 13 percent live plant hits).

The percentages of live cover for Indian ricegrass (Oryzopsis hymenoides) (fig. 10) for the BU and BG treatments covary and are of the same magnitude during the initial 9 years of the study, but both are higher than for the UG treatment. The UG treatment generally shows the lowest percentage live plant cover of all treatment combinations from 1983 to present. The percentage cover by Indian ricegrass within the BG treatment shows an increase (approximately 7-14 percent live plant hits) from 1989 to present, whereas cover within the BU and UG

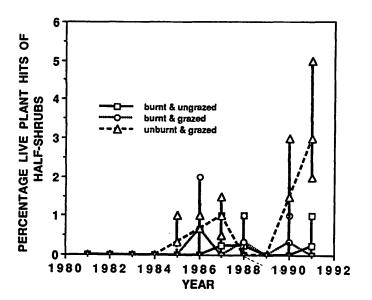


Figure 7—Percentage live half-shrub hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

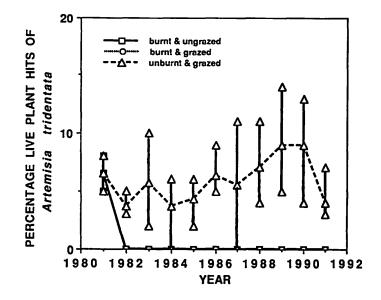


Figure 8—Percentage live Wyoming big sagebrush hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

treatments appears steady (approximately 5 and 3 percent live plant hits respectively) within the same time period.

Bluegrass (*Poa* spp.) (fig. 11), bottlebrush squirreltail (*Sitanian hystrix*) (fig. 12) and needlegrass (*Stipa* spp.) (fig. 13) generally constitute less than 5 percent live plant cover and are characterized by a lack of distinct long-term trends. During the latter 5 years of the study, the highest abundances of bluegrass occurred within the UG treatment, the lowest within the BG treatment, whereas the BU treatment appears intermediate. Percentage live plant

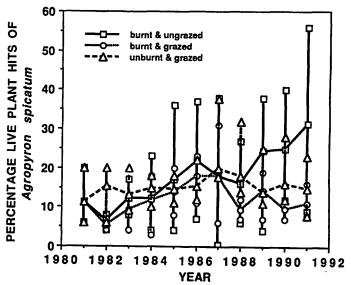


Figure 9—Percentage live bearded bluebunch wheatgrass hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

cover is consistently less in the BU treatment for needlegrass during the last 7 years. No distinct differences exist between treatments for bottlebrush squirreltail.

Percentage live cover of cheatgrass (fig. 14) is the most dynamic of all those presented within this paper. All treatments show a dramatic increase in cover following wildfire and cattle disturbance, with a maximum during the second year following the initial wildfire. The covariation of percentage cover is similar for all three treatments. The magnitudes for the BU and BG treatments are similar (approximately 50 percent live plant hits) and considerably larger than that for the UG treatment (approximately 25 percent live plant hits). All treatments show a negligible percentage cover by cheatgrass during the latter 2 years of investigation (1990 and 1991). The rate of decline of percentage cover following 1983 is lower than the rate of increase to the year of peak cover.

Russian thistle (Salsola kali) was first detected (approximately 1 percent live plant hits) in 1989 within the BG treatment and increased to approximately 13 percent during the final year of investigation (fig. 15). Russian thistle was noted within the BU treatment in 1990 and increased to approximately 6 percent in 1991. Russian thistle was first monitored (approximately 1 percent live plant hits) within the UG treatment in 1991.

DISCUSSION

The observed trend of cheatgrass establishment, invasion, and die-back may be unusual, or it may reflect the lack of long-term studies monitoring community change in sagebrush semidesert. The last 4 years of this study have shown lower than average rainfall. This may have played a part in the decrease of cheatgrass, since establishment

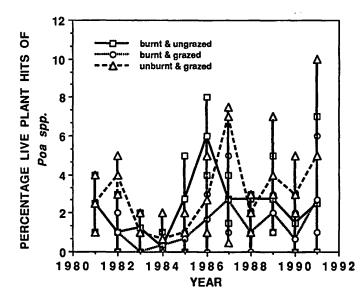


Figure 11—Percentage live bluegrass hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

of cheatgrass has been linked to high rainfall years. The reestablishment of perennial grasses is due to the continued presence of vegetatively produced culms following the 1981 wildfire. The lack of a serious wildfire since 1981 (perhaps due to a low fire load as a result of the drought years and heavy grazing) may have been important in the maintenance of the perennial grasses. These factors all need to be taken into account when interpreting data such as these.

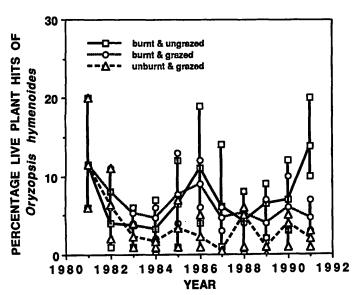


Figure 10—Percentage live Indian ricegrass hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

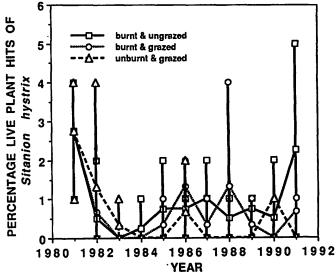


Figure 12—Percentage live bottlebrush squirreltail hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

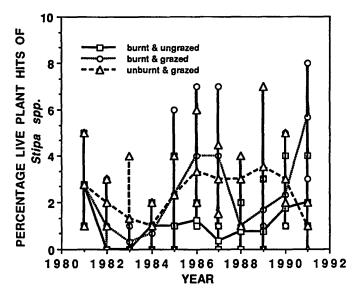


Figure 13—Percentage live needlegrass hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

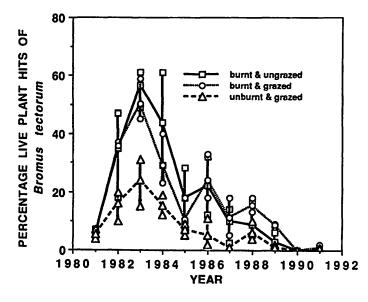


Figure 14—Percentage live cheatgrass hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

The similar trends and large magnitudes of cheatgrass percentage cover for the BU and BG treatments relative to the UG treatment inexorably link cheatgrass impact with fire events. The larger magnitudes of cheatgrass within treatments encompassing a burn is understandable within the context of fire being regarded as an acute disturbance (total removal of foliage at one instance in time), whereas grazing is a chronic disturbance (partial removal of foliage over a longer time period). The decline of cheatgrass for all treatment combinations in the face of heavy grazing is of considerable interest in view of

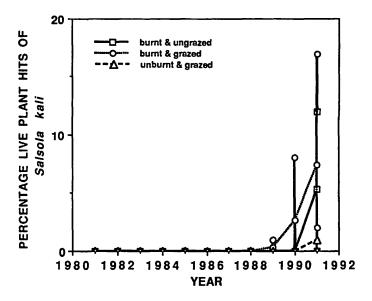


Figure 15—Percentage live Russian thistle hits for burnt and ungrazed, burnt and grazed, and unburnt and grazed treatments (1981-91).

presently held notions. It is interesting to note that the decline of cheatgrass within the UG treatment (chronic disturbance only) to minimum levels preceded that for the treatments encompassing a burn (acute disturbance).

The lack of clear difference between the BU and BG treatments signifies that cattle grazing does not have a clear impact on vegetation dynamics following a burn. However, this must be interpreted within the context of the community—for example, the long-term trends of perennial grasses and sagebrush also need to be considered.

Let us consider some of the changes that have occurred within other growth forms and individual species.

The removal of sagebrush within the treatments encompassing a burn is normal. Lack of regeneration may be due to unsuitable conditions for germination and persistence of seedlings. Sagebrush establishment may depend on the co-occurrence of specific requirements, resulting in a cohort effect. The slight decline in sagebrush within the UG treatment may be ascribed to natural mortality, or partial die-back in individual plots as a result of cattle disturbance.

The apparent difference in percentage cover of perennial grasses (primarily bearded bluebunch wheatgrass) between the BU and other treatments (BG and UG) may be for several reasons. The higher cover by perennial grasses may simply reflect a differential consumption or an accumulation of litter (although care was taken to differentiate between present year's and previous years' growth); or reflect differential reestablishment (primarily vegetative). The establishment of bottlebrush squirreltail (a shorter lived perennial grass) appears similarly enhanced by wildfire, but remains relatively unaffected by grazing. Clearly, the lack of grazing following the wildfire appeared beneficial in terms of establishing higher cover by perennial grasses.

Forbs are difficult to monitor on a cover basis within the sagebrush-steppe system because of their naturally low cover. The relatively low cover by forbs within the BU treatment for the last 2 years may be indicative of a condition commonly observed within vegetation exclosures a trend toward complete lack of shorter lived plants (Tueller and Tower 1979). The establishment of Russian thistle within some of the macroplots may herald future changes.

Some caution should be taken when interpreting results from the macroplots to larger spatial scales. It should be remembered that the macroplots are embedded within a larger burnt and heavily grazed system. It is likely that this has influenced vegetation dynamics within the macroplots studied. For example, there may have been a mass effect (Hatton and Carpenter 1986) that resulted in a higher presence of cheatgrass within the UG treatment than would have occurred within a complete system that remained unburnt. Past history of a site may only become apparent many years after the occurrence or initiation (in the case of grazing) of a disturbance event. This is illustrated by the fact that several figures show divergence of long-term trends between treatments within the latter years of the study.

This paper illustrates some of the problems involved with initiating and maintaining long-term studies. It is often luck that guides the ecologist to the right place at the right time (in this case, immediately prior to a wildfire). Considerable foresight is required to envisage beneficial experimental designs. Interpretation of results is often difficult because of the many perspectives possible (individual species, populations, communities, growth forms). This means that the objectives of a study need to be clearly stated. Maintenance of long-term studies is aided if the method of data collection is efficient in time and personnel (two persons for 1 day per year, in this case).

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HISTORY AND APPLICATIONS OF THE INTERMOUNTAIN GREENSTRIPPING PROGRAM

Mike Pellant

ABSTRACT

The size and frequency of wildfires are rapidly increasing on rangelands in the Intermountain area of the Western United States. One of the major contributors to increased wildfires is alien annual grasses, primarily cheatgrass (Bromus tectorum). Because these annual grasses dry earlier than native species and are highly flammable, they promote the rapid spread of fire. To reduce the size and impact of rangeland wildfires, a wildfire presuppression program called "greenstripping" was initiated in Idaho by the Bureau of Land Management in 1985. Greenstripping is the strategic placement of 30- to 400-ft-wide strips of fire-resistant vegetation on fire-prone landscapes. To date, 451 mi (16.280 acres) of experimental and operational greenstrips have been established. The objectives of the greenstripping program include protecting native rangelands and private properties from wildfire damage, as well as reducing fire suppression and rehabilitation costs.

INTRODUCTION

Wildfire impacts are of increasing concern to resource managers and the public in the Great Basin Desert (northern Nevada, eastern Oregon, southern Idaho, and western Utah) of the Intermountain West. Historically, wildfires occurred at return intervals of 32-70 years in sagebrush (*Artemisia* sp.) vegetation types in the Great Basin (Wright and others 1979). However, the frequency and size of wildfires today is considerably higher than historical levels. Between 1984 and 1993, 2,909 wildfires burned 1,956,840 acres of rangeland in Idaho alone (USDI 1993).

Conversion of native, shrub-steppe vegetation to annual grasses was initiated in the mid-1800's with overgrazing by domestic livestock (Yensen 1980). A significant reduction in native herbaceous vegetation occurred and, concurrently, alien annual species were introduced and soon dominated large areas within the Intermountain area (Young and others 1972).

Cheatgrass is a wildfire hazard because it matures earlier than native species and provides easily ignited fuels that promote a rapid rate of firespread (Stewart and Hull 1949). Whisenant (1990) found a significant correlation between fire frequency and relative frequency of cheatgrass in southern Idaho. Greater fire frequencies were also found to cause lower species richness in native communities. The trend of increased wildfire frequency on cheatgrass rangelands observed by Stewart and Hull (1949) is continuing today (Pellant 1990).

Cheatgrass was recognized as an "ecologic intruder" as early as 1949 (Stewart and Hull 1949) and is now a major component of the vegetation on over 17 million acres of Great Basin rangelands (Pellant, in press). The ecological and economic implications of the invasion of cheatgrass and other alien weeds and the concurrent increase in wildfires are enormous (Young and others 1987). The adverse impacts of cheatgrass expansion and wildfire increases in the Intermountain area have recently received national attention in a popular magazine (Devine 1993).

Although many consider this region a "lifeless desert," these rangelands support a wide variety of wildlife and plant species, provide watershed and recreation values, and support an important livestock industry. A proactive wildfire management approach to reduce wildfire impacts on natural and fiscal resources was needed to maintain the character and ecosystem functions in the Intermountain area. The use of fire-resistant vegetation (greenstripping) to reduce wildfire spread offered an alternative to reverse this trend.

BACKGROUND

The concept of using vegetation that resists burning as a tool to reduce wildfire spread is not new. Early researchers working with crested wheatgrass (Agropyron cristatum and A. sibericum) in southern Idaho recognized the value of this introduced, perennial grass in lessening the cheatgrass fire hazard (Hull and Stewart 1948; Stark and others 1947). The practical benefit of crested wheatgrass as a fire control tool was recognized after an August 1949 wildfire northeast of Shoshone, ID. A 15,000-acre wildfire burned to the perimeter of a crested wheatgrass seeding and stopped, prompting the Bureau of Land Management (BLM) fire control officer to report, "The reseeded area of Owinza Butte, which has a good stand of crested wheat, shows without doubt the value of this type of planting in fire control work" (USDI 1948).

The establishment of vegetative fuel breaks in cheatgrass rangelands was proposed in 1946 in Oregon (Platt and Jackman 1946). These authors suggested that cheatgrass rangelands be broken at suitable intervals, especially along highways, with "strip plantings" of fireresistant vegetation such as crested wheatgrass.

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Bureau of Land Management personnel in Idaho first applied the concept of planting fire-resistant vegetation along roadways in 1981-82 in the Shoshone District. A 25-mi system of crested wheatgrass "roadstrips" was planted after a large wildfire (USDI 1982). Establishment of crested wheatgrass was poor because of annual grass competition and large expanses of rocky, shallow soils in the treatment area. However, results from early research and wildfire contacts with seedings were sufficiently promising that the BLM decided in 1985 to incorporate the use of fire-resistant vegetation into its Emergency Fire Rehabilitation program to reduce future fire occurrences after an initial fire (USDI 1985).

The establishment of vegetative fuel breaks to reduce wildfire spread is not limited to the Great Basin area. In 1957, the "Fuel-Break Research and Demonstration Program" was organized in southern California to expand construction of wide fuel breaks in chaparral areas (Green 1977). Planting perennial grasses that remain green into the summer was recommended for California firebreaks.

BEGINNING OF THE GREENSTRIPPING PROGRAM

In 1985, Idaho BLM personnel initiated the greenstripping program to reduce the impacts of wildfires. Strips of fire-resistant vegetation are planted at strategic locations on the landscape to slow or stop wildfires. The previous section clearly indicates that the use of fire-resistant vegetation to reduce wildfire impacts is not a new concept. Why did BLM initiate this new wildfire presuppression program? The answer is simple: to incorporate improved plant materials and new seeding and site preparation equipment and technology into the implementation of a vegetative fuel-break program. Greenstripping, a proactive approach to wildfire management, was implemented to augment the reactive programs of fire suppression and Emergency Fire Rehabilitation (Pellant 1990).

In 1987, two tasks were accomplished to formally implement the greenstripping program. First, an interagency workgroup completed a handbook that identified greenstrip criteria and procedures (USDI 1987). Second, Congressional funding was obtained to establish operational greenstrip projects and implement a cooperative research program. Goals of the BLM's Intermountain Greenstripping and Rehabilitation Research Project are to evaluate and select fire-resistant plant materials and equipment to improve greenstripping and fire rehabilitation practices. Six research cooperators are currently working to accomplish these goals.

In 1991, an internal evaluation of the greenstripping program recommended program expansion to public land in Utah, Oregon, and Nevada (USDI 1991). Pilot greenstrip projects were established in these three States in 1992-93, and multistate coordination on greenstrip projects and research continues to this day. The author provides technical assistance about greenstrip planning and implementation to other land managers in the Intermountain area.

PROGRAM OBJECTIVE

The objective of the greenstripping program is to slow or stop the spread of wildfires by the strategic placement of strips of fire-resistant vegetation on the landscape (fig. 1). By reducing wildfire frequency and size, the following benefits are realized:

1. Reduced loss of plant diversity and shrub cover on sagebrush-steppe and salt-desert shrublands. With longer intervals between wildfires, loss of plant diversity, especially shrubs, will be slowed on fire-prone landscapes and eventually native species may increase (West 1978; Whisenant 1990; Young and Evans 1978).

2. Reduced loss of private structures and properties on urban/rural interfaces with public rangelands.

3. Reduced fire suppression and rehabilitation costs.

FUELS MANAGEMENT STRATEGY

Vegetative fuelbreaks, including greenstrips, are simply fuels modification actions whereby vegetation that is susceptible to igniting and carrying a fire is replaced by vegetation that is less likely to ignite or carry a wildfire. Standing dead material and current growth of plants and litter constitute the bulk of rangeland fuels. Fuels are the only element of the fire behavior triangle that can be influenced by management actions, as neither weather nor topography are easily manipulated. By modifying fuel properties, extreme fire behavior can be reduced.

Fuels available for combustion depend on the proportion of fuel that is dead, fuel particle size, moisture content, and fuel continuity (Anderson and Brown 1988). With other factors being equal, the likelihood of a fire start and rate of fire spread increases as fuel availability



Figure 1—This greenstrip project near Mountain Home, ID, was seeded with crested wheatgrass in 1985. Seedbed preparation on this 30-ft-wide greenstrip was done with road patrol to reduce weedy plant competition. Note absence of cheatgrass in interspaces in this 1992 photo.

increases. Rangelands infested with alien, annual grasses are more prone to ignition and fire spread than native rangelands, since the proportion of available, contiguous fuels is higher on the former than the latter.

The effectiveness of greenstrips, or any fuels modification project, in reducing wildfire spread is enhanced by three factors:

Disrupting Fuel Continuity—Fuel continuity can be disrupted by replacing cheatgrass or other annual grasses, which grow in a matlike pattern, with caespitose grasses such as crested wheatgrass, which have large spaces between individual plants (fig. 1). Spread of surface fires is interrupted in discontinuous fuels and can be more easily suppressed (Anderson and Brown 1988).

Reducing Fuel Accumulations and Volatility— Rangelands with a high density of shrubs generate longer flame lengths and increase the probability of fire spotting (Schmidt and Wakimoto 1988). The high monoterpene and sesquiterpene content of sagebrush (Kelsey 1986) increases fire intensity in shrubs. Fire suppression actions are easier and safer to carry out in light fuels than in heavy fuels; for example, backfiring is less risky in perennial herbaceous vegetation than in dense stands of shrubs. The probability of fires spreading laterally can be greatly reduced if shrub stands are thinned to maintain a minimum distance of 10 ft between plants (Schmidt and Wakimoto 1988).

Increasing the Density of Plants With a Higher Moisture Content—The length of time during the fire season that fuels and fire behavior remain hazardous and ignition potential is high is largely reflected in the moisture content of the various species in the plant community (Anderson and Brown 1988). Increasing the proportion of plants with high moisture and low volatile oil content can reduce both the potential for ignition and rate of fire spread.

Forage kochia (*Kochia prostrata*), an introduced half shrub, was found to have a fourfold and tenfold higher moisture content in August 1992 than crested wheatgrass and cheatgrass, respectively (USDI 1992). This plant is effective in retarding wildfire spread and can compete well in a weedy environment (fig. 2).

PLANNING AND IMPLEMENTATION

A host of factors must be considered in the planning and implementation of a greenstrip project. The use of an interdisciplinary team that "designs" a greenstrip based on a site-specific evaluation is essential. The following factors should be considered when designing and implementing a greenstrip project.

Project Area

Selection of sites to implement greenstripping projects is determined by an interdisciplinary team. This team reviews land-use plans that identify high-value habitat,



Figure 2—Forage kochia plant (foreground) in a marginally established greenstrip near Mountain Home, ID. Forage kochia is still green in this August 1990 photograph. A wildfire started off Interstate 84 (background) burned to this greenstrip and stopped because of the sparsity of contiguous fine fuels in the seeding.

watershed, and cultural and plant communities that are at risk if disturbed. Both fire history and potential for repeated wildfires are also considered.

High fire-frequency areas are generally associated with cheatgrass and tend to reburn at frequent intervals (Whisenant 1990). Greenstripping can break large blocks of cheatgrass-infested rangeland into smaller, more manageable units, thereby reducing fire suppression costs and spread of wildfires into unburned shrublands.

Land Ownership

Land ownership patterns are an important consideration in greenstrip planning. Greenstripping across "checkerboard" land ownership patterns requires easements from private or State land owners. "Gaps" left in greenstrips due to the presence of nonfederal land can severely limit the effectiveness of a greenstrip in stopping or slowing a wildfire.

Fire Behavior

Topography, vegetation types (fuel loads), and weather patterns are fire behavior characteristics that must be evaluated and incorporated into locating greenstrips on the landscape. Expected fire behavior is included in the design of a greenstrip project by considering prevailing wind direction, slope, and fuel quantities and continuity. Fire management specialists are included in the planning process to ensure proper consideration of fire behavior variables in selecting greenstrip locations.

Soils

Soil productivity and the amount of surface rock affect seeding establishment and persistence. Deeper soils generally support a better stand of seeded vegetation than do rocky, shallow soils. Therefore, greenstrip width is increased to compensate for reduced density of greenstrip species on rocky or shallow soils.

Greenstrip Width

Greenstrip width generally varies from 30 to 400 ft depending on fire prevention objectives, topography, expected fire behavior, and soils. Most greenstrip projects in Idaho average 300 ft in width and have been seeded along highways or railroads to reduce human-caused fire starts and create a wider fire barrier. As fuel height and volatility increase, greenstrip width should be increased to reduce the potential for fire spotting that may occur over the greenstrip.

Visual Impacts

Greenstrips can have a significant impact on the visual characteristics of a landscape. Adverse visual impacts can be minimized by avoiding straight-line seedings and increasing plant and structural diversity in greenstrip plantings.

Plant Materials

The selection of proper seed mixtures for greenstrip plantings is critical for the successful establishment and persistence of seeded species. General criteria for selecting species for rehabilitation are discussed by Plummer and others (1968). Extensive research on reseeding abandoned farmland (Stark and others 1946) and cheatgrassinfested rangelands (Hull and Stewart 1948; Hull and Holmgren 1964; Klomp and Hull 1971) is available for planning greenstrip projects. Plants selected for seeding greenstrip projects should also be:

1. Fire resistant during a majority of the wildfire season.

2. Drought tolerant and adapted to persist on semiarid sites.

3. Palatable to herbivores.

Fire tolerant to survive occasional burns.

5. Capable of establishing and persisting in competition with annual species.

Plant materials meeting all of these criteria are not readily available. Introduced wheatgrasses (Agropyron sp.), Russian wildrye (Elymus junceus), dryland alfalfa (Medicago sp.), Lewis flax (Linum lewisii), and small burnett (Sanguisorba minor) are the most common herbaceous species seeded in greenstrip projects.

Shrubs generally increase fuel loads and flammability, increasing the probability that a greenstrip could be breached by a wildfire. Therefore, use of shrubs in greenstrips is minimal. One exception is forage kochia, which is limited in use only by seed availability and cost. There are also concerns that this plant may spread outside of greenstrip project boundaries and compete with native plants.

Fourwing saltbush (*Atriplex canescens*), a native shrub, is occasionally used to enhance diversity of greenstrips and to trap winter snowfall.

Site Preparation and Seeding

Most sites selected for greenstripping are dominated by weedy species such as cheatgrass, either as an annual grass monoculture or as the dominant understory species under sagebrush. Site preparation to reduce competition from annual plants is required prior to seeding perennial vegetation (Evans and Young 1977; Stark and others 1947). Evans (1961) reported that cheatgrass densities as low as 64 plants per square foot greatly increased mortality of crested wheatgrass seedlings.

Mechanical, herbicidal, and burning treatments (or combinations of them) are effective in controlling annual species under the right conditions. Mechanical seedbed preparation techniques have been used extensively and evaluated in the greenstripping program. Disking is most effective if the treatment is done in early spring prior to cheatgrass seed maturity (fig. 3). Seeding greenstrip species with a rangeland drill is done in the fall following the disking treatment. Labor and equipment costs to mechanically prepare seedbeds and distribute seed were estimated at \$20 to \$25 per acre by Pellant (1990). He reports that these costs are considerably reduced (\$8.50 per acre for labor) with the use of a disk chain that buries unwanted vegetation and distributes seed in one pass.

Use of fire as a site preparation technique can be effective if burning is done prior to seed dispersal by cheatgrass (Hull and Stewart 1948; Pechanec and Hull 1945). Costs to burn cheatgrass rangelands are generally under \$5 per acre.



Figure 3—Towner plow used to reduce annual plant competition in May 1993 on a greenstrip project near New Plymouth, ID. Rangeland drills were used to plant a diverse greenstrip mixture in October 1993.

Herbicides offer another alternative for cheatgrass control prior to seeding (Eckert and others 1974).

Several herbicides are being field tested in Idaho and Nevada to determine their effectiveness in reducing cheatgrass competition. Twenty-one herbicides are approved for use on public land to meet specific vegetation treatment objectives (USDI 1991). Economics, environmental impacts, selectivity, and effectiveness are several of many factors that must be considered prior to selecting an herbicide for site preparation in cheatgrass-infested rangelands.

Management

Livestock season-of-use and wildlife use patterns must be considered in greenstrip planning. Livestock and wildlife are often attracted to green vegetation, causing overuse and eventual loss of palatable greenstrip plants. Additionally, greenstrips along roads or railways may attract livestock and wildlife to the road or track, causing accidents.

An adequate period of herbivore exclusion during the plant establishment period is also essential. Seeding prescriptions for greenstrips should only include species that will establish during the grazing exclusion period and species that will not be selectively overgrazed and eventually lost from the greenstrip. However, livestock can serve a useful role in proper greenstrip management by reducing fine fuels through grazing and trampling.

PROGRAM STATUS

From 1985 to the end of 1993, 451 mi (16,280 acres) of greenstrips were seeded on public land in Idaho (Pellant 1993). Pilot greenstrip projects were completed in Oregon, Nevada, and Utah in 1992 with technical assistance from the Idaho Greenstrip Program Manager.

Two wildfires have burned into established greenstrip projects. In 1988, a greenstrip project north of Grasmere, ID, was effective in stopping a wildfire along 6 of 7 mi of the contact area.

This allowed suppression forces to concentrate their efforts on a fire front of only 1 mi instead of 7. In 1990, a greenstrip adjacent to a major interstate highway near Mountain Home, ID, limited a wildfire to 15 acres (fig. 3). From 1980 to 1989, the average area burned in the same vicinity was 1,800 acres.

The Intermountain Greenstripping and Rehabilitation Research Project has been transferred to the Department of the Interior's National Biological Survey. Research is continuing in 1994.

SUMMARY

The Intermountain landscape has been permanently altered by the introduction and spread of alien annual species, especially cheatgrass, which are more competitive and flammable than native species. In 1965, a group of land managers and research specialists met in Vale, OR, to discuss solutions to the management problems posed by cheatgrass. Noted revegetation researcher, A. C. Hull, Jr., summed up the situation by stating, "The more cheatgrass the more fire, and the more fire the more cheatgrass" (USDI 1965). In many respects, this situation is little changed 28 years later. Therefore, it is probable that wildfire impacts will continue to increase unless proactive measures, such as greenstripping, are applied. Greenstripping is not the ultimate solution to the cheatgrass-wildfire problem, but one of many tools that must be applied to control wildfires on rangelands dominated by annual plants.

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PRESCRIBED BURNING CONSIDERATIONS IN SAGEBRUSH ANNUAL GRASSLAND COMMUNITIES

G. Allen Rasmussen

ABSTRACT

Prescribed burning can be an effective tool to manage sagebrush grasslands. However, burning prescriptions for sagebrush grasslands vary depending on the management objectives, species composition of the community, and location. To develop successful fire prescriptions in these communities, consideration must first be given to the management objectives. Second, the past and future management of the area has to be considered to determine if prescribed burning is a viable alternative. Once these have been established, the species composition, fuel load, fuel continuity, and weather are considered. These factors will determine the burning prescription used and follow-up management needed for prescribed burning to be successful in sagebrush-grassland sites with cheatgrass (Bromus tectorum). Prescribed burning will only decrease cheatgrass in the short run, so it should only be used as a seedbed preparation technique where cheatgrass dominates the understory.

INTRODUCTION

Prescribed burning has been defined as the judicious use of fire to achieve specific management objectives. However, research has found fire is one of the primary disturbance agents that has allowed cheatgrass (*Bromus tectorum*) to dominate many sagebrush (*Artimesia* spp.)bunchgrass communities.

Many managers feel prescribed fire has no place in managing sagebrush-grassland communities. The objective of this paper is to discuss considerations that need to be addressed when using prescribed fire in sagebrushgrasslands and general prescriptions that could be used.

MEETING OBJECTIVES

The first step in determining when fire should be used would be to determine the objective for the area. Objectives range from maintaining or improving forage production for wildlife or livestock, to altering the plant community, to helping prepare the seedbed. The next step would be to determine the site characteristics.

Two important site characteristics are species composition of the current plant community and climatic conditions. The species composition should be inventoried to determine the possible plant community that would follow the prescribed burn. Fire acts as a top removal technique that can give the competitive advantage to resprouting species and annuals that have a seed reservoir in the soil (Wright and Bailey 1982). Some strong resprouting shrubs, for example, rabbitbrush (Chrysothamnus spp.) can easily dominate sagebrush communities following fire. Perennial herbaceous plants are affected by fire depending on their growth form (cespitose vs. rhizomatous), fuel load adjacent to the meristematic tissue, and phenological growth stage when the fire occurs (Wright and Klemmedson 1965). When precipitation is below 30 cm/yr caution should be used to ensure the desired plant response.

If fire can still meet the management objectives, the next step is to determine the fire prescription that would be most appropriate. General burning prescriptions tend to be very broad to allow flexibility. This flexibility is needed to overcome the variability in fuel loads, fuel moisture, fuel continuity, relative humidity, temperatures, and windspeed. However, experience with fire behavior and local conditions is required to determine when prescribed burning will meet the management objectives.

CHEATGRASS-DOMINATED SITES

Sites with cheatgrass as the dominant understory species generally have good fuel continuity following good precipitation years. The burning prescription can be fairly flexible since this good fuel continuity of cheatgrass will carry the fire. Prescribed burning can reduce cheatgrass the following year if the area is burned at the appropriate time.

Pechanec and Hull (1945) found that burning in the summer would decrease the cheatgrass seedlings the following year (table 1). The likely reason for fire reducing cheatgrass seedlings is that the plants have matured and senesced, but the seeds have not shattered. Since the seeds are still up in the fuelbed, heat from the prescribed burn can destroy the seeds. Heat from grassland fires is generally not of sufficient duration or high enough at groundline to damage seeds. Once the cheatgrass seeds have shattered and are on the ground, fire will have little impact on them.

Reducing cheatgrass densities with fire is only temporary. Observations suggest densities normally return within 2 years, provided weather conditions are favorable. Reseeding would be required to help reduce the density of cheatgrass.

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Table 1-Date of burn and number of cheat-
grass plants the following spring
(adapted from Pechanec and Huli
1945)

Month of burn	Cheatgrass plants per m ²
June	150
July	120
August	440
October	480
November	1,330

A disadvantage of summer burns is the damage to existing native perennial grasses. These grasses are at a susceptible phenological stage. If numerous desired perennial herbaceous plants are found on the area, early summer burns are not advisable (Wright and Klemmedson 1965). Prescribed burning should be carefully considered to ensure it would meet the desired objectives.

BURNING PRESCRIPTIONS

When considering prescribed burning prescriptions, the fine-fuel load and sagebrush canopy cover have a direct relationship with the prescribed burning success; this has been discussed by Britton and Ralphs (1979). In northern Utah, prescriptions have been developed for both spring and fall burns (table 2). Fall burns are the most common. These fall burns probably are favored because fire is not often used until the sagebrush canopy cover has increased to the point that fine-fuel loads are often below 250 kg/ha, and the sagebrush canopy must carry the fire. This generally requires a higher intensity fire and environmental conditions that occur in the late summer, early fall period. This has led to problems of soil erosion, generally when weather conditions were not favorable for revegetation. Spring burns allow the greatest flexibility to ensure a

Table 2—General prescribed burning conditions for sagebrushdominated rangeland in northern Utah

Condition	Acceptable	Ideal
1-h fuel moisture (pct)	5-12	5-8
Green herbaceous fuel	<5 cm new growth	
Cloud cover (pct)	0-60	<25
Temperature (°C)	10-35	15-32
Relative humidity (pct)	10-35	12-20
Windspeed (m.p.h.)	5-20	8-20

desired plant response to prescribed burning because the soil moisture is known before the burn is conducted. However, the window of opportunity is greatly reduced.

Spring burns have fewer days that meet the prescription and require the burn manager to be more aware of daily environmental conditions and flexible enough to burn when these conditions are appropriate. Because of cooler environmental conditions, spring burns require a better herbaceous fuel load and continuity to meet the burn objectives compared to summer and fall burns.

In northern Utah with spring burns, temperatures rarely get above 21 °C before the green herbaceous fuel dominates the understory. The most success has been found at temperatures between 15 and 18 °C when the relative humidity is less than 20 percent. However, in central Utah there is less effective moisture and lower herbaceous fuel loads for the corresponding canopy cover. This generally requires the temperature to be above 29 °C and the relative humidity to be less than 20 percent.

CONCLUSIONS

Prescribed burning can help alter sagebrush-annual grasslands. However, perennial herbaceous plants are at a susceptible phenological stage during early and midsummer burns, which are most damaging to annual grasses in the Intermountain West. In most situations where annual grasses dominate the herbaceous understory there are not sufficient perennials available to take advantage of the reduced cheatgrass competition following prescribed burns or wildfires. Additional revegetation methods are required to supply the needed seed source for a perennial herbaceous plant community.

If the site objective is to maintain the perennial herbaceous vegetation, prescribed burning would be most effective if it was used before sagebrush dominates the site and effectively excludes the perennial herbaceous plants. This would reduce the need for reseeding following the burn. If the desire is to maintain the sagebrush, prescribed burning has very limited applicability.

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EFFECTS OF FIRE ON SALT-DESERT SHRUB RANGELANDS

Neil E. West

ABSTRACT

Fire was not thought to be a driving variable in saltdesert shrub ecosystems prior to 1983. The El Niño related extreme wetness of 1983-85 resulted in a profusion of mostly exotic annuals followed by wildfires. Unfortunately, the most productive sites, near the upper boundary of the type, have been most often affected. Major species such as shadscale (Atriplex confertifolia) and budsage (Artemisia spinescens) do not resprout following fire. Winterfat (Ceratoides lanata), saltbush (Atriplex nuttallii), gray molly (Kochia americana) and black greasewood (Sacrobatus vermiculatus) do resprout, but subsequent populations appear reduced.

INTRODUCTION

Just a decade ago I would have not ever dreamed of addressing this topic. In fact, in my (West 1983) review of salt-desert shrub ecosystems, I explicitly said that fire was not part of that environment. Blaisdell and Holmgren (1984) also fail to mention fire in their more managementoriented review. There was no literature or experience at the time of writing for us to say otherwise. In another review (West 1988) only 5 years later, I had to recant that view.

The difference is due to the extremely wet conditions of 1983-85, the profusion of mostly exotic annuals, and subsequently, wildfires. Before we discuss the consequences of those events in the 1980's, let us define the environment and biota of the ecosystems under consideration here.

FEATURES OF THE SALT-DESERT SHRUB ECOSYSTEM TYPE

The term "salt-desert shrub" tells three important aspects of its character—that it is climatically dry, the soils are usually salty, and the vegetation is dominated by shrubs. Such circumstances are found over about 17x10⁶ ha of lowlands in all four regional deserts of North America, plus parts of the Great Plains and the San Joaquin Valley of California (West 1983). The dominant perennial plants are either shrubs or half-shrubs within the Chenopodiaceae.

There are usually three kinds of salt-desert sites occurring in a catena from valley bottom to pediment slope. The valley bottoms are either largely barren salt pans or wet meadows to marshes, depending on drainage. The wet meadows and marshes usually have free water extending at the surface, for at least half of the year. Thus, these segments of the gradient do not usually support fire. The next higher segment has high water tables, but water does not usually stand on the soil surface. Here the hydrohalophytes dominate. The major shrub there is black greasewood (*Sarcobatus vermiculatus*). The major original grass was Great Basin wildrye (*Elymus cinereus*). Alkali saccaton (*Sporobolus airoides*) has survived unrestricted grazing much better, however.

The most extensive portion of the salt-desert shrub type occurs on the well-drained uplands. The xerohalophytes that occur there are more diverse, including species in saltbushes (*Atriplex*), *Kochia*, winterfats (*Ceratoides*), hopsages (*Grayia*), rabbitbrushes (*Chrysothamnus*), and horsebrushes (*Tetradymia*). Variations in community composition and productivity are intimately related to soil salinity and texture. Total plant cover and production is least on marine shales and greatest on slightly gravelly sites due to the inverse texture principle (Noy-Meir 1973). The latter kind of sites are usually where enough continuous fine fuel can be produced during exceptionally wet years to carry subsequent fires.

LIVESTOCK GRAZING-FIRE-CLIMATE INTERACTIONS

It is now becoming more apparent that livestock grazing has not had an exclusive role in allowing the expansion of introduced annuals, especially cheatgrass (Bromus tectorum). While livestock trampling of microphytic soil crusts is sometimes invoked as a cause (West 1990), annuals can be found on relicts without livestock grazing (Svejcar and Tausch 1991). Whisenant and Wagstaff (1991) have shown that even the moderately grazed Desert Experimental Range has shown increased cheatgrass. Heavy spring-use paddocks had a comparatively greater increase in cheatgrass than other combinations of intensity and timing of sheep grazing. While the general truncation of season of use and reduced numbers of livestock on salt-desert ranges can be followed by enhanced abundances of native perennials on some of the Bureau of Land Management's (BLM) salt-desert ranges (Yorks and others 1992), cheatgrass will still remain and even increase. Without livestock consumption of some of these fuels, susceptibility of these lands to fire could increase further.

The shrub "dieback" phenomenon centered on 1983-84 (Nelson and others 1989; Price and others 1992) freed up space and resources that could be utilized by annuals.

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With the annuals came finer and more continuously arrayed fuels that dried up sooner than the original shrubland. Although the shrubs are recovering in some of these areas (Ewing and Dobrowolski 1992), fire may intervene and return them to annual dominance. Wind and water erosion could remove and dilute the soil organic matter and attendant nutrient concentrations around the shrubs (Charley and West 1975), and the consequent safe sites for seedling survival they provide (West 1982; West and Goodall 1986). After fire has eliminated the native perennials, essential mycorrhizae may be extirpated (Wicklow-Howard, these proceedings).

EVIDENCE OF FIRE IMPACT

The above reasons are from the sparse available literature on the topic. Are there concrete examples to demonstrate these patterns? I have come across four circumstances that illustrate the role of fire in effecting change on salt-desert rangeland.

The uppermost segment of the salt-desert shrub type in Curlew Valley, northwestern Utah, has been studied by our department since the 1950's. Gates and others (1956) described the vegetation and soil thoroughly. Cook (1971) described the changes on species populations, regrowth, and carbohydrate reserves following utilization. Rice and Westoby (1978) described the lack of successional recovery in the vegetation of the exclosures established in the early 1950's. Duba (1976) described the population biology of some of the introduced annuals. These studies predating the particularly wet period of 1983-84 allow us to appreciate the extent of change since.

By happenstance, Kevin Connors, a technician in the Forage and Range Laboratory of the USDA Agricultural Research Service, was in Curlew Valley on July 7, 1983. perhaps the most ecologically important day in the history of Curlew Valley this century. Fortunately, Kevin had a camera and the presence of mind to take some slides at permanently locatable points. Comparing those slides with a recent field examination shows that the major fuels in 1983 were bottlebrush squirreltail (Sitanion hystrix) grass in the winterfat stands, but tansy mustard (Descurainia pinnata) and pepperweed (Lepidium perfoliatum) elsewhere. Cheatgrass was less abundant that year than it had been before or since. Although shadscale (Atriplex confertifolia)- and saltsage (Atriplex gardneri)-dominated plots were burned as well as the winterfat (Ceratoides lanata) plots I do not have preburn slides from them. Drawing on Rice and Westoby's (1978) data taken last in 1973 for all three types, we observed that only winterfat and saltsage resprouted after this fire. The shadscale plot had the most cheatgrass of the three and has been altered the most.

The Dugway Proving Ground is another place where some earlier work on salt-desert vegetation was done (Vest 1962). Vest's map shows that shadscale dominated the southwestern corner of that property. Recent monitoring efforts have taken us back to that area. Security reasons prevent me from being able to present photographic evidence, so you will have to take my word for it that shadscale is gone and introduced annuals dominate even though livestock have not been there since 1948. The sources of fire are somewhat unique. While lightning ignites most fires elsewhere, the more common sources at Dugway are from military ordinance. This area is adjacent to an artillery training ground. How many times this area has burned since Vest made his map, I do not know. I can tell you, however, that the FIREX operations of 1987 led to extensive fires because they escaped to adjacent BLM areas and resulted in intensive efforts at revegetation (Tom Roberts, personal communication 1989). Sparks and others (1990) noted from repeat observations at section corners that fires had changed upper salt desert areas in nearby Skull Valley, UT, some probably prior to the 1980's. The changes were more pronounced and widespread on the more heavily impacted east than west side of the valley.

A fourth instance of fire in salt-desert shrub communities has been pointed out to me by Jim Young. This took place west of Winnemucca, NV, in 1986. Over 600,000 acres were burned, including some shadscale-dominated areas on the upper bajada of the Sand Dunes Allotment of the T Quarter Circle Ranch (Emmerich and others 1992). Abundant cheatgrass carried the fire there. Very little recovery of shadscale was observed in the spring of 1992.

In contrast to these known instances of major fires over some salt-desert shrub rangeland, we also know that some of the most well-studied salt-desert areas have not burned. For instance, no fires have occurred at the Desert Experimental Range (R. Holmgren, personal communication 1990) or farther south in Pine Valley, UT (Yorks and others 1992). There have also been no fires on the longterm study plots of Sharp and others (1990) in Raft River Valley, ID.

It would be nice to be able to say how much of the saltdesert shrub rangeland has been burned and when. This will require agreement on what constitutes the salt-desert shrub type and a consistent way to record fires. Perhaps this can be solved in the future with remote sensing and procedures associated with synoptic monitoring plans such as EMAP (Hunsaker and Carpenter 1990).

If readers know of further examples of fires in saltdesert shrub communities that have some documentation, I would appreciate knowing about them. We can use them as natural experiments to build up our understanding of how this relatively new kind of disturbance influences such vegetation, soils, and wildlife habitat.

RESPONSES OF MAJOR SALT-DESERT PLANT SPECIES TO FIRE

The best that we can presently do to summarize what we know about fire in salt-desert shrub ecosystems is to note the response of major plant species to fire (table 1). This information was assembled from the Fire Effects Information System (Fischer and Wright 1987), Intermountain Fire Sciences Laboratory, Intermountain Research Station, USDA Forest Service, Missoula, MT, personal experience, and volunteered comments obtained at the symposium.

Some major species can resprout after the tops are scorched (*Ceratoides lanata, Kochia americana, Sarcobatus vermiculatus*); others must recover from seed (*Atriplex*

Species a	nd Location	Lifeform ¹	Resprout	Killed (musi regenerate from seed)
Up	lands			<u> </u>
Spiny hopsage	Atriplex (Grayia) spinosa	S	x	
Budsage	Artemisia spinescens	S		x
Shadscale	Atriplex confertifolia	S		X
Little greasewood	Sarcobatus baileyi	S	x	
Fourwing saltbush	Atriplex canescens	S	x	
Torrey saltbush	Atriplex torreyi	S	X	
Gardner saltbush	Atriplex gardneri	Ĥ	X	
Winterfat	Ceratoides (Eurotia) lanata	н	X	
Gray molly	Kochia americana	H	X	
Forage kochia	Kochia prostrata²		X	
Great Basin wildrye	Leymus (Elymus) cinereus	G	Х	
Indian ricegrass	Oryzopsis hymenoides	G		х
Bottlebrush squirreltail	Sitanion hystrix	G	X	
Low	riands			
Black greasewood	Sarcobatus vermiculatus	S	x	
Samphire	Salicornia utahensis	Ĥ	?	
Torrey seepweed	Suaeda torreyana	Ĥ	?	
lodine bush	Allenrolfea occidentalis	н	?	
Saltgrass	Distichlis stricta	G	?	
Alkali sacaton	Sporobolus airoides	G		Х

Table 1-Response of major perennial plants of salt-desert shrublands to fire

'S = shrub, H = half shrub, G = grass.

²Major introduced species used in revegetation efforts.

confertifolia, Artemisia spinescens) (table 1). This difference in response could drastically alter the course of secondary succession on these lands for many decades.

PROSPECTS FOR THE FUTURE

With the now wider presence of introduced annuals, I see increased chance of burning of salt-desert shrub rangelands. Global warming is expected to result in wider variations in temperature and precipitation. Thus, even though the longer term trends in temperature could be higher, we will probably have more extremely wet years as well as deeper droughts. This along with the fertilization effects of increased CO₂ should result in more fuel because cheatgrass and red brome (*Bromus rubens*) growth is enhanced by an atmosphere richer in CO₂ (Smith and others 1987).

Thus, unless we can use knowledge of when to expect wetter conditions from El Niño events to more successfully reseed these rangelands to less fire-susceptible perennials such forage *Kochia* (*Kochia prostrata*), we are in for some more difficult times in managing some of the salt-desert shrublands.

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A TECHNICAL COMPARISON MODEL: CLASS A FOAM COMPARED TO WATER AS AN EXAMPLE

Paul M. Schlobohm

Water has been used to fight fire for centuries. The Bureau of Land Management (BLM) relies on a fleet of over 400 water engines as its primary fire suppression technology in Great Basin fuels.

Class A foam is a relatively new approach to fire suppression. The foam concentrates were introduced in the early 1980's (Schlobohm and Rochna 1987). Proportioning and foam-generating devices have been modified to meet the demands of the wildland fire workplace.

There are two arguments against the use of Class A foam. First, the use of foam technology requires investment beyond that necessary to operate a conventional water-pumping system. For example, foam concentrate that may cost \$9.00 per gallon and is proportioned at 0.5 percent will cost \$22.50 for every treatment of a 500-gallon tank. Installing a foam proportioner will cost anywhere from \$200 to \$4,000. Aspirating nozzles cost between \$20 and \$500. Compressed air foam systems range from \$5,000 to \$20,000, depending on components.

A second argument is that the improvements foam may offer are unnecessary. As a result of years of experience with water, engines are managed to handle the typical workload of fire frequency and behavior. The argument is that extreme fire situations, such as large numbers of large fires in a few hours which tax the capabilities of water engines, would do the same for foam engines.

Advocates for the use of Class A foam argue that foam makes water more productive. For example, when engines using water extinguished 100 chains of fireline in grass and brush fuels of the Lakeview BLM District, similar engines using foam extinguished 133 chains (Schlobohm and Rochna 1987). The difference was attributed to water engines routinely doubling back to catch rekindles while foam engines continued moving ahead.

No documented method exists to determine if an investment in Class A foam is cost effective. Is there a fire scenario for which the use of foam saves money? For which fireline intensity levels does foam use cost more than water alone? Fire managers must guess the answers to these questions as they consider dispatch to fires and offseason investment in their engines.

PURPOSE

The purpose of this paper is to develop a process or model for comparing a new technology against an existing technology. The comparison is based on productivity, cost, and workload parameters. The parameters determine annual expected values for each technology. Differences in expected values are tested for significance. The process can help the fire manager assess the role of the new technology in local resource, fuel, and fire conditions.

THE COMPARISON MODEL

The model for comparing fire suppression technologies is presented in figure 1. The model is designed to quantify the annual efficiency of differing suppression forces against identical historical fire scenarios. Suppression forces for each technology are defined by production, effectiveness, and cost. Fire scenarios are defined by size and perimeter over time. The efficiency of each technology is determined by optimizing the dispatch of the forces to each fire scenario. This is the measure of efficiency analysis.

Workload is defined by frequency of fires described by fireline intensity level. One relationship of efficiency and workload is expected value, which is determined through a decision-tree analysis. This is the expected value analysis.

The difference in expected values is evaluated for significance by a test of the null hypothesis. The null hypothesis test supports a decision either for the current or the new technology. This is the statistical analysis of the null hypothesis.

A second relationship of efficiency as a function of workload examines those portions of the workload for which each technology is the choice. This is the workload analysis.

Although the model is generic, each step will now be explained in detail with the example of Class A foam and water.

ALTERNATIVES

A test of the null hypothesis requires the analysis of two alternatives:

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^{1.} There is no difference between the use of water and the use of foam.

^{2.} There is a difference between the use of water and the use of foam.

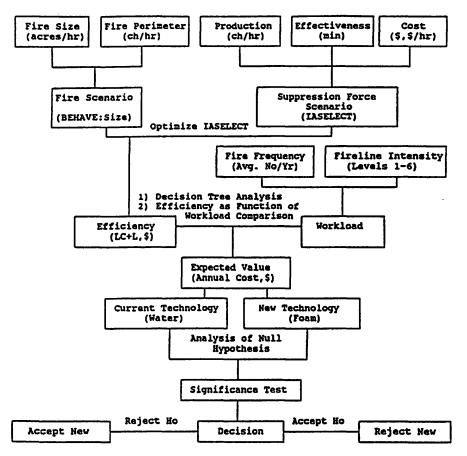


Figure 1—The fire suppression technology comparison model.

Current (water) technology in this case is a set of suppression forces modeled after a BLM district in the Great Basin. The water forces set includes 12 identical ICS type 5 water engines, two water tenders, and one type 2 bulldozer.

New (foam) technology is defined as the current technology plus or minus those characteristics that make it different from the current technology. The foam forces set includes the exact same 12 engines and their complement of tenders and bulldozer. The engines, however, have foam equipment and concentrate appropriate for Great Basin fires. Specifically, each foam engine has the least expensive automatic proportioner and enough concentrate to work one 8-hour shift. A very wet foam is made from standard water nozzles that have the same flow rate as those on the water engines.

MEASURE OF EFFICIENCY ANALYSIS

Optimizers—In this model, least cost plus resource loss (LC+L) is a measure of efficiency for a specific fire. LC+L is a function of production, effectiveness, and cost.

Computer programs such as IASELECT (Wiitala 1990) and the Initial Attack analyzer have been developed to obtain values for efficiency measures as a function of these parameters. IASELECT optimizes suppression force dispatch based on LC+L for specific fires. It is used in this model because (1) it performs the desired optimization calculations, (2) it can be narrowed in scope, and (3) it is readily adjusted.

The Suppression Forces Scenario—IASELECT requires several descriptive inputs for its analysis. Suppression forces are described as accurately as possible.

Each suppression force is assumed to be always available in the analysis to simplify the comparison and reduce the number of externalities. In reality, each suppression force is rarely available for each fire.

Suppression force effectiveness or use duration indicates how long apparatus or personnel are useful once they arrive on a fire. Use duration is how IASELECT accounts for time when a suppression force is not productive, such as an engine returning to a water source for a tank refill.

Use duration for the engines is determined by tank capacity and water flow rate. Each engine has an 850gallon tank. Each engine is assumed to flow 5 gallons per minute continuously until the tank is empty. Since this flow rate is appropriate for both water and foam on applications to Great Basin fuels, effectiveness is assumed to be equal for each technology:

> 850 gallons @ 5 gallons/minute = 170 minutes = use duration

Production rates for water engines and bulldozers are taken from the National Wildfire Coordinating Group Fire Line Handbook. Foam engine production is based on water engine production rates. Table 1-Fire growth scenario for FM1 FIL6

Ignition to containment	Fireline to be built	Area of fire
Hours	Chains	Acres
1	291	402
2	583	1,607
3	874	3,615
4	1,166	6,427
5	1,457	10,042
6	1,749	14,460
7	2,040	19,681
8	2,332	25,706

Production is a critical element of this analysis because it is a key measure of the difference between the technologies, and yet the values for water and foam are weakly supported. Water engine production rates are widely used, but their origins are no different than production rate values currently available for foam: they are best guesses.

The production rate selected for foam is from the Lakeview example described in the introduction. Foam engines were one-third more productive than accompanying water engines. This production rate is selected because it is based on fuels and flow rates similar to those in the model.

Costs are derived from district planning data for equipment and personnel costs. For simplification, each engine is assumed to be equally staffed.

Foam engine costs are identical to water engines except for the additional cost of foam-related materials. These materials include a \$2,000 automatic proportioner amortized over 10 years at \$0.14 per hour and foam concentrate used at 0.5 percent to water. The cost schedule for foam concentrate is \$14 per hour based on concentrate cost of \$9.33 per gallon. These materials are appropriate for the tactics and fuels in this model.

The Fire Growth Scenario — The suppression forces are compared by their efficiency at containing fires of historically recorded growth. Fire growth scenarios consisting of area and perimeter increase data are located from records or created from fire growth models and input into IASELECT.

Two fuel models are most common to the Great Basin BLM lands: Fire Behavior Prediction System FM 1 (FM 1), short grass, and FM 5 (FM 5), brush (2 feet). The model has been run to make the foam-water comparison in both fuel models. These two models characteristically have 1-day burning periods. Therefore, time inputs are in hours from 1 to 8. Fires are assumed to ignite in early to midafternoon. A scenario of fire growth is computed for each fire intensity level. Table 1 is one of 12 scenarios (6 FILs per Fuel Model) created for the water-foam comparison. Growth was computed from historical rate of spread records (10-year average at 50th percentile).

Selection of Least Cost + Resource Loss-

IASELECT now combines each fire growth scenario with each suppression force scenario. The analyzer will select a subset of the suppression forces to contain each fire at every possible timeframe for the smallest cost. Three additional factors affect this selection: resource value change, mop-up costs, and cost of uncontained fires. Resource value loss estimates are found in district planning data. Mop-up costs are not included in this example because mop-up is limited in FM 1 and FM 5 and mop-up is often simply a method of staging suppression forces.

Every fire may not be contained in the 8-hour timeframe. If the resources cannot achieve containment, the least cost plus resource loss of an "escaped" fire is estimated by the sum of the resource loss and cost of all equipment and personnel after 8 hours.

Table 2 summarizes the least cost plus resource loss for each fire scenario.

EXPECTED VALUE ANALYSIS

The Workload Scenario—Improvements in efficiency alone may not justify a change in the current technology. Historical records for some jurisdictions indicate low fire frequency burning about 1 acre per year x total. Does this workload demand improved suppression technology?

Workload is the annual frequency of fire intensity levels. Annual frequencies were taken from Firefamily for two fire management zones (FMAZ) in the Boise District from 1980 to 1989. FMAZ 1 is dominated by the grass fuel model; FMAZ 2 by the brush model. These are the frequencies in table 2.

Expected Value—A common technique for relating costs per event to event frequency is an expected value analysis. In this model the expected value is the total annual cost anticipated, given the least cost plus resource loss per fire (LC+L) and the fire frequency. Table 2 is arranged like a decision tree to display this analysis. Expected cost plus loss per fire (EC+L) is the LC+L times the probability of annual occurrence. Expected annual cost per fire is the sum of the EC+L. The expected value or total annual cost for all fires is the annual cost per fire times the number of fires.

In FM 1, the expected value for foam is \$761,217 less than the value for water. In FM 5, the expected value for foam is \$335,838 less than the value for water.

STATISTICAL ANALYSIS OF THE NULL HYPOTHESIS

Paired Comparison—Foam and water technologies are compared against the same fire scenario in a paired comparison. Each fire scenario provides a measure of the differences in the efficiencies of the technologies. For example, differences for LC+L by fire scenario are as shown in table 3. A paired comparison evaluated these differences. For FM 1 and FM 5, the null hypothesis can be rejected with certainty at the 99 and 98 percent levels, respectively.

WORKLOAD ANALYSIS

Workload is examined with respect to the difference in least cost plus resource loss. The difference indicates an economic advantage and advantages can be arranged to suggest when each technology is appropriate (table 4).

Table 2-Least cost	plus resource loss b	y fire intensity level

Fire scenario	Acres burned	Least cost + loss per fire	Avg. annual frequency	Prob. of occur.	Exp. cost + loss per fire	Exp. total annual cost/fire	Exp. val: total annual cost
Water							
FM1FIL1	13	\$ 192	14	0.179	\$ 34		
FM1FIL2	165	688	23	.295	203		
FM1FIL3	288	1,766	28	.359	634	\$39,226	
FM1FIL4	1,304	75,776	10	.128	9715		\$3,059,652
FM1FIL5	6,978	394,874	2	.026	10,125		
FM1FIL6*	25,706	1,444,184	1	.013	18,515		
FM5FIL1	25	192	6	.176	34		
FM5FIL2	315	2,264	10	.294	666		
FM5FIL3	485	2,752	12	.353	971	59,051	
FM5FIL4 ¹	5,574	194,365	4	.118	22,866		2,007,726
FM5FIL51	10,873	372,831	1	.029	10,966		
FM5FIL6 ¹	23,405	800,619	1	.029	23,548		
Foam							
FM1FIL1	13	192	14	.179	34		
FM1FIL2	93	639	23	.295	188		
FM1FIL3	288	1,654	28	.359	594	29,467	
FM1FIL4	733	43,595	10	.128	5,589		2,298,435
FM1FIL5	3,101	176,706	2	.026	4,531		_,,
FM1FIL6	25,706	1,445,376	ī	.013	18,530		
FM5FIL1	25	192	6	.176	34		
FM5FIL2	315	1.976	10	.294	581		
FM5FIL3	485	2,513	12	.353	887	49,173	
FM5FIL4	3,135	111,347	4	.118	13,100	,	1,671,888
FM5FIL51	10.823	373.822	1	.029	10,995		.,
FM5FIL61	23,405	801,610	1	.029	23,577		

"Escaped" fire: not contained by suppression forces in 8 hours.

This examination suggests that there are distinct fire intensities, not just fuel models, for which one technology is more appropriate than the other.

No advantage occurs when fires are small enough to be contained with a less expensive technology (the bulldozer). Foam use is economically advantageous on fires that foam suppression forces can contain in the 8-hour

Table 3-Differences for LC+L by fire scenario

Fire scenario	LC+L water	LC+L foam	Difference
		Dollars	
FM1FIL1	192	192	0
FM1FIL2	688	639	49
FM1FiL3	1,766	1,654	112
FM1FIL4	75,776	43,595	32,181
FM1FIL5	394,874	176,706	218,168
FM1FIL6	1,444,184	1,445,376	(1,192)
FM5FIL1	192	192	0
FM5FIL2	2,264	2,264	288
FM5FIL3	2,752	2,513	239
FM5FIL4	194,365	111,347	83,018
FM5FIL5	372,831	373,822	(991)
FM5FIL6	800,619	801,610	(991)

period. This is especially true of fires causing measurable resource damage (FIL 4-5 in this example) because foam use reduces acres burned. The difference in efficiency during escaped fires is equal to the difference in equipment cost between the two technologies. Water is cheaper to use when the fire cannot be contained.

SELECTION OF ALTERNATIVE

The example use of this comparison model supports the use of foam for fire suppression in FM 1 and 5. Expected values predicting annual savings in fire suppression costs of \$761,217 and \$335,838, respectively, are statistically supported by the rejection of the null hypothesis that no savings would occur.

DISCUSSION

Limitations to the model and the example used to describe it are due to simplification. Tactics, effectiveness, production rates, availability, and fire growth rates are some of the parameters that must be more accurate.

The strength of the model is its flexibility. Parameters such as production, cost, and fire size are based on the most accurate information available. Yet a resource allocation program such as IASELECT is designed to facilitate

Table 4—Workload with respect to difference in least cost plus resource loss

FM	FIL	LC+L Difference	Advantage
1	1	0	None
1	2	49	Foam
1	3	112	Foam
1	4	32,181	Foam
1	5	218,168	Foam
1	6	1,192	Water
5	1	0	None
5	2	288	Foam
5	3	239	Foam
5	4	83,018	Foam
5	5	991	Water
5	6	991	Water

changes in inputs. Fire managers can play the "What if?"game. For example, a manager may be considering the purchase of Class A foam equipment. Is this a good idea in the first place? If so, how much investment is necessary? The manager can make (at least) two comparisons using this model: the first, a comparison of water to foam priced at an entry level; the second, a comparison of water to foam priced to meet all possible fire scenarios.

Class A foam is a technology not unlike other new ideas in that we are struggling to define its role. Stories are common. Facts are not as common. When relevant data arrive, a method of sorting out if and when to use each technology will be necessary. Managers can guess what role foam has for them, but a model like the one presented can help justify their actions toward foam and water. The workload analysis suggests a decision to send water or foam to a fire could be based on fuel model and expected fire intensity. Dispatch could be prioritized to send suppression forces to fires at which they are most advantageous.

In this example of the model, the resource loss of fires with FIL 5 and 6 is more important to determining total LC+L than the increase in production foam offers. But if a manager can anticipate a majority of moderate fire intensities, then smaller fires, earlier containment, and lower costs with foam use are supported by the example.

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NEVADA LIVE FUEL MOISTURE SAMPLING PROJECT—IMPLICATIONS FOR FIRE BEHAVIOR

Marcus Schmidt

For many years it has been known that live fuel moisture is one of the important factors in determining fire potential and fire behavior. Fuels can be considered as a heat sink or a heat source depending on how much moisture the fuels contain. Because of their high moisture content, living fuels will seldom burn by themselves in their natural arrangement. Heat from burning dead fuel is needed to dry the living material sufficiently to allow it to burn and add to the heat output of the fire. Fuels typically go from one to the other over the course of a season.

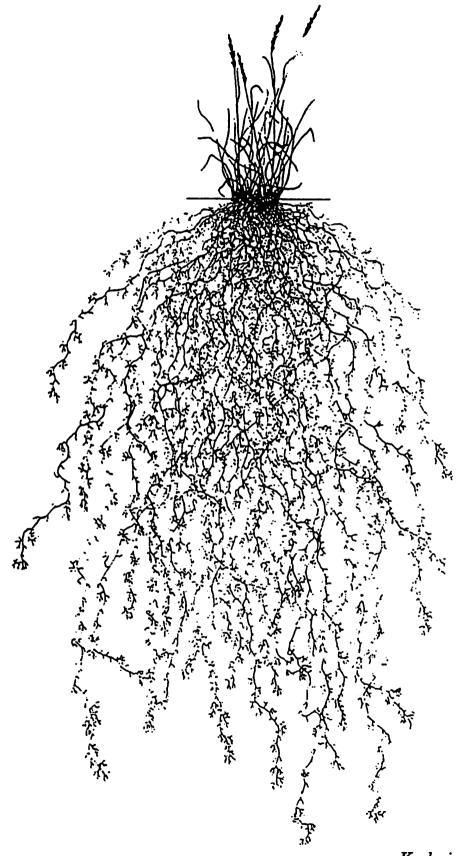
Nevada has tracked this seasonality for sagebrush live fuel moisture since 1984. There are currently 33 sites in the Great Basin. The sampling period is generally from early spring (before greenup) to late fall (when the plants become dormant). The greatest benefit to the fire manager is to visualize what their live fuel moistures are before the fire season as compared to historic data. By using the average seasonal trend line to project future fuel moisture readings, managers can determine at which time of the summer the fuel moistures will be the lowest, which could indicate the greatest fire activity. A fire behavior and tactics chart has been made using many computer runs from the Fire Behavior Prediction System—BEHAVE. This gives the firefighter information on potential fire behavior in the sagebrush fuels based on live fuel moistures taken on their own sites.

Much work has been done in Nevada to streamline the live fuel moisture determination process using many common software products. Sample disks are available for demonstration and copying.

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Ecology



Koeleria cristata

MANAGEMENT IMPLICATIONS OF YELLOW STARTHISTLE ADAPTATIONS IN THE PACIFIC NORTHWEST

Gary L. Kiemnec Michael L. McInnis

ABSTRACT

Yellow starthistle (Centaurea solstitialis) management must take into account the environmental variables that can be used to assist in control of this weed. Biological factors affecting starthistle growth are discussed with emphasis on the planting of desirable grasses to compete with starthistle. Using such a method would require a grass that can effectively compete for water by early growth and good lateral root spread. Survival characteristics of starthistle seed are also discussed.

INTRODUCTION

Plants are adapted to surviving and spreading in certain environments. A number of environmental or ecological factors that favor or restrict survival are present at any one time, to varying degrees and levels of interactions. The aboveground factors include biology, gas, and light, while soil factors include biology, nutrients, and water. Manipulation of these factors may provide for management of yellow starthistle (Centaurea solstitialis L.).

ATMOSPHERIC GAS

Atmospheric gas concentration does not change to any large degree over the growing season, and practically cannot be manipulated so as to be used as a management tool. Carbon dioxide levels are not changeable in the short term. Over the past 30 years, the atmospheric carbon dioxide level has been increasing (Miller 1990). It is unknown at this time what the long-term effect of increased carbon dioxide levels will be on weed species competitiveness.

BIOLOGY

Biological factors include insect and disease pests that will attack starthistle and also other plants that limit its competitiveness in the environment. Seed head fly (Urophora sirunaseva) has been successfully introduced into Oregon, but its ability to control starthistle has yet to be

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evaluated (Coombs and others 1987). Fungal rust (Puccinia jaceae) is being investigated as a method of control of starthistle. The spread of disease depends on climatic factors, which can vary considerably from year to year.

WATER

In arid environments water availability is a limiting factor in the successful spread of yellow starthistle. If an understanding of the water needs of yellow starthistle can be achieved, some appropriate management choices could be made in control efforts.

Competition for water may provide a means for control of yellow starthistle. Desirable grasses can create competition for water, but the soil volumes from which water is extracted by grasses and starthistle must overlap. However, in the first year, many grasses grow more in a vertical direction than in a horizontal spread (Troughton 1957), and thus do not provide for competition in the interplant area.

Initial grass establishment in an area already infested with starthistle is difficult due to the different growth characteristics of yellow starthistle compared to arid grasses. In the initial year, annuals such as yellow starthistle will have faster growth than perennials since they are trying to produce seeds while the perennials are trying to produce a greater root system. Water competition by the grasses will not be great-in fact, starthistle will be more competitive for available water in the surface soil and perhaps in the subsoil, as studies have shown starthistle to produce a long taproot (Sheley and Larson 1992).

Only after the grass stand has established will competition be effective. Given this observation, it becomes necessary to reduce the competitive edge that yellow starthistle has through application of mechanical control, for example, tillage, and/or chemical control (herbicides). Picloram (4-amino-3,5,6-trichloropicolinic acid) has been beneficial in this respect (Larson and McInnis 1989). Other herbicides such as clopyralid (3,6-dichloropicolinic acid), 2,4-D (2,4dichlorophenoxyacetic acid), dicamba (3,6-dichloro-o-anisic acid), chlorsulfuron (2-chloro-N[(4-methoxy-6-methyl-1,3,5 triazin-2-vl) aminocarbonvl]-benzenesulfonamide), and metsulfuron (methyl 2-[[[[(4-methoxy-6-methyl-1,3,5triazin-2-yl)-amino]carbonyl]amino]sulfsonyl]benzoate) can be effective but have different effects on desirable grasses (Northam and Callihan 1989).

From the foregoing discussion two grass characteristics are critical to successful grass establishment and competition against yellow starthistle: (a) fast growth rate; and (b) large root system with good lateral spread.

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NUTRIENTS

Limited experimentation with fertilizer application to help in grass establishment has shown that competition from grass has not been increased to the point where starthistle populations have been adversely affected (Larson and McInnis 1989; Prather and others 1988). Not enough work has been done to identify whether this effect is one of water and/or nutrient competition. These experiments have broadcast the fertilizer, thus providing a uniform distribution of nutrients that would benefit the starthistle to the same or greater degree compared to grasses. If starthistle root growth is faster than grass root growth, then the soil volume explored by starthistle would be greater than that of the grasses and would therefore benefit more than grass from added nutrients.

Additionally, starthistle may be more efficient than grasses at removing nutrients from the soil. If nutrients are to be added to give an advantage to grasses the nutrients should be banded with, or close to, the seed. It might be anticipated (but not proven) that uniform (broadcast) fertilizer applications on older grass stands would assist competition from grasses.

Expectations would be that, if competition is used as a control method, eradication would not be the end result. Some survival of yellow starthistle would be expected.

SOIL

The geographic spread of starthistle depends on the interaction between climate and soil factors. Whether starthistle can survive under stresses such as salt and/or water is important in determining its areal spread.

Seed germination is the first step in establishment. Research has shown that starthistle germination can take place under saline soil conditions (Larson and Kiemnec, in preparation). Seedling survival under salt stress has yet to be determined, thus establishment in saline soils is still in question. Water stress on germination can be imposed by exposure of seed to polyethylene glycol (PEG). Yellow starthistle germination can occur at stresses of -0.5 MPa. Germination differences between plumeless and plumed seed under stressed or nonstressed conditions suggest that starthistle seed may be able to survive through dispersal in time, thus making a long-time infested site especially difficult to manage. In the soil seed bank, starthistle seeds lose viability with time (Joley and others 1992; Northam and others 1989). However, some seeds can remain viable for years (Northam and others 1989). Even if seed rain can be prevented, tillage of an infested site would bring buried, viable seeds to a germinable position.

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PRISTINE VEGETATION OF THE JORDAN CRATER KIPUKAS: 1978-91

Robert R. Kindschy

ABSTRACT

During the past 14 years, information has been gathered concerning the pristine vegetation of the two major kipukas within southeastern Oregon's Jordan Crater Research Natural Area. Such information is valuable when assessing the status of vegetation on comparable sites under management. Cheatgrass is present in minor amounts in all the plant communities. Variation in abundance is apparently related to the amount of timely precipitation in a given year. Cheatgrass awaits a disturbance, which reduces the competitiveness of native perennials, to establish temporary dominance.

INTRODUCTION

Approximately two to three thousand years ago (Mehringer 1987) a major eruption of basalt lava covered 6,880 ha (16,995 acres) of sagebrush steppe near Jordan Valley in southeastern Oregon (43°10' N. latitude and 117°20' W. longitude). Unusually nonviscous lava isolated two areas of land, forming islands or kipukas. Neither site has been influenced by human activities, including grazing by livestock. As such, they provide "benchmark" information about pristine plant communities within the Owyhee Upland Province (Franklin and Dyrness 1973). The entire lava flow was declared a Research Natural Area (RNA) in June 1975 (Kindschy and Maser 1978).

The eastern kipuka is 3.5 ha (8.6 acres) in area, while the western is smaller at 1.4 ha (3.4 acres). However, the more rugged west kipuka has a greater variety of habitats and, consequently, greater plant species richness. Elevations are similar, 1,335 m (4,380 ft) at the west kipuka and 1,274 m (4,180 ft) at the eastern. Soils differ between the kipukas (table 1).

METHODS

Both kipukas are accessible only by helicopter or by rather arduous hiking across the lavas. Each was visited on an irregular basis throughout the past 14 years of monitoring. Plant production was determined using standard plot clip and weight techniques with conversion to air dry weights employed. Line intercept transects were randomly run to measure frequency and density by plant species and land barren of vegetation. Foliar cover of sagebrush was determined using the variable plot method (Cooper

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. Robert R. Kindschy is a biologist with the Bureau of Land Management in Vale, OR 97918. 1957). Cryptogam frequency was measured both by line intercept and by systematic points taken at 1.5-m intervals.

Sagebrush height was directly measured on all plants within belt transects. Age class characterization of sagebrush was by consensus of three range scientists. Decadent plants exhibited >50 percent dead material.

Soils were described in 1983 by soil scientists Daniel E. Brown and James A. Pomerening, Bureau of Land Management, U.S. Department of the Interior.

RESULTS

Vegetative cover in rangeland communities is always of interest to biologists. In 1991, the east kipuka exhibited 59 percent of the ground barren of vegetation; 21.4 percent of this was rock. Figure 1 shows the percentage of ground cover. Bluebunch wheatgrass (Agsp) accounted for 24.6 percent of cover. Sandberg's bluegrass (Posa) represented 3.6 percent. More significant were the forbs, *Lomatium* (5.9 percent) and *Crepis* (1.7 percent). Such palatable forbs appear to diminish under grazing pressure by livestock. Wyoming big sagebrush comprised 5.2 percent of the intercept.

Plant frequency, determined in June 1978, documented the ratio of grasses:forbs:shrubs on the east kipuka. Figure 2 illustrates this relationship. Frequency of native, perennial forbs is of interest. At 30 to 45 percent of the vegetation, forbs within this pristine environment appear to be more prevalent than on similar sites subjected to domestic livestock use.

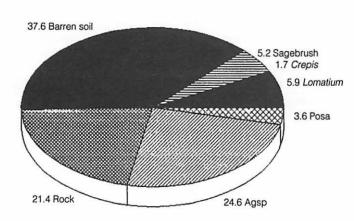
Figure 3 portrays percent composition of vegetation on the east kipuka in June 1978. Again, it is significant that the forb, *Lomatium*, comprised 25.5 percent of species. *Crepis* represented over 4 percent. Bluebunch wheatgrass (Agsp) approached half the vegetation present at 49.1 percent. Figure 4 depicts plant production during 1978. *Lomatium*, by far, was the maximum producer at 462 kg/ha. Bluebunch wheatgrass (Agsp) was second at 182 kg/ha.

Wyoming big sagebrush crown cover varied little between 1986 measurements and those of 1991 (fig. 5). The range was between 5 and 7.5 percent. Sagebrush height, which averaged 84.6 cm, was remarkably consistent (fig. 6). Of interest was the density of sagebrush by age class (fig. 7). It was apparent that this stand on the east kipuka was in trouble.

Whether this was due to the persistent drought is questionable, although stress may have contributed to the loss of older sagebrush plants. A lack of seedlings and young may be related to the competition from well-established perennial grasses and forbs. Sagebrush reproduction appears common on many grazed rangelands elsewhere in southeastern Oregon during the continuing drought.

Table 1-Summary of soils data for Jordan Crater kipukas

	East kipuka	West kipuka
Soil type	Anawalt variant (mesic) silt loam.	Old camp very gravelly silt loam.
Classification	Clayey, montomorillonetic, mesic.	Loamy-skeletal, mixed mesic.
	Lithic Xerollic Haplargid.	Lithic Xerollic Haplargid.
Parent material	Residium from Pliocene olivine basalt. Basaltic residium results in a more clayey and a less sketetal soil than the rhyolitic residium of the west kipuka.	Residium from Miocene rhyolite.
Physiography	Slopes are 1 percent to 5 percent on the crest and about 20 percent to 30 percent around the outer margin. Rimrock common around outer margin.	Slopes are 3 percent to 8 percent. The edge of the surrounding lavas is about 2 m higher than the kipuka.
Stoniness	Stones are 0.7 to 1.5 m apart on the surface (Class 3). Rock outcrop is exposed on about 2 percent of area.	Stones are 0.2 to 9 m apart (Class 2). Rhyolite pebbles cover 50 percent of soil surface. Rock outcrop exposed on 10 percent to 15 percent of area.



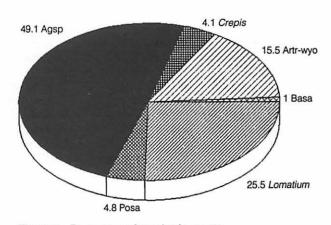
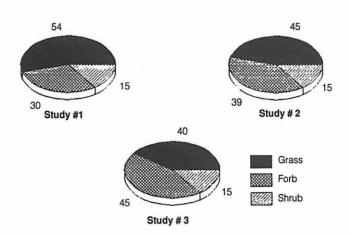


Figure 1—Ground cover percentages at east kipuka in 1991.



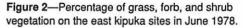


Figure 3—Percentage of species in vegetation of east kipuka, June 1978.

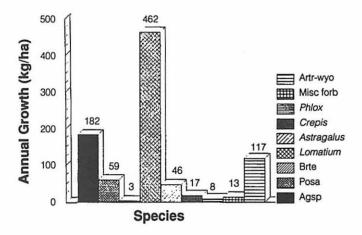


Figure 4—Annual plant growth (kg/ha) on east kipuka during 1978.

Vegetation on the west kipuka is favored by site diversity but restricted by a more-limiting soil. Interestingly, the vegetation within the Wyoming big sagebrush/ bluebunch wheatgrass community changed little between

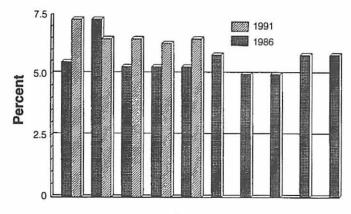
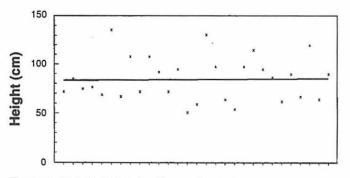
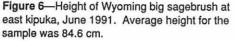


Figure 5—Wyoming big sagebrush crown cover (percent) at east kipuka, 1986 and 1991.





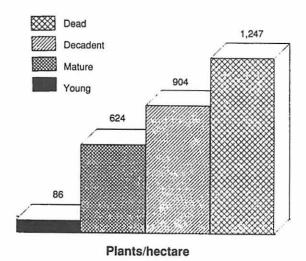


Figure 7—Density of sagebrush by age class at east kipuka, July 1991.

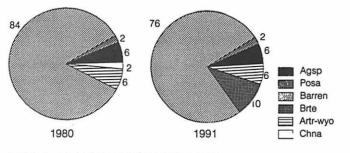


Figure 8—Transect vegetation components (percent), west kipuka, 1980 and 1991.

1980 and 1991 (fig. 8). Most significant was the increase in cheatgrass (*Bromus tectorum*) from undetected in 1980 to 10 percent of the foliar intercept in 1991. Soil previously barren of vegetation appeared to have been populated by cheatgrass. No loss in perennial grasses, forbs, or shrubs was noted. Unusually heavy spring rainfall in 1991 may have created an environment conducive to annuals, such as cheatgrass, in the interspaces between existing perennials.

Comparison of data among the various pristine communities on the west kipuka showed the differences in vegetation (fig. 9) among various communities. Frequency of occurrence data on the west kipuka illustrates the differences among the various communities (fig. 10).

Cryptogam occurrence on the west kipuka is shown in figure 11. Two samples in 1987 showed little difference between plant communities. Mosses and lichens comprised roughly 42 percent of the "hits" (frequency of occurrence) in pristine habitats. These soils were loose and fluffy.

Figure 12 illustrates the results of a study conducted during 1991 on the west kipuka. Cheatgrass was present in all the pristine plant communities, but was most abundant in the deeper soils of the basin big sagebrush site.

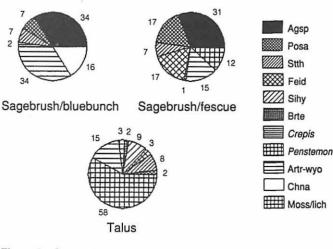


Figure 9—Canopy intercept if vegetation (percent), west kipuka, September 1980.

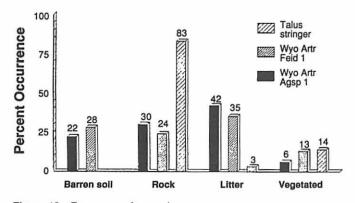


Figure 10—Frequency of ground cover occurrence (percent), west kipuka, September 1980.

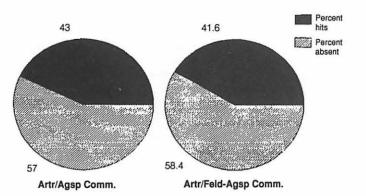


Figure 11—Frequency of moss and lichen occurrence (percent), west kipuka, 1987.

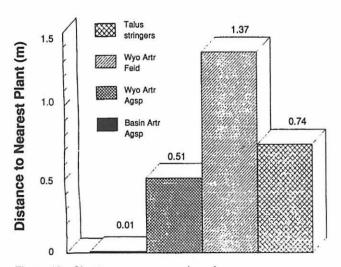


Figure 12—Cheatgrass occurrence in various plant communities, west kipuka, September 1991.

CONCLUSIONS

Pristine vegetation has been influenced through the introduction of flora from other areas over time. Such is the case with the kipukas of the Jordan Crater RNA. Cheatgrass is presently a component of the ecosystem. It will likely remain so for many millennia. Cheatgrass abundance appears to be governed by opportunity. Stress on perennial plants from drought, fire, or biological agents creates an opportunity for temporary abundance and perhaps dominance of annuals such as cheatgrass.

Future monitoring of the kipuka vegetation will determine plant species composition change. This paper documents the rather stable vegetative assemblage during the 1980's.

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MEDUSAHEAD: NATURAL SUCCESSOR TO THE CHEATGRASS TYPE IN THE NORTHERN GREAT BASIN

M. Hironaka

ABSTRACT

Medusahead (Taeniatherum asperum) has replaced cheatgrass (Bromus tectorum) and other annual grasses over extensive areas in California, Idaho, Oregon, and Washington during the past 40 years. It has low palatability, injurious and pesky awns, and completely dominates affected areas. Avoidance by livestock and resistance to rapid decomposition result in medusahead stands with thick accumulations of old growth. Wildfires are common. Recovery to preburn levels of biomass and density is achieved in a few years. One perennial-grass candidate to replace medusahead is bottlebrush squirreltail (Sitanion hystrix). Seedlings of this grass possess some needed traits to endure the stresses of annual grass competition during the first growing season.

INTRODUCTION

Medusahead (*Taeniatherum asperum*) was first reported in the Pacific Northwest near Roseburg, OR, in 1887 (Furbush 1953) and shortly thereafter in eastern Washington near Steptoe in 1901 (St. John 1937). The introduction of medusahead to the Palouse region was only a few years after cheatgrass (*Bromus tectorum*) (Mack 1981).

The spread of medusahead was not as spectacular as that of cheatgrass. In the Great Basin, medusahead was first collected near Payette, ID, in 1944 by J. F. Pechanec, about 300 miles south of G. R. Vasey's 1901 collection site (St. John 1937). After its discovery by Pechanec, it had spread rapidly in southern Idaho and adjacent Oregon. A 1957 Bureau of Land Management report indicated that more than 700,000 acres were infested with medusahead in southern Idaho (Bovey 1959). Today, a conservative estimate of infested acreage in the Intermountain region would more than double that amount.

Medusahead is a winter annual grass that has the potential of successionally replacing cheatgrass in the 11-inch and above precipitation zone in the northern Great Basin. Nearly all of the spread of medusahead has been at the expense of cheatgrass and associated bromes. The invasion has been and continues to be restricted to the higher precipitation zones of the cheatgrass type. At the drier edge of its infestation, medusahead tends to be associated with swales and heavier textured soils (Dahl and Tisdale 1975).

The appearance of mature medusahead is menacing. The long, wavy, retrosely barbed awns on the glume and seed make the seed head physically unattractive to livestock. In addition, it is of low palatability. The high silicon dioxide content is suspect for its unattractiveness, being more than 10 percent of the dry weight and probably contributes to its low palatability and slow rate of decomposition (Bovey and others 1961). The large amount of old growth because of avoidance by livestock and slow decomposition is especially conspicuous. Accumulations of several thousand pounds per acre of old growth and litter are common. The accumulation delays soil warming in the spring and retards soil surface evaporation, and contributes to shifting the competitive advantage to medusahead over cheatgrass. The slow decomposition of old growth slows nutrient cycling, especially nitrogen, and this is thought to favor medusahead (Brannon 1972) over cheatgrass. Needless to say, medusahead provides excellent ground cover.

REPLACEMENT PROCESS

The process as to how medusahead has been able to replace cheatgrass has been of great interest. The replacement process is not the same as the Russian thistlemustard-cheatgrass sequence reported by Piemeisel (1951). The growth development of cheatgrass and medusahead is lock-step from germination to resumption of shoot growth in the spring. Even the root growth activity of the two during winter is similar (Harris 1967; Hironaka 1961). After resumption of aboveground growth in the spring, cheatgrass develops much more rapidly and reaches seed maturity 10 to 20 days earlier than medusahead. This earlier maturity of cheatgrass suggests that cheatgrass would have the advantage in the lower precipitation zones, but does not explain how medusahead replaces it where moisture is sufficient for both.

After testing for allelopathic effects, which proved negative, no apparent reason for the rapid replacement of cheatgrass could be found. Though not tested with a critical experiment, it was found that the overwintering mortality of cheatgrass was consistently higher than medusahead by 5 to 10 percent. This differential in overwintering mortality, coupled with reduced seed production per unit area for cheatgrass because of fewer and smaller plants due to shared density with medusahead, rapidly favors domination by medusahead. This differential in winter mortality is believed to be the primary mode of population shift that favors medusahead.

The rapidly diminishing seed production of cheatgrass due to replacement by medusahead leads to a prolonged

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domination by medusahead, until it is successionally replaced by another species. During medusahead domination, the most noticeable thing is the accumulation of old growth and litter during the early years. However, after some years, one notices a decline and stabilization in the amount of old growth. It is speculated that the soil microbial populations gradually catch up and old-growth accumulation is greatly reduced.

The large amount of fine fuel material associated with medusahead brings with it the problem of fire. Wildfires are common occurrences, which periodically devastate large continuous blocks of rangeland in certain years. Normally, soil surface damage is minimal, and soil erosion is generally not a serious problem. Enough caryopses escape damage to produce a thinned, vigorous stand of multiculmed plants the year following fire. Within a few years stand densities approach what they were before the fire.

REPLACEMENT PROSPECTS

To control and replace medusahead with a more desired species is slow and difficult. Much of the medusahead type is on terrain that is too steep or rocky for rangeland tillage and seeding equipment. For areas where medusahead competition can be controlled and seeding is economically feasible, seeding to perennial grasses with introduced perennial grasses is recommended. For the most part, however, this is wholly impractical and other strategies must be considered.

Succession, natural and assisted, seems to be the only practical alternative. Options to effectively reduce medusahead competition directly by treatment to enhance and encourage establishment of perennials are prohibitive due to costs or legislation. For example, the use of herbicides to temporarily control medusahead might have been feasible and acceptable 20 or 30 years ago, but it is no longer an available option on public lands because of environmental concerns. Moreover, economics with respect to land value and cost of land treatment reduce the number of options available.

Establishing perennials by successional replacement might be more easily accomplished in the medusahead type than the drier cheatgrass type in the northern Great Basin. The greater amount of precipitation associated with the medusahead type means we have more latitude, ecologically speaking. In the natural replacement process each succeeding community is dominated by species individuals that have longer longevity. Perennials, once established, are difficult to dislodge, and for the species to gain dominance in the community they need only to establish individuals when the suitable conditions arise. Annuals, on the other hand, must reestablish yearly or frequently to hold their place in the community.

Harris (1967) and Harris and Goebel (1976) provided an explicit explanation as to why the native bluebunch wheatgrass (Agropyron spicatum), the climax bunchgrass that had been replaced, was not able to return in the face of cheatgrass competition. Bluebunch wheatgrass seedling roots remain inactive over winter, whereas roots of cheatgrass seedlings continue to grow, enabling cheatgrass to be competitively superior for soil moisture. Overwinter root activity of medusahead is similar to that of cheatgrass (Hironaka 1961).

SQUIRRELTAIL COMPETES

A native bunchgrass whose seedlings are able to successfully compete with medusahead is bottlebrush squirreltail (*Sitanion hystrix*), a relatively short-lived perennial (Hironaka and Sindelar 1973). Preliminary studies indicate that squirreltail seedling roots are capable of growth under low soil temperature conditions. This enables squirreltail seedlings to have root penetration as deep as the roots of medusahead and cheatgrass by the beginning of the spring season. Bluebunch wheatgrass is unable to do this (Harris 1967).

Squirreltail seedlings establish with difficulty in medusahead communities, but some are able to establish in spite of the competition. Each succeeding year, the established individuals become larger and because of their perenniality gain an additional edge on the use of resources, as well as physically depriving annuals of space. Once mature, the squirreltail plant becomes an annual seed source for the site. The gradual takeover of site by squirreltail makes for a wholly different environmental condition for seedlings of other long-lived perennials species. It is probable that site occupancy by squirreltail provides a different moisture-depletion regime than when annual grass dominance prevails, even though there may be little difference in the total amount of soil moisture utilized. The altered moisture depletion regime would improve the chances of perennial seedlings surviving in a squirreltail community, while they could not establish in medusahead- and cheatgrass-dominated communities.

Under these new conditions, it is likely that the slowdeveloping wheatgrass seedlings would have a better chance of establishing in a squirreltail community and, once established, gradually replace the squirreltail grass.

This last scenario has not been observed in the field, but with a little encouragement with seed introduction and coverage, the chance of safe site opportunities (Harper 1977) for bluebunch wheatgrass or other longlived perennial grasses would be greatly increased. With well-planned management, long-lived perennials could be inserted in squirreltail communities, and gradually they would again dominate the difficult and rugged landscapes presently dominated by medusahead.

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ECOLOGICAL RELATIONSHIPS BETWEEN YELLOW STARTHISTLE AND CHEATGRASS

Larry L. Larson Roger L. Sheley

ABSTRACT

Ecological relationships between alien annual weed species are dominated by reproduction and resource allocation strategies. The reproductive strategy of cheatgrass (Bromus tectorum) relies on a large number of plants with fewer large seeds per plant and a concentrated seed drop. In contrast, starthistle (Centaurea solstilialis) relies on fewer plants, greater seed production, and two distinct periods of seed drop. Annual fluctuations in community dynamics between these two species are largely influenced by their compatibility with annual climatic patterns.

INTRODUCTION

The loss of native perennial vegetation on extensive areas of North American rangelands has been followed by the establishment of alien annual weed populations. The grassland steppe of the Pacific Northwest and the California Annual Grasslands, once dominated by native perennial grasses such as bluebunch wheatgrass (*Pseudoroegneria spicata* [Pursh.] Love), are examples of rangelands where perennial vegetation loss has been followed by cheatgrass (*Bromus tectorum* L.) domination (Mack 1981). Rangeland ecologists are becoming increasingly concerned as yellow starthistle (*Centaurea solstitialis* L.), a more recent alien annual, has begun to occupy cheatgrass range, resulting in further land use deterioration (Hironaka 1990; Roche and Roche 1988; Sheley and others 1992).

The ecological relationships and community dynamics that permit rangeland domination by annual weeds are complex. It is generally recognized that organisms are capable of budgeting energy or resources in order to complete their life cycles successfully (Radosevich and Holt 1984). The amount, timing, and juxtaposition of photosynthate allocated to root, shoot, leaf, and reproductive effort, and the amount of time spent in dormancy, maintenance, and growth are important attributes that govern plant species success.

Differential resource capture and allocation form plant strategies and are closely linked with species survival and

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Larry L. Larson is Associate Professor and Roger L. Sheley is Graduate Research Assistant, Department of Rangeland Resources, Oregon State University, Corvallis, OR 97850. community dynamics (Harper 1977). Hironaka (1990) proposed a successional pattern for rangelands favoring occupation by species that exhibit a winter annual strategy. He suggests that community dynamics, following rangeland deterioration, would favor later maturing winter annuals that would produce greater numbers of seed and ultimately dominate the site. The objective of this paper is to describe preliminary results from life history research on yellow starthistle and cheatgrass grown in association.

LIFE HISTORY STRATEGY

The study site was located 14 km west of Walla Walla, WA. The area receives an annual precipitation of 229-305 mm and is dominated by Walla Walla silt loam soil (coarse-silty, mixed, mesic Typic Haploxeroll).

The study was initiated in June 1991 in a vegetation community dominated by cheatgrass and starthistle. Sampling occurred at 2-week intervals and was continued through two complete life cycles. The sampling strategy followed the generalized model developed by Sager and Mortimer (1976).

The soil seed bank reserve was determined by sifting and separating cheatgrass and starthistle (plumed and nonplumed) seed from 30 randomly located 686-mm³ soil samples removed from the top 80 mm of the soil profile.

Density of mature individuals was determined by counting plants in 30 randomly located 2- by 5-dm plots. Density of seedlings and established plants was determined by counting individuals in 5 percent and 50 percent of the plot area, respectively, in 20 randomly placed 2- by 5-dm plots.

Cheatgrass seed production was determined by harvesting 20 mature individuals at each plot location. Seeds were separated from the parent plants, and the seed production estimate for the plot was adjusted to reflect mature cheatgrass density. Yellow starthistle seed production was determined by calculating the average number of seedheads per plant and randomly harvesting a single seedhead from each of 10 individuals at each plot location. Seeds were separated into plumed and nonplumed categories, and the number of seeds per plot was determined.

Seed rain was estimated using wooden sticky traps (37 by 300 mm) coated with a smooth surface of lithium-based grease and placed flush on the soil surface. Forty traps were randomly placed within the study area. Seeds were counted by species and type at each 2-week visit.

Analysis of variance was performed on each set of samples. Confidence intervals were calculated at the 5 percent level of confidence. Life history data are presented on a square-meter basis.

ROOT GROWTH STRATEGY

Seeds of cheatgrass and yellow starthistle were pregerminated, and four seedlings were transplanted into circular polyvinyl chloride tubes. The tubes (800 mm in length) were filled with sterilized 'A' horizon soil from the study site and brought to field capacity. Tubes were arranged in an environmental chamber (10 °C with 12-h daylength) as a randomized complete block design with five blocks and 10 tubes for each species per block. Sampling took place 10, 14, 18, 22, 26, 30, 34, 38, 44, and 46 days after planting. Sampling consisted of extracting above- and belowground plant parts to determine depth of root penetration, root length (Comair Corp., Melbourne, Australia), aboveand belowground biomass, and leaf area (Licor-3100 with conveyer belt, Li-Cor, Inc., Lincoln, NE). Data were analyzed using the analysis of variance procedures found in SPSS/PC+ (SPSS Inc., Chicago, IL).

LIFE HISTORY STRATEGY RESULTS

The study was conducted during a drought in an area co-dominated by cheatgrass and yellow starthistle. The annual cycle for cheatgrass began with 660 mature plants/m², producing an average of 11 seeds/plant for a total of 7,000 seeds/m² (27 g) (table 1). The seed was released in July with little loss occurring between crop production and seed rain deposition. The seed rain was added to a seed bank representing 4 percent of the annual seed crop. In contrast, the starthistle population contained 180 mature plants/m², yielding an average of two seedheads or 120 seeds/plant for a total of 21,000 seeds/m² (31 g). The seed crop contained 70 percent plumed and 30 percent nonplumed seeds. The plumed seed was released in August with 30 percent loss. The nonplumed seed was released in December and had 65 percent loss. The seed rain joined a seed bank equivalent to 14 percent of the annual crop.

Seed bank reserves act as a stabilizing factor that serves to ensure species survival (Radosevich and Holt 1984). Our data suggest that starthistle contributes a greater portion of its reproductive effort into this seed pool than cheatgrass. In addition, two distinct patterns of reproductive resource allocation exist between cheatgrass and yellow starthistle. Cheatgrass produced fewer, heavier seeds (one seed type), while starthistle produced more, lighter seeds (two seed types). High seed production by starthistle may provide increased probability of successful dispersal, safe site occupation, and genotypic variation (Harper 1977). Fewer heavier seeds may provide cheatgrass with an advantage by providing sufficient reserves to become well established before it requires independent assimilation, and may allow emergence from greater soil depth (Grime and Jeffrey 1965: Harper and others 1970). Cheatgrass and starthistle have different patterns of seed release. Cheatgrass matured early, released its seed by midsummer, and had minimal seed loss. In contrast, starthistle matured later, had two periods of seed dispersal, but had greater seed loss.

Seedlings of both species emerged in November. Approximately 90 percent of the cheatgrass seed rain had produced seedlings by January. Mortality reduced the cheatgrass population to 540 mature plants/m² by late April. In comparison, 57 percent of the starthistle seed rain produced

Table 1-Summarized life	history of	cheatgrass	and starthistle
(attribute/m ²)			

Attribute	Cheatgrass	Starthistle
Mature plants	660	180
Seed production	7,000	21,000
		(15,000 plumed)
-		(6,000 nonplumed
Seed rain	7,000	13,000
		(11,000 plumed) (2,000 nonplumed
Seed bank	300	3.000
Fall seedlings	6,200	7,500
Spring seedlings	2,000	5,000
Mature plants	543	<u> </u>

seedlings by January, and by late April the established seedling count was 3,000 seedlings/m². Both species showed significant rates of mortality through the winter months. A second wave of mortality is anticipated for starthistle this spring and summer. The level of mortality will likely be determined by climatic events during that time period.

ROOT GROWTH STRATEGY RESULTS

Shoot weight, root weight, leaf area, and total root length were similar for both species, and combined means are presented (table 2). Individual T-tests at each harvest failed to show differences between species. The ability of cheatgrass to grow rapidly has been widely documented (Harris 1967; Hull 1963; Svejcar 1990). Our results suggest that starthistle shares this competitive characteristic. Hironaka (1961) found similar results comparing the later maturing medusahead with cheatgrass.

Soil depth penetration was greater for starthistle than cheatgrass (table 3). Starthistle soil depth penetration surpassed cheatgrass after 22 days and was nearly twice the

Table 2—Summary of shoot weight, root weight, leaf area, and total root length for yellow starthistle and cheatgrass

Days from planting	Shoot weight/ plant	Root weight/ plant	Leaf area/ plant	Total root length/ plant
	mg	mg	cm²	ст
10	1	т	0.3	41
14	2	1	.5	131
18	4	3	.9	257
22	8	3	1.6	317
26	13	5	3.2	437
30	28	13	5.8	970
34	45	23	9.1	1,233
38	107	42	16.6	1,652
42	143	57	22.2	2,017
46	328	138	41.3	3,858
_SD(0.05)	53	13	4.5	363

Table 3[Depth of s	oil pen	etration	(mm) by	cheat-
\$	grass and	yellow	starthis	lle root s	ystems ¹

Day	Cheatgrass	Starthistle	
10	81	93	
14	120	150	
18	114	184	
22	150	259	
26	165	324	
30	209	427	
34	265	521	
38	335	567	
42	382	715	
46	404	767	

¹LSD (0.05) for any two row means = 88.

penetration of cheatgrass at the end of the 46-day experiment. Deeper soil penetration provides niche differentiation between these species and likely contributes significantly to the later maturing characteristic of starthistle.

Deep silt loam and loam with few coarse fragments are the most common soils associated with starthistle domination (Talbott 1987). Under dry conditions, the early maturing cheatgrass would have an advantage over starthistle by utilizing moisture and completing its life cycle ahead of the later maturing species. This could limit the resources available to starthistle and thereby limit viable seed production. Hironaka (1961) proposed the same scenario for cheatgrass and the later maturing medusahead. Under moderate and wet moisture conditions, starthistle would have an advantage of continuing growth later, producing more seed than cheatgrass, distributing seed through time, and maximizing safe site occupancy.

High plant density can produce growth conditions that simulate dry conditions (Radosevich and Holt 1984). Under high-density conditions, rapid and deep soil penetration may allow the avoidance of interspecific competition and depleted soil moisture. This niche differentiation should prove advantageous for starthistle when grown in dense communities of cheatgrass. However, species plasticity is one of the more powerful density reactive mechanisms that contribute to the regulation of reproductive output by a population (Harper 1977). Thus, additional research in the area of density response needs to be conducted.

Our preliminary results suggest that cheatgrass and starthistle have evolved complex life strategies. When

these species are found in association, community dominance will be dynamic. Shifts in community dominance will fluctuate to reflect the interface of life strategies with the prevailing edaphic and climatic conditions.

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POTENTIAL INTERACTIONS BETWEEN GLOBAL CHANGE AND INTERMOUNTAIN ANNUAL GRASSLANDS

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ABSTRACT

Productivity of C3 plants apparently has risen with the increase in atmospheric CO_2 since preindustrial times, and continued increases are expected. Variation among C3 species in their relative growth responses to increasing CO_2 may cause changes in vegetation of the Intermountain West, but the extent of such variation is poorly understood. Even in the absence of variation among C3 species in response to CO_2 , interactions between CO_2 effects and characteristics associated with plant lifeform may shift competitive relationships among annual grasses, perennial grasses, and shrubs, or influence abiotic factors such as the frequency and intensity of wildfires.

INTRODUCTION

The CO₂ concentration of the atmosphere has increased by almost 30 percent since the beginning of the Industrial Age, from about 275 to 350 ppm (Keeling and others 1982). It is expected to double again in the next century, primarily because of intensive combustion of fossil fuels (Trabalka and others 1985). Ehleringer and others (1991) reviewed evidence of even wider fluctuation in atmospheric CO₂ over geologic time; CO₂ levels may have been as high as 3,000 ppm in the mid Cretaceous, about 100 million years ago, decreased to about 300 ppm in the Paleocene, and were as high as 1,000 ppm in the Eocene, 50 million years ago. For the last 160,000 years, CO₂ levels have been below today's concentration of 350 ppm, and may have been as low as 160 ppm from 20,000 to 15,000 years ago (Barnola and others 1987; Delmas and others 1980). Atmospheric CO_2 rose to about 275 ppm at the end of the last ice age, 10,000 years ago, and remained fairly constant until the anthropogenic increase began in the early 19th century (Neftel and others 1985; Stuiver and others 1984).

Continued, rapid increases in atmospheric CO_2 and other trace gases are viewed with alarm because of possible increases in temperatures of the lower atmosphere and other climatic perturbations associated with intensification of the "greenhouse effect" (Schneider 1989; Watson

Herman S. Mayeux is Range Scientist and Hyrum B. Johnson and H. Wayne Polley are Ecologists, Agricultural Research Service, U.S. Department of Agriculture, 808 East Blackland Road, Temple, TX 76502. and others 1990). Changes in temperatures and precipitation patterns could influence species composition and productivity of terrestrial plant communities (Gates 1990; Joyce and others 1990; Perry and Borchers 1990; Peters 1990), but accurately predicting the consequences of a changing climate is difficult when its theoretical cause is also the primary raw material for plant growth (Long 1991; Long and Hutchin 1991).

FUTURE EFFECTS OF INCREASING CO, ON VEGETATION

A major source of uncertainty in predicting the response of vegetation to rising levels of atmospheric CO₂ is the lack of sufficient understanding of the direct effects of increased CO₂ on plant performance and how this "CO₂ fertilization effect" will interact with possible changes in abiotic factors such as temperatures and evaporation rates (Long 1991). Recent research suggests that physiological and whole-plant processes like photosynthesis, phenological development, leaf area and biomass accumulation, and reproductive output are often accelerated or increased at the CO₂ levels expected in the next century, while respiration and transpiration rates are suppressed (Bazzaz and Fajer 1992; Bunce 1990; Idso 1989; Mooney and others 1991; Strain 1987). Other responses, such as changes in the way carbon is partitioned within the plant and morphological and phenological adjustments, may not represent immediate increases in biomass but can strongly affect ecological success (Bazzaz 1990).

Future shifts in species composition have been proposed because these effects are more strongly expressed in some plant species than in others (Patterson and Flint 1980). In general, plants with C3 metabolism (or the C3 photosynthetic pathway) are much more responsive to increased CO₂ than those with C4 metabolism at current and future CO_2 levels. C4 photosynthesis is nearly CO_2 saturated at current atmospheric concentrations, but C3 photosynthesis is not (Pearcy and Ehleringer 1984). This difference may give a competitive advantage to C3 species where the two functional groups occur together, as has been shown under controlled conditions (Carter and Peterson 1983; Johnson and others 1993; Marks and Strain 1989). In the field, elevated CO_2 increased shoot density and standing crop of a C3 grass but had no effect on two associated C4 species (Curtis and others 1989).

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EFFECTS OF INCREASING CO₂ ON CURRENT VEGETATION

Our current understanding of historic and prehistoric changes in atmospheric CO_2 levels suggests that the presettlement vegetation of the Intermountain West, as elsewhere on Earth, developed in an atmosphere with relatively low concentrations of CO_2 ; current levels are twice that of the last glaciation and 30 percent greater than they were about 200 years ago. The potential importance of this change in shaping the structure and species composition of contemporary plant communities becomes evident if the beneficial effects of additional CO_2 on plants, summarized earlier, occurred over the range of CO_2 concentrations of the past.

The assumption that the increase in CO_2 since preindustrial times selectively favored C3 over C4 plants, as has been predicted to occur with future CO_2 increases, provided the basis for our hypothesis that the 30 percent rise already experienced contributed to vegetation change, particularly the concomitant increase in abundance and density of C3 shrubs on the C4 grasslands of the American Southwest and the southern Great Plains (Johnson and others 1993; Mayeux and others 1991).

EFFECTS OF CO₂ ON VEGETATION OF THE INTERMOUNTAIN WEST

In the Intermountain West, however, the vegetation is not clearly divided into those two dominant functional groups, C3 shrubs and C4 warm-season grasses. Most Intermountain species are C3, including almost all of the dominant grasses, native and introduced. Few important C4 grasses occur, such as galletagrass (*Hilaria jamesii*) in the southern Great Basin. The genus Atriplex, including the saltbushes and shadscale (A. confertifolia), consists of C4 plants; all other shrubs are C3. Russian thistle (Salsola iberica) and halogeton (*Halogeton glomeratus*) are important C4 invaders, but others are C3.

Little is known about the response of these species to increasing CO₂. A native lovegrass (Eragrostis orcutianna) responded to elevated CO_2 to a greater extent than would be expected (Smith and others 1987). Productivity of an introduced C3 annual grass, soft chess (Bromus mollis), also increased at elevated CO₂ (Larigauderie and others 1988). Big sagebrush (Artemisia tridentata var. tridentata) may be the only Intermountain species that has been studied at subambient, ambient, and superambient CO₂ levels (Johnson and Lincoln 1990). Increasing atmospheric CO₂ from the preindustrial level of 270 ppm to the current 350 ppm increased ovendry weight of big sagebrush seedlings by 60 percent, while elevating CO_2 to 650 ppm further increased plant biomass by only 10 percent. The larger response of big sagebrush to the subambient increase supports the contention that historical increases in CO₂ may be more important than future increases in terms of direct effects on vegetation.

If increased CO_2 has played a role in the changes in species composition of vegetation observed in the Intermountain West, the positive effects of increased CO_2 on plant performance must be expressed to varying degrees

among the dominant C3 species. The extent to which plants within each of the two major metabolic groupings, C3 and C4, vary in their ability to respond to increasing CO₂ is not yet known, but limited evidence suggests that sufficient variability exists to influence species composition in natural vegetation (Johnson and others 1993). For instance, Smith and others (1987) grew three C3 grasses and one C4 grass native to the Great Basin in atmospheres with near-current (340 ppm) and future (680 ppm) CO₂ concentrations and recorded a number of physiological and whole-plant responses. All C3 species responded favorably to higher CO₂, but wide variation was observed among cheatgrass (Bromus tectorum), Indian ricegrass (Oryzopis hymenoides), and western wheatgrass (Agropyron smithii) in responses such as tillering. aboveground biomass, and root:shoot ratios. They identified the annual cheatgrass as the C3 species most responsive to CO_2 . For instance, cheatgrass was the only one of these C3 grasses in which leaf area increased in response to a doubling of CO₂.

Woody and perennial herbaceous C3 plants may also be highly responsive to additional CO_2 , but the possibility exists that inherent characteristics associated with lifeform and life history may modify the role that CO_2 effects play in vegetation change, especially in arid environments where advantageous characteristics of preadapted annuals allow them to rapidly respond to change (Young and others 1972).

We constructed a large growth chamber to test the hypothesis that increases in atmospheric CO₂ over the range experienced since the last glaciation and since the beginning of the Industrial Age have influenced plant performance, especially that of C3 annuals (Mayeux and others, in press). Plants are grown in an elongated soil container with a relatively large volume of about 12 m³, with topgrowth enclosed in an elongated, transparent polyethylene film chamber. The chamber is 38 m long, has a diameter of less than 1 m, and is enclosed in a vented glasshouse. Movement of air through the chamber creates a continuous daytime CO₂ gradient from nearcurrent ambient, 350 ppm, to below Ice Age levels, usually 150 or 200 ppm, by photosynthetic depletion. Dewpoint and dry-bulb temperatures are automatically reset to conditions within the glasshouse at five equally spaced locations along the 38-m length to reduce temperature and humidity gradients.

The annuals oats (Avena sativa) and wild mustard (Brassica kaber) were grown alone and in mixtures in the chamber from 150 to about 340 ppm to compare responses of a graminoid and a broadleafed C3 herbaceous plant to CO₂ (Polley and others 1992). Stomatal conductance of both species decreased with increasing CO₂, but decreased conductance did not prevent a linear increase in net CO₂ assimilation of 300 percent in oats and an even greater proportional increase in wild mustard. Leaf area/plant of the two species increased linearly from about 0.6 m² at 150 ppm to 1.2 and 1.8 m² at 270 and 340 ppm, respectively. Increased assimilation per unit leaf area and comparable increases in total leaf area/plant combined to cause aboveground biomass/plant of oats to increase from about 5 g at CO₂ concentrations below 200 ppm to 12 g at 270 ppm and 20 g at 340 ppm at flowering. The biomass response of mustard was almost as large.

A subsequent experiment with two cultivars of dayneutral spring wheat (*Triticum aestivum*) substantiated the magnitude of physiological and growth responses of C3 annuals to subambient increases in CO₂. The dayneutral, spring wheat cultivars 'Yaqui 54' and 'Seri 82' were grown to maturity under two watering regimes. Soil water content was restored to field capacity weekly through the duration of the 100-day experiment or watering was terminated at 50 days, during early anthesis. Under continuously well-watered conditions, total aboveground biomass of Seri M82 increased from about 300 g/m² at about 200 ppm CO₂ to 520 g/m² at 275 ppm, and to 700 g/m² at near-current CO₂ concentrations at maturity (fig. 1). Aboveground biomass of the older cultivar Yaqui 54 increased even more dramatically under well-watered

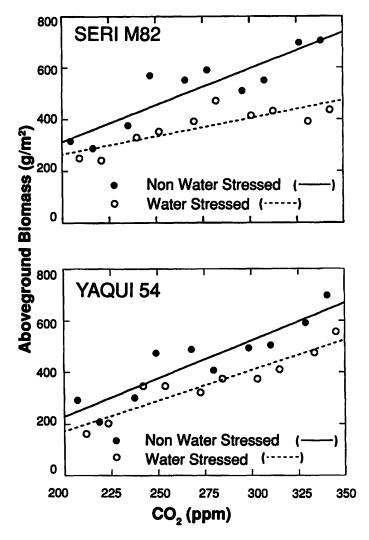


Figure 1—Total ovendry aboveground biomass of two cultivars of day-neutral spring wheat grown for 100 days along a continuous daytime CO₂ gradient from about 200 to 350 ppm in the subambient CO₂ chamber at Temple, TX.

conditions, from 220 to 660 g/m². Water stress during the last half of the growing season decreased yields of both cultivars across the range of CO_2 concentrations, and decreased the rate of biomass accumulation relative to well-watered Seri M82, but both cultivars responded positively to increasing CO_2 .

Like total aboveground biomass, grain yields of the two varieties more than doubled over the entire CO₂ gradient, and increased 50 and 54 percent as CO₂ rose from the level of 200 years ago to that of today (data not shown). Wheat used the same amount of soil water regardless of CO₂ level or yield, so water use efficiency increased proportionally with herbage and seed yields. Similar improvements in performance of other wheats (Gifford 1977: Neales and Nicholls 1978) and other C3 crops (Allen and others 1991; Baker and others 1990) have been demonstrated as CO₂ increased over subambient levels. The relative magnitude of the improvements in performance of C3 plants to increases in CO₂ representative of the Holocene or just the last 200 years is greater than that observed for C3 plants when the current CO₂ concentration is doubled, which averages about 30 percent (Kimball 1983).

Increases in the productivity of oats and wheat suggest that other annual C3 grasses may also be more productive and efficient than they were, if these annual C3 crops are acceptable models for other C3 annual grasses. This poses the possibility, relevant to recent vegetation changes on intermountain rangelands, that productivity of C3 plants like cheatgrass is increasing with CO_2 and has been since its introduction.

GLOBAL CHANGE, CHEATGRASS, AND FIRE

Ryan (1991) reviewed the relationships between climate, vegetation, and wildfire and considered in detail the possible impacts of global warming on fuel characteristics, ignition sources, weather, and other factors which influence the frequency and intensity of wildfires. He concluded that global warming may alter fire frequency and intensity by modifying several factors that control wildfire, resulting in an even greater role of fire in shaping vegetation in the future. Smith and others (1987), in considering the implications of the highly positive effects of elevated CO₂ on cheatgrass, noted that cheatgrass invasion has been associated with a possible increase in fire frequency (Young and Evans 1978) and thereby plays a role in vegetation change (Billings 1990). They concluded that "a substantial increase in productivity in Bromus under high CO₂ could exacerbate this condition and possibly increase the number and severity of wildfires in the Great Basin." These suggestions raise an important point. The effects of global change on ecosystems may not be manifested straightforwardly as differences among plants in their response to increasing CO_2 or higher temperatures, but rather indirectly as CO₂ or climate effects on abiotic factors like fire frequency and intensity.

Nonetheless, if the 30 percent increase in atmospheric CO₂ over the last 200 years has dramatically increased standing crop of C3 annuals like cheatgrass, as suggested by the results of experiments conducted in the subambient CO₂ chamber, historical increases in CO₂ may have contributed to the successful invasion by introduced annuals. Other C3 plant lifeforms also likely benefited from increased CO₂, but highly efficient dispersal mechanisms, breeding system, and other characteristics of cheatgrass relative to native perennials (Piemeisel 1951; Young and others 1972) may have interacted with CO₂ effects in ways that selectively favor cheatgrass in the current Great Basin environment. Furthermore, the suspected occurrence of more frequent and severe wildfires over recent decades (Billings 1990; Peimeisel 1951; Pickford 1932) may be attributable to more uniform and dependable fuel loads associated with increased herbaceous productivity where cheatgrass occurs because of its response to increased CO₂, in a manner similar to that described for forests in the future by Ryan (1991).

It is tempting to assume that positive responses of cheatgrass productivity to CO_2 contributed to increased fire frequency by increasing fuel loads, but an extensive comparison of fuel characteristics on Idaho's Snake River Plains indicated that total amounts of fuel per unit area decrease with increased abundance of cheatgrass, although fuel continuity was improved by cheatgrass (Whisenant 1990). Higher flammability and other physical characteristics of cheatgrass relative to native perennials may also be a factor in wildfire behavior.

Similarly, historical increases in the abundance and density of C3 woody species like big sagebrush (Arno and Gruell 1983, Branson 1985) and junipers (Juniperus sp.) (Blackburn and Tueller 1970; Burkhardt and Tisdale 1976; Christensen and Johnson 1964; Cottom and Stewart 1940) in the Great Basin could have been encouraged by the favorable effects of increased CO₂ on growth and water-use efficiency over the last two centuries (Mayeux and others 1991). Woody plants (Idso and others 1991), including conifers, are highly responsive to elevated CO₂ (Conroy and others 1990; Higginbotham and others 1985; Kaushal and others 1989), and their growth appears to have been favored by historical increases in CO₂ (Graumlich 1991; Kauppi and others 1992; Kienast and Luxmoore 1988; LaMarche and others 1984). Elevated CO₂ increased mycorrhizal density on roots of Virginia pine (Pinus echinata), enhancing nutrient acquisition and supporting additional biomass increases (O'Neill and others 1987).

A wealth of information is accumulating concerning CO_2 effects at the leaf and individual plant level, and plant species appear to vary widely in the extent and nature of their reponses to additional CO_2 (Johnson and others 1993) and climate change (Graham and Grimm 1990). Despite limitations of scale and the individualistic nature of plants' responses, we consider future effects of global change on natural vegetation by extrapolating to plant assemblages, landscapes, and even larger spatial scales (Cohn 1989; Emanuel and others 1985; Joyce and others 1990; Mayeux and others 1991; Perry and Borchers 1990; Ryan 1991; Verstraete and Schwartz 1991).

Even when the limitations are recognized, much of what we propose in terms of vegetation response to global change is speculation. The same complaint applies to our efforts to reconstruct effects of changing climate and other factors on rangeland vegetation over the recent past (Branson 1985), a period in which interpretation should be aided by a rich written and photographic record. Nonetheless, recent research strongly suggests that the direct effect of increased atmospheric CO_2 on plants is a factor not sufficiently considered in seeking the causes of historical and current changes in intermountain and other vegetation, and changes in CO_2 levels will continue to influence the structure and species composition of vegetation in the future as concentrations continue to rise.

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ASSESSMENT OF BIOLOGICAL CONTROL OF EXOTIC BROADLEAF WEEDS IN INTERMOUNTAIN RANGELANDS

Joseph P. McCaffrey Linda M. Wilson

ABSTRACT

Since 1948, more than 30 biological control agents (primarily insects) have been released against 15 noxious broadleaf weeds of intermountain rangelands in Idaho and surrounding States. Biological control of St. Johnswort (Hypericum perforatum) represents the oldest and most successful program in the region, and yellow starthistle (Centaurea solstitialis) one of the newest programs. Despite the success of biological control, annual grassland systems are prone to successive invasions by exotic, broadleaf weeds, potentially resulting in the development of a biological control treadmill. Biological control must be considered in the context of an overall vegetation management program if successful rangeland restoration is the objective.

INTRODUCTION

Since 1948, more than 30 biological control agents (primarily insects) have been released against 15 noxious broadleaf weeds of intermountain rangelands in Idaho and surrounding States (Harmon and McCaffrey 1989; PNW Weed Control Handbook 1992). Table 1 summarizes the number of agents released against nine weed species. These target weeds represent established programs with limited effort currently under way to release additional bioagents.

The St. Johnswort (goatweed) (Hypericum perforatum) program represents the oldest and one of the most successful programs. Initiated in the late 1940's to early 1950's, three agents including two leaf-feeding beetles, *Chrysolina quadrigemina* and *C. hyperici*, and a root-boring beetle, *Agrilus hyperici*, have contributed to the successful control of this weed in the Intermountain West (Campbell and McCaffrey 1991). In northern Idaho, the overall abundance of *H. perforatum* fluctuates around an amount estimated at about 3 percent of that present in 1948 (Tisdale 1976). Canyon grasslands, in particular, have experienced excellent reduction of St. Johnswort in northern Idaho. This has been largely due to *C. quadrigemina* and *A. hyperici* (Campbell and McCaffrey 1991).

Paper presented at the symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. Joseph P. McCaffrey and Linda M. Wilson are Associate Professor of Entomology and Research Assistant, respectively, Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID 83843. In British Columbia large amounts of the weed persist in cooler, moister areas dominated by *C. hyperici* (Williams 1985). The lack of control in these areas might be partially explained by the absence of *A. hyperici*. Cooler, moister areas of northern Idaho that are dominated by *C. hyperici* have *A. hyperici*, but do not have persistent St. Johnswort stands (Campbell and McCaffrey 1991).

NEW PROGRAMS

Table 2 summarizes several of the biological control programs currently "in progress," representing programs where new bioagents are being acquired and introduced. The program aimed at control of yellow starthistle (*C. solstitialis*) was initiated in the early to mid-1980's (Turner and others, in press). Five insects have been cleared for release in Idaho, Washington, Oregon, and California.

All the insects are endophytic within the capitulum, and four of the five insects are already established within the region (table 3). It will take several years for these insects to increase their populations and disperse. Given that *C. solstitialis* reproduces only by seed, it is expected that these insects will cause a significant reduction in the plant population.

SUCCESSIVE COMMUNITIES

The stability and value of successive plant communities have differed within areas following biological weed control. For example, in California the void created by St. Johnswort

Table 1-Biological control of rangeland weeds

established programs

Weed species	Number of agents established ¹
St. Johnswort (goatweed)	3 (2)
Rush skeletonweed	3
Mediterranean sage	1
Musk thistle	2
Plumeless thistle	2
Canada thistle	2 (1)
Russian thistle	1
Tansy ragwort	3
Puncturevine	2

¹Numbers in parentheses represent potential new species that might be released or "inherited" from other programs.

Table 2—Biological control of rangeland weeds active prog

Weed species	Agents established ¹	New agents		
Diffuse knapweed	4	2		
Spotted knapweed	4	3		
Yellow starthistle	3	2		
Leafy spurge	3	4		
Dalmation toadflax	1 (2)	?		
Yellow toadflax	1 (2)	?		

¹Numbers in parentheses represent bioagents not intentionally released.

Table 3—Biological control agents for yellow starthistle

Agent	Туре	Status
Bangasternus orientalis	weevil	established
Chaetorellia australis	fiy	established
Urophora siruneseva	fly	established
Eustenopus villosus	weevil	established
Larinus curtus	weevil	released in 1992

reduction was largely filled by a desirable perennial grass, Danthonia californica Bol., plus annual grasses, legumes, and forbs of varying forage value (Huffaker 1951; Huffaker and Kennett 1959). In northern Idaho, the forage species that replaced the weed have not resolved the problem of unstable plant communities. For example, Tisdale (1976) reported that St. Johnswort populations reduced by biological control were largely replaced by the same seral grasses (Bromus spp.) and forbs that were dominant prior to St. Johnswort's invasion of northern Idaho in the early 1900's.

Unfortunately, many of those replacement species were introduced annual grasses. The annual grasses provided an improvement in forage value when compared to St. Johnswort, but resulted in unstable plant communities subject to invasion by other weedy forbs and grasses (Tisdale 1976). In fact, yellow starthistle has replaced St. Johnswort as a major weedy forb in the Clearwater, Snake, and Salmon River canyons of northern Idaho (Campbell and McCaffrey 1991). This situation illustrates the importance of evaluating biological weed control within the context of a broader strategy for ensuring the establishment of stable plant communities following weed control. Otherwise, the situation may eventually result in a "biological control treadmill" where successive biological control efforts are required to deal with invasive, exotic weedy forbs following biological control of the previous invaders. As noted by Harshman (1956), the next noxious weed may not be so amenable to biological control.

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QUANTITATIVE VARIATION WITHIN AND AMONG CHEATGRASS POPULATIONS: THE ROLE OF MULTIPLE INTRODUCTIONS

Stephen J. Novak

ABSTRACT

Variation within and among populations of cheatgrass (Bromus tectorum) was determined for 35 quantitative traits. Substantial population differentiation was detected for most of the 35 traits. Phenotypic plasticity accounts for the variation seen for most of these traits. Genetic variation for these traits is usually partitioned among populations and regions. Populations from North America possessed higher levels of variation among families, suggesting the possible importance of multiple introductions in increasing quantitative variation in alien species.

INTRODUCTION

Genetic variation for individuals and populations can be described as residing at three distinct levels: DNA sequences, single-locus traits, and multilocus (quantitative) traits. Quantitative traits such as time to emergence, growth rate, time to reproduction, and fecundity are critical components of the life history of a species because they can influence the growth and persistence of the species (Dingle and Hegmann 1982). Venable (1984) states that studies of quantitative trait variation "...present an interesting bridge between the fields of ecology and evolution because they are directly interpretable ecologically as adaptation for survival and reproduction." Additionally, variation in quantitative traits can be genetically based or the result of phenotypic plasticity (Bradshaw 1965: Clausen and others 1940). Either mechanism allows a species to survive under variable environmental conditions (Lewontin 1957).

The ability to survive in a variable or novel environment is potentially made even more difficult for invading species because founder events and population bottlenecks result in a reduction in genetic variation following immigration (Barrett and Husband 1990; Barrett and Richardson 1986; Brown and Marshall 1981). The potential difficulty in avoiding extinction is accentuated for selfing-introduced species since they partition most of their genetic variability among rather than within populations (Brown 1979; Hamrick and Godt 1990; Loveless and Hamrick 1984). Cheatgrass (*Bromus tectorum*) is a highly selfing annual grass species that occurs worldwide in temperate grasslands. The native range of this species extends from the Mediterranean Basin, including northern Africa, to Tibet and southern Pakistan (Pierson and Mack 1990). Cheatgrass has been introduced into many locations and was first observed in eastern North America as early as 1790 (Muhlenberg 1793) and in the Intermountain West about 1889 (Mack 1981).

Previous results from electrophoretic analysis of cheatgrass show little genetic variation in North American populations (Novak and others 1991, also reviewed by Pyke and Novak, these proceedings). Regional differences in the distribution of allozyme variation as well as the presence of several novel allelic variants indicate this species has experienced a complex introduction history in North America. Some populations in the West appear to have resulted from the combining of genotypes following multiple introduction of different genotypes from the native range and subsequent gene flow (Novak and others, submitted). Furthermore, allozyme data suggest a higher level of population differentiation in the native range than in the introduced range. Populations from North America partition their genetic variation evenly within and among populations, most likely the result of multiple introductions (Novak and Mack, in preparation).

The objectives of this study were to determine the level and distribution of variation for quantitative traits in six native and six introduced populations of cheatgrass. I was interested in how genetic variation for these traits is partitioned within and among families and populations and among regions in this widespread selfing weed. Using a comparison of heritable variation within populations from Eurasia and North America, I asked whether there is evidence for a reduction in variation for quantitative traits due to founder effects. Alternatively, would an increase in variation in quantitative traits be detected within populations as a result of multiple introductions?

MATERIALS AND METHODS

Plant Material—Seeds from individual maternal plants (families) were collected from a total of 12 populations from the native and introduced ranges of cheatgrass (table 1). The six native populations span the Mediterranean Region: Jordan, Turkey, Yugoslavia, France, and Morocco. Populations from North America were sampled across the introduced range of cheatgrass and in several cases their locations correspond to sites at or near putative points of introduction (7, 9, 10, and 12).

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. Stephen J. Novak is a Postdoctoral Research Associate, Department of Botany, Washington State University, Pullman, WA 99164-4238.

Table 1—Populations from the native and introduced ranges of cheatgrass used in the analysis of quantitative variation

Range	Population			
Native	1. Amman, Jordan			
	2. Algada, Jordan			
	3. DeGoreme, Turkey			
	4. Cemerno, Yugoslavia			
	5. Conquerac, France			
	6. Touna Station, Morocco			
Introduced	7. Philadelphia, PA			
	8. Lexington, KY			
	9. Provo, UT			
	10. Smoot Hill, WA			
	11. Rattlesnake Springs, WA			
	12. Cache Creek, BC			

Greenhouse growouts were performed for one generation to reduce environmental effects on the expression of the traits to be measured (Roach and Wulff 1987; Schall 1984). Seeds from field-collected plants of each population were sown into wooden flats (50 by 40 by 20 cm) containing standard greenhouse potting media and placed in an unheated greenhouse. Plants were watered as needed, and the position of the flats on the greenhouse bench was rotated regularly until the plants reached maturity. Flats were rotated to minimize the effects of microclimate differences within the greenhouse on the traits being measured (Schall 1984). In the spring the mature plants were harvested and placed separately in envelopes; 10 plants were chosen at random as the families for the subsequent experiment.

In the fall of 1988, seeds from 10 families, each consisting of 10 individuals, from each of the 12 populations were individually weighed with a Cahn Instruments electrobalance to the nearest 0.001 mg. Seeds from all families and populations were randomly positioned in a grid in flats at a density of 550 seeds/m² and maintained under the same conditions described above. This sowing density is lower than plant densities usually observed in the field for cheatgrass (Mack and Pyke 1983) and was chosen to minimize intraspecific competition (Mitchell-Olds and Rutledge 1986).

Plants were scored for 35 quantitative traits (Novak 1990). In this paper I will report on a subset of these traits, including initial seed weight, time to emergence, plant height at 30-day intervals and at harvest, time to flowering (defined as the days needed for the panicle to exert through the leaf sheath), and mean seed number per plant. Plants were harvested individually, when chlorophyll pigmentation was no longer observable within the panicle, and were ovendried (70 °C) for 48 h. Plants were stored with dessicant for 48-72 h before taking morphometric measurements and dry weight readings.

Data Analysis—Analysis of variance was performed to detect trait differences among all populations and to test for family differences within each population. A nested analysis of variance was performed for all populations using the NESTED program of SAS (SAS Institute 1985) to partition total phenotypic variation within and between families, populations, and ranges. Intra-class correlation coefficients (t) were used to determine the amount of differentiation among families within each population (Zar 1974).

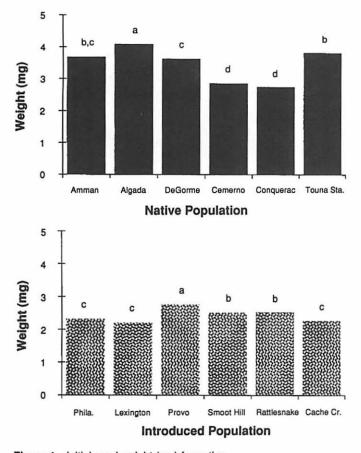
Previous electrophoretic analyses revealed that outcrossing is exceedingly rare in cheatgrass: zero in the introduced range and 0.17 percent in the native range (Novak and Mack, in preparation). Given these results, I assume complete selfing and that the progeny from all families used in this study are genetically identical full sibs. Under the assumption of full-sib families the withinfamily variance is considered to be due to the environment (phenotypic plasticity), and the total genetic variation for each trait is partitioned into the family, population, and range variance components. The proportion of genetic variation among families (PGVAF), among populations (PGVAP), and among ranges (PGVAR) is reported as a proportion of the total genetic variance (Venable and Burguez 1989). These values allow the distribution of the total genetic variance to be compared at several hierarchical levels.

RESULTS AND DISCUSSION

Phenotypic means differ among populations for all quantitative traits except percent reproductive biomass (%REPBIOM) and percent vegetative biomass (%VEG-BIOM), indicating substantial population differentiation for most of these traits (data not shown). Initial seed weight was uniformly higher in native range populations than in introduced populations (fig. 1). Of the introduced populations, Provo, UT, had the largest initial seed weight (2.76 mg), while only two populations from the native range, Cemerno, Yugoslavia (2.85 mg) and Conquerac, France (2.74 mg), possessed comparable values. The initial seed weight does not appear to influence time to emergence in the cheatgrass populations used in this study (fig. 2). In fact, there may be an inverse relationship between initial seed weight and time to emergence since the population from both the native and introduced ranges with the largest initial seed weight also possessed the longest time to emergence (Algada, Jordan, and Provo, UT, respectively).

Initial seed weight and plant height (at least at the early time intervals) does appear to possess a positive relationship. Mean plant heights at the 30-, 60-, and 90-day intervals for all populations of cheatgrass from the native range are larger than those observed for the populations from the introduced range (fig. 3). However, the mean plant height for the introduced populations at 120 days exceeds that observed for native populations. By the time of harvest, differences in plant heights between the native and introduced ranges are considerable (fig. 3). The patterns suggested by the relationship between seed weight and plant height appear to be a function of increased growth rates that are found in plants possessing large seeds. Interestingly, initial seed weight apparently has a larger influence on plant heights than on time to emergence.

Time to flowering also appears to be related to large early season plant heights and generally with initial seed weight. Populations that had the fastest growth rates in



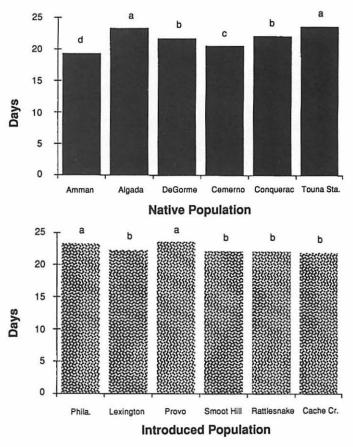


Figure 1—Initial seed weight (mg) for native (top) and introduced (bottom) populations of cheatgrass. Different letters at the top of columns indicate significant differences (P < 0.05).

consistently the first populations to initiate flowering (fig. 4). The mean time to flowering for all native populations is 95.1 days; the introduced populations initiated flowering in 103.4 days. The variation in time to flowering observed for native populations circumscribes that observed for introduced populations: the Algada, Jordan, population had the shortest time to flowering (68.54 days) while the Cemerno, Yugoslavia, population had the longest (121.87 days). Time to flowering for introduced populations ranged from 93.42 days (Rattlesnake Springs, WA) to 116.14 days (Lexington, KY).

A large amount of variation for mean seed number was observed in the populations used in this experiment (fig. 5). Introduced populations produced more seeds (41.9) than populations from the native range (38.8), suggesting that there is a benefit associated with delayed flowering. Indeed, the two populations from the native range with the longest time to flowering, DeGoreme, Turkey, and Cemerno, Yugoslavia, produced the largest number of seeds (41.5 and 63.4, respectively). The same trend generally held for the introduced populations, with the exception of the population from Lexington, KY. This population had the longest time to flowering in North America (fig. 4); however, it also produced the smallest number of seeds (fig. 5).

Different patterns emerge when these quantitative traits are compared between the native and introduced

Figure 2—Days to emergence for native (top) and introduced (bottom) populations of cheatgrass. Different letters at the top of columns indicate significant differences (P < 0.05).

cheatgrass populations. The native populations generally have larger seeds, larger plant heights in the early time intervals, shorter time to flowering, and produce fewer seeds when compared to their North American counterparts. The pattern described for native range populations

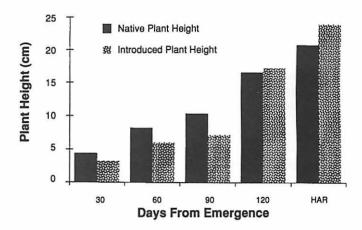
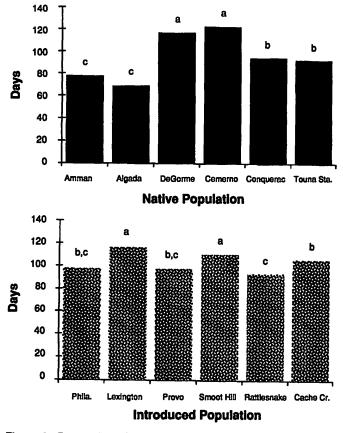
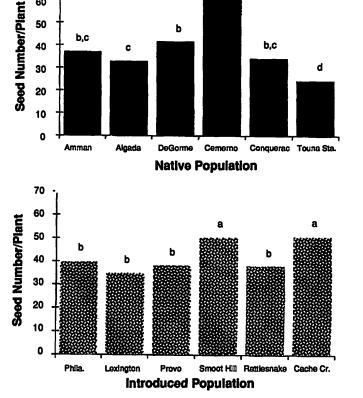


Figure 3—Plant heights (cm) for native and introduced populations of cheatgrass at 30 day intervals and at harvest.





b

a

b,c

Figure 4-Days to flowering for native (top) and introduced (bottom) populations of cheatgrass. Criteria used to define the initiating of flowering are explained in text. Different letters at the top of columns indicate significant differences (P < 0.05).

appears to be consistent with a life history adapted to extremely arid environments (Fox 1990). Plants in such environments flower quickly before the onset of summer drought, but they do so at a cost because they also produce fewer seeds. In the face of such drastic selection pressures, however, the production of even a small number of seeds ensures that these plants (and their genotypes) will be represented in the next generation.

Hierarchical Analysis—The nested ANOVA was used to partition the total phenotypic variance for all 35 quantitative traits into a hierarchical series (individuals, families, populations, and ranges) (data not shown). The range variance component accounts for differences among the native and introduced ranges for a trait, while the population component accounts for differences among populations. The within-population variation is divided into the family and individual variance components. For 30 of 35 of these traits the individual variance component accounts for most of the phenotypic variation for these traits. The individual variance component is assumed to be due to the environment and indicates that for these 30 traits most of the variation is due to phenotypic plasticity. The sum of the family, population, and range variance components comprises the total genetic variation for each trait. The total genetic variation was partitioned among families, among populations, and among regions and

Figure 5-Seed numbers in native (top) and introduced (bottom) populations of cheatgrass. Different letters at the top of columns indicate significant differences (P < 0.05).

70

60

50

40

b.c

reveals a fairly even distribution of genetic variation among these hierarchical levels (among families = 10 traits, among populations = 15 traits, and among ranges = 10 traits).

These results indicate that the majority of genetic variation for 25 of these traits is partitioned among populations and regions and suggest that genetic variation for quantitative traits in cheatgrass is distributed over an enormous geographical area (three continents). The ranges of environments and habitats from which these plants were collected are extensive and suggest that differentiation among populations and ranges may be the result of local selection. The analysis of adaptive significance for these traits is confounded because the populations were grown in the greenhouse (Venable 1984). It should be noted, however, that this was not the goal of the current study; I was interested in detecting genetic variation among and within populations and the nearly uniform greenhouse environment makes this possible (Schall 1984).

Among-Family Variance—Intraclass correlation (t) analysis was used to identify among-family differences for all 35 quantitative traits within each native and introduced population. Genetic variation within populations of selfing species is usually characterized by the amount of variation found among families of that population

Table 2—Significant intraclass correlation coefficients (t) for ea	ıch
native and introduced population of cheatgrass. A to	tal
of 35 traits were examined in each population	

Range	Population	t values	
Native	Amman	25	
	Algada	15	
	DeGoreme	20	
	Cemerno	8	
	Conquerac	14	
	Touna Station	13	
Introduced	Philadelphia	23	
	Lexington	25	
	Provo	23	
	Smoot Hill	22	
	Rattlesnake Springs	25	
	Cache Creek	19	

(Allard and others 1968). The mean number of significant t values in native populations was 16; however, there is considerable variability in the number of significant values for these populations (table 2). The population from Amman, Jordan, had the highest number of significant t values (25), while the population from Cemerno, Yugoslavia, had the lowest (8). The range of significant t values for introduced populations is much less; the highest number of significant value was detected for the Lexington, KY, population (25) and the lowest value was detected for the Cache Creek, BC, population (19). The introduced range populations (23) had a greater mean number of significant t values when compared to native populations (16).

Large amounts of within-population genetic variation (among-family differences) were detected for most of the cheatgrass populations analyzed. Considerable quantitative genetic variation has previously been reported within populations of other highly selfing plant species (Clay and Levin 1989; Iman and Allard 1965; Kannenberg and Allard 1967; Law and others 1977; Venable and Burquez 1989). There clearly are large differences in the distribution of qualitative and quantitative genetic variation within populations of selfing plants such as cheatgrass.

Equally surprising was the observation that the number of traits with significant intraclass correlation coefficients (among-family variation) was higher for populations from North America. Founder effects and genetic bottlenecks associated with the introduction and range expansion of this species would be expected to reduce genetic variation in North America (Nei and others 1975); yet the opposite was observed. The higher within-population genetic variation in North American populations compared to home range populations of cheatgrass may be the result of multiple introductions. This hypothesis attributes the observed among-family variability within populations in the introduced range to the presence of different quantitative genotypes from the native range.

These results for the distribution of quantitative genetic variation provide independent support for the conclusions obtained using starch gel electrophoresis. The distribution of quantitative and electrophoretic variation among populations was similar, and generally high. In contrast, higher than expected (for a selfing species) levels of within-population variability were detected in North American populations for both electrophoretic and quantitative traits. Both results suggest that multiple introductions can play an important role in influencing the level of genetic variation within populations of introduced plant species.

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DISTRIBUTION OF TWO EXOTIC GRASSES ON INTERMOUNTAIN RANGELANDS: STATUS IN 1992

Mike Pellant Christi Hall

ABSTRACT

Alien annual grasses have dramatically altered ecosystem functions on rangelands throughout the Intermountain area in the Western United States. Cheatgrass (Bromus tectorum) and medusahead wildrye (Taeniatherum asperum) are the primary alien grass invaders of fire altered or disturbed rangelands. In 1992, the current distribution and potential for expansion of these two grasses were delineated on maps by Bureau of Land Management resource specialists in Nevada, Oregon, Utah, Washington, and Idaho. These maps indicate that 3.3 million acres of rangeland administered by the Bureau of Land Management in those States are dominated by cheatgrass and medusahead wildrye. Additionally, another 76.1 million acres of public rangeland are classified as infested or susceptible to invasion by the two alien grasses.

INTRODUCTION

Alien annual grasses complicate the management of public rangelands in the Intermountain West. Cheatgrass and medusahead wildrye have altered ecosystem functions causing a significant increase in the frequency and extent of wildfires (Stewart and Hull 1949; Young and others 1972, 1987; Whisenant 1990). In turn, wildfires have adversely affected many resource values and are responsible for rising fire suppression and rehabilitation costs (Pellant 1990).

Although growth and physiological requirements of cheatgrass and medusahead wildrye are relatively well known, there is little information on the current and potential distribution of these two annual grasses. Consequently, resource managers are hindered in their efforts to plan and fund management actions and improve fire suppression strategies.

A brief summary of historical references pertaining to cheatgrass and medusahead wildrye distribution follows.

Cheatgrass

Cheatgrass is adapted to a wide range of habitats from salt desert shrub communities (2,000 ft elevation), which receive around 7 inches of annual precipitation, to lower elevational forests (7,000 ft elevation), which receive up to 22 inches of precipitation annually (Hull and Pehanec 1947).

Mack (1986) reported that cheatgrass was introduced into the Intermountain West in the 1880's and reached its present distribution by 1930. He included a map of cheatgrass distribution in his publication; however no acreages of cheatgrass infestation were included. A. C. Hull (1965) described a "survey" indicating that cheatgrass occurred on at least 60 million acres in 11 western states. No source of information was cited for this survey.

Several authors discuss cheatgrass distribution on a state basis. Stewart and Hull (1949) report cheatgrass to be a "dominant" species (75 to 95 percent of the herbage production) on about 4 million acres of Idaho rangeland. They described another 10 to 15 million acres of Idaho rangeland as infested with cheatgrass (trace to 20 to 25 percent of the herbage production).

Fleming and others (1942) reported "several million acres of rangeland" to be infested with cheatgrass making it one of Nevada's "predominant grasses in both abundance and distribution."

Platt and Jackman (1946) indicated that cheatgrass was introduced into Oregon around 1900 and began a rapid expansion around 1916. They stated that cheatgrass was "in command on about 10 million acres" by 1942.

Medusahead Wildrye

Medusahead wildrye was introduced into the Intermountain West from the Mediterranean area in the late 1800's and is adapted to a wide range of climatic conditions (Young and Evans 1970). It grows best on soils with a high clay content and its distribution often overlaps rangelands infested with cheatgrass.

Several references describe medusahead wildrye distribution on a state basis in the Intermountain West. Hironaka (1963) reported that medusahead wildrye spread from isolated areas to 750,000 acres in just 15 years in southern Idaho. Over 2 million acres of rangeland in Oregon are within the boundary of known infestations of medusahead wildrye (Turner and Poulton 1963). Medusahead wildrye infestations occur on 120,000 to 150,000 acres in eastern Washington (Goebel and others 1969). Young and Evans (1970) reported medusahead wildrye invading seral plant communities in northeastern California, northern Nevada, and western Utah. No acreages were reported.

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Recent surveys documenting cheatgrass and medusahead wildrye distribution and extent in the Intermountain West have not been conducted. A survey to update the status of cheatgrass and medusahead wildrye infestations in a five-state area was initiated in 1991 by the Idaho State Office of the Bureau of Land Management (BLM), U.S. Department of the Interior.

METHODS

Resource specialists at the BLM field office level identified and mapped cheatgrass and medusahead wildrye distribution on large scale maps (generally 1/100,000 acre). Acreages of infestation were then calculated from maps using the appropriate dot acreage grid. Only public lands administered by BLM are included in the survey; although it is likely that some state and private lands were inadvertently included in acreage determinations.

States included in this survey are Idaho, Oregon, Washington, Utah, and Nevada. This survey relied upon the experience and knowledge of local field personnel along with pertinent monitoring and inventory data to identify areas of cheatgrass and medusahead wildrye infestations. Criteria provided to field personnel to assist in mapping annual grass distribution are:

1. Delineate three categories of infestation based upon the species composition by weight of cheatgrass or medusahead wildrye in the plant community (fig. 1, 2, and 3). Categories are "monoculture," "understory," and "potential."

2. Exclude all units of cheatgrass and medusahead wildrye from the mapping process that are less than 5,000 acres in area.

3. Map cheatgrass and medusahead wildrye separately whenever possible.

This qualitative approach minimized the time spent by field personnel to complete the survey. However, this approach also resulted in several obvious discrepancies in



Figure 1—Area representative of the "monoculture" category of cheatgrass or medusahead wildrye infestation. Over 60 percent of the species composition by weight is composed of one or both of these annual grasses.



Figure 2—Area representative of the "understory" category of cheatgrass and/or medusahead wildrye infestation. Between 10 to 59 percent of the species composition by weight is composed of one or both of these annual grasses.



Figure 3—Area representative of the "potential" category of cheatgrass and/or medusahead wildrye infestation. Less than 10 percent of the species composition by weight is composed of one or both of these annual grasses. As shown by the cheatgrass in the background of this photo; such areas are at risk of invasion by annual grasses following disturbance.

vegetation mapping units along state and BLM district boundaries (fig. 4). Unfortunately, no reconciliation of these discrepancies were made.

RESULTS

According to this survey, 3.3 million acres of rangeland are classified as cheatgrass/medusahead wildrye monocultures; nearly 14 million acres are infested with one or both of these grasses; and 62.1 million acres are at risk of invasion by the two grasses if a disturbance occurs (table 1).

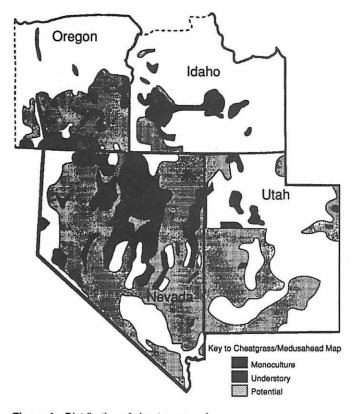


Figure 4—Distribution of cheatgrass and medusahead wildrye in the Intermountain West. Category boundaries represent broad types that include private and state land in addition to public land. Vegetation units of 5,000 acres or less are not included in this map. Original maps prepared by the field office personnel are available for inspection at the BLM's Idaho State Office.

The geographic distribution of these exotic grass infestations are portrayed graphically in figure 4. Maps for cheatgrass and medusahead wildrye distribution were not provided for Washington; therefore this State is not represented in figure 4. However, acreages of exotic grass infestation were provided for Washington and are included in tables 1 and 2.

Table 1—Cheatgrass and medusahead wildrye status on rangelands administered by BLM in Idaho, Oregon, Washington, Utah, and Nevada. Total public lands in the five-States are approximately 98 million acres

Category ¹	Acres	Public lands affected		
		Percent		
Cheatgrass:				
Monoculture (>60%)	2,908,000	3		
Understory (10-59%)	13,987,000	14		
Potential (<10%)	62,098,000	63		
Medusahead wildrye:				
Monoculture (>60%)	414,000	<1		
Total	79,407,000	>80		

¹Percent values refer to the estimated species composition by weight of cheatgrass or medusahead wildrye in the plant community.

Differences in the application of the survey criteria and inventory/monitoring data by the BLM personnel at different field offices diminishes the accuracy of this qualitative survey. The "monoculture" and "understory" values in tables 1 and 2 are generally more accurate than the values displayed in the "potential" category. Predicting the potential for alien grass invasion is more subjective and therefore more difficult, than identifying known infestations of cheatgrass and medusahead wildrye.

Acres of rangeland infested with cheatgrass and medusahead wildrye are displayed by State in table 2. The authors consider that the acreage estimated to have cheatgrass/medusahead "potential" in southern Nevada to be high. Conversely, the acreage designated as cheatgrass and medusahead "understory" in southern Idaho, especially in the southeastern portion of the State, is underestimated.

Comparison of historical reports about cheatgrass and medusahead wildrye extent and distribution with this survey is not feasible because different criteria were used (only BLM-administered rangelands were considered in this survey). However, since 80 percent of the public lands in the five States are either infested or at risk of invasion by these two alien grasses, new resource management

Table 2-	Acres of public lands either infested or at risk of infestation by cheatgrass in a
	five-State area. Medusahead wildrye (not included in this table) was identified
	as occurring on 322,560 acres in Idaho (in combination with cheatgrass) and
	as a monoculture on 92,160 acres in Oregon

State	Monoculture (>60%1)	Understory (10-59%1)	Potential (<10%1)
Idaho	1,082,880	1,751,040	1,221,120
Utah	297,600	1,082,880	11,635,200
Oregon	437,760	2,004,480	9,169,920
Washington	85,500	142,500	72,000
Nevada	1,004,000	9,006,000	40,000,000
Total	2,822,240	13,844,400	62,026,240

¹Percent values refer to the estimated species composition by weight of cheatgrass in the plant community.

strategies will be required to maintain or restore ecosystem functions and accomplish resource objectives.

SUMMARY

The qualitative nature of this survey combined with the large numbers of personnel who prepared the maps calls for caution in the uses and interpretation of this product. However, given the magnitude of the current cheatgrass and medusahead wildrye infestations and potential for future expansion in distribution and abundance, *all* resource managers in the Intermountain West should be concerned and open to proactive management and restoration strategies. If Intermountain managers do not apply proactive approaches to slow the spread of exotic weeds and break the cheatgrass-wildfire cycle; the next alien annual grass survey will paint a far more bleak picture than this survey.

ACKNOWLEDGMENTS

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EFFECTS OF SIMULATED FALL AND EARLY SPRING GRAZING ON CHEATGRASS AND PERENNIAL GRASS IN WESTERN NEVADA

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ABSTRACT

Potential effects of grazing on cheatgrass and perennial grass productivity were investigated on burned and unburned areas of a sagebrush community north of Reno, NV. Clipping was used in fall and early spring, early spring only, and late spring to simulate grazing for cheatgrass control. Cheatgrass biomass did not differ between the fall plus early spring treatment and the control over four sites with varying cheatgrass abundance over 2 years. Fall clipping increased cheatgrass production for both years. Late spring clipping had the largest reduction in both density and biomass of cheatgrass. All three treatments significantly reduced perennial grass biomass.

INTRODUCTION

Cheatgrass (Bromus tectorum L.) has invaded and become the dominant plant species on more than 41 million hectares in the Intermountain West (Mack 1981; Young and others 1987; Young and Tipton 1990), including extensive areas of western Nevada sagebrush-grass rangelands (Morrow and Stahlman 1984). In sagebrush-grass communities, cheatgrass quickly dominates on disturbed sites (Billings 1990; Young and Evans 1973) and is capable of invading undisturbed areas (Harris 1967; Hulbert 1955; Hunter 1990, 1991; Klemmedson and Smith 1964; Svejcar and Tausch 1991). Invasion by cheatgrass alters the population dynamics and fire history of sagebrush-grass communities (Klemmedson and Smith 1964; Morrow and Stahlman 1984; Stewart and Hull 1949; Young and Evans 1973; Young and others 1987). Altered fire dynamics caused by cheatgrass convert many areas from productive, perennial communities to less reliable, annual-dominated communities with increased fire management problems.

The presence of cheatgrass decreases the productivity of perennial rangeland grasses following fire (Melgoza and others 1990) or without fire (Harris 1967; Wilson and others 1966). In greenhouse experiments, production of both crested wheatgrass (Agropyron cristatum [L.] Gaertn.) and western wheatgrass (Agropyron smithii Rydb.) was significantly reduced by the presence of cheatgrass (Evans 1961; Rummell 1946). Much of this competitive ability appears related to exploitative root growth patterns in cheatgrass that deplete soil moisture down to 1.3 m (Harris 1967, 1977; Hulbert 1955; Melgoza and others 1990; Stewart and Hull 1949). However, competitive interactions with cheatgrass vary by species and by season (Cline and others 1977; Day 1975; Harris 1967, 1977). Thus, grazing at different times of the year may shift the competitive balance between cheatgrass and other species in the community.

This research investigated changes in the productivity of cheatgrass and perennial grass species in burned and unburned areas of a sagebrush community. Potential competitive interactions between cheatgrass and perennial grass species were studied utilizing three simulated grazing treatments. The three grazing periods used were selected to evaluate possible differential impacts on perennial grass and cheatgrass during different portions of the growing season.

STUDY SITE

A location on Bedell Flats, 35 km north of Reno, NV, was selected for the study. This location was stratified into four sites representing a range of cheatgrass abundance from over 50 percent of production to less than 5 percent. All four sites are within 0.5 km of each other, have the same slope and aspect, and vary in elevation by only 6 m. Soils on all four sites are fine loamy mixed mesic xerollic haplargids. Sites I, II, and III had burned at least a decade prior to the study. They are now dominated by annual grass, perennial grasses, forbs, and rabbitbrush (Chrysothamnus viscidiflorus [Hook.] Nutt.). Site IV is an unburned sagebrush (Artemisia tridentata wyomingensis Beetle) dominated community that had the lowest level of cheatgrass abundance. For convenience, we designated sites I through IV by their relative cheatgrass abundance: high, medium-high, medium-low, and low, respectively.

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EXPERIMENTAL DESIGN

Each site had nine treated and control plots; three for each treatment organized into three blocks of three paired plots each (fig. 1). Paired plots were arranged in a 3 by 3 Latin Square design to maximize dispersion on each site (Dowdy and Wearden 1983; Hulbert 1984). The treated and control plots were randomly selected within each pair. Additional treated and control areas were located adjacent to the actual plots at each site for destructive sampling. The treated area for all plots was 7 by 7 m in size. The area sampled for perennial species was 5 by 5 m in size centered within the 7- by 7-m plot; this provided a 1-m buffer strip of treatment around each sampled area.

Three simulated grazing treatments were applied: (1) late fall and early spring, (2) early spring only, and (3) late spring only. These periods were selected because they are those when cheatgrass is potentially the most sensitive to grazing pressure (DeFlon 1986). Treatments were repeated for 2 years (fall 1986 through spring 1987 and fall 1987 through spring 1988). The fall treatment was one clipping in mid to late November. Early spring treatments included three clippings from the end of March to the end of April. Late spring treatments included two clippings from the end of April to mid May and coincided with the early-boot stage of cheatgrass. Actual dates varied between years to match phenological stages as closely as possible. Perennial grass phenology was 1 to 2 weeks behind cheatgrass. All grazing treatments simulated heavy grazing.

SAMPLING METHODS

We determined total herbage production for the grasses and forbs and total leaf biomass for the shrubs by nondestructive methods. For the shrubs and perennial grasses, dimensional relationships between crown volume and leaf biomass were determined by species and by year (Freedman 1984; Ludwig and others 1975; Tausch 1989; Tausch and Tueller 1990). Plant measurements for shrub crown volume were: longest crown diameter, diameter perpendicular to the longest, and height of the foliage-bearing portion of the crown (Tausch 1989). For perennial bunchgrasses, the measurements were: longest basal diameter, diameter perpendicular to the longest, and average height of the culms (Johnson and others 1988; Tausch 1989). All measurements were in the 5- by 5-m inner area of the 7- by 7-m plots and were made during June of each year to coincide with the peak standing crop of each species.

Relationships between crown volume and leaf biomass were determined in treated and control areas that were specifically designated for destructive sampling. Twelve individual shrubs were destructively sampled for each species present at each site for each year. Eight individual bunchgrass plants were also destructively sampled from both the treated and untreated destructive sampling areas for each species present at each site for each year.

Crown volume for the shrubs was computed as one-half of an ellipsoid and for the perennial grasses as a cylinder. Nonlinear regression (Tausch 1989; Tausch and Tueller 1990) was used to determine the relationship between

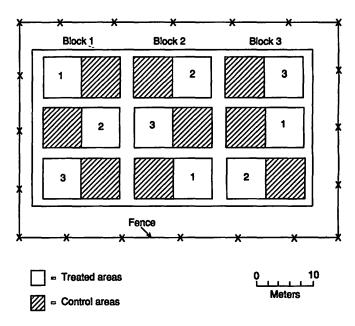


Figure 1—Experimental design for each site with three grazing treatments randomized within three blocks. Treatments are: (1) fall and early spring, (2) early spring only, and (3) late spring only.

crown volume and foliage biomass by species and by year for both treated and control situations.

The reference unit method was used for sampling cheatgrass and forbs (Andrew and others 1979, 1981; Cabral and West 1986; Kirmse and Norton 1985; Tausch and Tueller 1990). Both cheatgrass and forbs were sampled in three $1-m^2$ plots randomly located within each 5- by 5-m sample area. Calibration of the reference unit methods utilized a double sampling technique by site and year (Carpenter and West 1987) and occurred in the same destructive sampling treated and control areas used for the dimensional methods with the perennial species. Ten $1-m^2$ plots, half of them treated, were randomly located within the destructive sampling areas for double sampling at each site.

STATISTICAL ANALYSES

For the analyses in this paper, the three control plots in each block (fig. 1) were averaged to provide a balanced model of three replications for each of the treatments and for the control. For analysis of variance with the full data set, the error degrees of freedom for site and block were partitioned off prior to the determination of the significance between treatments and years (table 1). Interactions between treatment and site, treatment and year, and treatment, year, and site were also analyzed for the full model. Individual analysis of variance results by year and for each site were used to help interpret the results of the full model. Significance was determined at the 5 percent level or better for difference between treatments, between years, and for interaction between treatment and year. Table 1—Format for analysis of variance for four sites with three randomized blocks within each site and four treatments per block. Analysis parameters are the degrees of freedom (DF), sum of squares (SS), mean square (MS), and F-test (F). Significance tests are for treatment and year and interaction between treatment and site, treatment and year, and among treatment, year, and site using the cheatgrass total plot biomass results as an example

Source	DF	SS	MS	F
Site	3	2.68E+6		
Block	2	1.24E+5		
Site/Block				
(error)	6	1.35E+5		
Treatment	3	3.55E+5	1.18E+5	²24.41
Treatment/Site	9	2.38E+5	2.65E+4	¹ 4.79
Treatment/Site/Block				
(error)	24	1.33E+5	5.53E+3	
Year	1	1.86E+5	1.86E+5	²27.35
Treatment/Year	3	3.55E+4	1.18E+4	1.74
Treatment/Year/Site	12	4.95E+5	4.12E+4	² 6.05
Treatment/Year/Site/				
Block (error)	32	2.18E+5	6.82E+3	
¹ <i>P</i> ≤0.01.				

²P≤0.001.

RESULTS

The 1986-87 and 1987-88 winters represented drought years with 1988 drier than 1987 (fig. 2). The lack of fall precipitation in 1986 resulted in no fall germination of cheatgrass. Spring 1987 germination occurred in late February and early March. Fall rains in 1987 allowed fall germination of cheatgrass, and most new plants survived the winter despite the general lack of snow. Spring rains in March and April 1988 provided moisture for growth of the cheatgrass that germinated the previous fall.

Three species of shrubs and five species of perennial grasses were common on one or more of the four sites (table 2). One bush of smooth horsebrush (*Tetradymia glabrata* Gray) was also found in one plot of site III. Squirreltail and two species of *Stipa* were the most common bunchgrasses. One rhizomatous perennial, western wheatgrass, was present in some plots where it was sampled by the reference unit method (table 3). In addition to cheatgrass, tansy mustard (*Descurainia pinnata* [Walt.] Britt.) was a common annual (table 3).

Because analyses showed that individual bunchgrass species had similar responses to treatment, we present the results as a group to reduce repetition. Allometric relationships for bunchgrasses were found to be uniform within control areas over all four sites within each year. The same was true within treated areas. Dimensional relationships differed between treated and control areas as a result of the clipping. Shrub dimensional relationships were similar among sites and between treated and control plots within each year. Dimensional equations for the prediction of shrub and perennial grass biomass (table 2) were comparable to the results of Tausch (1989), Tausch and Tueller (1990), and Johnson and others (1988). The percent errors for our double sampling validation of the reference unit estimations (table 3) were comparable to the percent errors of Carpenter and West (1987).

The total leaf biomass values for cheatgrass, annual forbs, perennial forbs, perennial grass, and shrubs were averaged for the control plots within each site by year (fig. 3). Although total leaf biomass for each site declined from 1987 to 1988, reflecting the lower precipitation in 1988, the relative proportion of total leaf biomass at each site that was represented by cheatgrass was similar in both years.

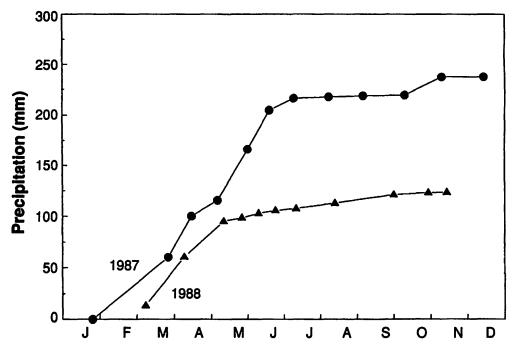


Figure 2-Precipitation for the 2 study years at the Bedell Flat study location.

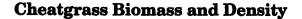
Table 2—Species sampled by dimensional methods and the results of nonlinear regression analysis (r²) and Standard Error of the Estimate (SEE) for the combined data from four Bedell Flat study sites for 2 years

		1987			1988				
	T	Treated		Untreated		Treated		Untreated	
Species	r ²	SEE(g)	r ²	SEE(g)	r ²	SEE(g)	r ²	SEE(g)	
Shrubs									
Artemisia tridentata wyomingens	sis ¹ *	•	0.81	35.31	٠	٠	0.92	14.15	
Chrysothamnus viscidiflorus	*	*	.72	15.09	٠	*	.88	12.91	
Leptodactylon pungens	٠	•	.74	3.15	•	٠	.81	5.10	
Perennial grass									
Agropyron cristatum	0.79	0.637	.92	2.32	0.50	0.925	.79	2.94	
Oryzopsis hymenoides	.53	1.44	.65	6.12	.53	1.23	.59	2.28	
Sitanion hystrix	.72	.311	.76	3.36	.80	.567	.73	2.25	
Stipa species comata + thurberiana	.62	.610	.82	2.11	.91	.717	.74	1.09	

¹Shrubs did not receive the clipping treatment.

Table 3—Species receiving double sampling analysis and their estimated average relative percent error for reference unit method sampling of plant biomass (g/m²). Data from five 1-m² treated and untreated sacrifice plots were averaged over the four Bedell Flat study sites for each of 2 years

	Relative percent error					
		1987	19	88		
Species	Treated	Untreated	Treated	Untreated		
Perennial grass Agropyron smithii	41.18	24.17	13.06	26.34		
Annual grass						
Bromus tectorum	17.20	27.82	22.62	22.85		
Perennial forbs						
Astragalus lentiginosus	40.02	41.71	21.19	32.90		
Lupinus caudatus			18.29	22.02		
Phlox longifolia			12.67	13.89		
Annual forbs						
Descurainia pinnata	24.99	45.14	29.44	39.14		
Erodium cicutarium	38.83	20.20	9.61	38.48		
Lygodesmia spinosa	55.47	46.23	28.28	38.82		



The average total biomass of cheatgrass from the site with the highest cheatgrass abundance was nearly twice the biomass of the medium-high site, over three times that of the medium-low site, and over ten times the biomass of the low abundance site (table 4). Average plant biomass per individual cheatgrass plant was highest on the medium-high site and lowest on the low site. Density followed the same trend as the total plot biomass.

Total leaf biomass of cheatgrass per plot differed significantly between treatments (tables 1 and 5) and years (table 6). The fall plus early spring treatment biomass was larger than that of the control, but not significantly. However, the early spring only and late spring treatment biomass levels were significantly different from each other and significantly less than both the control and the combined

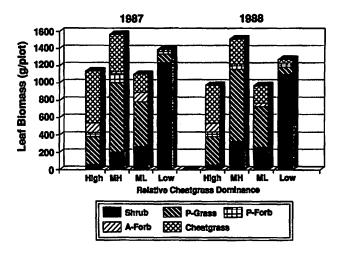


Figure 3—Comparison of total leaf biomass for the control plots for each study year, averaged over four sites of varying cheatgrass abundance. Cheatgrass is compared with similarly pooled data for the species groups of shrubs, perennial grass, perennial forbs and annual forbs.

fall and early spring treatment levels (table 5). Total cheatgrass biomass was reduced by almost a third in the drier year of 1988 (table 6).

Interaction between treatment and site for cheatgrass plot biomass was significant. This resulted from a decrease in the differences between treated and control plots as cheatgrass presence declined from the high to low abundance sites. On the low abundance site, only the difference between the control and the late spring treatment was significant. The three-way interaction of treatment, site, and year resulted from the above differences, plus an overall larger reduction in cheatgrass plot biomass in the treated plots relative to the control plots in the drier year of 1988.

Average biomass per individual cheatgrass plant was significantly different between treatments (table 5) and years (table 6). Average plant size for cheatgrass from the late spring treatment significantly differed from that of the

Table 4—Means of total biomass per plot and average biomass per plant for cheatgrass and perenn	ial
grass, and density for cheatgrass and perennial grass on four sites with a range of cheatgr	ass
abundance	

	Relative cheatgrass abundance by site			
	High	Medium-high	Medium-low	Low
Cheatgrass				
Plot biomass (g/25 m ²)	492.7	273.4	174.7	33.88
Plant biomass (g)	0.0954	0.1349	0.0710	0.0461
Density (No./m ²)	449.1	323.2	264.3	44.51
Perennial grass				
Plot biomass (g/25 m ²)	129.9	340.5	251.1	43.54
Plant biomass (g)	2.055	3.064	2.927	1.774
Density (No./25 m ²)	64.32	106.9	91.67	23.65

Table 5—Means¹ of total biomass per plot and average biomass per plant for cheatgrass and perennial grass, and density for cheatgrass and perennial grass from analysis of variance (table 4) for four treatments

	Treatment			
	Control	Fall+early spring	Early spring	Late spring
Cheatgrass				
Plot biomass (g/25 m ²)	281.1	310.2	233.8	149.5
Plant biomass (g)	0.103	0.0984 _{ab}	0.0807 _{ab}	0.0650
Density (No./m ²)	291.9 _a "	326.2 _a	278.6 _a	184.4 _b ັ
Perennial grass				
Plot biomass (g/25 m ²)	427.9	103.9	110.0 _b	123.2
Plant biomass (g)	5.6 0 1	1.322	1.516	1.382
Density (No./25 m ²)	71.34	68.38	73.29	73.50

¹Means in each row with the same letter are not significantly different by LSD analysis at the $P \le 0.05$ level of significance.

Table 6-Means ¹ of total biomass per plot and average biomass p	Ðľ
plant for cheatgrass and perennial grass, and density for	•
cheatgrass and perennial grass from analysis of variance	Ð
(table 4) for 2 years	

	Year		
	1987	1988	
Cheatgrass			
Plot biomass (g/25 m ²)	287.7	199.6 _b	
Plant biomass (g)	0.153	0.0204	
Density (No./m ²)	69.86 _a	470.7 _b	
Perennial grass			
Plot biomass (g/25 m ²)	183.7	198.8	
Plant biomass (g)	2.57	2.34	
Density (No./25 m ²)	69.97	73.28 <mark>,</mark>	

¹Means in each row with the same letter are not significantly different by LSD analysis at the $P \le 0.05$ level of significance.

control plots, but not the other two treatments (table 5). Average plant biomass in 1988 was almost one-eighth that of 1987 (table 6). The interactions between treatment and both site and year were not significant, but the three-way interaction among them was significant. This resulted from the control and combined fall and early spring treatments being significantly different from the other two treatments on the high cheatgrass abundance site.

Cheatgrass density also significantly differed between treatments (table 5) and years (table 6). Cheatgrass density significantly differed only between the control and the late spring treatment. Cheatgrass density significantly differed between years with the density much higher in the drier year of 1988 (table 5). Only the interaction between treatment and year was significant because the differences between the late spring and the control treatments were significant only in 1988.

Perennial Grass Biomass and Density

Total plot biomass for perennial grass was highest on the medium-high cheatgrass abundance site, followed by the medium-low site, the high site, and finally the low site (table 4). Average plant biomass and density for perennial grass both followed the same trends over the sites as the total plot biomass.

Perennial grass plot biomass significantly differed among treatments (table 5), but not between years (table 6). Perennial grasses consistently had significantly less total foliage biomass in the treated than in the control plots. The late spring treatment had slightly higher perennial grass foliage biomass than the other two treatments. Only the interaction between treatment and year was significant. Differences between the control and all three treated plots were greater in 1987 than in 1988, although significant in both years.

Average leaf biomass per plant for perennial grass significantly differed among treatments (table 5), but not between years (table 6). Perennial grass consistently had significantly less average plant biomass in the treated than in the control plots (table 5). The early spring treatment had the highest average plant foliage biomass of the three treatments. Significant interaction again occurred only between treatment and year for the same reasons as for the total plot biomass interaction.

Perennial grass density for the full model significantly differed only between years (table 6), but not between treatments (table 5). Only the three-way interaction among treatment, site, and year was significant. This resulted primarily from an increase in density of crested wheatgrass on the medium-high and medium-low cheatgrass abundance sites in 1988. Unlike the total and average plant biomass analyses, there were some density response differences among the perennial grass species. The combined fall and early spring treatment significantly reduced crested wheatgrass density compared to the other two treatments. Both the *Stipa* species and crested wheatgrass increased overall, and squirreltail decreased, in density in 1988 compared to 1987. The squirreltail density decrease was the greatest on the high cheatgrass abundance site.

Shrubs were not clipped and only small, nonsignificant changes occurred between treatments or years over the period of the study.

DISCUSSION

Late spring clipping (early boot stage) consistently had the largest negative impact on both total foliage biomass and density of cheatgrass. This treatment also had a slightly less negative impact on the total biomass of the perennial grass species. Removal of fall regrowth on the perennial grasses by late fall clipping consistently boosted the production of cheatgrass over all sites and over both years of data. Fall clipping apparently reduced the ability of perennial plants to compete with cheatgrass the next spring, even in the presence of the early spring clipping treatment. This reduced competitive ability occurred both when cheatgrass germinated in the spring and in the previous fall. A similar negative impact of mowing on perennial grass growth was observed on a nearby site by Young and Evans (1978).

The reduction of the total biomass of the perennial grasses by the three treatments was less in 1988 compared to 1987. The reverse was true for cheatgrass plot biomass. Density for the perennial grasses also increased in 1988 primarily from recruitment of new, small crested wheatgrass plants in 1988. The 2 years were substantially different in the average biomass and density of cheatgrass plants. Even though the much smaller cheatgrass plant size in 1988 was compensated for by a much higher density in 1988, the 1987 total leaf biomass was still only just over two-thirds of the 1988 level. The greater suppression of cheatgrass by the treatments, compared to perennial grass, in 1988 than in 1987 may indicate cheatgrass control by grazing is possible. Additional studies of this type over longer periods of time will be needed to verify this possibility.

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PATTERNS OF ANNUAL GRASS DOMINANCE ON ANAHO ISLAND: IMPLICATIONS FOR GREAT BASIN VEGETATION MANAGEMENT

Robin J. Tausch Tony Svejcar J. Wayne Burkhardt

ABSTRACT

Anaho Island National Wildlife Refuge, northeast of Reno, NV, is dominated by annuals despite a general absence of human-caused disturbance and fire. Four species of annual grass dominate areas that are segregated by elevation, aspect, and slope. A previous study and aerial photographs show annual grasses were present throughout the island well before the early 1960's and beginning to dominate in scattered areas by the early 1970's. By the early 1980's areas where annual grasses had replaced perennials were larger in size, and by 1991 covered about a third of the vegetated areas.

INTRODUCTION

In a previous paper Svejcar and Tausch (1991) reported on the dominance of annual invader species on the Anaho Island National Wildlife Refuge. Anaho Island is located in Pyramid Lake northeast of Reno, NV. It is currently about 200 ha in size and is the largest island in Pyramid Lake. Pyramid Lake is one of three remnants of the former pluvial Lake Lahontan. The island was established as a wildlife refuge in 1913 to protect breeding populations of primarily pelicans but also cormorants and California gulls. Anaho Island has a long history of minimal disturbance by humans.

The only resident mammal on the island is the deer mouse, and the primary predator is the Great Basin rattlesnake (Woodbury 1966). There are reports of limited attempts to use the island for raising sheep, goats, and pigs, but such attempts ended early in the 19th century (Henry 1990; Janik and Anglin 1991). The island has been under protection for nearly 80 years. Visitors to the island are accompanied by U.S. Department of the Interior Fish and Wildlife Service personnel. As a result, vegetation competition on the island for the last several decades has existed in the absence of significant mammalian herbivory or human disturbance.

Cheatgrass (Bromus tectorum L.) was introduced to North America in the late 1800's, reached a stasis in its expansion by the 1930's (Mack 1986), and may have reached Anaho Island during this period. Later, red brome (B. rubens L.) probably followed a similar but less well-documented establishment pattern. Despite the absence of herbivory or human disturbance on Anaho Island, the presence and dominance of cheatgrass and red brome are similar to that observed for other areas in the Great Basin (Billings 1990; Young and others 1987). More recently the ranges of both species have again been expanding (Hunter 1990; Young and Tipton 1990). Recent vegetation trends on the island (Svejcar and Tausch 1991) appear similar to the increasing occurrence of these species and increasing dominance of red brome in other disturbed and undisturbed communities (Hunter 1991) over the last two decades.

In a Master's thesis done on the island in the early 1960's Woodbury (1966) reported red brome to be present on less than half of the island. On most of the areas where he found red brome, it was not the dominant in the herbaceous layer. Svejcar and Tausch (1991) observed that large areas where Woodbury (1966) listed cheatgrass as dominant and red brome as absent were red brome dominated. The possible climatic, genetic, and competitive processes behind these patterns of change on Anaho Island, and throughout the Great Basin, have significant implications for management (Baker 1986; Bazzaz 1986; Roberts 1991).

This paper used aerial photography for a more detailed look at the 1991 distributions of annual grass species and the patterns of perennial plant replacement over the island. We have also used a series of aerial photographs of the island dating from 1954 to 1991 to estimate possible patterns and rates of change from perennial to annual dominance.

STUDY SITE

Anaho Island rises to 1,334 m above sea level and about 180 m above the level of Pyramid Lake (fig. 1). Over half the current area of the island has been exposed since 1911 when Derby Dam was constructed upstream of the Truckee River to divert water to the Fallon area for irrigation. Prior to the construction of Derby Dam, Pyramid Lake was at the level of Mud Slough where it overflowed into the Winnemucca Lake Basin to the east. The area of Anaho Island above this level is about 90 ha in size and is

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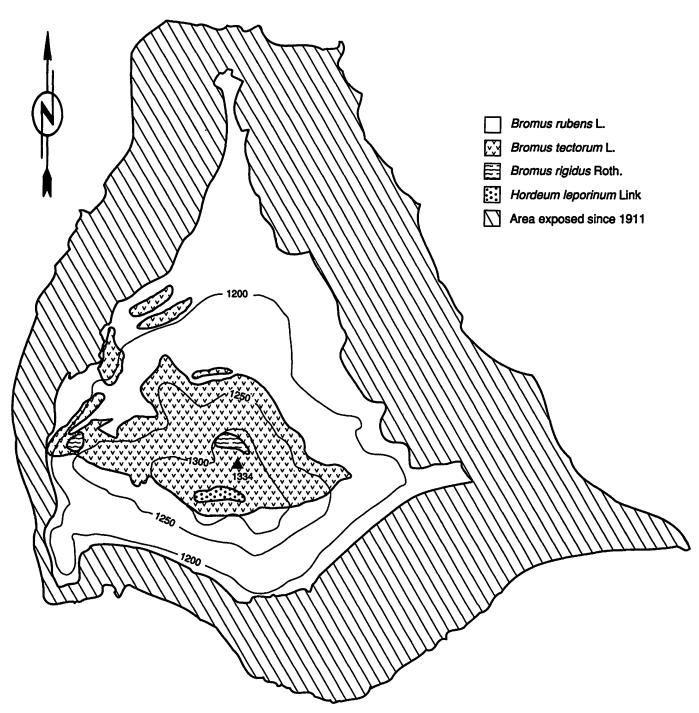


Figure 1----Map of Anaho Island showing locations where four annual grasses dominate the forb layer.

the subject of this paper. The area below the 19th century shoreline also has some interesting vegetation dynamics of colonization and community development, but these will not be discussed here.

Anaho Island receives 12 to 18 cm precipitation annually. Native vegetation is composed of plant species common to the salt-desert shrub zone throughout the Great Basin. The four species of annual grass found on Anaho Island are cheatgrass, red brome, rip-gut brome (*B. rigidus* Roth), and annual foxtail (*Hordeum leporinum* Link). All four species were present when Woodbury (1966) studied the island and in 1991 each dominated the herbaceous layer on different parts of the island.

METHODS

Two types of aerial photographs were used to map the patterns of annual grass dominance on Anaho Island. First, a 1:24,000 vertical color infrared aerial photograph taken in July 1991 was enlarged, and second a series of oblique color aerial photos were taken in December 1991. Both types of photos were used to estimate the distribution and relative dominance of annual grasses and dominant perennial species. These comparisons were confined to the area of the island above the 19th century water line (fig. 1) and excluded rock outcrops and pelican rookery areas.

The aerial photographs were first used to map the distributions of dominance by the four species of annual grass. Field reconnaissance was used to verify the mapped distributions. The photographs were then used to divide the vegetation into three cover types. These cover type designations were also verified with field reconnaissance. The first cover type is areas where we estimated the dominant perennial cover to have a consistent distribution or presence on twothirds or more of the area. Gaps in the perennial cover from one to a few dead individuals for this first cover type were estimated to total less than one-third of the area.

The second cover type is areas where the dominant perennial cover had a consistent distribution or presence on less than one-third of the area. In these areas perennials occurred as scattered individuals with annual species the only cover on over two-thirds or more of the area. The third cover type is the remaining area that was estimated to be between the first two categories.

Aerial photographs from various sources for 1954, 1956, 1970, 1971, 1973, 1980, and 1991 were used to estimate the pattern over time of the conversion of island vegetation to dominance by annuals. These included black-and-white, color, and color infrared types. Quality and scale varied considerably among the photos, and none was equal to the quality or resolution of the 1991 photographs. Because of the limited quality of these photographs, and the small size and scattered nature of areas showing loss of perennials, they were not useful for mapping.

ANNUAL GRASS DISTRIBUTION

In 1991 annuals grew on all parts of the island. Red brome was the dominant herbaceous species on about 44 ha (60 percent) of the area above the 19th century water line, other than rock outcrop (fig. 1). It was dominant on areas where Woodbury (1966) indicated cheatgrass to be dominant and red brome to be absent. Red brome dominated most of the southerly aspects and lower elevation areas of the island.

Cheatgrass was the dominant herbaceous species on about 25 ha or over 35 percent of the area (fig. 1). Cheatgrass dominance was largely confined to the upper elevation and northerly aspects of the island. Where dominant on lower elevations, cheatgrass was on steeper northerly facing slopes of beach terraces. Filaree (*Erodium cicutarium* [L.] L'Her) and barbwire Russian-thistle (*Salsola paulsenii* Litv.) were also common throughout the island on both red brome- and cheatgrass-dominated areas.

Together, annual foxtail and rip-gut brome occupied slightly over 1 percent of the area (fig. 1). The annual foxtail-dominated area was located on a level area near the top of the island. This area was reported by Woodbury (1966) as the possible location of a pelican rookery earlier in this century. The two rip-gut brome locations were both on sites adjacent to large tufa-covered rock outcrops that may increase effective site moisture.

ANNUAL GRASS DOMINANCE PATTERNS

Rock outcrops comprised about 20 ha or 22 percent of the total area above the 19th century water line (fig. 2). Active pelican rookeries covered about 6 ha or 7 percent of the same area.

Areas where the dominant perennials were estimated to have two-thirds or more of their original cover represented about 13 ha or 18 percent of the nonrock outcrop area above the 19th century water line (fig. 2). The most common community in this type was mixed desert shrub with shadscale (Atriplex confertifolia [Torr. & Frem.] Wats.), spiny hopsage (Grayia spinosa [Hook.] Moq.), rubber rabbitbrush (Chrysothamnus nauseosus [Pallas] Britt.), bud sagebrush (Artemisia spinescens D.C. Eaton), and winterfat (Ceratoides lanata [Pursh] J. T. Howell). Communities of pure stands of four-wing saltbush (Atriplex canescens [Pursh] Nutt.) and winterfat also were recorded. Even in these communities a dense understory of annuals was evident.

The areas where the dominant perennial cover had a consistent distribution or presence on less than one-third of the area covered 21 ha or about 30 percent of the nonrock outcrop area (fig. 2). In these areas perennials occurred as scattered individuals with annual species the only cover on over two-thirds of the area. This cover type was most common on the southerly and lower elevation areas of the island but occurred on all aspects and elevations. The loss of perennials has not been confined to shrub-dominated communities. A former desert needlegrass (*Stipa speciosa* Trin. & Rupr.)-dominated community on the west side of the island has been largely replaced by red brome.

The remaining cover type where dominant perennials covered between one-third and two-thirds of the area was approximately 36 ha (fig. 2), or about 51 percent of the nonrock outcrop area of the island above the 19th century water line. Throughout the island existing perennial vegetation, both shrubs and grasses, was composed mostly of mature to decadent plants. Perennial seedlings or juveniles were largely absent. The reduction in perennial dominance, combined with the absence of herbivory on the island, has resulted in robust growth by some individuals of the remaining perennials.

CHANGES OVER TIME

The series of 1954 to 1991 aerial photographs of the island (not shown) allowed a general estimation of the possible patterns and rates of conversion from perennials to annuals. Because the quality of the photographs prior to 1991 was not sufficient for mapping, direct estimation of the areas involved was not possible.

Pictures of Anaho in the thesis by Woodbury (1966) showed annual grasses to be prevalent in the understory in the early 1960's. From the 1954 through to the 1973 aerial photographs the perennial cover appeared generally uniform. Areas that appeared to be annual dominated were small and scattered and more frequent on the south slopes. By 1973 the scattered areas of possible annual dominance appeared to be about twice the size of those in 1956. The total area in 1973 that was not perennial dominated was

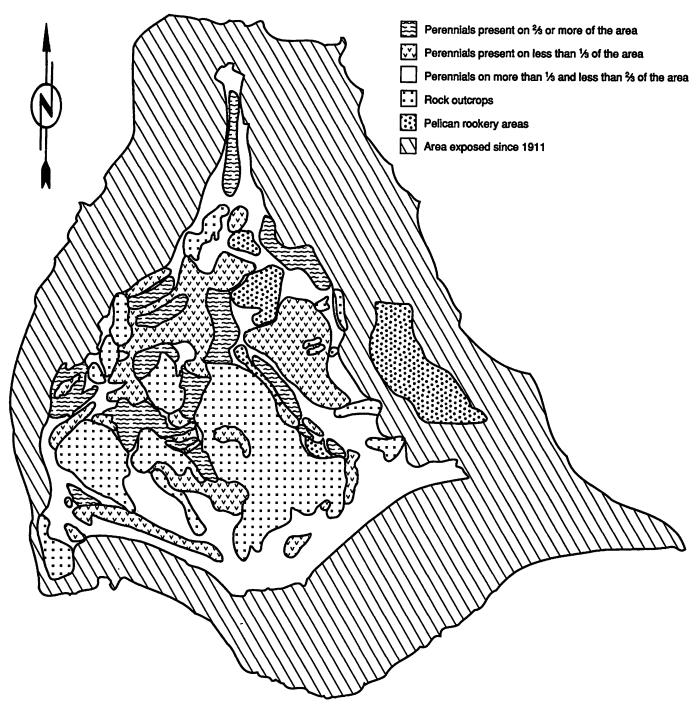


Figure 2—Map of Anaho Island showing three classifications of the relative dominance of perennials and annuals.

still small, accounting for less than about 20 percent of the vegetation cover on the island above the 19th century water level.

Although much of the 1980 aerial photograph had limited usefulness because of a low sun angle, some large areas that appeared to be dominated by annuals were present. These annual-dominated areas were possibly up to half or more the size of areas present in the same locations in 1991. Most of the replacement of perennials by annuals on Anaho Island appears to have occurred in about the last 20 years. As much as half or more of the change may have occurred in the last decade. The pattern of change appears to be one where many small areas of annual dominance have enlarged over time and coalesced into fewer large areas. The timing of these changes appears to coincide with the increasing dominance of annual grasses in dry sagebrush and salt-desert communities in other areas of the Great Basin, including protected areas such as the Nevada Test Site (Hunter 1990, 1991; Young and Tipton 1990).

DISCUSSION

Interpreting the patterns of 1991 annual grass dominance and the patterns of past change, we conclude that the majority of the island vegetation could be dominated by annual grass by the end of the decade. For most of the island the annual grass species involved are the same as in other areas of the Great Basin salt desert (Hunter 1990, 1991; Young and Tipton 1990). The annual foxtail-dominated area on the top of the island is an exception.

The most important implication for management is the increase in annual grass dominance despite the absence of significant herbivory or other disturbance from human activity or fire. Those changes appear related to the competitive superiority of annuals for the limited available moisture (Melgoza and others 1990). The absence of herbivory may also be important. In California grasslands, many areas protected from grazing can have a higher or even total dominance by annuals compared to adjacent grazed areas (Edwards 1992). The associated heavy thatch in these California grasslands also restricts the growth of perennial seedlings.

Annual grass-dominated areas on Anaho Island have a substantial thatch cover and little successful perennial reproduction (Svejcar and Tausch 1991). These conditions are not present on the adjacent shoreline that has both native herbivory and year-long livestock use. The cryptogamic cover of lichens and mosses on Anaho Island is also less evident in high annual grass cover areas of the island where the ground surface is covered by thatch. The combined effects of abundant annual grasses appear to be suppressing the reproduction of the perennials. That many of the older perennials have died over the last two decades is evident from the common presence of dead plants. Without younger plants to replace them the sites became annual dominated. Effective management to control annual grasses will require a better understanding of the biotic and abiotic conditions that can result in the patterns apparent on Anaho Island.

Nesting activities of pelicans and other birds have been confined to a small part of the eastern shore during most of the 19th century. In the past, however, these use patterns have apparently varied. Earlier in the century a rookery site was reported in the area now dominated by annual foxtail (Woodbury 1966). Recently available information indicates that annuals are better able to compete with perennials under improved nutrient conditions (Harper, these proceedings). The unusual presence of foxtail and its dominance of one site may represent a nutrient effect from past use of the location for nesting. Other still unknown factors may also be involved.

The dominance by annuals on Anaho Island appears related to its aridity. A more mesic site about 800 to 1,000 m higher in elevation on the Virginia Mountains on the west side of Pyramid Lake supports relatively large relict areas dominated by bluebunch wheatgrass (Agropyron spicatum [Pursh] Scribn. & Sm.). One of these areas burned about 15 years ago and has since returned to even greater wheatgrass dominance despite the presence of cheatgrass. This area is lightly used by livestock because of rugged terrain. The boundary for the higher moisture zone represented by the bluebunch wheatgrass relict areas is currently unknown, but appears to be approximated in this area by the boundary between Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis Beetle) and mountain big sagebrush (A. t. vaseyana [Rydb.] Beetle).

The drier Anaho Island annuals outcompete perennials because of their ability (in this moisture-limited environment) to utilize available soil moisture before the native perennials can complete their annual growth and reproduction cycles (Melgoza and others 1990). On the Virginia Mountains relict sites, soil moisture may remain after the annuals complete their life cycle. Somewhere between these two moisture conditions is a transition zone where perennials persist despite the presence of annual grass as long as there is no disturbance by fire. Once such a disturbance occurs in this zone, a threshold is crossed (Laycock 1991) and an annual-dominated community results. Large areas of western Nevada appear to be somewhere in this transition zone.

Annuals do not gain dominance under all circumstances and the patterns by which dominance occurs, when it is possible, also vary (Mooney and others 1986). The adaptations involved in changes such as the recent range expansions and competitive interactions of cheatgrass and red brome need to be better understood for effective management of affected areas (Baker 1986). To manage Great Basin communities for sustainable uses requires an ability to recognize relationships between the encroachment of annuals and important environmental controls such as annual soil moisture patterns, the variation of other environmental factors associated with a site, and site differences in patterns of competitive interactions between annual and perennial species.

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GREAT BASIN ANNUAL VEGETATION PATTERNS ASSESSED BY REMOTE SENSING

Paul T. Tueller

ABSTRACT

Cheatgrass-infested wildfire scars are readily identifiable on various scales of aerial photography including Landsat images if the burns are recent. Measurements were made from four Landsat MSS images and 11 NASA high-altitude color infrared aerial photographs of a scale of 1:29,000. Individual Landsat bands and various ratio and coefficient-based vegetation indices can separate burned from unburned sites using image processing techniques. Several vegetation indices were useful in linear models describing range sites with increasing amounts of cheatgrass.

INTRODUCTION

In recorded history, many hundreds of wildfires have occurred throughout the Great Basin and Intermountain region. The majority of these have occurred in the sagebrush vegetation that covers an estimated 19.5 million hectares throughout the region (Tueller 1989a). These wildfires vary considerably as to number and acreage involved. Many thousands of hectares have been impacted. The result has generally been the creation of an annual grass type dominated by cheatgrass (*Bromus tectorum*). The number, extent, and location have not generally been recorded for future reference.

This paper considers the potential uses of remote sensing technology for examining the extent of and changes in the annual cheatgrass vegetation types found in the Great Basin. Consideration has been given to the measurement of these sometimes monospecific plant communities where cheatgrass is the dominant or codominant species on both small and large areas. Lengthy ecotones have been formed. These have been evaluated by interpretation and measurements from aerial photographs and the measurement of these same attributes on satellite-derived computer compatible data with image processing. Procedures for monitoring successional trajectories are discussed. The spectral signatures associated with burned sagebrush or pinyon/juniper plant communities have been examined.

CHEATGRASS

There is ample evidence in the literature that cheatgrass is strongly competitive in the sagebrush/grass vegetation in the Great Basin and Intermountain region. Young and others (1971) state that annual species, like cheatgrass, are highly evolved to occupy a low seral niche caused by fire or grazing. Native species have never evolved to occupy these niches. These niches are not present in pristine big sagebrush-perennial bunchgrass communities, but when a perturbation occurs such as fire, alien annuals readily invade. Part of their success is attributable to their highly developed reproductive system, which makes them tough competitors after they have been established. Cheatgrass, sometimes called downy brome, readily invades a low seral niche created by a disturbance. The presence of plant litter and a rough microtopography are key seedbed characteristics permitting cheatgrass establishment, although success on bare ground is not high (Young and Evans 1972).

Even though cheatgrass caryopses are greatly reduced after fire, the surviving caryopses respond dynamically to the released environment potential. The response may include hybridization and recombination. Cheatgrass has the inherent competitive ability to close the new seral community to seedlings of native perennial grasses and annuals, and its dominance predisposes the site to recurring wildfire perturbation and cyclic environmental degradation (Young and Evans 1977). Cheatgrass is able to rapidly occupy the belowground space and actively utilize soil resources competing with native species for soil water. This negatively affects their soil-water status, aboveground biomass production, and root-length density, giving a strong competitive advantage to the cheatgrass, which then dominates the site (Melgoza 1989).

Young and others (1969) conclude that the important factors in the dynamics of downy brome populations are: (a) large numbers of viable caryopses are carried from one year to the next in the litter and soil; (b) downy brome caryopses production is density dependent; and (c) the simultaneous germination characteristics of freshly harvested downy brome caryopses can be conditioned environmentally to continuous germination.

Wright and Klemmedson (1965) compared the experimental burning of four species of grasses—Sandberg bluegrass (*Poa secunda*), bottlebrush squirreltail (*Sitanion hystrix*), needle-and-thread (*Stipa comata*), and Thurber needlegrass (*Stipa thurberiana*)—to understand their compatibility with cheatgrass. Sandberg bluegrass and squirreltail proved to be fairly resistant to fire, with squirreltail being damaged only in June and the bluegrass

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not at all. Needle-and-thread appeared to be the most susceptible to fire. Burning in June and July caused extreme damage to needle-and-thread, but in August it was relatively resistant. Thurber needlegrass had a similar response as needle-and-thread but less severe. Season of burn determined the extent of damage to both needlegrass species, and size of plant became increasingly important in determining damage in late summer.

DeFlon (1986) describes positive aspects of cheatgrass. Cheatgrass is one of the few grasses that will invade and flourish in the alkaline soils associated with the marginal rainfall of the Great Basin. He goes on to say that it should not be grazed in the summer, but in the winter it can be grazed when it is more palatable and nutritious than crested wheatgrass. He feels the case of cheatgrass as a grazeable species should be reexamined.

Raison (1979) has drawn several conclusions relative to the management of controlled burns. Effects of fire vary with each ecological situation, and currently insufficient data exist to allow accurate prediction of its full long-term effects on many ecosystems that are regularly burned. Furthermore, there needs to be an integrated regional study of the long-term effects of fire on plant communities; regularly burned areas need to be established and maintained so that fire ecology can be better researched and understood. Remote sensing technology has a role to play in this endeavor.

REMOTE SENSING

Remote sensing techniques hold considerable promise for the inventory and monitoring of natural resources in arid regions. They have the potential to integrate various systems for rangeland management (Tueller 1989b) leading to more efficient utilization of forage resources from rangelands by wildlife species as well as domestic livestock and wild horses. However, there has been a fundamental reason why applications have not been forthcoming—a significant lack of information concerning basic spectral characteristics of rangeland/aridland vegetation and soils. Without such basic information relevant to the sensors that are now available to rangeland resource managers, it has been and will remain difficult to develop the desired applications.

Soil substrate plays a significant role in vegetation assessments from spectral data. Similar plant communities can appear different if they have different soil types. Vegetation biomass tends to be overestimated on dark substrates and underestimated on light substrates (Elvidge and Lyon 1984). The typical spectra from rangeland scenes are closely correlated with the soil line developed by Kauth and Thomas (1976). Huete and Jackson (1987) found that senesced grass and weathered litter significantly altered the spectral response of the range vegetation canopy in the first four Thematic Mapper wavebands and thus seriously hamper the use of spectral vegetation indices in assessing green phytomass levels. However, pixel modeling may allow phytomass estimations (Huete 1986).

Data transformations involving such things as differences, sums, and ratios both with the red and infrared spectral space can be evaluated to determine if such data manipulation procedures will have predictor value for parameters such as vegetation biomass, species composition, phenology, species cover, and vegetation changes (plant succession) based on Landsat TM data (Tueller 1989). Most vegetation indices have been developed under humid conditions. In arid zones the ability to interpret spectral information based on vegetation indices is restricted because of the usual small portions of green phytomass and generally low percentages of shrub cover. In semi-arid regions with large areas of bare soil (50-100 percent) most ratio-based indices are known to be adversely affected by differences in soil brightness (Elvidge and Lyon 1985; Huete 1986). Differing spectral responses on changing soil types significantly limit the accuracy of vegetation estimates (Heilman and Boyd 1986; Jackson 1983).

Huete and Jackson (1987) found both ratio and orthogonal vegetation indices to be unreliable for detecting green phytomass of range canopies. Site-specific soil lines and coefficients can reduce the soil background influence and thus improve the estimate of greenness. Huete (1988) developed a soil-adjusted vegetation index (SAVI) to minimize the soil brightness spectral influence.

Ratio-based indices include the Ratio Vegetation Index (RVI), the Normalized Difference Vegetation Index (NDVI), the Transformed Normalized Difference Vegetation Index (TNDVI), the Modified Normalized Difference Vegetation Index (MNDVI), the Soil Adjusted Vegetation Index (SAVI), and the Transformed Soil Adjusted Vegetation Index (TSAVI).

Paltridge and Barber (1988) applied a modified normalized difference vegetation index (MNDVI) (NIR-1.2*RED)/ (NIR+RED). They used a 1.2 factor to adjust the NDVI to arid rangeland conditions in Australia. N-space indices include the Greenness Vegetation Index (GVI), the Soil Brightness Index (SBI), and the Perpendicular Vegetation Index (PVI). Jackson (1983) gives a clear example of how to calculate the coefficients of n-space vegetation indices, GVI, and SBI using the Gram-Schmitt orthogonalization process (Frieberger 1960) to obtain vectors. Four linear combinations of Landsat MSS bands known as "brightness," "greenness," "yellowness," and "nonsuch" originate from a four-band Landsat MSS orthogonal linear combination as described by Kauth and Thomas (1976).

The two-dimensional Perpendicular Vegetation Index (PVI) measures the orthogonal distance of a pixel back to a pre-established soil line (Richardson and Wiegand 1977). The farther a pixel is away from the soil line, the higher the green vegetation contribution to the pixel. We found that the PVI is highly correlated to shrub cover on salt desert and sagebrush-dominated rangelands (r = 0.91). Other indices to consider include the WDVI (Weighted Difference Vegetation Index) (Clevers 1989) and the TSAVI (Transformed Soil Adjusted Vegetation Index) (Baret and Guyot 1991).

Corrections for atmospheric variability are important to normalize spectral data recorded from high altitudes. Atmospheric corrections can be made for satellite data by using linear regressions of light and dark standard reflectance targets on the ground (Marsh and Lyon 1980). Path radiance corrections can increase the classification accuracy of the data (Kowalik and others 1983). Elvidge and Lyon (1985) also describe a useful method for defining the atmospheric influence on digital counts for the TM bands. A modified AVHRR vegetation index was found to be related to "grassland" fuel-moisture content in a study near Victoria, Australia. The AVHRR system as a whole proved extremely valuable for monitoring potential fire danger areas of the State. The relationship was based on the dominant control of leaf moisture status on satelliteobserved vegetation indices (Paltridge and Barber 1988).

Yue-Hong and others (1990) compared spatial weighting functions and found that the contiguity weight can be used to define the spatial term of neighborhood effects on wildfire. Data overlays of multiple GIS layers derive the explanatory variables for modeling the distribution of wildfires from logistic regressions. The model improves when the spatial term is included. Their results suggest that neighborhood effects are a primary factor in the distribution of wildfires.

Burned and unburned grass canopies had distinctly different diurnal surface radiative temperatures, and measurements of surface energy balance components revealed a difference in partitioning of the available energy between the two canopies, which resulted in the difference of their measured surface temperatures. Additionally, the timing of measurements and topographic conditions affect the magnitude of the difference in surface temperatures (Asrar and others 1988).

A geographic information system (GIS) can be used to identify and analyze not only the type and amount of change on a burn site, but also those classes which did not change. A GIS restricts change analysis to the fireaffected area by masking out unaffected vegetation through overlay operations. Furthermore, the flexibility afforded by a GIS allows additional data sets from preceding or succeeding dates to be added, creating a database for the study of long-term change within the study site (Jakubauski and others 1990).

METHODS

Three data sets were developed for this study. First we examined 10 burns in the sagebrush or pinyon/juniper woodland vegetation from three Landsat subscenes in western and central Nevada. Homogeneous areas were selected for burned and unburned sites at these 10 burn locations. From these homogeneous sites 20 pixels of Landsat Thematic Mapper data were obtained for analysis. Data for each of the TM bands (one through five and seven) except the thermal band were summarized (table 1). Then 11 vegetation indices were computed for each site based on TM Band four (Near Infrared) and TM Band three (red). Formulas for these vegetation indices are listed in table 2. No ground data were available for these 10 burn-unburn comparisons. The various vegetation indices were chosen and interpreted based on their potential to distinguish between burned and unburned vegetation sites during June. Means and standard deviations were calculated along with a Student's t statistic in order to compare burned with unburned sites.

A second data set was analyzed as part of another study we are working on designed to model pixels for their various components based on various vegetation indices. Ten unburned shrub-dominated range sites in western Nevada (or they had not been recently burned) with differing

Table 1—Landsat TM bands acquired a	and vegetation indices
computed in this study	

	_	
TM1 Th	em	atic Mapper Band1
TM2 Th	em	atic Mapper Band2
TM3 Th	em	atic Mapper Band3
TM4 Th	em	atic Mapper Band4
Shrub C)ov	er Percent
BRTE C	òv	er Percent
DVI	=	Difference Vegetation Index
RVI	8	Ratio Vegetation Index
TNDVI	=	Transformed Normalized Difference Vegetation Index
81	=	Normalized Difference Vegetation Index
PVI	=	Perpendicular Vegetation Index
MNDVI	=	Modified Normalized Vegetation Index
SBI	=	Soil Brightness Index
GVI	=	Greenness Vegetation Index
SAVI	=	Soil Adjusted Vegetation Index
TSAVI	8	Transformed Soil Adjusted Vegetation Index
WDVI	8	Weighted Difference Vegetation Index

amounts of cheatgrass mixed in the stand were sampled. The data set consisted of ground measurements of cover and both reflectance and radiance data from a 20-pixel sample from the same ground locations of western Nevada shrub-dominated range sites. The 20 radiance values for each TM band were used to compute several vegetation indices as described earlier in the paper. For this paper I have examined only the linear relationships with ground-measured dominant shrub (usually sagebrush) cover, bare ground, and cheatgrass cover as the dependent variable against a number of independent variables (vegetation indices).

A third data set consisted of interpreting and studying four Landsat MSS images and 11 NASA high-altitude frames of a scale of 1:29,000. These were analyzed by photo interpretation techniques. For these scenes we identified and measured each burn in the scene (most were in the sagebrush vegetation) and determined the acreage and length of perimeter of the burn.

Table 2-Vegetation indices used in this study

Vegetation index	Formula			
RVI	TM4/TM3			
NDVI	TM4-TM3/TM4+TM3			
TNDVI	V (TM4-TM3/TM4+TM3)+0.5			
MNDVI	TM4-1.20*TM3/TM4+TM3			
PVI	V (Rgg5–TM3) ² +(Rgg7–TM4) ²			
SBI	(0.664*TM3)+(0.747*TM4)			
GBI	(0.747*TM3)+(0.664*TM4)			
DVI	TM4-TM3			
WDVI	TM4-0.08*TM3			
SAVI	TM4-TM3/(TM4+TM3+0.5) * (1.0+0.5)			
TSAVI	a1(TM4-a1*TM3-b1)/			
	[a1-TM4+TM3-a1*b1+0.08(1+a12)]			

'For variable names see table 1.

RESULTS AND DISCUSSION

Increasing amounts of cheatgrass are usually associated with site degradation by overgrazing, wildfire, or other potential perturbations. Burns that are only a few years old are reasonably easy to identify on the Landsat Thematic Mapper images displayed on the image processing monitor. Tables 3 and 4 show the results from two of the 10 sites, a fire on the Gund Ranch in central Nevada and one on Fort Sage Mountain in western Nevada. Statistical comparisons with each band comparing the burned and unburned sites easily record significant differences using a simple t test.

While it is easy to record the difference using such a procedure, not much is really learned about the spectral characteristics of these rather simple ecosystems. Rather there is a need to carefully do some pixel modeling in order to determine the information content of the individual pixels or pixel samples for the site.

Data comparing these same 10 burns using several vegetation indices described earlier show that some indices show significant differences and some do not. Data from four of these indices, RVI, GVI, NDVI, and TNDVI, showed potential for describing differences among burned and unburned sites (table 5). In this case the RVI and the PVI were not successful in differentiating among the burned and unburned sites. However, the NDVI and the TNDVI were useful vegetation indices in this regard. These two indices among several others seem to be sensitive to the small amounts of vegetation reflectance from these cold desert sites.

For predicting the level of cheatgrass amount on a site I refer the reader to the second data set that was not completed on burned and unburned sites (fig. 1). The adjusted R^2 value of 0.9661 for this data set is somewhat suspect since two seeming outliers accounted for the strength of the relationship. Further sites with cheatgrass will be required to determine the real value of this relationship. However, cheatgrass tends to be abundant on a site or not abundant depending on disturbance, and

Table 3—A comparison of Landsat TM bands as simple comparative signatures for burned and unburned pixel samples from the Gund Banch study site in central Nevada

Site: Gund	Mean	S.D.	S.E.	T	P
TM1					
Burned	79.85	2.796	0.6252	9.54	0.0000
Unburned	73.10	1.483	.3317	9.54	.0000
TM2					
Burned	42.50	1.638	.3663	17.92	.0000
Unburned	35.50	.607	.1357	17.92	.0000
тмз					
Burned	74.65	2.207	.4935	29.55	.0000
Unburned	59.00	.858	.1919	29.55	.0000
TM4					
Burned	72.50	1.960	.4383	38.35	.0000
Unburned	54.05	.887	.1983	38.35	.0000
TM5					
Burned	147.60	1.932	.4321	41.01	.0000
Unburned	121.50	2.089	.4672	41.01	.0000

Table 4-A comparison of Landsat TM bands as simple compara-
tive signatures for burned and unburned pixel samples
from the Fort Sage study site in western Nevada

Site: Fort Sage	Mean	S.D.	S.E.	Т	Ρ
TM1					
Burned	74.80	1.4730	0.3293	10.06	0.0000
Unburned	69.05	2.0890	.4672	10.06	.0000
TM2					
Burned	40.35	.7452	.1666	10.88	.0000
Unburned	36.70	1.3020	.2911	10.88	.0000
ТМЗ					
Burned	66.50	1.0000	.2236	13.71	.0000
Unburned	57.75	2.6730	.5977	13.71	.0000
TM4					
Burned	67.95	.8256	.1846	30.44	.0000
Unburned	58.75	1.0700	.2392	30.44	.0000
TM5					
Burned	147.50	1.6700	.3735	27.17	.0000
Unburned	126.80	2.9610	.6620	27.17	.0000

the two outliers reflect disturbed sites with high cheatgrass cover.

The percentage of the dominant shrub on our 10 western Nevada study sites was predictable based on a combination of the two vegetation indices, the NDVI and MNDVI, giving an adjusted R^2 of 0.8066. A prediction based on TM4A and TM2A gave an even higher adjusted R^2 (0.9002) value. It is gratifying to find that a reasonable estimation of the dominant shrub on these cold desert sites can be made with Landsat data alone. The increased adjusted R^2 based on ground reflectance of the site-dominant shrub in bands two and five is difficult to explain and requires further research.

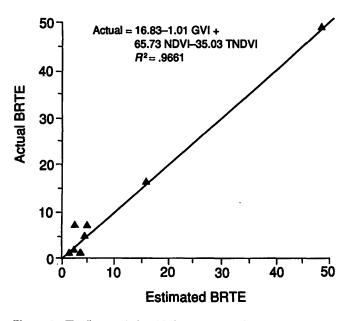
The third data set involved the photo interpretation of several burn sites in the sagebrush grass. Photo interpretation criteria used to identify these sites include such factors as lighter tones associated with the burned area when compared with the darker tones of the sagebrush vegetation and the irregular shape of the burns. Some of the burns were bounded by tracks made by heavy equipment used in the suppression process. Table 6 and table 7 summarize these data. For the 11 NASA high-flight color infrared photographs we found that the burn size varied from 26.8 acres to 113.2 acres. Perimeters for these burns varied from 0.9 to 10.98 miles in length. Ratios of size to perimeter were from 30/1 to 138/1. In other words for each mile of perimeter there were from 30 to 138 acres of burned ground. Each of the 11 frames represented about 50,000 acres. The recent burns identified and studied represented only 1.9 percent of the total area.

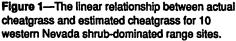
The four Landsat MSS images that we studied represented approximately 6,400,000 acres per frame. With an average of 16,446 acres of recently burned ground per frame the area burned represented only 0.25 percent of the total. With periodic analysis of new imagery, monitoring would provide good data on the amount of burned ground possibly on an every 2 or 3 year basis. On these four frames the ratios of acreage to perimeter in miles varied from 41/1 to 83/1.

Table 5—Selected vegetation index values for 10 northern Nevada burned and unburned range sites1

		RVI	PVI		ŇDVI		TNDVI	
	B	U	В	U	B	U	В	U
	0.461	0.463	5.381	4.573	0.010	0.008	0.715	0.713
	.444	.477	9.938	8.226	.054	.064	.745	.751
	.457	.505	6.583	10.119	.019	.056	.511	.746
	.491	.445	3.183	.275	.015	.044	.697	.675
	.504	.462	7.619	5.975	.025	.023	.725	.72
	.466	.525	3.920	6.628	.005	.033	.704	.72
	.505	.668	6.734	14.974	.026	.177	.725	.823
	.583	.797	16.542	19.734	.199	.281	.836	.884
x	.512	.475	2.821	3.644	.022	.008	.692	.70 1
	.695	.586	10.189	13.597	.064	.130	.751	.794
	.512	.540	7.287	8.774	.044	.083	.710	.754
	.024	.036	1.307	1.864	.018	.028	.026	.020
	t -0.91		-1.39		-2.45		-1.85	
	Ρ	0.3873	0.	1979	1	0.0350	0.	0976

¹B = burned; U = unburned.





CONCLUSIONS

Efforts directed toward using satellite remote sensing data to measure burned sites in the sagebrush/grass vegetation will eventually be routine data inputs to resource management and GIS. Also, such data can be used to monitor changes in rangelands resulting from management or from various perturbations.

Satellite radiance data alone can provide information relative to burned vs. unburned sagebrush/grass sites in the Great Basin and Intermountain region. However, the difficult task is the business of establishing satellitebased signatures that can be used to extract meaningful information about burns in the sagebrush/grass resulting in annual grassland. The difficulty extends to the concept of extending the signature to different sites (spatially) and different dates (temporally) and still have a signature based on a vegetation index or some other satellite dataderived index, that can describe specified environmental parameters and follow changes in them for monitoring purposes. This will require enhanced procedures for assessing the quantitative aspects of pixel components for the sites to be studied and monitored. Also, analysis and

Table 6—Burn acreage to burn perimeter miles and the ratio of acreage to perimeter for wildfires in northern Nevada of 11 NASA color infrared photographs (panoramic)¹

Frame No.	Acreage	Perimeter	Acre/ PM	Plant community
180	26.8	.9	19.78:1	Pinyon-Juniper/ Sagebrush
162	85.8	4.7	18.26:1	Pinyon-Juniper/ Sagebrush
111	64.4	1.4	46.0:1	Sagebrush
106	333.8	8.0	41.73:1	Sage/Mountain Mahogany
88	648.	5.5	117.82:1	Sagebrush
85	1,132.	8.2	138.05:1	Sagebrush
81	579.	4.5	128.67:1	Sagebrush
72	33.5	.9	37.22:1	Sagebrush
50	391.	5.5	85.0:1	Pinyon-Juniper/ Sage
37	344.6	4.6	74.91:1	Sagebrush
30	911.	10.98	82.97:1	Salt Desert Shrub
$\frac{\Sigma x}{\overline{x}}$	4,549.9	55.18		
x	413.63	5.0	71:1	

¹Scale-1:29,000; date: June 21, 1979.

Frame	Total burn acreage	Total perimeter miles	Ratio acreage/PM
Ruby Mountains	26,344.5	317.59	82.951:1
Santa Rosa	12,840.1	202.384	63.444:1
Coils Creek	15,206.1	365.274	41.629:1
Black Rock Desert	11,393.1	210.028	54.246:1
Σχ	65,783.9	Σx 1,095.3	
x	16,446.0	x 273.8	x 60.57:1

Table 7—Total average total burn perimeter and the ratio of perimeter to acreage for wildfires in northern Nevada on four MSS images from 1973¹

10.25 percent of the area burned.

interpretation of remote sensing systems with higher spectral resolution may be helpful.

Predictions of changes in shrub cover, perennial grass cover, annual grass cover, bare ground, and other surface soil parameters with satellite-derived remote sensing data will allow better management of these cold desert ecosystems. Establishment of descriptive signatures based on satellite data alone may be the most useful. However, the signatures for describing scene components may be improved in some cases by acquiring ground-based reflectance data to include in the model.

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VA MYCORRHIZAL STATUS OF BURNED AND UNBURNED SAGEBRUSH HABITAT

Jan E. Gurr Marcia Wicklow-Howard

Sagebrush is considered to be an obligate vesiculararbuscular mycorrhizal plant. Some studies have shown that burning lowers the mycorrhizal inoculum potential (MIP) of the soil (Klopatek and others 1988, 1990; Wicklow-Howard 1989). If this happens, then sagebrush may take longer to reestablish after fire.

A study was performed to investigate the relationship of vesicular-arbuscular mycorrhizae (VAM), Wyoming big sagebrush (*Artemesia tridentata* Nutt. var. *wyomingensis* [Beetle and Young]) and burned vs. unburned soils. The purpose of the study was to:

1. Investigate whether planting mycorrhizal inoculated sagebrush seedlings in burned soils would enhance reestablishment.

2. Monitor the mycorrhizal inoculum potential (MIP) of soils before and after a fire.

3. Compare mycorrhizal root colonization in wild sagebrush found growing in burned soil with that of wild sagebrush growing in unburned soil.

STUDY SITE

The study site is a 300- by 400-meter section of the Orchard Range Plant Test Site located about 20 miles east of Boise, ID.

The two soil types studied are Tindahay fine sandy loam and Power-Chardoton silt loams. The area is sagebrush dominated with islands of cheatgrass-dominated habitat.

In September 1989, one half of the site was burned, including both sagebrush- and cheatgrass-dominated areas.

SAGEBRUSH SEEDLINGS

Sagebrush seeds were harvested at the site, grown at the Intermountain Research Station Shrub Sciences Laboratory in Provo, UT, and then planted at the site in May 1990.

Treatment areas consisted of: (a) burned sagebrush, (b) burned cheatgrass, and (c) unburned cheatgrass. Three randomly selected replicate plots per treatment were planted with mycorrhizal inoculated (M+) seedlings and noninoculated (control) seedlings. VAM inoculant (species *Glomus intraradices*) was purchased from NPI of Salt Lake City, UT.

Roots were harvested in October 1990 and in June 1991, preserved in a solution of formalin, acetic acid, and alcohol (FAA), and later assessed for VAM colonization using the Magnified Intersections Method of McGonigle and others (1990). Arbuscular, vesicular, and hyphal intersections were counted and calculated on a per total root intersections per sample basis. Survivorship and height were assessed.

MIP IN SOILS

Tindahay and Power-Chardoton soils were randomly sampled in June 1989, before burning, and again in June 1990 and June 1991, after the burn.

A bioassay was run on the soils using sudangrass. Roots were harvested after 6 weeks, preserved in FAA and stained according to the procedure of Philips and Hayman (1970). MIP was calculated by counting the number of VAM-colonized root segments per 100 per sample.

VAM IN WILD SAGEBRUSH

In June 1991 (1 year and 8 months after burning) wild sagebrush roots were randomly sampled in the burned sagebrush site and in the unburned sagebrush site.

Roots were preserved in FAA, later stained with lactoglycerin trypan blue, mounted on microscope slides, and checked for VAM colonization using the Magnified Intersections Method.

SEEDLING RESULTS

Burned Cheatgrass—Seedlings in this treatment did not survive past the first growing season.

Unburned Cheatgrass—Arbuscular colonization was not significantly different between M+ and the control (fig. 1). The dates were also not significant. Hyphal colonization (fig. 2) remained significantly greater between M+ and the control through June 1991. There was no difference in survivorship between inoculated and noninoculated seedlings.

Poster paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992.

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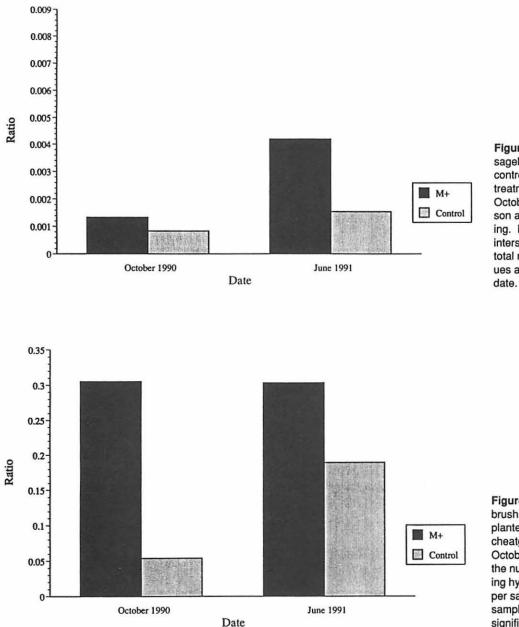


Figure 1—Arbuscular colonization of sagebrush seedling roots (M+ and the control) in the unburned cheatgrass treatment. Roots were sampled in October 1990 after the first growing season and in June 1991, 1 year after planting. Ratio given is the number of root intersections containing arbuscules per total root intersections per sample. Values are means of samples from each date. There was no significance.

Figure 2—Hyphal colonization of sagebrush seedling roots (M+ and the control) planted in May 1990 in the unburned cheatgrass treatment and harvested October 1990 and June 1991. Ratio is the number of root intersections containing hyphae per total root intersections per sample. Values are means of the samples from each date. M+ remained significantly greater than the control.

Burned Sagebrush—Arbuscular colonization was not significant (fig. 3). Hyphal colonization (fig. 4) was significantly greater in M+ than in the control for October 1990 but not by June 1991, 1 year after planting. Survival and growth of seedlings were the same among inoculated and noninoculated seedlings.

More seedlings (both M+ and the control) survived and height measurements were greater in the burned sage site than in the burned or unburned cheatgrass sites.

MIP RESULTS

MIP (fig. 5) increased the first year after the fire in the Tindahay soil, then decreased the second year after the fire. In the Power-Chardoton soil MIP decreased each year after the fire. The decrease in MIP was not statistically significant, however.

WILD SAGEBRUSH ROOTS

Wild sagebrush roots (fig. 6) from the burned site had significantly less arbuscular and vesicular colonization than wild sagebrush roots from the unburned site.

CONCLUSIONS

VAM-inoculated seedlings did not exhibit increased arbuscular or vesicular colonization, but they did have

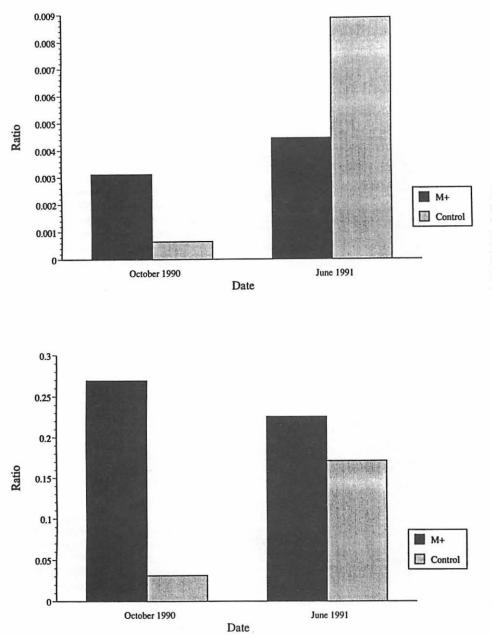


Figure 3—Arbuscular colonization of sagebrush seedling roots (M+ and the control) in the burned sagebrush treatment site. Ratio is the number of root intersections containing arbuscules per total root intersections per sample. Values given are the means of samples from each date.

Figure 4—Hyphal colonization of sagebrush seedling roots (M+ and the control) harvested from the burned sagebrush area after the first growing season (October 1990) and 1 year after planting (June 1991). Ratio is the number of root intersections containing hyphae per total root intersections per sample. Values given are means of samples from each date. Mean values were significantly different for October 1990.

an increase in hyphal colonization. This may not be due to VAM colonization. It could be hyphal colonization from other fungal species.

Seedlings in the burned cheatgrass and unburned cheatgrass sites did not survive, or they did not survive as well, as those in the burned sagebrush site.

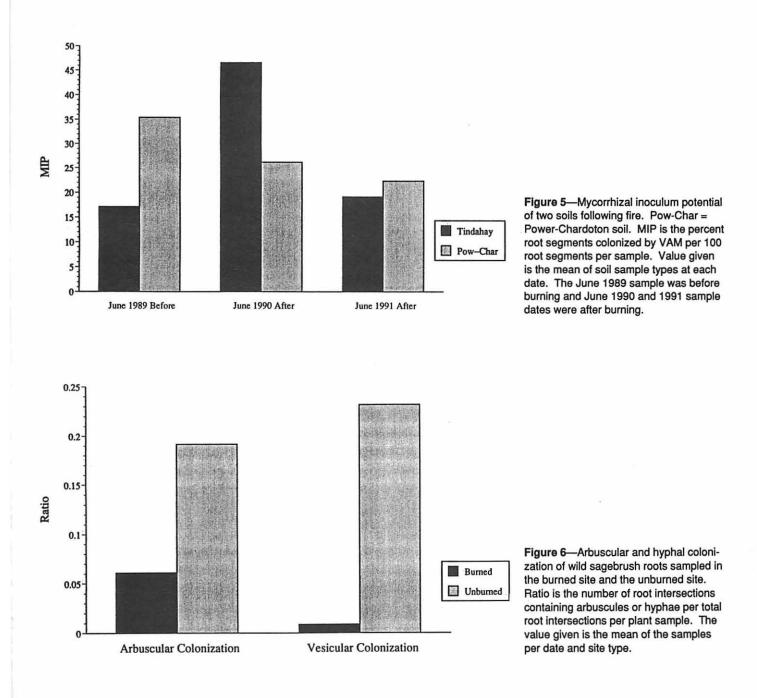
Although MIP of the two soil types was not significantly lower after burning, the VAM infection level of sagebrush seedlings was low. VAM infection level of wild sagebrush coming up in the burned site was significantly lower than in the unburned site.

Additional research is needed to assess the effects of commercial VAM inoculant. Another inoculant species

may work better. Attention should be paid to various planting techniques. Perhaps a study of seeds vs. seedlings should be done incorporating tilled vs. nontilled soil.

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GROWTH, REPRODUCTION, AND LIFE HISTORY FEATURES OF FOURWING SALTBUSH GROWN IN A COMMON GARDEN

B. K. Pendleton D. C. Freeman E. D. McArthur R. L. Pendleton

The reproductive biology of diclinous plant species, species having more than one sexual morph, is of considerable research interest. Differences in the reproductive biology of the sexual morphs may, in turn, influence the relative allocation of resources to growth, reproduction, and maintenance. If, as first proposed by Darwin (1877), females allocate a greater portion of resources to reproduction than do males, and if resources are finite, then an increase in reproductive costs should result in a decrease in resources available to current growth as well as future growth and reproduction (Agren 1988; Freeman and others 1976; Horvitz and Schemske 1988; Lloyd and Webb 1977; Putwain and Harper 1972; Willson 1979).

In this common garden study, life history features and possible secondary sex characteristics were examined using fourwing saltbush (*Atriplex canescens*), a species which exhibits three genotypic gender states: staminate, pistillate, and a labile hermaphroditic genotype (Barrow 1987; McArthur 1977; McArthur and Freeman 1982). The common garden permits examination of the biology of each sexual morph without the confounding effects of differences in age structure and habitat found in natural populations. The following questions were addressed:

• Do the sexual morphs differ in intensity of flowering or inflorescence structure?

• Are there differences between the sexual morphs in growth and habit?

• Are the responses to irrigation treatment equal among the sexual morphs?

• Are there population differences in growth, reproduction, and response to treatment?

METHODS

Stem cuttings of male, female, and hermaphrodite plants from two contrasting tetraploid populations, Spanish Fork Canyon and Kingston Canyon, were rooted in peat pellets kept moist through periodic misting. The resulting ramets were planted at the Rush Valley experimental garden in spring 1982. Ten ramets from each clone were planted in both irrigated and control portions of the garden. All clones had the same relative position in both the control and treatment portions. Ramets were planted 2.4 meters apart. All plants were watered during 1982 to aid in establishment. Plants in the irrigated portion received an additional 5 liters of water per month during the 1983 growing season.

In August of 1983, the following data were recorded for all ramets:

- Mortality.
- Height.
- Crown diameter.
- Branch length—five branches per ramet.
- Sexual phenotype-male, female, or hermaphrodite.
- Number of inflorescences.
- Length of five randomly selected inflorescences.

• Number of flowers per inflorescence — determined microscopically for two inflorescences from each of four flowering ramets.

Table 1—1982-83 mortality and flowering percentages of cloned ramets from Spanish Fork and Kingston Canyon populations

	Females	Males	Hermaphrodites			
	Percent					
Mortality						
Spanish Fork ramets						
Irrigated	2.0	10.0	4.5			
Control	8.0	7.5	4.0			
Kingston Canyon ramets						
Irrigated	6.1	6.7	8.0			
Control	5.4	8.3	17.0			
Flowering						
Spanish Fork ramets						
Irrigated	93.8	97.2	85.7			
Control	76.3	94.6	85.7			
Kingston Canyon ramets						
Irrigated	58.7	89.3	72.8			
Control	72.1	87.3	80.8			

Poster paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992.

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MORTALITY

Mortality, both between the sexes and between the populations, was quite uniform, with the exception of KC hermaphrodite clone three (table 1). Most mortality was attributable to factors other than sexual morph (for example, transplant shock and herbivory). The likelihood that a sexual morph would flower, males being most likely, hermaphrodites next most likely, and females least likely, was approximately the same in both populations.

Kingston Canyon and Spanish Fork Canyon ramets did not have a similar response to irrigation treatment. Spanish Fork females showed a positive response to irrigation; Kingston Canyon females showed a negative response. Spanish Fork ramets, regardless of sexual morph, flowered with greater frequency than Kingston Canyon ramets.

GROWTH

Spanish Fork Population—Male ramets had the smallest mean values for all growth measures (table 2). Female ramets were consistently larger than male. Hermaphrodite ramets were intermediate in most cases, with a significantly larger crown diameter in the control environment. Hermaphrodite ramets were most like female in growth pattern. Irrigation treatment produced an increase in all growth measures. Males and females responded to the irrigation treatment in a similar manner. Kingston Canyon Population—Male ramets had the smallest growth measures (table 3). Females were consistently larger than males. The few exceptions to these trends, irrigation height and crown diameter, were nonsignificant. Hermaphrodite ramets were most like female with the exception of the height per crown (HPC) ratio, which was nonsignificant.

There were no significant differences between sexual morphs for height, crown diameter, and HPC measures in the irrigation environment. Irrigation treatment produced an increase in height and crown for all sexual morphs, and an increase in branch length of male ramets. Hermaphrodites and females responded to the irrigation treatment similarly.

REPRODUCTION

Spanish Fork Population—Female ramets on average had longer but fewer inflorescences than did male ramets (table 2). Hermaphrodite inflorescences were intermediate in length. Flowers per inflorescence did not vary significantly between sexual morphs in either environment. Male and female ramets increased the number of inflorescences under irrigation; males by 81 percent and females by 33 percent. Hermaphrodite ramets, which had the greatest number of inflorescences in the control environment, were unaffected by irrigation.

Kingston Canyon Population—Hermaphrodite ramets had the longest inflorescences and the most flowers per

Trait	Sexual morph	Control environment	Irrigation treatment	Population mean
Height	Female	311.85 a	370.94 a	341.86
•	Male	240.14 b	289.44 c	264.45
	Hermaphrodite	297.18 a	340.91 b	320.63
Crown diameter	Female	316.57 b	421.20 a	369.71
anch length	Male	292.79 b	383.61 a	337.58
	Hermaphrodite	355.60 a	382.86 a	370.21
Branch length	Female	71.00 a	79.33 a	75.28
-	Male	28.70 c	32.19 c	30.54
	Hermaphrodite	45.38 b	53.87 b	49.93
Height per	Female	1.03 a	.96 a	.99
crown ratio	Malə	.83 b	.77 b	.80
	Hermaphrodite	.88 b	.93 a	.91
Number of	Female	37.15 b	49.57 b	44.09
inflorescences	Male	44.21 b	80.21 a	62.21
	Hermaphrodite	59.52 a	60.25 b	59.92
nflorescence	Female	34.63 a	36.15 a	35.48
length	Male	13.54 c	15.70 c	14.64
-	Hermaphrodite	21.92 b	28.87 b	25.80
Flowers per	Female	75.14 a	86.11 a	80.58
inflorescence	Male	86.84 a	87.34 a	87.89
	Hermaphrodite	87.70 a	102.63 a	95.74

Table 2—Mean values of the growth and reproduction measurements for the Spanish Fork Canyon population. All length measurements are in millimeters. Means followed by the same letter are not significant at the 0.05 level

Trait	Sexual morph	Control environment	Irrigation treatment	Population mean
Height	Female	320.71 a	336.57 a	328.85
•	Male	243.20 b	320.45 a	282.17
	Hermaphrodite	292.71 a	311.79 a	303.35
Crown diameter	Female	323.92 a	375.36 a	350.32
	Male	262.04 b	384.64 a	323.89
	Hermaphrodite	299.73 ab	361.04 a	333.91
Branch length	Female	79.69 a	78.80 a	79.22
	Male	43.84 b	67.66 b	55.83
	Hermaphrodite	76.22 a	74.13 ab	75.05
Height per	Female	.95 a	1.05 a	1.00
crown ratio	Male	.95 a	.86 a	.91
	Hermaphrodite	1.01 a	.90 a	.94
Number of	Female	19.73 b	34.41 b	27.32
inflorescences	Male	53.35 a	68.02 a	60.84
	Hermaphrodite	29.47 b	44.63 b	37.76
Inflorescence	Female	24.11 b	28.75 b	26.24
length	Male	16.71 c	19.07 c	17.87
-	Hermaphrodite	37.28 a	37.87 a	37.60
Flowers per	Female	93.55 a	84.14 b	88.97
inflorescence	Male	66.56 a	118.35 b	93.82
	Hermaphrodite	121.68 a	168.25 a	150.87

 Table 3—Mean values and standard deviations of the growth and reproduction measurements for the Kingston Canyon population. All length measurements are in millimeters. Means followed by the same letter are not significant at the 0.05 level

Table 4—Percent of variance by clone (genotype) and various environmental components for Spanish Fork Canyon growth and reproductive parameters

Sexual morph	Source	Height	Crown diameter	Number inflorescences	Branch length	inflorescence length
Female	Treatment	0	5.44	0	0.47	0.06
	Clone Treatment	15.05	20.19	23.15	32.46	31.32
	x clone	21.45	13.80	28.85	13.92	6.35
	Ramet	_	-		37.67	48.91
	Error	63.49	60.57	48.00	15.47	13.44
Vale	Treatment	13.30	0	0	2.04	1.61
	Clone Treatment	39.93	0	4.28	33.94	15.59
	x clone	0	0	0	15.52	14.15
	Ramet	_	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	23.19	32.21	
	Error	47.76	100.00	95.72	25.31	35.43
Hermaphrodite	Treatment	26.39	25.68	0	10.00	12.56
	Clone Treatment	44.14	9.11	29.57	.21	13.76
	x clone	0	8.16	11.21	14.77	15.26
	Ramet	—		-	34.65	20.06
	Error	29.47	57.05	59.22	50.38	38.36

inflorescence, although the difference was not always significant (table 3). Female ramets had longer but fewer inflorescences than did male ramets. All three sexual morphs increased the number of inflorescences under irrigation. Male and hermaphrodite ramets also increased the number of flowers per inflorescence.

VARIANCE PARTITIONING

Mean squares values from the ANOVA were partitioned into their variance components following Bulmer (1980). Sexual morphs differed markedly in the variation percentage accounted for by each source. For example, the clone term for number of inflorescences accounts for 23.15 percent of the variation in female clones, 4.28 percent of the variation in male clones, and 29.57 percent of the variation in hermaphrodite clones. Irrigation treatment accounted for a small percentage of the variation in male and female clones (an average of 5.1 percent and 1.9 percent, respectively), but accounted for an average of 20.7 percent of the hermaphrodite variance (table 4).

The clone term was significant across all variables and sexes, and accounted for a significant fraction of the total variation in all cases, indicating a high degree of genetic variation within the Spanish Fork Canyon population. The high percentage of variance accounted for by the ramet term of the analysis indicates that substantial microenvironmental variation can occur across relatively short distances within the common garden.

CONCLUSIONS

1. Differences between sexual morphs in growth and flowering schedules suggest tradeoffs in resource allocation between growth and reproduction. Males flowered with the greatest frequency and intensity, while producing the smallest growth parameters. Females had the largest measures of vegetative growth and flowered with the least frequency and intensity.

2. Hermaphroditic plants have a growth and reproductive biology distinct from males and females. Values were most like females in growth, but more like males in intensity of flowering. Hermaphrodites have the largest number of flowers per inflorescence.

3. Mean values for growth and reproductive characters examined were quite similar between the Kingston Canyon

and Spanish Fork populations. Growth and reproduction trends of the sexual morphs were also similar, but less pronounced in the Kingston Canyon population. The unusually high precipitation experienced during the 1982 and 1983 growing seasons created relatively lush conditions for the more xeric KC plants, minimizing differences between sexual morphs.

4. Irrigation treatment accounted for over four times the variation in hermaphroditic plants as it did for either male or female plants. This observation is consistent with the hypothesis that hermaphrodites are better able to respond to environmental change than either males or females.

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POTENTIAL ROLE OF SOIL MICROORGANISMS IN MEDUSAHEAD INVASION

James D. Trent James A. Young Robert R. Blank

Medusahead (*Taeniatherum caput-medusae* ssp. asperum) is an annual grass that is invading western rangelands. Once it invades native communities or replaces cheatgrass (*Bromus tectorum*) in degraded communities, utilizable forage for domestic livestock and seeds for granivores are sharply reduced, wildfires are perpetuated, and secondary plant succession is disrupted. Medusahead and cheatgrass appear to respond favorably to nitrogen (N) addition to soils (Kay and Evans 1965) and may occupy and dominate disturbed sites where N mineralization is high. Tilman (1988) proposes a model of succession that describes changing plant dominance based on zero net growth isolines of different plant species with different resource requirements.

We propose that vegetation removal and soil disturbance results in elevated levels of mineral N, which favors medusahead over the perennial seedlings. A decrease in soil mineral N over time may eventually favor perennial seedlings that are more competitive at lower levels of mineral N. In addition, disturbance alters detrital food webs, shifting food webs from those dominated by fungi to those dominated by bacteria (Hendrix and others 1986). Bacterially dominated systems are characterized by rapid decomposition and nutrient mineralization, while localization of organic matter in surface soils of less-disturbed soils promotes fungal-dominated systems that are characterized by lower decomposition rates and net nutrient immobilization (Hendrix and others 1986). According to this hypothesis, undisturbed sagebrush (Artemisia spp.) soils should be characterized by fungal domination and net N immobilization, while disturbed soils containing medusahead would be dominated by bacteria, resulting in net N mineralization.

The purpose of this study was to: (1) determine whether soil N status differs among heavily disturbed, moderately disturbed, and undisturbed sites and to relate such differences to microbial dominance by either fungi or bacteria; and (2) manipulate soil mineral N by adding either fertilizer, sugar, or a nitrification inhibitor to determine the effect of mineral N on medusahead seed germination.

METHODS

An observational study and an N fertilization experiment were conducted. The observational study was conducted in Lahontan sagebrush (Artemisia arbuscula ssp. longicaulis)/Sandberg bluegrass (Poa sandbergii) plant communities near Susanville in northeastern California. Three sites with different disturbance histories were chosen for comparison: (1) an undisturbed site, which lacked cheatgrass and medusahead (UNSAG = soil takenbeneath sagebrush; UNINT = soil taken in the shrub interspaces); (2) a site moderately disturbed, with cheatgrass and medusahead invading the sagebrush community (MODSAG = soil taken beneath sagebrush; MODINT = soil taken in the shrub interspaces); (3) a heavily disturbed site, which historically had been subjected to heavy sheep grazing. This site had burned, so it lacked sagebrush and was dominated by medusahead with some recent squirreltail (Elymus hystrix) colonists (DISEL = soil adjacent to *Elymus*; DISMED = soil in medusahead).

Soil was taken between 1 and 20 cm below the litter layer. Four replications of dune and interdune soils were sampled on September 17, 1991. Soil smears of bacteria and actinomycetes were stained with Europium trifluoroacetonate and and fluorescent brightner (Anderson and Slinger 1975) and counted at 1000x with a UV microscope. Actinomycetes were less than 1 μ m in diameter and fungi were generally greater than 1.5 μ m in diameter. Fungal hyphae were stained and quantified (400x) using an Irgalan black membrane filter technique. Organic carbon, pH, anaerobic N mineralization, aerobic N mineralization, and total N were determined using standard methods (Page and others 1982). Microbial biomass carbon was measured using a chloroform fumigation/potassium sulfate extraction procedure (Sparling and West 1988).

In a second study, five N manipulations were imposed in the heavily disturbed medusahead soils in November 1991. In the first three treatments, soils were fertilized with 30 kg/ha N ammonium sulfate, urea, or calcium nitrate. In the fourth treatment, sucrose was applied at 230 kg/ha in an effort to induce net immobilization of mineral N. The fifth treatment was an application of the nitrification inhibitor, N-serve. The treatments were replicated four times as a randomized complete block design. On April 7, 1992, ocular estimates of percent cover, squirreltail leaf lengths, and seedling densities were quantified using a 0.01-m² quadrat.

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Table 1—Organic carbon and soil nitrogen parameters for undisturbed soils (UNSAG = soil beneath the sagebrush canopy; UNINT = soil between sagebrush plants), moderately disturbed soils (MODSAG = soil beneath the sagebrush canopy; MODINT = soil between sagebrush plants), and heavily disturbed soils (DISEL = soil adjacent to *Elymus hystrix*; DISMED = soil beneath medusahead litter)

Location	ORGCAR	ANAEROB NH4-MIN	AEROBE N-MIN	TOT N	C:N	H20 pH	CaCl₂ pH
	Percent		· · · · · (µg/g) · · · ·				
UNSAG	0.96 ab ¹	17.64 a	1.11	524 ab	20	6.85 b	6.31 bc
UNINT	.46 c	2.74 b	1.38	214 b	22	6.92 b	6.17 c
MODSAG	1.24 a	19.93 a	2.44	869 a	15	6.78 b	6.56 b
MODINT	.64 bc	1.14 b	1.29	353 b	18	6.88 b	6.65 b
DISEL	.60 bc	7.52 ab	.91	509 ab	14	7.50 a	7.26 a
DISMED	.50 bc	4.91 b	.80	298 b	17	7.46 a	7.27 a
P-VALUE ²	0.016	0.022	0.34	0.055	0.15	0.0001	0.0001

¹Values in columns followed by the same letter are not significantly different at *P* < 0.05 according to mean separations by Least Significant Differences. ²Probability values obtained using ANOVA.

RESULTS

Differences in microbial populations and soil properties among sites were found (tables 1 and 2). Soil pH was significantly greater in the heavily disturbed site. Soils beneath sagebrush had greater levels of organic carbon than soils from other sites. Total N and anaerobic N mineralization was greatest in soils collected beneath sagebrush. Total N and anaerobic N mineralization was least in soil collected from sagebrush interdunes and heavily disturbed medusahead soils. Heavily disturbed soils containing squirreltail were intermediate. Aerobic N mineralization and C:N ratios were not significantly different among sites. Bacterial numbers were not significantly different among sites. Heavily disturbed, moderately disturbed, and undisturbed soils in general had similar fungal hyphal lengths; however, undisturbed interdune soils had distinctly lower hyphal lengths. Actinomycete numbers and hyphal lengths were significantly greater in heavily and moderately disturbed soils, when compared to undisturbed soils. Microbial biomass carbon was greatest in soils adjacent to squirreltail and sagebrush, and least in medusahead and interdune soils.

In the N manipulation study, medusahead germination was significantly greater in all fertilization treatments (table 3). Medusahead density was six, four, and four times greater than controls in the calcium nitrate, ammonium sulfate, and urea treatments, respectively. Medusahead density in the sugar, N-serve, and control treatments was not significantly different. Squirreltail leaf length was also stimulated by N fertilization and slightly inhibited by N-serve application.

DISCUSSION

In contrast to what has been observed in agroecosystems after soil disturbance (Hendrix and others 1986), we did not find a significant shift from fungaldominated to bacterial-dominated systems with increased disturbance. The low levels of fungal hyphal length would suggest that nutrient cycling in general is largely dominated by bacteria at all sites, regardless of disturbance history. The higher numbers of actinomycetes in disturbed soils may be a consequence of the change in soil structure observed after disturbance. After fire and heavy grazing, the loss of sagebrush and the thin sandy

Table 2—Microbial carbon (MIC CARB), bacterial numbers (BACT #), actinomycete numbers (ACTIN #), actinomycete hyphal length (ACTIN), and fungal hyphal length (FUNGI) (location descriptions are in table 1)

Location	MIC CARB (x 10 ⁷)	BACT # (x 10 ⁷)	ACTIN #	ACTIN	FUNGI
	μ <i>g/g</i>			m/	g
UNSAG	671 ab ¹	66.0	1.78 d	56.4 c	3.5 a
UNINT	370 c	43.8	1.61 d	26.6 c	.7 b
MODSAG	852 a	114.0	14.01 a	376.0 a	2.8 ab
MODINT	504 bc	101.0	3.73 cd	95.8 c	3.0 ab
DISEL	617 abc	113.3	10.13 ab	305.4 ab	4.6 a
DISMED	480 bc	87.2	6.67 bc	155.7 bc	3.6 a
P-VALUE ²	0.026	0.34	0.0001	0.0031	0.091

¹Values in columns followed by the same letter are not significantly different at *P* < 0.05 according to mean separations by Least Significant Differences.

²Probability values obtained using ANOVA.

Table 3-	-Medusahead density, cover, and Elymus hystrix leaf
	length in relation to soil nitrogen manipulations.
	Treatments imposed in November 1991, and
	measurements taken April 7, 1992

Treatment	Medusahead seedlings/0.01 m ²	Medusahead cover	Elymus leaf length cm	
	··· ····························	Percent		
Control	5 c ¹	6 C	12.4 b	
Sugar	4 c	4 c	11.6 bc	
N-serve	6 C	5 c	9.7 c	
NH4SO4	20 b	23 b	17.8 a	
Urea	20 b	25 b	18.1 a	
CaNO ₃	32 a	52 a	19.1 a	

¹Values in columns followed by the same letter are not significantly different at P < 0.05 according to mean separations by Least Significant Differences.

veneer at these sites results in the exposure of smectitic clays. Clays typically are more heavily colonized by bacteria and actinomycetes than fungi (Stotzky 1986).

Laboratory incubations indicated that soils beneath sagebrush plants had a greater potential for nitrogen mineralization than sagebrush interspace and medusahead soils. We have also shown that N fertilization can stimulate medusahead germination. Hence, removal of sagebrush by fire should result in patches of soil with high levels of mineral N that should stimulate medusahead germination. Sugar additions to the medusahead seedbed did not reduce medusahead seed germination. Lack of a sugar effect could mean that (1) controls are already low in mineral N, resulting in minimum germination; (2) sugar is not an adequate carbon substrate for reducing mineral N below control levels; or (3) germinating seeds already received nitrate priming from the previous year and sugar would have a greater effect in the second year of the study. N-serve inhibits the transformation of ammonium to nitrate, which should reduce the pools of nitrate in the soil and lower germination. However, there was no effect of N-serve on germination. As with the sugar treatment, germinating seeds may have already received enough nitrate from the previous year; therefore, an N-serve effect may be more evident in the second year of this study.

Innovative methods in managing these microbial processes may allow us to reduce the competitive ability of medusahead after soil disturbance or vegetation removal by fire. The effect of nitrification inhibitors or organic amendments on soil mineral N and medusahead germination should be investigated in greater detail. Manipulations that reduce soil nitrate should reduce medusahead germination and favor perennial grasses such as squirreltail. In addition, further research into biocontrol of medusahead and other weeds should consider the soil microbial community structure of each particular ecosystem. In the heavily disturbed medusahead ecosystem, bacteria and actinomycetes dominate over fungi, hence a bacterial or actinomycete biocontrol agent may be more effective than a fungal biocontrol agent.

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CONTROLLING EROSION ON LANDS ADMINISTERED BY THE BUREAU OF LAND MANAGEMENT, WINNEMUCCA DISTRICT, NEVADA

Michael J. Zielinski

The Bureau of Land Management (BLM) Winnemucca District consists of approximately 4 million hectares. The Winnemucca District is located in the northern Great Basin. The extremes of climate, relief, aspect, and geologic type all combine to produce a diverse environment. Numerous wildfires occur within the district. The dominant vegetative communities where fire occurrence is most frequent are the Wyoming big sagebrush (Artemisia tridentata wyomingensis) and the shadscale (Atriplex confertifolia) communities.

The following information is extracted from the "Ten Year Fire History Report" for the district or the "Burn Area Reports" for each fire.

In the past 10 years, 602 fires have burned 305,000 hectares. Fire size varies, but fires between 17,000 and 46,000 hectares are not uncommon. The peak fire year was 1985, burning 208,800 hectares.

Seeding projects have been conducted on 25,500 hectares. The objectives of the fire rehabilitation program are:

1. Prevent loss of soil through erosion and loss of onsite productivity of ecological sites. ("Ecological site" and "range site" are synonymous; an ecological site or range site is a distinctive kind of rangeland that differs from other kinds of rangeland in its ability to produce a characteristic natural plant community; definition from section 302.1 National Range Handbook.)

2. Prevent damage to property on and off site (such as loss of structures, roads, irrigation systems, power and communication lines).

3. Prevent the invasion of burned areas by highly flammable annual plants that produce a high potential for a reburn and additional site deterioration.

NATURAL REVEGETATION

Natural revegetation is the principle rehabilitation method for 92 percent of the burned areas (this information is extracted from the district fire reports). Areas are closed to livestock grazing for a minimum of two growing seasons. Livestock closure applies to all treatment methods.

Livestock closure support facilities are necessary to control livestock grazing. These facilities create physical barriers to livestock to assure that grazing does not take place. Rest from grazing provides the native species sufficient time for seed germination and for development of adequate seedling root growth to prevent uprooting by grazing. It also allows perennials and seedlings to develop good vigor and produce viable seed.

SEEDING

Seedings are implemented in areas that lack sufficient perennial species for natural revegetation. Rangeland drills or broadcast seeders are used. Rangeland drills can be used on slopes up to 25 percent. Aerial seeding is not used in the district because of vesicular crusting and low annual precipitation. No broadcasted seed is planted into Wyoming big sagebrush or shadscale communities, unless seed is covered by chaining or harrowing.

Of the hectares seeded (25,500), 78 percent (19,900 hectares) occurs in the Wyoming big sagebrush communities, 14 percent (3,600 hectares) in the basin big sagebrush (*Artemisia tridentata tridentata*) communities, 5 percent (1,300 hectares) in the mountain big sagebrush (*Artemisia vaseyana*) communities, and 3 percent (800 hectares) in the shadscale communities.

Seed prescription is based on pure live seeds per square foot (PLS/ft²). Seeding rates have a minimum of 20 PLS/ ft² for drills; rates range between 20 to 40 PLS/ft². The rate for broadcasted seed is double the drill rate.

VEGETATIVE WATERWAYS

Vegetative waterways are drainage channels that have been seeded by broadcasting seed. Seed prescriptions are a combination of grasses and forbs. This method is used in steep terrain, where access by rangeland drills is not possible.

EROSION MATS

Erosion mats have been used to armor headcuts or line drainage channels. Erosion mats are tough, waterpermeable fabrics. Before placing the erosion mat, the area is broadcast seeded. The erosion mat is rolled onto the ground surface and is anchored.

GREENSTRIPPING

The greenstripping treatment is intended to slow or stop the spread of wildfire by placing strips of fireresistant vegetation strategically on the landscape to

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reduce wildfire size and frequency (Pellant 1990). This treatment is used principally in the Wyoming big sagebrush communities. A seedbed is prepared by removing existing vegetation.

A common method of removing vegetation and preparing a seedbed is spring plowing, which is done to set seed of annual species, to reduce competition. The strips lay fallow during the summer and early fall. Drill seedings are completed in the fall, from mid-October through November. The strips are generally 100 meters wide and adjacent to existing roads. The roads serve as access points for fire suppression crews.

TREND DETERMINATION

Treatments discussed here are based on monitoring (Community Structure Analysis and Density Studies) and observation of fires beginning in 1984. Studies are read for 3 consecutive years, then at 5-year intervals to determine trend.

NATURAL REVEGETATION

Natural revegetation areas lack sufficient perennial species for natural recovery or are inaccessible to mechanical equipment. To determine areas that have natural recovery potential, the soil and ecological site must be determined. Third-order soil surveys are the basis for determining ecological sites.

From the ecological site, the ecological status or seral stage can be determined. Ecological status or seral stage is determined by comparing the present plant community with that of the climax community. A rating of 0-25 is early, 26-50 mid, 51-75 late, and 75-100 climax. Successful natural recovery will occur in late or climax status. Seeding failures will result in areas of late status, due to competition from existing perennial species.

Four vegetative communities will be discussed: the shadscale, the Wyoming big sagebrush, the basin big sagebrush, and the mountain big sagebrush.

Shadscale—Shadscale communities in late ecological status naturally recover within 5 years. Natural recovery results in two to five shrubs per meter. The reestablished shrubs are from seed reserves in the soil.

It is essential that areas are rested from livestock grazing for a minimum of 2 years. First-year shadscale seedlings lack spines and are highly susceptible to grazing. Plants develop spines in the second year. Without livestock controls, these plant communities will be dominated by annual species. Early and mid status communities will be dominated by annual species.

The common soil subgroups for these plant communities are: Duric or Typic Camborthids, Duric or Typic Natrargids, Typic Durorthids, and Typic Nadurargids. Precipitation is between 4 and 8 inches. The potential vegetative composition is about 70 percent shrubs, 25 percent grasses, and 5 percent forbs.

Wyoming Big Sagebrush — Wyoming big sagebrush communities have the poorest natural recovery for shrubs. Eight years of monitoring indicate that no Wyoming big sagebrush recovery has occurred. These plant communities are highly susceptible to annual plant invasion by cheatgrass (*Bromus tectorum*).

The common soil subgroups for Wyoming big sagebrush communities are: Durixerollic or Xerollic Camborthids, Durixerollic or Xerollic Haplargids, Durixerollic or Xerollic Natrargids, Xerollic Durorthids, and Xerollic Nadurargids. Annual precipitation is between 8 and 12 inches. The potential vegetative composition is about 55 percent grasses, 40 percent shrubs, and 5 percent forbs.

Basin Big Sagebrush—Basin big sagebrush communities have poor natural recovery for shrubs, from a trace to one plant per meter. The common soil subgroup for the basin big sagebrush communities is Xeric Torripsamments. Annual precipitation is between 8 and 10 inches. The potential vegetative composition is about 55 percent grasses, 35 percent shrubs, and 10 percent forbs.

Mountain Big Sagebrush — Mountain big sagebrush communities' natural recovery occurs within 15 years and has been one to two shrubs per meter. In mid status, shrubs will recover, but native grasses and forbs will be lacking.

The common soil subgroups for the mountain big sagebrush community are Typic Haploxerolls and Typic Argixerolls. Annual precipitation is between 12 and 16 inches. The potential vegetative composition is 65 percent grasses, 25 percent shrubs, and 10 percent forbs.

SEEDINGS

Seeding treatments are based on soil suitability as rated by the Nevada State Seeding Guide, and ecological status. Soil suitability is determined by reviewing the third-order soil survey and by an on-site investigation. If left to natural rehabilitation, areas would be invaded by less-desirable annual plant species. Sites with similar characteristics, after past burns, have become dominated by annual plant species such as cheatgrass, halogeton (*Halogeton glomeratus*), mustards (*Brassica*), and Russian thistle (*Salosola kali*).

Areas that are dominated by annual species have a high potential for recurring wildfires, which eventually degrade a site beyond its ability to naturally regain the potential ecological community it was once capable of producing. Young and Evans (1978) stated, "The reestablishment of downy brome (cheatgrass) dominance predisposes the vegetation to recurring wildfires and cyclic environmental degradation. Downy brome has the inherent competitive ability to close seral communities to seedlings of perennial grasses. Downy brome is the symbol of environmental degradation if the pristine vegetation is used as the benchmark of judging range condition."

Seedings provide sufficient competition to prevent total annual species invasion. This in turn maintains site productivity by preventing frequent wildfires.

SEEDING SUCCESS BY PLANT COMMUNITIES

Seedings in shadscale have resulted in failure. Seeding success is between 50 and 75 percent in the Wyoming big

sagebrush areas. Seeding success is less then 25 percent in the basin big sagebrush (sandy) areas. Aerial seeding in the mountain big sagebrush areas has resulted in failure. Drilled seedings have not been conducted in these areas; steep slopes have been the limiting factor.

SEED PRESCRIPTIONS

Seed prescriptions are based on surface texture, moisture regime, available water capacity, salinity, sodicity, and surface morphological type. Each seed prescription is adapted to the particular soil type and ecological site. A slight soil difference can make the difference between a success or failure.

For example, consider an 810-hectare burn composed of 485 hectares of a Duric Natrargid in late status and 325 hectares of a Durixerollic Natrargid in mid status. Soil characteristics are identical except for percent organic carbon-0.4 to 0.6 and 0.6 to 0.8, respectively. What is the best rehabilitation option? Seed the entire area, allow for natural recovery, or provide a combination of both?

The Duric Natragids will recover naturally. A seeding of crested wheatgrass will have less than a 50 percent chance of survival. The Durixerollic Natragids will be dominated by annual species, unless the area is seeded. If the objective of seeding is erosion control, then adapted species must be planted. A seeding failure will not remedy the situation. Seed prescriptions thus include native and introduced species.

COVER CROPS

Seedings of cover crops for erosion control of blowing sands have two purposes: (1) erosion control and (2) protection of existing perennial species for reestablishment. Controlling wind erosion is a major problem within the Winnemucca District. Fine sand surface textures left barren after fires have created severe erosion problems. Rapid erosion control treatments are essential to prevent damage to resources. Wind erosion can remove 6 to 19 millimeters, or 62 to 185 tons of soil per hectare per year. Cover crops of cereal rye are a quick solution to this problem, as they stabilize the surface for reestablishment of perennial or annual vegetation.

Cover crops have been used to prevent dust hazard along roads or adjacent to urban development. Strong winds periodically create severe dust hazards, which have limited visibility on State highways and Interstate 80. Traffic has been forced to stop or to travel only one way. The potential exists for vehicular accidents and serious personal injuries. The worst accident was a chain collision of 23 vehicles on Interstate 80.

VEGETATIVE WATERWAYS

Vegetative waterways are an effective erosion control treatment in mountainous areas. Vegetative waterways are natural drainage channels, seeded to grasses and forbs. Seeding success has been 100 percent on eight projects. The vegetation serves as a filter to trap sediment and decreases velocity of runoff, preventing gully formation. Livestock have had a detrimental effect by severely grazing established vegetation, which has reduced the effectiveness of this treatment.

The common soil subgroup for this treatment is Fluventic Haploxerolls. Annual precipitation is between 12 and 16 inches.

EROSION MATS

This treatment is rarely used, because the cost of installation is generally prohibitive. This treatment is used to lessen sediment in watershed areas that have viable fisheries.

GREENSTRIPPING

Greenstripping is a new technique used for slowing or stopping the spread of wildfires. This technique was first tried in the mid-1980's in Idaho. Success of the program has resulted in implementation of similar projects in the Winnemucca District.

Reducing wildfire frequency and size results in important benefits. By protecting fire-susceptible vegetation types from wildfire, important rangeland resources such as wildlife habitat, livestock forage, and watershed stability are maintained. Loss of private structures and properties on urban/rural interfaces with public rangelands is reduced. Large annual rangelands are broken into smaller, more fire-manageable blocks. Suppression and rehabilitation costs are reduced (Pellant 1990).

Sagebrush vegetation types in the Great Basin evolved in an environment that included wildfire at return intervals of 32 to 70 years (Wright and others 1979). Alien annual species were introduced and rapidly expanded in extent and dominance on degraded rangelands (Young and others 1972). Cheatgrass is one of the alien annual plants that is highly flammable, has a high potential for reburn, and causes additional site deterioration. The recurring wildfires eventually degrade the sites beyond their ability to naturally regain the ecological community they once could produce (Young and Evans 1978). Greenstripping is a treatment used to reverse this trend.

CONCLUSIONS

Third-order soil surveys provide information resource managers need to develop cost-effective and successful vegetative erosion control treatments. Management options and success can be related directly to the predictability of the soil type's response to treatment, which is determined through analysis of the area's soil and ecological status. The objectives of the fire rehabilitation program can be accomplished.

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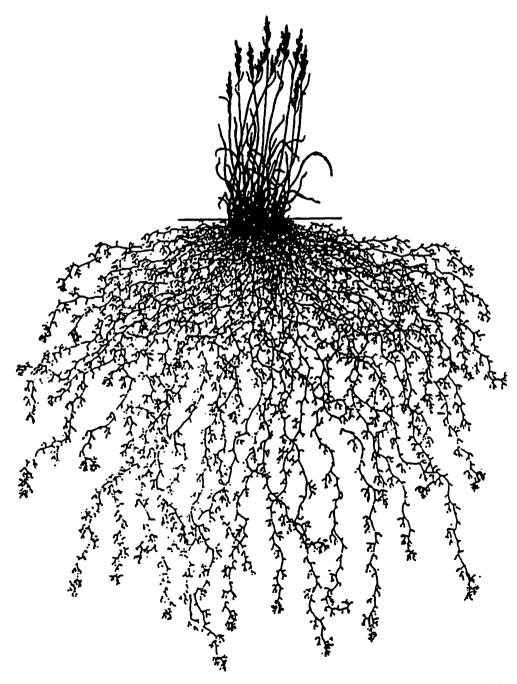
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Resources



Poa sandbergii

WASHINGTON STATE SHRUB-STEPPE ECOSYSTEM STUDIES WITH EMPHASIS ON THE RELATIONSHIP BETWEEN NONGAME BIRDS AND SHRUB AND GRASS COVER DENSITIES

Frederick C. Dobler

ABSTRACT

Fifty-five shrub-steppe sites were surveyed to determine bird species composition. Bird and plant diversity were positively correlated. Range condition was also correlated to bird diversity. Sagebrush cover density was positively related to occurrence for seven birds, including sage thrasher, sage sparrow, and Brewer's sparrow. Long-billed curlew and savanah sparrow showed the opposite relationship. Annual grass cover density was negatively related to occurrence for four birds, including sage thrasher and sage sparrow. No species showed the opposite relationship.

INTRODUCTION

When the first settlers arrived in eastern Washington they found an expansive landscape of sagebrush and bunch grass. At first considered "worthless for agriculture," it provided unbroken habitat for many species of wildlife adapted to this arid environment. Soon the seemingly limitless shrub-steppe was being grazed and then tilled, as wave after wave of pioneers made claims on the land. Today about 59 percent of the original shrub-steppe habitat in Washington has been converted to agriculture, leaving much of what remains fragmented and degraded.

While some workers have made extensive studies of shrub-steppe birds (Rotenberry and Wiens 1978, 1980; Wiens and Rotenberry 1981, 1985), the Washington Department of Wildlife thought in 1988 that more effort was needed to assess the condition of the nongame bird community at large, and especially in Washington. Most of the nongame animals that use the shrub steppe remained poorly understood, and while most were not yet thought to be in critical need (although some notable exceptions occurred), a feeling of concern had grown as agricultural development continued to reduce the remaining shrub-steppe area. While recognized by a few, the value of shrub steppe to wildlife was not easily demonstrated, since its complex relationships were not easily quantified.

The Department of Wildlife therefore set out to describe and quantify wildlife and habitat relationships in Washington's shrub steppe. While an extensive library

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of work exists on the management of rangeland, it nearly always views management with regard to livestock production or game habitat. We decided to approach our studies from a community-based approach rather than from a single-species approach with the hope that the important needs and management strategies would reveal themselves with as little prejudice as possible.

STUDY AREAS

Potential site locations were found using LANDSAT Thematic Mapper data to locate areas of shrub-steppe habitat in the Columbia Basin of Washington. Sample sites were chosen using a stratified random scheme with modifications. The 1988 study area was restricted to habitat north of Interstate 90, and 31 sites were chosen in three counties. In 1989 the study area was expanded to include the area south of Interstate 90. Twenty-four sites were selected for this area. Twenty-one of the 1988 sites were randomly selected for use in the 1989 and 1990 censuses, making a total of 45 survey sites in those years, and a total of 55 sites for all years.

Once the sites were selected, transect locations were chosen using a random starting point to place the 500meter north-south transect, with no point on the line closer than 50 meters to an edge.

BIRD SURVEYS

In 1988 and 1990 the transects were surveyed four times, but in 1989 there were only three runs of each transect. All surveys occurred between April 1 and June 6 of each year. An attempt was made to spread the repetitions out over the entire sample period to reduce seasonal bias. Transects were staked at each end with wooden stakes and surveyed following procedures outlined by Mikol (1980).

VEGETATION MEASUREMENT

Line intercept and microplot measurements were made of each transect on a parallel line 5 meters west of the flagged transect. Beginning at either end, the transect was divided into 10 equal 50-meter segments. Every other segment was selected for vegetation sampling. Line intercept was used to measure shrub cover along the entire length of each selected segment. Only the live parts

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of the shrub canopy were counted, and open spaces within the shrub larger than the range seen in healthy growing parts were not included in the summation. This range was estimated visually and was qualitative rather than quantitative. Ten microplots (Daubenmire 1959) were placed along each of the selected segments, beginning at 0 meters and then one every 5 meters.

Annual grasses were grouped together when measuring cover classes, as were annual forbs. Perennial grasses were separated to species. Perennial forbs were keyed to genus except in cases where species determination was unambiguous, such as where only one species could be present, such as yarrow (*Achillea millifolia*), and then species was recorded. Shrubs were always separated to species.

VEGETATION MEASUREMENT RESULTS

Ninety-six perennial plants were recorded by the vegetation survey. Sixteen of those species were shrubs. The most common shrub species was big sagebrush (*Artemisia tridentata*), occurring on 76 percent of the transects. The next most common was grey rabbitbrush (*Chryso-thamnus nauseosus*) occurring on 58 percent of the transects. Table 1 gives occurrence values for these and the other woody species.

The average mean percent cover for big sagebrush for the 42 transects where it occurred was 6.7 percent. The mean percent cover by transect was as high as 19.2 percent. This cover was exceeded in 16 segments (a segment is 50 meters long) in 10 different transects where the greatest cover for a segment was equal to 31.7 percent.

Twenty species of perennial grasses were recorded by the microplot measurements. The most common grass was Sandberg bluegrass (*Poa sandbergii*), occurring on 98 percent of the transects and in 68 percent of the combined plots. The mean percent cover ranged as high as 33.9 percent by transect, and the average for the 54 transects where it occurred was 16.8 percent. Next most common was bluebunch wheatgrass (*Agropyron spicatum*), occurring on 75 percent of the transects and in 27 percent of the plots. The mean percent cover ranged as high as 41.9 percent by transect, and the average for the 41 transects where it occurred was 12 percent.

Annual grasses were combined in the microplot measurements, but cheatgrass (*Bromus tectorum*) was by far the most common annual grass. The occurrence of annual grasses was almost universal; they were present on every transect and in 76 percent of the microplots. The percent cover values ranged higher than any other plant measured by the plots, reaching 75.7 percent on one transect, and had an average value for all transects of 20 percent, higher than any other species, shrubs and forbs included.

Fifty-eight perennial forbs were recorded in the microplot measurements. Six were present on more than half the transects. They were *Phlox, Lomatium,* yarrow, *Lupinus, Erigeron,* and *Eriogonum.* Except where a forb occurred on only one transect, no forb had average cover values exceeding 3 percent (average for only the transects where the forb was recorded).

Annual forbs were combined in the microplot measurements, and the group comprises an undetermined number of individual species, with no single species dominating, unlike cheatgrass for the annual grasses. Annual forbs were found on every transect and in 74 percent of the plots. The percent cover values ranged as high as 49.7 on one transect and had an average of 12.3 percent for all transects combined. Table 2 gives percent occurrence and mean percent cover for grasses and forbs.

	Occu	rrence	Perc	ent cover	
Species	Number	Percent	Mean	Range	
Artemisia tridentata	42	76.4	6.7	0.3	19.2
Chrysothamnus nauseosus	32	58.2	1.0	.0	3.7
Chrysothamnus viscidiflorus	22	4.0	.9	.1	2.8
Artemisia rigida	18	32.7	2.6	.1	7.2
Artemisia tripartita	17	3.9	1.4	.2	3.6
Tetradymia canescens	11	2.0	.6	.0	1.6
Artemisia arbuscula	5	9.1	1.6	.2	5.9
Ribes aureum	5	9.1	.8	.1	1.4
Rosa nutkana	5	9.1	.9	.2	2.1
Populus spp.	3	5.5	2.4	.3	3.8
Prunus spp.	3	5.5	1.7	.0	4.0
Purshia tridentata	2	3.6	4.0	2.6	5.3
Sarcobatus vermiculatus	2	3.6	1.0	.6	1.4
Symphoricarpus albus	2	3.6	3.3	2.8	3.9
Amelanchier alnifolia	1	1.8	_	_	_
Berberis repens	1	1.8	—	_	
Holodiscus discolor	1	1.8		_	
Leptodactylon pungens	1	1.8	_	_	_

Table 1—Occurrence, percent occurrence, and mean percent cover for shrubs and trees found on 55 shrub-steppe transects, measured by line intercept. Mean percent cover calculation does not include transects where the species is absent

Table 2—Percent occurrence by transect and plot, mean percent cover for all transects combined, and the range of percent cover. Mean
percent cover does not include transects where species was absent

O menian	N1	Occurrence	Desistent	88	Percent cover	Donas
Species	Number	By transect	By plot	Mean		Range
GRASSES						
gropyron cristatum	2	3.6	1.1	5.4	3.5	7.
Agropyron dasystachyum	2	3.6	.3	.8	.4	1.:
Agropyron intermedium	1	1.8	.2	1.3		-
gropyron spicatum	41	74.5	27.4	12.1	.1	42.
nnual grass	55	100.0	76.0	20.1	.1	75.
Distichlis	4	7.3	1.5	4.2	.3	11.
Elymus cinereus	13	23.6	1.2	1.9	.1	9.
Elymus glaucus	2	3.6	.1	.4	.1	-
estuca idahoensis	15	27.3	5.2	4.7	.8	14.
lordeum jubatum	4	7.3	1.6	4.9	.3	12.
Coeleria cristata	4	7.3	.4	1.2	.1	2.
Dryzopsis hymenoides	4	7.3	.8	4.8	.1	16.
Poa ampla	7	12.7	.5	.4	.1	1.
Poa bulbosa	4	7.3	.3	.1	.1	
Poa cusickii	6	10.9	1.3	2.4	.1	10.
Poa pratensis	8	14.5	2.6	6.1	1.1	26.
Poa sandbergii	54	98.2	67.9	16.8	3.1	51.
Sitanion hystrix	54	14.5	78.8	.1	.1	1.
Stipa comata	18	32.7	5.3	4.2	.3	22.
Stipa occidentalis	13	23.6	4.5	4.9	.3	20.
Stipa thurberiana	8	14.5	3.0	5.8	.3	27.
ORBS						
Achillea millefolium	31	56.4	7.9	2.2	.1	11.
Agoseris glauca	4	7.3	.8	1.5	.1	5.
Vlium	8	14.5	.7	.5	.1	1.
unnual forb	55	100.0	73.9	12.3	1.0	49.
Intennaria	9	16.4	.4	.4	.1	1.
Artemisia douglasiana	1	1.8	.0	.8		-
Arnica fulgans	1	1.8	.1	1.8	—	-
Aster	5	9.1	.6	1.4	.3	3.
Astragalus	21	38.2	1.8	.5	.1	1.
Balsamorhiza careyana	¹ 1	1.8	.3	7.0		-
Balsamorhiza hookeri	9	3.6	.3	.2	.1	1.
Balsamorhiza rosea	1	1.8	.0	.1	—	-
Balsamorhiza sagittata	7	12.7	1.3	3.1	.3	6.
Brassica	2	3.6	.1	.2	.1	
Carex filifolia	15	27.3	5.4	7.0	.1	21.
Calochortus macrocarpus	1	12.7	.4	1.1	.1	-
Castilleja thompsonii	1	1.8	.0	.3	_	-
Chaenactis douglasii	5	9.1	.6	.6	.1	1.
Cirsium vulgare	1	1.8	.0	.8	—	-
Comandra umbellata	2	3.6	.4	1.4	-	-
Crepis atribarba	5	9.1	1.3	1.9	.1	4.
Delphinium	8	14.5	1.8	1.3	.3	5.
Erodium circutarium	1	1.8	.0	.1	—	-
Erigeron	28	50.9	4.4	1.3	.1	4
Eriogonum	28	50.9	6.5	1.9	.1	6
Frasera	1	1.8	.1	.3		•
Fritillaria pudica	1	1.8	.1	.1		-
Gaillardia aristata	4	7.3	.3	.5	.1	1
Galium	9	16.4	1.1	.7	.1	1
Geranium	2	3.6	.1	.8	—	-
Gilia	1	1.8	.1	.6	_	-
Haplopappus stenophyllus	1	1.8	.0	.1	_	-
Hieracium	7	12.7	1.0	1.3	.3	3
ris	1	1.8	.1	1.1		
luncus	t	1.8	.0	1.3	_	-
Lowisia	i	1.8	.0	.1	_	
Linum perenne	1	1.8	.3	4.8	_	
Lithosperma ruderale	4	7.3	.2	.5	.1	1

Table 2 (Con.)

		Occurrence			Percent cover	
Species	Number	by transect	By plot	Mean	Range	
Lithophragma	1	1.8	.0	.1	_	_
Lomatium	33	2.4	8.6	1.3	.1	5.0
Lupinus	29	4.0	6.4	2.2	.1	7.2
Medicago sativa	1	1.6	.1	.9	—	_
Microseris troximoides	2	.8	.3	.5	.3	.6
Oenothera	3	1.4	.6	.8	.1	1.9
Orthocarpus	11	1.2	1.7	.7	.1	1.6
Oxytropis	1	.1	.0	.1	—	
Penstemon confertus	1	12.8	.3	7.0	—	_
Phlox	36	2.2	7.6	1.2	.1	5.6
Potentilla	4	2.7	.3	1.5	.1	3.5
Psoralea	1	.7	.1	.4	—	
Ranunculus	1	.6	.1	.3		_
Rumex venosus	2	1.9	.3	1.1	.9	1.2
Sedum	2	1.1	.1	.6	.6	.6
Sisyrinchium	1	.1	.1	.1		_
Sporobolus	1	1.9	.1	1.1	_	_
Trifolium	4	3.8	5.0	2.1	.3	5.2
Urtica dioica	1	.1	.0	.1	_	
Vicia	2	.4	.1	.2	.1	.3
Viola trinervata	2	1.7	.5	.9	.1	1.8

BIRD MEASUREMENT RESULTS

In the 3 years of survey, 93 species of birds were recorded on the 55 transects. Table 3 gives for each species the total number, number of observations, number of transects where the species was present, and number of runs where the species was seen. In 1988, 71 species of birds were observed in four replicate samples; in 1989, 58 species were observed in three replicates; and in 1990, 62 were observed in four. Only one species of bird was seen in 100 percent of the sample sites, the western meadowlark (*Sturnella neglecta*). It was seen in over 96 percent of all runs in every year. A run is one survey of a transect. The next most ubiquitous

 Table 3—Bird occurrence by species, giving the total number observed, the total number of independent observations, and the percent occurrence by all transects combined and by all runs combined. A run is a single survey on a transect. Species with one observation are listed at the bottom of table

	Total	Total	Percent occurrence		
Species	birds	observations	Transects	Runs	
1988 TRANSECTS					
Western meadowlark	717	641	100.0	98.4	
Brewer's sparrow	467	444	83.9	70.7	
Vesper sparrow	446	408	96.8	87.8	
Horned lark	425	286	80.6	65.9	
White-crowned sparrow	371	138	77.4	43.1	
Sage thrasher	100	98	61.3	48.8	
Savannah sparrow	88	82	51.6	26.8	
Brewer's blackbird	142	70	45.2	20.3	
American robin	58	49	25.8	16.3	
Brown-headed cowbird	60	48	38.7	19.5	
Mourning dove	46	40	38.7	20.3	
Sage sparrow	38	36	22.6	14.6	
Starling	50	33	35.5	17.1	
Killdeer	33	27	32.3	17.9	
Common raven	31	24	41.9	17.1	
Ring-necked pheasant	25	24	22.6	16.3	
Chukar	26	20	16.1	8.1	
Grasshopper sparrow	18	18	9.7	6.5	
American kestrel	18	18	41.9	13.8	
				(con.)	

Table 3 (Con.)

	Total	Total	Percent occ	
Species	birds	observations	Transects	Runs
Rufous-sided towhee	19	18	12.9	8.1
American goldfinch	26	17	12.9	5.7
Common flicker	18	17	19.4	10.6
Valley quail	16	15	16.1	9.8
Song sparrow	15	15	12.9	8.1
Gray partridge	25	15	25.8	11.4
Rock wren	14	14	12.9	7.3
Red-winged blackbird	18	12	22.6	8.9
Black-billed magpie	14	12	19.4	7.3
Canada goose	136	10	22.6	7.3
Northern harrier	10	9	25.8	7.3
Red-tailed hawk	8	8	16.1	6.5
Loggerhead shrike	8	8	12.9	5.7
House wren	9	8	3.2	3.3
Mailard	12	7	22.6	5.7
Violet-green swallow	17	7	19.4	10.6
Lark sparrow	7	6	12.9	3.3
Common snipe	6	6	9.7	4.9
Say's phoebe	6	6	9.7	4.1
Pine siskin	7	5	9.7	4.1
Dark-eyed junco	5	5	12.9	4.1
Yellow-rumped warbler	16	4	6.5	3.3
Cliff swallow	15	4	9.7	2.4
Clark's nutcracker	5	4	6.5	3.3
Yellow-headed blackbird	9	4	12.9	3.3
Sage grouse	6	3	3.2	1.6
Ruby-crowned kinglet	7	3	6.5	2.4
American wigeon	4	2	6.5	1.6
Green-winged teal	6	2	3.2	8. 8.
Northern oriole	2	2	3.2	.0
1989 TRANSECTS				
Western meadowlark	740	715	100.0	98.5
Horned lark	461	424	88.9	73.3
Brewer's sparrow	300	289	44.4	38.5
Vesper sparrow	247	245	51.1	50.4
Sage thrasher	123	123	33.3	30.4
Grasshopper sparrow	98	95	51.1	29.6
White-crowned sparrow	156	71	62.2	27.4
Sage sparrow	41	40	20.0	11.1
Savannah sparrow	41	34	26.7	10.4
Brown-headed cowbird	56	33	40.0	16.3
Long-billed curlew	36	31	31.1	17.0
Black-billed magpie	37	27	26.7	14.8
Rock wren	26	26	13.3	9.6
Mourning dove	35	26	33.3	14.1
Brewer's blackbird	26	22	28.9	12.6
Chukar	23	20	20.0	10.4
Common raven	24	18	28.9	11.9
Ring-necked pheasant	18	18	28.9	11.9
Lark sparrow	14	13	13.3	6.7
Killdeer	14	13	17.8	8.9
American robin	13	12	15.6	5.9
Red-winged blackbird	19	11	11.1	5.9
Northern harrier	11	9	20.0	6.7
House finch	14	8	8.9	3.0
Valley quail	7	7	4.4	3.0
Rock dove	11	6	6.7	3.0
Mallard	6	5	2.2	1.5
American kestrel	5	5	6.7	3.7
Loggerhead shrike	5	5	11.1	3.0
Yellow-headed blackbird	6	5	4.4	3.0
Cinnamon teal	9	4	6.7	3.0
Canada goose	7	4	4.4	2.2
-				(con.)

Table 3 (Con.)

And-Lalled hawk 3 6.7 2.2 Rough-legged hawk 4 3 4.4 1.5 Rough-legged hawk 3 3 6.7 2.2 Common filoker 3 3 6.7 2.2 Common filoker 3 3 6.7 2.2 Rufous-sided towhee 3 3 2.2 7.7 Buffehad 2 2 2.2 7.7 Putflehad 2 2 4.4 1.5 Sandhill crane 33 2 2.2 4.4 1.5 Barn exallow 2 2 4.4 1.5 5 Sandhill crane 33 2 2.2 4.4 1.5 Barn exallow 2 2 4.4 1.5 5 Sandhill crane 33 408 7.5 5 5 5 Barn exallow 20 33 19 80.0 35.0 3 3 3 3 3		Total	Total	Percent oc	
Rough-legged hawk 4 3 4.4 15 Common Bicker 3 3 2.2 1.5 Common Bicker 3 3 2.2 1.5 Rufeus-citcled towhee 3 3 6.7 2.2 Standing 2 2.2 7 Bufflenad 2 2.2 7 Standhil carne 33 2 2.2 7 Standhil carne 3 2 2.2 7 Standhil carne 3 2 2.2 7 Standhil carne 3 1.0 0.0 96.1 Horneol Lark 877 708 91.1 75.6 Standtraspratrow 400 46.7 2.9 13.9 Brown-beastner 77 50 44.8.9 1	Species	birds	observations	Transects	Runs
Rough-legged hawk 4 3 4.4 1.5 Common fileker 3 3 6.7 2.2 Common fileker 3 3 6.7 2.2 Rufous-aided towhee 3 3 6.7 2.2 Staffing 4 3 2.2 7.7 Buffichead 2 2.4 1.5 Sandhill cane 33 2 2.2 7.7 Barn swallow 2 2.4.4 1.5 1690 TRANSECTS 1690 TRANSECTS 11 7.56 Western meadowlark 847 7.86 100.0 66.1 1690 TRANSECTS 16 104 66.7 25.9 Pring-necked pheasant 97 61 60.0 92.6 Sage thrasher 75 71 42.2 26.7 Sage thrasher 75 71 42.9 13.9 Direver-heads dyneasant 97 61 60.0 92.6 Sage phraxow 33 37.6 <td>Red-tailed hawk</td> <td>3</td> <td>3</td> <td>6.7</td> <td>2.2</td>	Red-tailed hawk	3	3	6.7	2.2
Great-homed own 3 3 6.7 22 Gray participe 5 3 6.7 22 Starting 4 3 2.2 7.7 Mutous-cided towhee 3 6.7 2.2 7.7 American goldfinch 5 2 2.2 7.7 American goldfinch 5 2 2.4.4 1.5 Starting 2 2 4.4 1.5 Starting 2 2 4.4 1.5 Starting 77 788 90.0 96.1 1.75.6 Starting 77 708 91.1 75.6 56.6 75.6 56.7 23.9 31.1 <td>Rough-legged hawk</td> <td>4</td> <td></td> <td>4.4</td> <td>1.5</td>	Rough-legged hawk	4		4.4	1.5
Common Bicker 3 3 2.2 1.5 Rufue-aided towhee 3 3 6.7 2.2 Rufue-aided towhee 3 3 2.7 2 Buffishaad 2 2.2 7.7 Buffishaad 2 2.2 7.7 Bant Bead 2 2.2 7.7 Bant Bead State 2 2.4 1.5 Sandhill crane 33 2 2.4 1.5 Sandhill crane 33 2 2.4 1.5 Been TRANSECTS 1960 TRANSECTS 1966 104.0 66.7 5.6 5.56 Stearm meadowlark 847 7.96 90.0 35.0 3.6 3.6 Stearm meadowlark 847 7.6 1.1 2.2 6.7 3.6		3		6.7	
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1990 TRANSECTS Western meadowlark 847 798 100.0 96.1 homed lark 877 706 91.1 75.6 Brewer's sparow 607 566 75.6 55.6 Grasshopper sparow 203 199 60.0 35.0 Mite-cowned sparow 156 104 66.7 23.9 Ring-neckd pheasant 97 91 60.0 36.7 Sage thrasher 75 71 42.2 26.7 Sage sparow 76 69 28.9 13.9 Brown-headed cowbird 74 57 51.1 23.9 Brown-headed cowbird 74 57 51.1 23.9 Brown-headed cowbird 74 57 51.1 23.9 Brown-headed cowbird 74 67 50.48.9 19.4 Brown-headed cowbird 74 78 33.3 12.8 Song sparow 33 30.3 31.1 10.6 Commor raven <td< td=""><td></td><td></td><td></td><td></td><td></td></td<>					
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Homed lark 677 708 91.1 756 Brewer's sparrow 607 566 75.6 55.6 Grasshopper sparrow 203 199 60.0 35.0 Mite-conved sparrow 156 104 66.7 23.9 Ring-necked pheasant 97 91 60.0 35.0 Sage thrasher 75 71 42.2 26.7 Sage sparrow 76 69 28.9 13.9 Brown-headed cowbird 74 57 61.1 23.9 Brown-headed cowbird 74 57 61.1 23.9 Darch-billed mappie 46 33 37.8 15.6 Song sparrow 33 30 31.1 10.6 Song sparrow 17 16 22.2 6.7 <		0.47	700	100.0	00.4
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White-rowmed sparow 156 104 66.7 23.9 Sage thrasher 75 71 42.2 26.7 Sage thrasher 75 71 42.2 26.7 Sage sparow 76 69 28.9 13.9 Brown-headd cowbird 74 57 51.1 23.9 Brown-headd cowbird 74 46 48.9 19.4 Brackbilled magpie 46 37 28.9 13.9 Long-billed curlew 48 33 37.8 15.6 Song sparow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Sam swallow 20 15 22.2 6.7 Kildear 17 16 22.2 6.7 Satify 25 12 15.6 5.0 Satify 25 12 15.6 5.0 Satify 35 26 7.2 1.1 3.3 Sh					
Ring-necked pheasant 97 91 60.0 36.7 Sage thrasher 75 71 42.2 26.7 Sage sparrow 76 69 28.9 13.9 Brown-headed cowbird 74 57 51.1 23.9 Brown-headed cowbird 74 57 51.1 23.9 Brown-headed cowbird 104 46 48.9 19.4 Black-billed mappie 46 37 28.9 13.9 Long-billed curlsw 48 33 37.8 15.6 Song sparrow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Savannah sparrow 17 16 22.2 6.7 Kildeer 15 14 17.8 72 Ban swallow 20 15 22.2 6.7 Kildeer 15 14 17.8 5.0 Ouggerhead shrike 15 12 13.3 3.9 Red-winged blackbird 19 11 11.1 4.4 N	Grasshopper sparrow				
Sage thrasher 75 71 42.2 26.7 Sage sparow 76 69 28.9 13.9 Brown-haded cowbird 74 57 51.1 23.9 Mouring dove 67 50 48.9 19.4 Brower's blackbird 104 46 48.9 19.4 Black-bilde mapie 46 37 28.9 13.9 Long-billed curlew 48 33 37.8 15.6 Song sparrow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Chukar 27 21 20.0 8.3 Ring-billed gull 36 17 8.9 3.9 Savannah sparrow 17 16 22.2 6.7 Kildeer 15 14 22.2 7.2 Loggenhead shrike 15 12 13.3 3.9 Red-winged blackbird 19 11 11.1 4.4	-				
Sağe sparow 76 69 28.9 13.9 Brown-headed cowbird 74 57 51.1 23.9 Mourning dove 67 50 48.9 19.4 Brekvelide mappie 46 37 28.9 13.9 Long-billed curlew 48 33 37.8 15.6 Song sparow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Savannah sparrow 36 17 8.9 3.9 Savannah sparrow 17 16 22.2 6.7 Kildeer 15 14 22.2 7.2 Loggerhead shrike 15 14 22.2 7.2 Loggerhead shrike 15 12 13.3 3.9 Red winged blackbird 19 11 11.1 4.4 Short-aced owl 9 9 17.8 5.0 Armerican robin 15 12 13.3 3.9	Ring-necked pheasant	97	91	60.0	36.7
Brown-headed cowbird 74 57 61.1 23.9 Mourning dove 67 50 48.9 19.4 Brewer's blackbird 104 46 48.9 19.4 Black-billed mappie 46 37 28.9 13.9 Long-billed curlew 48 33 37.8 15.6 Song sparow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Bring-billed gull 36 17 8.9 3.9 Barn swallow 20 15 22.2 6.7 Starting 25 12 15.6 5.0 American robin 15 14 21.5 5.0 American robin 15 12 15.6 5.0 American robin 15 12 15.6 5.0 American robin 15 12 15.6 5.0 American robin 15 12 16.6 5.0 <t< td=""><td>Sage thrasher</td><td>75</td><td>71</td><td>42.2</td><td>26.7</td></t<>	Sage thrasher	75	71	42.2	26.7
Mourning dove 67 50 48.9 19.4 Brawer's blackbild maple 46 37 28.9 13.9 Long-billed curlew 48 33 37.8 15.6 Song sparow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Chukar 27 21 20.0 83 Savannah sparow 17 16 22.2 6.7 Killdeer 15 14 22.2 6.7 Killdeer 15 14 22.2 7.2 Deggerhead shrike 15 14 17.8 7.2 Starling 25 12 13.3 3.9 Red-winged blackbird 19 11 11.1 4.4 Northeared owl 9 9 17.8 5.0 Canada goose 39 8 15.6 4.4 Valley quail 7 2.2 1.7 Malard 13 7<	Sage sparrow	76	69	28.9	13.9
Brewer's blackbird 104 46 48.9 19.4 Black-billed mappie 46 37 28.9 13.9 Black-billed mappie 46 33 37.8 15.6 Song sparrow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Ring-billed gull 36 17 8.9 3.9 Savannah sparrow 17 16 22.2 6.7 Killdeer 15 14 22.2 7.2 Loggenhead shrike 15 14 22.2 7.2 Loggenhead shrike 15 12 13.3 3.9 Red-winged blackbird 19 11 11.1 4.4 Northern harrier 9 9 17.8 5.0 Canada goose 39 8 15.6 4.4 Valley quail 7 7 11.1 4.4 Northern harrier 9 9 17.8 5.0	Brown-headed cowbird	74	57	51.1	23.9
Brewer's blackbird 104 46 48.9 19.4 Black-billed mappie 46 37 28.9 13.9 Black-billed mappie 46 33 37.8 15.6 Song sparrow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Ring-billed gull 36 17 8.9 3.9 Savannah sparrow 17 16 22.2 6.7 Killdeer 15 14 22.2 7.2 Loggenhead shrike 15 14 22.2 7.2 Loggenhead shrike 15 12 13.3 3.9 Red-winged blackbird 19 11 11.1 4.4 Northern harrier 9 9 17.8 5.0 Canada goose 39 8 15.6 4.4 Valley quail 7 7 11.1 4.4 Northern harrier 9 9 17.8 5.0		67		48.9	19.4
Black-billed magpie 46 37 28.9 13.9 Long-billed curlew 48 33 37.8 15.6 Song sparrow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Shing-billed gull 36 17 8.9 3.9 Savannah sparrow 17 16 22.2 6.7 Barn swallow 20 15 22.2 6.7 Barn swallow 20 15 22.2 6.7 Saring 25 12 15.6 5.0 American robin 15 12 13.3 3.9 Red winged blackbird 19 11 11.1 4.4 Short-sared owl 9 9 17.8 5.0 Canada goose 38 8 5.6 4.4 Valley quail 7 7 11.1 3.3 Canada goose 39 8 15.6 4.4 Valley quail	0	104	46		
Long-billed curlow 48 33 37.8 15.6 Song sparrow 33 30 31.1 10.6 Song sparrow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Chukar 27 21 20.0 8.3 Starnamic Sparrow 17 16 22.2 6.7 Barn swallow 20 15 22.2 6.7 Glideer 15 14 22.2 7.2 Starling 25 12 15.6 5.0 American robin 15 12 13.3 3.9 Red-winged blackbird 19 11 11.1 4.4 Northern harrier 9 9 17.8 5.0 Canada goose 39 8 15.6 4.4 Valley quai 7 7 11.1 3.3 Canada goose 39 8 15.6 4.4 Valley quai 7					
Song sparrow 33 30 31.1 10.6 Common raven 31 23 33.3 12.8 Chukar 27 21 20.0 8.3 Ring-billed gull 36 17 8.9 3.9 Savannah sparrow 17 16 22.2 6.7 Glideer 15 14 22.2 7.2 Loggerhead shrike 15 14 22.2 7.2 Loggerhead shrike 15 14 17.8 7.2 Starling 25 12 15.6 5.0 American robin 15 12 13.3 3.9 Red-winged blackbird 19 11 11.1 4.4 Apther marrier 9 9 17.8 5.0 Canada goose 39 8 15.6 4.4 Valley quail 7 7 11.1 3.3 Carlada goose 39 8 15.6 4.4 Valley quail 7<					
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Ring-billed gull 36 17 8.9 3.9 Savannah sparrow 17 16 22.2 6.7 Barn swallow 20 15 22.2 6.7 Barn swallow 20 15 22.2 6.7 Loggerhead shrike 15 14 22.2 7.2 Loggerhead shrike 15 14 17.8 7.2 Starling 25 12 15.6 5.0 American robin 15 12 13.3 3.9 Red-winged blackbird 19 11 11.1 4.4 Short-eared owl 9 9 11.1 4.4 Northern harrier 9 9 17.8 5.0 Canada goose 39 8 15.6 4.4 Valley quail 7 7 11.1 3.3 Caffornia gull 13 6 8.9 3.3 American kestrel 6 6 11.1 3.3 Common snipe 6 6 11.1 2.8 Gray partridge 11					
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Northern harrier 9 9 17.8 5.0 Canada goose 39 8 15.6 4.4 Valley quail 7 7 11.1 3.3 California gull 13 7 8.9 2.2 Rock wren 8 7 2.2 1.7 Mallard 13 6 8.9 3.3 American kestrel 6 6 11.1 3.3 Common snipe 6 6 11.1 3.8 Gauli spp. 35 5 2.2 .6 House sparrow 5 5 2.2 .6 House sparrow 5 5 2.2 .1 Sharp-tailed grouse 7 5 2.2 .1 Sage grouse 2 2 4.4 1.1 Common nighthawk 8 4 8.9 2.2 Yellow-headed blackbird 4 8.9 2.2 4.4 1.1 Sage grouse 2	Red-winged blackbird	19	11	11.1	4.4
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1988 TRANSECTS

Northern pintail House finch Western wood pewee Long-billed curlew Poorwill Chipping sparrow Eastern kingbird Wilson's warbler

1989 TRANSECTS

Blue-winged teal Prairie falcon Song sparrow Say's phoebe Eastern kingbird

1990 TRANSECTS

Northern goshawk American goldfinch Common flicker Hammond's flycatcher Western tanager Eastern kingbird

Species with only one observation for all runs¹

Rough-legged hawk American crow Ring-billed gull House sparrow Rufous hummingbird Tree swallow Western kingbird

Swainson's hawk Northern oriole Lazuli bunting Caspian tern Western kingbird

Great blue heron Swainson's thrush American crow Sandhill crane Mountain bluebird Hermit thrush Rock dove Gray-crowned rosy finch Osprey Red-breasted nuthatch Sharp-tailed grouse Orange-crowned warbler

Pine siskin Dark-eyed junco House sparrow Rough-winged swallow Wilson's warbler

House finch Lark sparrow Rock dove Macgillivray's warbler House wren

¹Percent occurrence by transects 3.2, and by runs 0.8.

species was the horned lark (*Erimophila alpestris*), occurring in 80, 88, and 91 percent of the sample sites in 1988, 1989, and 1990, respectively. Four species together made up over two-thirds of the total observations. They were the western meadowlark with 2,154, the horned lark with 1,418, the Brewer's sparrow (*Spizella breweri*) with 1,299, and the vesper sparrow (*Pooecetes gramineus*) with 1,061.

In contrast, 24 species were recorded only on one transect one time. One other species, hermit thrush (*Catharus* guttatus), was recorded on only one transect on two runs in 1988. None of these species are closely associated with shrub steppe and may be considered incidental. Thirteen species (included here is the sharp-tailed grouse, *Tympanuchus phasianellus*) were recorded on two transects, and nine species on only three (included here is the sage grouse, *Centrocercus urophasianus*). In all, 47 species were seen on three or fewer transects; 38 of these were seen on three or fewer runs, and represent only 111 observations from a total 8,727.

DISCUSSION

The primary goal of this study was to reveal relationships between shrub-steppe habitats and wildlife. One of the central themes of ecology is the concept of biodiversity. A generally accepted axiom states that as plant diversity increases wildlife diversity increases. This axiom appears obvious when comparing temperate woodlands to tropical rain forests, and in other comparisons of similar scale. I wanted to test whether wildlife in the shrubsteppe ecosystem would exhibit the same kind of response to changes in habitat complexity. The relationship between bird and plant diversity (Shannon-Weaver Index) is plotted for each of the 55 transects in figure 1, and reveals significant correlation of shrub-steppe plant and bird diversity. Only terrestrial birds were used in the figure.

This finding is important to managers, since plant diversity and range condition are very likely correlated. Range site descriptions used by the USDA Soil Conservation Service (SCS) list key native species present in undisturbed sites. A simple index of range condition can be created by dividing the number of native plant species occurring on each study site by the number of plant species predicted in climax by the SCS Range Site Descriptions. If this is done for each level of structure-grasses, forbs, and shrubs-the value can range between 0 (if no native plants are present) and 3 (if all the native species are represented). I calculated these condition index values for 37 of the transects that stayed for the most part within a single range type. The index is limited to comparisons of simple presence. Figure 2 shows a significant correlation between vegetation diversity and range condition index determined by occurrence of native shrubs, grasses, and forhs

This correlation is an important relationship to acknowledge, but it is not surprising since both indices are derived on similar principals. I must also point out that condition in this context is not referring to any specific use, except the climax vegetation described by the SCS Range Site Descriptions. Conceptually, this condition may not be the condition desired in a particular wildlife management application. However, in practice most wildlife managers would consider good-to-excellent condition range to be good shrub-steppe wildlife habitat. This may be in part due to training that emphasizes climax communities, but it also has a basis in the context that badly

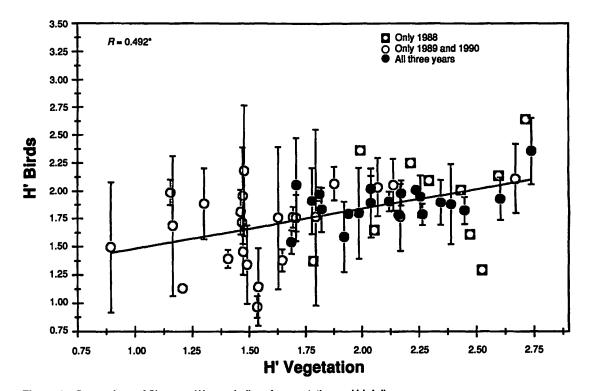


Figure 1—Comparison of Shannon-Weaver indices for vegetation and bird diversity for 55 shrub-steppe transects. Microplot values were used for the plants and total counts for the birds. Only terrestrial birds were used in the figure. *R* value significant at the 95 percent level.

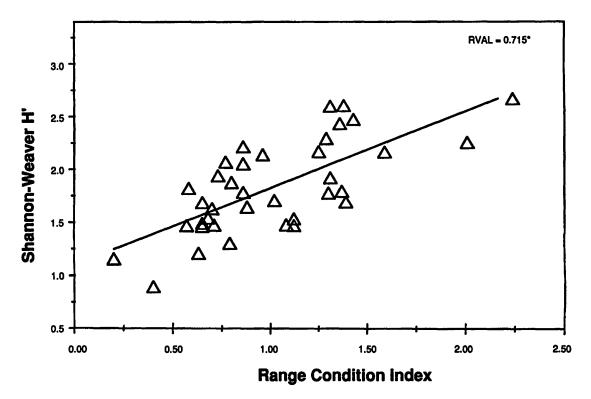


Figure 2—Comparison of Shannon-Weaver vegetation diversity indices and range condition indices. The range condition index is the sum of the ratios of actual native species to expected for shrubs, forbs, and grasses, and ranges between 0 and 3. *R* value significant at the 95 percent level.

degraded, poor-condition range offers little value to many species of wildlife. Figure 3 shows the significant correlation between bird diversity and range condition index, showing that bird diversity declines as range condition index declines.

Wildlife communities are comprised of single species, each of which react to components of the habitat in different ways. Some species, such as the sage sparrow (Amphispiza belli), sage thrasher (Oreoscoptes montanus), and Brewer's sparrow, are limited to shrub steppe, and closer examination of their responses to changes in habitat would establish the value of key habitat components, at least for those species. Other species, such as the western meadowlark and horned lark, are ubiquitous and generally successful in many kinds of habitats. Shrub-steppe habitat is not critical to their population, but by their common presence they contribute an important element to the shrub-steppe ecosystem and cannot be dismissed out of hand. Finally, some species, the vesper sparrow is an example, nest on the ground and can live in open grasslands and shrub steppe alike. While a common resident of the shrub steppe, they are not dependent on the presence of shrubs, but their responses may provide information about other aspects of the community. Because of the limited scope of my studies, I did not have opportunity to modify habitats to determine responses; however, the counts of birds in habitats of different conditions do permit some prediction based on the assumption that habitat modified to gain the same condition would hold the same numbers.

Shrub Cover

Shrubs, mostly big sagebrush, are the most obvious and dominant structural feature of the shrub-steppe community. The average cover of big sagebrush is thought to have been about 10 percent prior to introduction of livestock into Washington. Since livestock do not eat it, sagebrush cover often increases with grazing. On badly degraded ranges high cover of sagebrush may replace most other plants. On the other hand, sagebrush cover is often reduced, either intentionally to reduce competition with desirable livestock forage plants, or by wildfire.

Figures 4 and 5 show the relationships between two species of shrub-steppe birds and sagebrush cover. Only transects where the species were present are included in the figures, to reduce bias caused by including sites unsuitable for the species. The wildlife numbers shown are the sum of the counts by transect.

Sage thrasher shows the strongest relationship to big sagebrush cover. In both very low and very high sagebrush covers, the numbers of sage thrashers counted were lower than in the middle of the range. If the historical cover of big sagebrush is accurately estimated to be about 10 percent, it can be said that sage thrasher counts were highest at about historic levels.

Brewer's sparrow counts also show a strong relationship to big sagebrush cover. Counts in very low shrub densities were lowest, increasing as covers approached 10 percent. This supports other studies that have shown

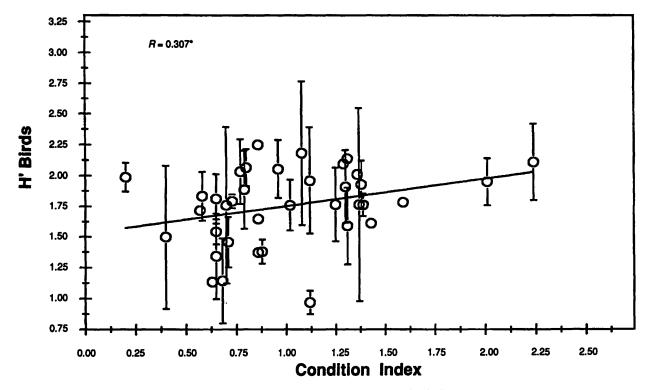


Figure 3—Comparison of Shannon-Weaver bird diversity indices and range condition indices. *R* value significant at the 95 percent level.

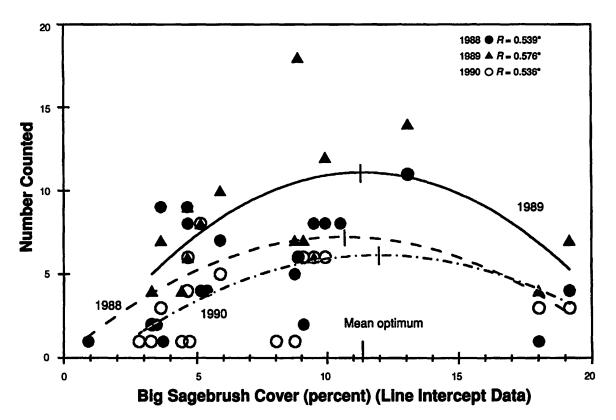


Figure 4—Comparison of big sagebrush cover and the number of sage thrashers counted. Only transects that had at least one sighting of sage thrasher were used in the figure. *R* values are significant at the 95 percent level or above. The mean optimum was 11.3 percent. The maximum sagebrush cover measured on any transect was 19.1 percent.

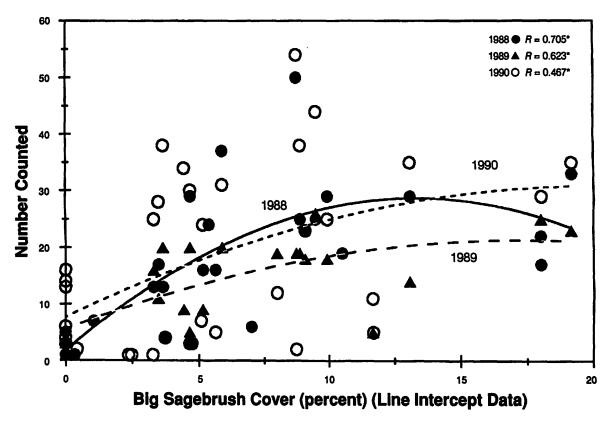


Figure 5—Comparison of big sagebrush cover and the number of Brewer's sparrows counted. Only transects that had at least one sighting of Brewer's sparrow were used in the figure. *R* values are significant at the 95 percent level or above.

that removal of sagebrush causes declines in Brewer's sparrow numbers (Best 1972; Castrale 1982). As cover increased above 10 percent, the count numbers did not decline, as with the sage thrasher. Covers above 20 percent are not shown by the data in figure 5 and, while only suggested by the data, there is likely a level above 20 percent where the count numbers would decline. It should be noted, however, that none of the 55 transects measured had a mean big sagebrush cover greater than 20 percent. although 10 different transects did have a total of 16 segments with densities higher than 20 percent, reaching a maximum cover of 31.7 percent. Therefore, while some sites might reach covers high enough to cause declines due to excessive big sagebrush cover. Brewer's sparrows are more apt to be sensitive to very low big sagebrush cover.

Other bird species did not show a significant correlation when counts were regressed against sagebrush cover values. In some cases this may not indicate that the species is independent of sagebrush cover, but rather that the data sampling was not sufficiently sensitive to the differences within the species' habitat. This might be especially important for species with fewer observations. For example, the sage sparrow, another sagebrush obligate, was rarer than the two species described above, being found on only 17 of the 55 transects, and then in only low numbers. However, by comparing transects that have at least one occurrence of sage sparrow to those that had none, we see that transects with sage sparrow have significantly greater big sagebrush cover than those without sage sparrow (fig. 6).

Other species that showed a similar positive correlation are loggerhead shrike (Lanius ludovicianus), brownheaded cowbird (Molothrus ater), and mourning dove (Zenaida macroura). Savannah sparrow (Passerculus sandwichensis) and long-billed curlew (Numenius americanus) showed an inverse relationship, with big sagebrush cover lower on transects where the species occurred.

Annual Grass Cover

Annual grasses have become a prominent feature in the ranges of the West. These grasses are usually one of several introduced bromes, and while all species were combined for our measurements, cheatgrass was by far the most common. These annual grasses are very efficient in competing for moisture in low-precipitation zones, and readily invade disturbed soil sites left following fire or overgrazing, but are present on even the best sites measured. In fact, 100 percent of the transects and 76 percent of the microplots showed at least some annual grass occurrence (table 2).

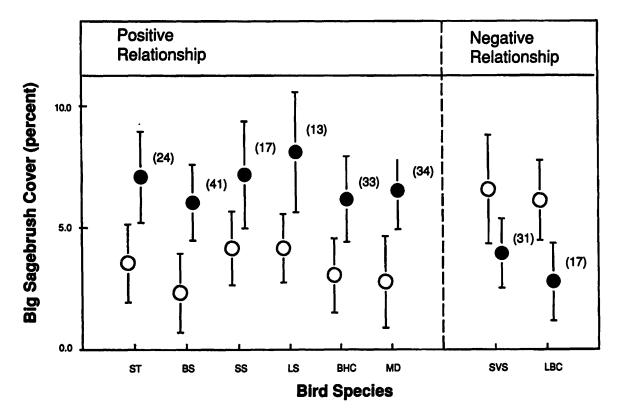


Figure 6—Comparisons of big sagebrush cover values (line intercept) for sites where shrub-steppe bird species occurred and where they did not. Filled circles represent sites where the species shown occurred. The number in parentheses is the number of sites out of 55 where the species occurred. Error bars show 95 percent C.I. ST = sage thrasher, BS = Brewer's sparrow, SS = sage sparrow, LS = loggerhead shrike, BHC = brown-headed cowbird, MD = mourning dove, SVS = savannah sparrow, LBC = long-billed curlew.

There is much interest in the effects of annual grass invasion on wildlife numbers, since range condition and the invasion of annuals are related. Brewer's sparrow count totals are negatively correlated with annual grass cover, with the highest counts found on transects with annual grass cover less than 20 percent (fig. 7). Three other species also exhibited a negative relationship to annual grass cover. By comparing sites where the species was present to sites where the species did not occur, figure 8 shows that annual grass cover was greater at sites where sage thrasher, sage sparrow, and brown-headed cowbird were absent than at sites where they were present. In no case was there a positive relationship for the 17 species with sufficient data to justify comparison.

Other Grasses

Similar comparisons of presence/absence showed that Brewer's blackbirds occurred more often on sites where Sandberg bluegrass cover was greater. Sage thrasher occurrence exhibited the opposite relationship to *Poa* and occurred more often where bluebunch wheatgrass cover was greater. Long-billed curlew occurred more often where bluebunch wheatgrass cover was lower. Finally,

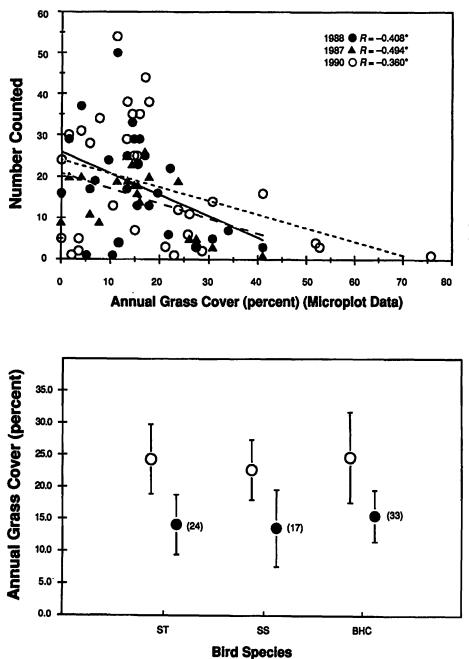


Figure 7—Comparison of annual grass cover and the number of Brewer's sparrows counted. Only transects that had at least one sighting of Brewer's sparrow were used in the figure. *R* values are significant at the 95 percent level or above. The solid line is 1988, the dashed 1989, and the fine dashes 1990.

Figure 8—Comparisons of annual grass cover values (microplot) for sites where shrub-steppe bird species occurred and where they did not. Filled circles represent sites where the species shown occurred. The number in parentheses is the number of sites out of 55 where the species occurred. Error bars show 95 percent C.I. ST = sage thrasher, SS = sage sparrow, BHC = brown-headed cowbird.

mourning dove occurred more often where *Stipa* cover was less. Six species with sufficient data for comparison showed no identifiable relationship.

CONCLUSIONS

These comparisons are informative, and one is tempted to draw conclusions of causality when such significant relationships are shown. Some such conclusions may be justified; for instance, shrub-nesting birds clearly need shrubs and would occur only where shrubs occur. However, I must urge caution when extending these conclusions very far. For example, at least one study (Petersen 1987) found that Brewer's sparrows did not decrease after a prescribed burn, which would indicate that reduction of shrub cover had no negative effect when used to create a patchy landscape. My study has not attempted to explain what has contributed to these relationships, and some of the relationships may be secondary in nature.

What can be said is that certain habitat features reflect well-documented management changes, and the presence of these features in some cases is strongly correlated with the presence or absence of wildlife species. As an example, the increase of annual grass cover is an indication that disturbance has occurred. In the extreme it would indicate very poor-condition range, as viewed by the cattleman. When it is largely absent, range condition is usually good. Brewer's sparrow count numbers are inversely related to annual grass cover, and without knowing the precise reason, management which would increase annual grass cover would likely reduce Brewer's sparrow numbers, or so the data would suggest.

It could be assumed then that poor-condition range is bad for Brewer's sparrows. That may be so, but poorcondition range can also occur where annual grass is not excessive but Sandberg bluegrass is the dominant grass species, and the data do not suggest a negative relationship with Sandberg bluegrass. Also, a high level of big sagebrush cover is usually an indication of poor condition, and yet the data show that Brewer's sparrow counts do not decline as shrub cover increases.

What conclusions can we make? First, of the 17 species shown for which comparisons were made, seven had a positive relationship with the cover of big sagebrush, two were inversely related, and eight were not related. Therefore, more shrub-steppe species would benefit by preservation of big sagebrush than by any other policy indicated by these data. Next, four of the 17 species showed an inverse relationship to annual grass. No species showed a positive relationship. Thirteen showed no relationship. Therefore, management that prevents annual grass invasion and reduces annual grass cover would benefit four species, two of which are important shrub-steppe species, and none would suffer. These two conclusions can be used to guide future research, but more important, we can conclude that wildlife management in the shrub steppe should strive to preserve shrub cover, particularly big sagebrush, and avoid disturbances that would increase annual grass cover.

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GRASSHOPPER COMMUNITY RESPONSES TO SHRUB LOSS, ANNUAL GRASSLANDS, AND CRESTED WHEATGRASS SEEDINGS: MANAGEMENT IMPLICATIONS

Dennis J. Fielding Merlyn A. Brusven

ABSTRACT

Grasshopper density and species composition were sampled at 42 sites arrayed along a disturbance gradient. Grasshopper density was lowest and species diversity was highest in vegetation types with shrub cover. Annual grasslands had the highest grasshopper densities and the lowest species diversity, and were dominated by generalist species with wide diet breadths. Management concerns that arise from the different characteristics (food habits, migratory propensity) of the dominant grasshopper species associated with the various plant communities were discussed. Management of grasshopper populations by habitat manipulation may be a viable alternative strategy.

INTRODUCTION

Grasshopper populations periodically reach outbreak proportions in the Intermountain region (Hewitt and Onsager 1983). In 1985, during a massive grasshopper outbreak, about 2.5 million ha of rangeland across southern Idaho were treated with broad-spectrum insecticides. This type of sledge-hammer approach to the control of insect pests applied on a landscape scale is becoming less acceptable. The undesirable aspects of broad-spectrum biocides (effect on nontarget arthropods, expense) make it compelling to find ways to manage grasshopper populations so that outbreaks are less frequent and of smaller extent. This project was undertaken to assess the role that range management actions have on grasshopper populations and to provide insights into the management of grasshoppers through habitat manipulation.

Like many areas of the Intermountain region, southcentral Idaho has suffered extensive habitat degradation and shrub loss due to increased fire frequency associated with the invasion of cheatgrass. The diminished resource values that result from this process of shrub loss have been documented by many studies. The response of rangeland grasshoppers to the conversion of native vegetation to annual grasslands has not been studied in detail.

There are well over 100 species of grasshoppers in the Intermountain region. Only four or five species attain very high densities and account for most of the outbreak populations. One of these, Melanoplus sanguinipes L., is particularly troublesome. In south-central Idaho, where there is an extensive interface between publicly owned rangeland and privately owned irrigated cropland, migration of grasshoppers from rangeland to cropland is a major problem. Melanoplus sanguinipes is well known for its propensity to migrate (McAnelly and Rankin 1986) and its broad range of food plants (Mulkern and others 1969) makes it a threat to a wide variety of crops, as well as rangeland forage species. Another abundant species in the Intermountain region is Aulocara elliotti. It differs from M. sanguinipes in several respects: it is restricted to feeding on grasses only (Mulkern and others 1969) and is seldom found in cultivated crops.

The objective of the present study is to identify patterns of grasshopper species composition among different vegetation types, and to determine whether the conversion of native plant communities to annual grasslands has an affect on the abundance of the major grasshopper pest species in south-central Idaho.

MATERIALS AND METHODS

Forty-two sites were sampled for plant and grasshopper species composition. These sites were all within the Davis Mountain SW USGS 7.5' quadrangle map (north of Bliss, ID). This area was selected because a wide spectrum of plant communities, from relatively undisturbed to dominance by exotic annual grasses (cheatgrass, *Bromus tectorum*, and medusahead, *Taeniantherum asperum*) and introduced perennial grasses (primarily crested wheatgrass, *Agropyron cristatum*), were all present within a small geographic area. The small scale of the study was intended to minimize the effects of local weather patterns on grasshopper community composition.

The current year's standing crop by plant species was estimated by the weight-unit method (USDA-SCS 1976). Ten, $1-m^2$ quadrats were estimated at each site in July of 1990 and 1991. Both years' data were averaged for subsequent analysis.

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. Dennis J. Fielding is Postdoctoral Fellow and Merlyn A. Brusven is Professor of Entomology, Department of Plant, Soil and Entomological Sciences, University of Idaho, Moscow, ID 83843.

Grasshoppers were sampled twice per year in June and late July and August. Densities were estimated by counting the number of grasshoppers flushed from $50, 0.1\text{-m}^2$ quadrats. Species composition was determined by capturing and identifying at least 30 grasshoppers at each site. Density of individual grasshopper species was estimated by multiplying the species' proportions by overall density on the site. Pooled grasshopper data from the four sampling dates were used for subsequent analysis.

Plant data were summarized and primary gradients identified using detrended correspondence analysis (DCA) (Hill 1980), an eigenvector ordination technique. Primary gradients in plant species composition were identified by nonparametric correlation (Spearman's r_s , Zar 1984) of shrub biomass, native perennial grasses (excluding *Poa* spp.), annual vegetation, and the percent exotic plant species with plant DCA axis-1 scores for the 42 sites. Trends in grasshopper community composition were also examined by nonparametric correlation with the plant DCA axis-1 scores.

RESULTS

The DCA ordination of the vegetation is shown in figure 1. The first axis, which accounted for 53 percent of the variation in plant data, may be interpreted largely as a disturbance gradient. The biomasses of shrubs and native grasses were negatively correlated with the plant DCA axis-1 scores $(r_s = -0.79 \text{ and } -0.72$, respectively, N = 42, P < 0.01), indicating less disturbed plant communities at the low end of axis-1 (fig. 1). Biomass of annual vegetation and the percentage of aboveground biomass represented by exotic plant species were positively correlated $(r_s = 0.59 \text{ and } 0.91$, respectively, N = 42, P < 0.01) with the plant DCA axis-1, indicating the dominance by introduced plant species at the high end of plant DCA axis-1.

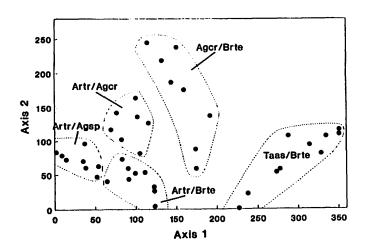


Figure 1—Detrended Correspondence Analysis ordination of 42 sites based on plant species aboveground biomass. Vegetation types are labeled according to the dominant plant species: Artr, big sagebrush (Artemisia tridentata); Agsp, bluebunch wheatgrass (Agropyron spicatum); Agcr, crested wheatgrass (Agropyron cristatum); Brte, cheatgrass (Bromus tectorum); Taas, medusahead wildrye (Taeniantherum asperum).

Table 1-Mean plant aboveground biomass (gram dry weight/
square meter) by vegetation type

	Vegetation type					
Plant	Artr/ Agsp	Artr/ Brte	Artr/ Agcr	Agcr/ Brte	Taas/ Brte	
Bromus tectorum	5.2	11.5	3.0	5.4	15.0	
Bromus japonicus	2.8	1.5	.5	<.1	1.0	
Taeniantherum asperum	<.1	1.4	.3	1.8	22.2	
Agropyron cristatum	.4	.7	19.0	21.8	.4	
Poa sandbergii	.8	1.5	4.8	5.7	2.5	
Agropyron spicatum	14.9	<.1	<.1	<.1	<.1	
Other native grasses ¹	4.8	.8	<.1	.3	<.1	
Artemisia tridentata	34.4	33.6	26.5	2.2	.3	
Chrysothamus spp.	1.9	3.2	4.8	.5	.2	
Annual and biennial forbs	.2	.7	.2	1.3	3.4	
Perennial forbs	.7	<.1	<.1	.3	<.1	
Number of plant species	12.1	9.3	5.6	8.0	7.6	

Includes Elymus cinereus, Sitanion hystrix, Stipa thurberiana, and Agropyron smithii.

Five somewhat subjective but nonoverlapping vegetation types were delineated on the ordination diagram and were labeled according to the two plant species with the greatest mean aboveground biomass within the vegetation type. Table 1 lists the mean composition of the five vegetation types.

Grasshopper species composition also differed among the vegetation types (table 2). *Melanoplus sanguinipes* showed a strong affinity for the annual grassland sites where it accounted for 66 percent of all grasshoppers collected (table 2). *Melanoplus sanguinipes* did not comprise more than 15 percent of the population in any of the other vegetation types. Density of *M. sanguinipes* was strongly

Table 2—Mean density and percentages of grasshopper species collected by vegetation type

		Vegetation type				
Density and species	Artr/ Agsp	Artr/ Brte	Artr/ Agcr	Agcr/ Brte	Taas Brte	
Overall density (per m ²)	0.22	0.31	0.68	1.18	1.63	
Percentage of population:						
Ageneotettix deorum	16	6	2	*	*	
Amphitornus coloradus	25	2	5	4	*	
Aulocara elliotti	5	34	50	63	13	
Circotettix undulatus	14	+	۰.	+	+	
Cordillacris occipitalis	•	8	•	*	•	
Cratypedes neglectus	1	3	9	3	•	
Dissosteira spurcata	•	•	+	+	2	
Hesperotettix viridis	1	10	9	•	•	
Melanoplus cinereus	1	•	+	٠	•	
Melanoplus sanguinipes	13	15	7	15	66	
Oedaleonotus enigma		13	6	5	14	
Phoetaliotes nebrascensis	1		*		•	
Spharagemon equale		2	4	5	1	
Stenobothrus shastanus	5	-	•	•		
	*	•	3	•		
Trachyrachys kiowa	2	2		•		
Trimerotropis gracilis Trimerotropis psuedofasciata	_	*	•	•	1	

correlated with the plant DCA axis-1 scores (fig. 2). Aulocara elliotti dominated the crested wheatgrass sites (table 2). Density of A. elliotti also was positively correlated with axis-1 scores, although it reached its highest densities near the middle of plant DCA axis-1, where the Agcr/Brte sites were located (fig. 3).

Both overall density and diversity (Shannon's H') of grasshoppers were strongly correlated with the plant DCA axis-1 scores (figs. 4 and 5). Sites high on plant DCA axis-1, the sites lacking sagebrush cover, had the highest grasshopper densities and the lowest diversity. In the lesser disturbed Artr/Agsp sites, 13 species comprised 95 percent of the grasshoppers collected from these sites (table 2). Progressively fewer species comprised 95 percent of the grasshoppers in the vegetation types arrayed from left to right along plant DCA axis-1 (fig. 1). Only four species accounted for 95 percent of the grasshoppers collected from the annual grassland sites.

DISCUSSION

Striking differences were observed in the grasshopper assemblages associated with natural and introduced plant communities in south-central Idaho. The pattern of reduced biodiversity associated with the conversion to exotic annual grasslands (Whisenant 1990; T. Rich, these proceedings) was reflected in the grasshopper assemblages within the study area. Grasshopper assemblages were composed of progressively fewer species along the primary disturbance gradient in the plant communities. Sagebrush was probably the single most important factor affecting grasshopper community structure. The vegetation types with sagebrush were all characterized by low overall density and high diversity without any single species dominating, except *A. elliotti* in the Artr/Agcr sites.

Much of the observed patterns were the result of the distribution of two of the most common species, *M. sanguinipes*

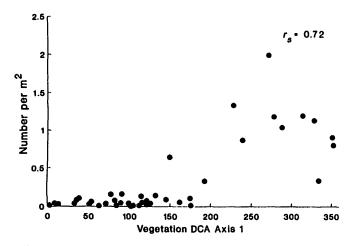


Figure 2—Relationship of *M. sanguinipes* density to vegetation DCA axis-1 scores.

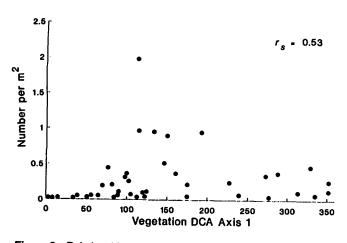


Figure 3—Relationship of *A. elliotti* density to vegetation DCA axis-1 scores.

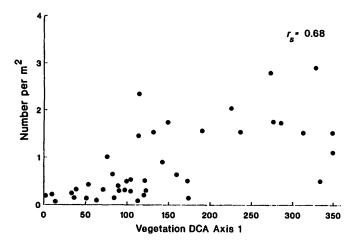


Figure 4—Relationship of overall grasshopper density to to vegetation DCA axis-1 scores.

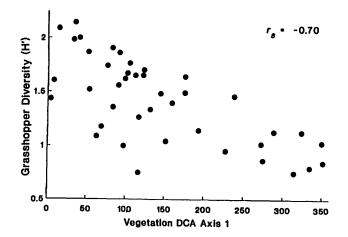


Figure 5—Relationship of grasshopper diversity to vegetation DCA axis-1 scores.

and A. elliotti. The annual grasslands were dominated by M. sanguinipes. Aulocara elliotti dominated the crested wheatgrass seedings. The relative abundance of their preferred host plants may account for much of their observed habitat preferences. Both species can subsist largely on cheatgrass early in the season, then switch to other foods as the cheatgrass dries. Crested wheatgrass is readily accepted by A. elliotti later in the season, while M. sanguinipes feeds largely on weedy forbs later in the season (Fielding and Brusven 1991). Annual and biennial forbs were most abundant on the annual grasslands (table 1).

The different life history strategies exhibited by M. sanguinipes and A. elliotti result in different management implications for these species. Aulocara elliotti is more of a specialist adapted to exploit a perennial grass resource. As a member of the grass-feeding subfamily Gomphocerinae, it is restricted in its host range to grasses. Phenologically it is well adapted to the perennial grasses of the area, maturing at about the same time as the plants. It appears that the life history strategy of A. elliotti is to specialize on a perennial resource, remain in a resource patch and tolerate conditions during adverse periods. Because A. elliotti tends to mature at about the same time as its host plants, it is less likely to migrate off the rangeland in search of more suitable habitat. In contrast, M. sanguinipes is a much more opportunistic feeder, and populations hedge their bets with a wide spread in hatching dates. A large proportion of the population of M. sanguinipes will mature well into the summer when most plants have dried, leading to a situation where they will be much more likely to migrate to irrigated cropland. Therefore, where migration to cropland is a concern, then high populations of *M. sanguinipes* may be considered undesirable. However, if destruction of forage grasses is the primary concern, then populations of A. elliotti will compete directly with livestock for available forage grasses, whereas M. sanguinipes will tend to feed first on less desirable weedy forbs.

Because populations of A. elliotti are usually more tightly synchronized than populations of M. sanguinipes (Onsager 1987), it is easier to assess the potential for damage from A. elliotti early in the season instead of waiting for hatching to be completed, as is the case for M. sanguinipes where a substantial proportion of the population may already be in the fourth instar (the ideal time for treatment) before all hatching has been completed.

Because of its high reproductive potential, it is probable that *M. sanguinipes* will be the dominant species in most vegetation types during outbreak years. However, in those habitats with a more equitable distribution of species, *M. sanguinipes* may be not be able to attain its full potential for explosive population growth. Few studies have found evidence of direct competition between grasshopper species; it seems especially unlikely that populations of *M. sanguinipes* will be inhibited by other grasshopper species in habitats where *M. sanguinipes* already dominates.

These results indicate that areas with shrub cover and an understory of perennial grasses will have lower overall grasshopper densities with a lower proportion of pest species. These data were taken during years of low grasshopper density; it may be expected that during outbreak years grasshopper density may exceed treatment thresholds in all vegetation types. Examination of nymphal survey data from 1985, a year of extremely high densities, indicates that, although densities were high across south-central Idaho, the relationship between annual grasslands and higher grasshopper densities prevailed (Fielding and Brusven in press). In the Shoshone Bureau of Land Management district in 1985, annual grasslands averaged 41 grasshoppers/m² compared to about 22/m² in sagebrushcovered areas (Fielding and Brusven in press). It may be argued that when densities exceed a certain threshold it does not matter whether there are 20 or 40 grasshoppers per square meter, it will be enough to cause hardships for farmers and ranchers. However, the evidence to date suggests that outbreaks would be less frequent, less intense, and cover less area in habitats with shrub cover than on frequently burned, cheatgrass-dominated landscapes.

If further research confirms that annual grasslands do experience more frequent grasshopper outbreaks, then rehabilitation of annual grasslands with shrubs and perennial grasses should be considered as a means of noncatastrophic management of grasshoppers. Because migration of M. sanguinipes from rangeland to irrigated croplands is a primary rationale for control operations in south-central Idaho, some of the highest priority areas for rehabilitation would be those areas adjacent to croplands. Although the costs of grasshopper control alone may not justify the expense of planting shrubs and perennial grasses over large areas, the benefits to game birds such as pheasant (Sands, these proceedings), other wildlife, and livestock may be enough to justify rehabilitation of high-priority areas. The management of grasshoppers by the manipulation of vegetation has the advantage of being an environmentally sound, long-term strategy that could benefit many other resources.

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RESOURCE IMPACTS OF CHEATGRASS AND WILDFIRES ON PUBLIC LANDS AND LIVESTOCK GRAZING

Thomas C. Roberts, Jr.

ABSTRACT

In the past decade, nearly 500,000 acres of rangeland have burned in the Salt Lake (Utah) District of the Bureau of Land Management. Most of the acreage consumed has been dominated by cheatgrass (Bromus tectorum). This paper addresses the resource impacts on lands dominated by cheatgrass and burned areas where cheatgrass was not dominant. Included are discussions of impacts on vegetation, forage, wildlife, and budgets.

INTRODUCTION

The previous days' sessions have included some ideas on revegetation, the ecology of cheatgrass, and fire ecology and management. This morning I will address some of the resource impacts of cheatgrass and wildfires on public lands and their management.

I will address some of the concerns that we have in the Salt Lake District of the Bureau of Land Management (BLM). Our District comprises over 3 million acres of public land in Box Elder, Rich, and Tooele Counties in the northern third of Utah. Elevations range from about 4,200 feet at the surface of the Great Salt Lake to over 12,000 feet at the top of the Deep Creek Mountains.

Some of the vegetation community types include: a limited acreage in the spruce-fir type; the aspen community type; the mountainbrush type; the pinyon-juniper type; the juniper type; the sagebrush-grass type; the salt desert shrub type; and the cheatgrass type.

In our District, most of the cheatgrass (Bromus tectorum) type is located in what was or is the salt-desert shrub community type. Unfortunately, in some parts of the Pony Express Resource Area, cheatgrass population is becoming more dense in the sagebrush-grass community type and the juniper community type. Consequently, its presence is becoming a factor in any vegetation management decision process.

However, my task today is to discuss the resource impacts of cheatgrass and wildfires on the public lands and livestock grazing in our District. In the last 10 or so years nearly 500,000 acres have burned in our District. Most of this acreage has been in cheatgrass wildfires. These are acres that have been dominated by cheatgrass in Tooele or Box Elder Counties. We also had some acreage burned under prescription and noncheatgrass wildfires.

NONCHEATGRASS FIRES

These comparatively few acres will be addressed first. In the early and mid-1980's, we had some wildfires go through Rich County. I will review a couple of them. At the south end of the county, a lightning strike the evening of July 24, 1981, caused a fire that consumed approximately 1.100 acres of sagebrush interspersed with juniper stands. The hot and dry conditions prior to fire contributed to the hot fire that in combination with high winds resulted in a very clean burn. The fire moved so fast through the country that cattle on the South Woodruff Allotment were nearly stranded and killed. Postfire evaluations resulted in rehabilitation efforts on the site. We used a mix of grasses and forbs in a rangeland drill, and we were also able to use a Dixon Land Imprinter. We found the Imprinter to be effective on this site, but because of a narrower swath and poorer control of seed dispersal, it was probably more expensive than the drill to use. Two years later some clipping studies showed that the net results of the fire were positive. An unburned plot vielded a clipped weight equivalency of 880 pounds to the acre while a burned plot nearby yielded the equivalency of nearly 1,500 pounds to the acre, an increase of 69 percent. The notes taken at the time indicate that those areas not reseeded had also greatly improved.

Clearly the net impact on range productivity was positive. Nonetheless, this fire did require two growing seasons of nonuse on the allotment and an additional workload on the part of the permittees, BLM resource area staff, Soil Conservation Service district staff, and the expenditure of funds by all concerned. The fire took place in what was then considered a critical deer winter range, and they were affected also, shifting their use elsewhere. The blowing and drifting soil that resulted from the fire and reseeding operations may have indicated some soil loss.

On August 25, 1983, a dry lightning strike caused a fire that burned through the Rabbit Creek area of northern Rich County. This fire involved parts of two allotments, the Duck Creek Allotment and the Rabbit Creek Allotment, both summer cattle allotments. The Rabbit Creek fire was apparently a fast-moving, cool fire in rangelands that were in pretty good shape with a diversity of grasses and shrubs, in the sagebrush-grass community type. The permittees had grazed it conservatively for years and the

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fuel load and diversity reflected it. When the fire occurred we were able to determine that the area would need only rest to return to better than prefire productivity. This assessment was confirmed in the clipping studies that showed there to be an increase in productivity of 257 percent, from an equivalent of 740 pounds to the acre to 2,640 pounds to the acre in one allotment and an increase from 680 pounds to the acre to 770 pounds to the acre in the other allotment. Because of the good condition on this piece of rangeland, the only loss was some nonuse for a couple of seasons. The gentle topography and good rootmasses probably held any soil losses to a minimum. These two fires may also illustrate the difference in postfire measures needed for sites that are in different conditions; the Rabbit Creek site needed no rehabiltitation work, while the burn in the South Woodruff area did need some work.

As described by A. C. Hull (1965), the fire frequency is less in a community type with a low frequency of cheatgrass, and our experience in Rich County, with less cheatgrass than the rest of the District, confirms his statement.

The major amount of the rest of the acreage that has been burned in the District over the past decade has been in the sagebrush-grass community type (with a sizable cheatgrass component) or in what had historically been the salt-desert shrub type gone to cheatgrass. A notable exception would be a fire that included a crested wheatgrass seeding while burning through the sagebrush-grass and salt-desert shrub types near the Tooele-Juab County line. This fire happened in July with high temperatures, high winds, and low relative humidities. In total, about 7,000 acres burned in the Richfield and Salt Lake Districts. Much of the acreage was reseeded with a mix of grasses, a few forbs, and a small amount of fourwing saltbush. The seeding took place in January and February and, except for fourwing saltbush, was fairly successful. This fire was beneficial to us in that it cleaned up a 20year-old chaining of trees and shrubs that were reinvading. It also illustrated that contrary to what some people may believe, a crested wheatgrass seeding can burn. The livestock forage impact of this fire was some displaced livestock grazing use. We were fortunate in our District that the amount of acreage was only about 1,500 acres, and the grazing use was transferred elsewhere in one allotment, while in the other allotment there were 2 years nonuse. This burn also illustrates that the more conservatively stocked and better condition an area is in prior to a fire, the better it will be after the fire. The fire encompassed two allotments, one that had been conservatively stocked under a cooperative Allotment Management Plan with the Forest Service, U.S. Department of Agriculture, and one operator, the other allotment with 10 operators, all with their own management goals. The area was in the transitional range for mule deer from the Sheeprock Mountains and probably rejuvenated some of the grass plants that had been getting rank. Some of the sagebrush plants are returning to the scene. For both native and domestic ungulates, the net result of the fire 6 years ago appears to be positive. However, this had been an expensive fire, both while it was happening and during the rehabilitation stage. While it was burning for 3 days the fire

crews of both the Forest Service and BLM were involved. The rehabilitation work took the commitment of two BLM Districts and the State Office.

The District has also had a couple of other fires in the edge of the juniper type that further extended into that community. One of them, believed to have been started by a motorcycle, was a fire that burned over 1,100 acres in August, 1986. This fire was assisted by the slope of the west side of the Onaqui Mountains. Due to the slope and community type involved, little suppression action was taken. However, a few years after the fire, the area is doing well with a strong population of bluebunch wheatgrass and Indian ricegrass. Because of the distance from water, the area was grazed very little by domestic livestock, and consequently there was little impact upon any human use of the area. The area now receives use by deer and wild horses.

CHEATGRASS FIRES

The greatest impact of fire in our District has been in the cheatgrass type, or in what was probably the saltdesert shrub community type. The problem is best illustrated by the following fire statistics. The Initial Attack Analysis Model, a part of the National Fire Management Planning Analysis System, is a system to track statistics on wildfires. District fires for the last 10 years (1981-90) have been broken into four classes, defined by fuel type, in our case analagous to the following vegetation types; cheatgrass, sagebrush-grass, pinyon-juniper, and fires along the National Forest boundary, generally at higher elevations. These models show the average number of fires per year to be 26 in the cheatgrass type, 15 in the sagebrush-grass type, 16 in the pinyon-juniper type, and only eight at the higher elevation Forest boundary.

The statistics can also be broken down by acreage per year. In 1981, there were 144 fires in the District burning nearly 34,000 acres. In 1982 there were 44 fires burning nearly 37,000 acres, and in 1983, 45 fires burned almost 275,000 acres. It would be an understatement to say that fire and fire rehabilitation took on a life of their own in 1983. The BLM acreage in that amount of land burned required the reseeding of over 46,000 acres with nearly 500,000 pounds of seed. The additional District funds for this total project were over \$800,000, requiring the efforts of a joint team consisting of personnel from the BLM State Office, the District and Area Offices, and the Soil Conservation Service. If the problems pertinent to cheatgrass had not been clear before, they were hammered home that year. The lack of dependability as a source of forage afforded by cheatgrass had always been a concern, but this was a solid demonstration. Using an estimated annual average productivity of 20 acres per animal unit month (AUM), the fires of that year caused the displacement of nearly 14,000 AUM's, affecting numerous ranching operations for two growing seasons. Another problem that we attempted to limit was the soil loss. Efforts included gulley plugs and bank stabilization work for an additional cost of \$48,000. The soil losses were evident with estimates of up to 6 feet of gulley erosion and 6 inches of

sheet erosion taking place that fall. The problems affiliated with rehabilitation projects of this size include: the disruption of daily routines; the hiring of temporary help, who may or may not be familiar with the needs of the land and project; and the high secondary costs, like extra vehicles, related to the startup and maintenance of projects of this size and immediate nature. Also consider that this was during a period when we may have been a little less sophisticated in our demands and skills in rehabilitation efforts.

I think that we have learned a lot since then, and hopefully not all that experience went for naught. That 1983 had a wet spring after a number of wet years and probably set us up for a bad fire year is now a moot point. That year, if nothing else, taught us that cheatgrass fires are expensive. If we use the average cost for fire suppression of \$5.00 per acre and a minimal rehabilitation cost of \$30.00 per acre for a total cost of \$35.00 per acre, we can see that cost of these fires to the taxpaver is also significant. Unfortunately, not all of our rehabilitation efforts were successful, and even where they were, we are left with a vegetation type conversion that many people (and birds or animals) find less than optimal. I also believe that because of the aggressive nature of cheatgrass as a cool-season annual that it exacerbated any condition that may have been peripheral to causing the shrub dieoff that we had in the District a few years ago.

Consequently, we have found the cheatgrass type or its invasion to be frustrating and challenging. Cheatgrass is an undependable forage source and is a fuel source for rangeland fires. These fires cause a loss of forage to the ranching community and wildlife most of us enjoy. Concomitant with that is the ultimate loss of diversity in the plant and animal communities that we administer. Add to this the risk of soil loss in an uncontrolled and unplanned fire situation in the precipitation belt where rehabilitation is difficult, and we have a much less than desirable condition. According to any common definition, the loss of diversity and soil would probably fit the term "desertification."

Is there a ray of light at the end of the tunnel? Yes, I think that there is. We are gaining knowledge in our skirmishes with cheatgrass. Although, as we have heard this week and as we have seen in our District, it is moving out into other community types, I think that we are becoming more skilled in planning and implementing rehabilitation projects. We are also more cognizant of the potential problems that an aggressive annual plant can cause, and we are more willing to try new ideas. And we are seeing the natural revegetation by salt-desert shrubs (shadscale, Gardner saltbush, and winterfat) in some areas where we thought they had been eliminated. Examples are along the Pony Express Trail in the Resource Area and a railroad section that had burned clean in 1984 that have shadscale returning on them. We are also more willing to attempt to use a diversity of plant materials, native and exotic, in rehabilitating these burned-over areas. Although the use of exotics like forage kochia is debated in some circles, it should be maintained in the arsenal of plant material to be used in some conditions. I also feel encouraged with the emphasis that the cheatgrass and native rangeland restoration problem is receiving in the research arena, including the research effort that the BLM is making.

CONCLUSIONS

We have found that, in general, noncheatgrass burn areas are less likely to need rehabilitation and, depending on the prefire management and condition, may not need any rehabilitation. Consequently these fires are cheaper and often beneficial from a resource viewpoint. Whereas fires are expensive to suppress and rehabilitate, cheatgrass burn areas often have a lower rate of success in rehabilitation. In general, a 2-year, sometimes longer, period is required after a fire to allow the area to come back, eliminating the use of the area by domestic livestock. Cheatgrass fires tend to be self perpetuating, decreasing the period between fires. Cheatgrass fires also decrease flora and fauna diversity in a time when we as a populace are becoming more concerned with biological diversity. However, to reiterate, the future is not all that bleak; we are seeing an increased emphasis on the research and restoration of our native rangelands, and in some cases a natural revegetation with native salt-desert shrubs. There is also an increased awareness of the importance of our native rangelands from an overall resource viewpoint, not just their grazing capacity. In conclusion, I see a future that is interesting, challenging, and has the potential for great successes.

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DISPLACEMENT OF RARE PLANTS BY EXOTIC GRASSES

Roger Rosentreter

ABSTRACT

Exotic grasses are displacing both rare and common plant species on western rangelands. Interspecific competition displaces valuable genetic resources in many parts of the world, including the Intermountain shrub-steppe communities. This problem is especially bad in the Intermountain West because of the invasion of exotic species preadapted to the arid conditions. Case studies of several rare plants, including Aase's onion (Allium aaseae Ownbey), Davis peppergrass (Lepidium davisii Rollins), slick-spot peppergrass (L. papilliferum [Henderson] A. Nels. & J.F. Macbr), inch-high lupine (Lupinus uncialis S. Wats), gymnosteris (Gymnosteris nudicaulis /Hook. & Arn.] Gray), and an annual buckwheat (Oxytheca dendroides Nutt.), illustrate the challenge these species have in surviving in environments modified by exotics. Even if grazing were properly controlled or regulated, rare plants would still be threatened unless exotic grasses and the resulting increased fire frequency were controlled.

INTRODUCTION

The displacement of rare plants by annual weeds is a major problem on Intermountain rangelands. Cheatgrass (*Bromus tectorum* L.) is now the dominant species on more than 40 million ha (100 million acres) of the Intermountain West (Mack 1981). Competition between rare plants and annual weeds is both direct and indirect. Indirect impacts caused by annuals include increased fire frequency and the associated conversion of shrub-steppe to nonshrub annual grasslands, and the associated increased plant litter (Billings 1990; Evans and Young 1970) and changes in nutrient availability. Prior to the arrival of white settlers, fire-return intervals in the sagebrush steppe probably varied between 60 and 110 years, but much of the region now burns at intervals of less than 5 years (Whisenant 1990).

The Exotic Annuals

The most prevalent exotic annual weeds in the Intermountain West are listed in table 1. These and other annuals may occur alone or in combination. Each year, depending on weather conditions, timing of precipitation events, soil texture, soil pH, and stochastic fluctuations in the availability of seed, exotic annual species may rapidly dominate a disturbed site. For example, medusahead wildrye is more prevalent on heavy clay soils; pale alyssum and filaree more typically occur on coarse sandy soils; and Russian thistle, kochia, halogeton, tumblemustard, and perfoliate peppergrass are common on alkaline sites.

The domination of a site by a particular species is not wholly dependent on soil chemistry, as these species may proliferate rapidly in an area following a soil-disturbing event. The species that stochastically has the greatest abundance of seed present in the seed bank is often the species to dominate.

Watershed Values

Sites converted to annuals have lost genetic, species, and structural diversity. They represent low-quality watersheds with increased susceptibility to soil erosion and are prone to desertification (Buckhouse 1985). Annual vegetation is more susceptible to drought, as its biomass accumulation fluctuates with the available soil moisture more than perennial vegetation does.

Stewart and Young (1939) found forage production of grasses varied much less for perennial grasses than for cheatgrass. They demonstrated that perennials produce twice the biomass of cheatgrass in a moist year and 12 times the biomass during a drought. Managing forage for domestic livestock on annual grasslands can be seen as a gamble under such production schedules (Roberts 1990). An error in planning or grazing management can cause habitat degradation during dry years and leave dangerous flash fuels in moist years. Rangeland users need a more dependable source of forage for proper grazing management (Roberts 1990).

Fire Frequency

Sites dominated by annuals typically have higher fire frequencies than sites where perennials dominate (Pellant

Table 1—Common exotic weedy annual species on Intermountain rangelands

Common name	Scientific name		
Cheatgrass	Bromus tectorum L.		
Medusahead wildrye	Elymus caput-medusae L.		
Filaree	Erodium cicutarium (L.) L'Her.		
Bur buttercup	Ranunculus testiculatus Crantz		
Perfoliate peppergrass	Lepidium perfoliatum L.		
Pale alyssum	Alyssum alyssoides L.		
Tumblemustard	Sisymbrium altissimum L.		
Tansymustard	Descurainia pinnata (Walt.)Britt		
Halogeton	Halogeton glomeratus Meyer		
Kochia	Kochia spp.		
Russian thistle	Salsola kali L.		

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1990). Exotic annuals produce a continuous bed of flash fuels that perpetuates an abbreviated fire cycle, a cycle unsuitable for persistence of most native plants (Wright 1985). The resulting loss of genetic and structural diversity is important to the functional dynamics of the system and as an indicator of ecosystem health.

Studies of rare species not only deepen our knowledge of these species, but they also deepen our understanding of common species, offering insights to questions of fundamental importance in ecology and evolutionary biology. Losses in vegetation diversity cause collateral declines in faunal diversity and shorten the time period of active plant growth (Parmenter and MacMahon 1983).

It is the reduced period of active growth and the associated reduction in community biomass that causes the decline in many animal populations. For example, loss of shrubs used as winter food and thermal cover for jackrabbits caused a decline in the use of the Snake River Birds of Prey Area by golden eagles (Nydegger and Smith 1986; Steenhof and Kochert 1988). A reduced period of active green vegetation means a reduced period when wildlife and domestic livestock can properly utilize an area.

Landscape Patterns

Annual grasslands that burn frequently are highly uniform, interspersed with very few patches of unburned vegetation remaining (Whisenant 1990). Large, species-poor sites have a strong isolating effect on the remaining native vegetation patches. The new fire regime results in areas with poor species richness, low landscape patchiness, and altered successional patterns. Mature sagebrush steppe is eliminated, as are many earlier successional species that occupy a site after minor disturbances within the mature community.

Loss of a dominant species such as sagebrush may cause the loss of sympatric species dependent on it, such as twisted moss (*Tortula ruralis* [Hedw.] Gaerth.), which grows in the shade of sagebrush. Likewise, spiny hopsage (*Grayia spinosa* [Hook.] Moq.) becomes established beneath canopies of mature shrubs (Nancy Shaw: personal communication). Some sagebrush grassland species are mutualistic, sharing mycorrhizal associations as well as complementing each other ecologically (Wicklow-Howard 1989). As one species is lost, associated species may also be threatened.

Shrubs

Biological relationships and their structural dependency are critical in the shrub-steppe of the Intermountain West. Shrubs intercept moisture, provide shade, recycle deep soil nutrients, and modify soil-surface temperatures by decreasing wind velocity (Murray 1975; Rosentreter and Jorgensen 1986). These structural features of steppe shrubs are comparable to values attributed to trees in forests. Conversion of shrub-steppe to annual grasslands represents a drastic and detrimental change in a community.

Ecosystem Stability

Loss of diversity generally causes ecosystem instability and, in portions of the Intermountain West, increases fire frequencies (Whisenant 1990). In addition to the biological "cost" of increased fire frequencies, the enormous monetary cost of fire in terms of suppression and rehabilitation provides a major incentive to maintain native perennial rangelands.

Annual fire suppression costs on Bureau of Land Management-administered lands in the State of Idaho alone averaged \$4,339,000 per year between 1987 and 1991. In 1992 the costs increased to \$10,253,000 (Bill Mitchell: personal communication). Without a conversion from the annual grassland vegetation back to a perennial type, these costs will recur as areas repeatedly burn, and traditional rehabilitation costs of these sites can be much higher than the appraised value of the land (Roberts 1990).

STUDY AREA

The results discussed later are based on several studies of rare plant populations in the Snake River Plain and adjacent foothills. The Snake River Plain is of basaltic origin, while the foothills are a mixture of granitic alluvium and fine silts and clays. Elevations range from 671 m (2,200 ft) to 1,676 m (5,500 ft) at midmountain. Soil moistures are classified as aridic; soil temperatures are classified as mesic. Cooler soil sites that are frigid soil temperature regime or cooler are not addressed in this treatment.

ABIOTIC FACTORS AND LANDSCAPE PATTERNS

Shrubs increase abiotic microsite variability by providing shade, decreasing wind, and capturing snow and rain on a local scale. This is especially important in areas like the Intermountain West where precipitation comes primarily in the winter as snow.

Abiotic factors change when a site is converted from shrubs to exotic annual grasslands, and the loss of shrubs is the major factor affecting abiotic changes (Billings 1990). With shrub loss, there is a decline in (1) forage production, (2) soil stability, (3) diversity, (4) consistent annual biomass production, (5) mineral cycling, (6) thermal and escape cover for wildlife, and (7) esthetic values (Parmenter and MacMahon 1983; Rosentreter and Jorgensen 1986). These local influences on the abiotic conditions are reflected in the vegetative cover at every level of scale on the landscape. For example, the composition of the local vegetation is simplified and the degree of landscape patchiness decreases with an increased prevalence of annual grasses, biotic changes which can persist for long periods due to the changes in the abiotic environment (Billings 1990; Whisenant 1990). In northern Nevada, Billings (1990) followed a sagebrush- steppe site for 41 years after it burned. He found that sagebrush did not return to this cheatgrass-dominated site.

In a climate where most of the annual precipitation comes in the form of snow, shrub presence or absence may determine the effective soil moisture throughout the year. At low and mid-elevations, the snow melts periodically, saturating the ground beneath the snowbank. Repeated occurrences of this snow-capturing and melting process contribute to a patchy vegetation pattern.

STRUCTURAL DIVERSITY

The structural diversity of a site is dramatically lowered as the shrub component declines. Shrubs provide important thermal and escape cover for wildlife, just as they provide favorable microsites for establishment of grass and forb seedlings.

The structure of the shrub community influences the pattern of snow accumulation and melting process and moderates soil temperatures both beneath individual shrubs and at the stand level. These differences influence animal and plant composition, dispersal, and vigor. Animals dependant on forbs and grasses in a shrub community find green forage for up to a month longer than in an adjacent annual grassland lacking structural diversity (Rosentreter, personal observation).

SUCCESSIONAL PATTERNS

It appears that the steppe ecosystem, once controlled by classical successional patterns (relay floristics), is now largely dominated by initial floristics due to the introduction of exotic annuals (Billings 1990). In southwestern Idaho, the first exotic seeds to arrive at a site have a great advantage over other species, often dominating the site for long periods of time (Whisenant 1990). This may be referred to as the "stochastic occurrence of seed." While seasonal fluctuations in precipitation or litter may affect the frequency of specific exotics, displaced native perennials typically do not vary seasonally in frequency (Evans and Young 1970). For example, with fall precipitation, cheatgrass grows rapidly and will dominate a site by the following spring. If fall moisture is minimal or lacking, bur buttercup (Ranunculus testiculatus Crantz) frequently dominates. Russian thistle (Salsola kali L.) emerges in spring and comes to dominate disturbed sites that receive summer precipitation. These exotics take advantage of the full spectrum of the phenologic and temperature niches available in the Intermountain steppe.

While exotic annuals exploit soil moisture at different times of the year, they do not utilize the entire soil profile. This may explain why, without fire, grazing, or other major disturbance, shrub-steppe habitats in good condition can exclude most exotic annuals. Most ecologists recognize the importance of competition for space above the soil surface, but in arid regions, interspecific competition is largely played out underground, in the soil profile. Shrubsteppe communities converted to annual grasslands generally lack deeply rooted species to utilize deep soil moisture. Shrubs recycle nutrients and moisture leached deep into the soil profile (Caldwell and Richards 1989; Murray 1975). Without the return of these deep nutrients and moisture, many sites may become increasingly impoverished, arid, and less productive (Billings 1990).

SPREAD OF EXOTICS

Initially, annual grasses may occur only where a fire or other major disturbance has taken place, but they may spread to adjacent sites. Exotic, nongrass species increase slowly after the disturbed site is dominated by cheatgrass. After a second fire, other exotics, in addition to cheatgrass, quickly invade the areas adjacent to the original disturbance. I believe this is largely determined by the "stochastic occurrence of seed."

CASE STUDIES

Direct Competition

Native Annuals—In portions of the Intermountain West cheatgrass has replaced native annuals such as gymnosteris (Gymnosteris nudicaulis [Hook. & Arn.] Gray), inch-high lupine (Lupinus uncialis S. Wats.), oxytheca (Oxytheca dendroides Nutt.), and langloisia (Langloisia punctata [Torr.] Greene). Most of these native species are now on the Idaho State sensitive plant list (Moseley and Groves 1990). Exotic annuals compete directly with native plants for space, moisture, and light. Gymnosteris is found in basin big sagebrush (Artemisia tridentata Nutt. ssp. tridentata) habitat (DeBolt and Rosentreter 1988). Label data from specimens collected 20 to 40 years ago state that it was "abundant" or "common" (College of Idaho Herbarium, Caldwell, ID [CIC]). Today this plant is rarely seen, with small colonies found only on good-condition rangelands when spring moisture is abundant. I collected extensively in two above-average moisture years in southwestern Idaho and found few populations of this species.

The inflorescences of gymnosteris plants collected in Idaho in the last 10 years are predominately yellow or white. Older collections exhibited a wider range of colors at each collection site, including white, yellow, pink, violet, and orange. This decline in color variation may represent a loss of genetic diversity caused by reduced genetic mixing of the remnant populations. The isolated patches of gymnosteris may have become reproductively isolated and may be experiencing genetic bottlenecks (Falk and Holsinger 1991). This decline in genetic diversity may decrease the vigor of individuals and populations.

Indirect Competition

Aase's Onion—Aase's onion is a rare (Federal category 1 species), small perennial that occurs on coarse, barren, sandy soils on east-, south-, and west-facing slopes in the Boise foothills (DeBolt and Rosentreter 1988). It is often associated with mature bitterbrush (*Purshia tridentata* [Pursh] DC.) on or near ridgetops. Aase's onion is restricted both ecologically and geographically. Its phenology is very early, with growth beginning in February and flowering in March and April. While its habitat is not optimal for the growth of cheatgrass, as the surrounding vegetation is converted to annuals, cheatgrass can be found invading Aase's onion habitat. As the occurrence of cheatgrass increases in areas adjacent to onion habitat, litter cover increases thereby modifying soil conditions

Table 2—Number of *Allium* umbels and cover class values of exotic annuals per quadrat. Annual cover classes: 1 = 1-5 percent, 2 = 6-25 percent, 3 = 26-50 percent, 4 = 51-75 percent

	Mean number of Allium umbels		and a start of the second s
1	11.5	8.9	38
2	8.4	5.9	14
3	5.6	4.9	12
4	4	2	3

and encouraging the growth of other exotic annuals such as filaree (*Erodium cicutarium* [L.] L'Her.) and pale alyssum (*Alyssum alyssoides* L.) (Young and Evans 1979). These exotics spread easily into sandy sites directly competing with the onion (table 2).

Table 2 data group cheatgrass, filaree, and pale alyssum together as annuals. Table 2 shows that the number of *Allium* umbels decreases as the percentage of annuals increases in a quadrat (unpublished data, Boise District, BLM files). Field observations of Aase's onion show an increase in filaree, pale alyssum, and cheatgrass on sites that have burned (table 2), with filaree the best adapted for sand. Growth of these annuals on coarse, sandy soil and adjacent areas causes an accumulation of litter and a nutrient flush. This litter is damaging to the onion, which is adapted to barren, nutrient-poor sites. Though no onion sites have been totally displaced by exotics to date, the extent of the onion's suitable habitat has decreased in size.

Davis Peppergrass—Davis peppergrass, a Federal candidate 2 species, is a caespitose perennial mustard restricted to hard-bottom playas (fig. 1) that are usually barren of other vegetation (DeBolt and Rosentreter 1988). The playas are poorly drained and often inundated with standing water in early spring. It occurs in eastern Oregon and southwestern Idaho.

Although cheatgrass does not grow on the playas with Davis peppergrass, it indirectly affects peppergrass survival. Playas in the Great Basin receive runoff from adjacent areas. When these adjacent areas are converted to exotic annual grasslands, siltation generally increases (DeBolt and Doremus 1989, 1990). Some playas adjacent to annual grasslands can receive over 1.5 cm of siltation in the spring following a summer wildfire (Ann DeBolt 1988: personal observation). Excess siltation may smother and kill individual Davis peppergrass plants.

A second and more direct threat created by the degraded grasslands is the growth of other annual weeds, especially Russian thistle (fig. 2). After death, Russian thistle, kochia, and tumblemustard plants dry and break

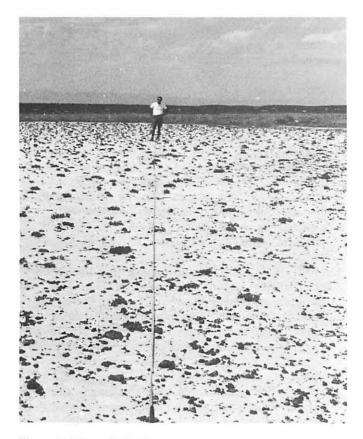


Figure 1—Playa with Davis peppergrass.

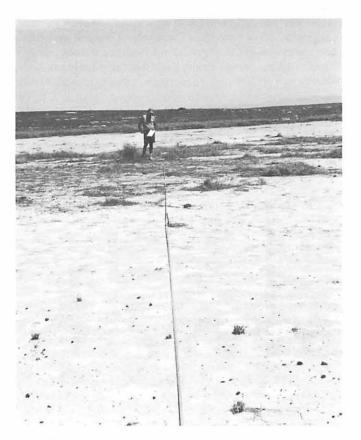


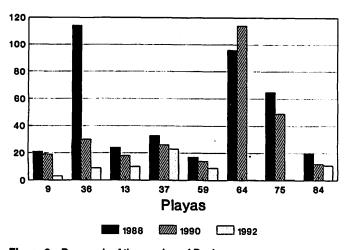
Figure 2—In this playa Davis peppergrass died due to the mulching effect of Russian thistle.

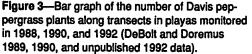
free from the ground to blow about as "tumbleweeds," occasionally coming to rest in the playas. Because playas are depressions in the landscape, they may collect large numbers of tumbleweeds to depths of a meter or more.

Tumbleweeds can act as a mulch, blocking light for extended portions of the year, and sometimes causing extensive peppergrass mortality. Several playas have been completely covered by tumbleweeds (fig. 3). Figure 3 shows data from two playas (number 64 and 75) where populations of peppergrass went from 114 and 65 plants respectively to none in a 2-year period. Six other playas (fig. 3) with Davis peppergrass have greatly decreased in population size due to the mulching effect of tumbleweeds (DeBolt and Doremus 1989, 1990, and unpublished 1992 data).

Slick-Spot Peppergrass—Slick-spot peppergrass is a small biennial mustard restricted to relatively barren "slick spots" within the Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) community type in southern Idaho (DeBolt and Rosentreter 1988). Slick spots are shallow soil sites or tiny playas also referred to as intercoppice areas (Eckert and others 1986). These sites are variable in size, but they are generally small (2-5 m²) and irregular in shape. They are sparsely vegetated by vascular plants, but are often carpeted with nonvascular microphytic plants, also called cryptogamic crusts (Rosentreter 1986).

For slick-spot peppergrass, cheatgrass is not a direct, but rather an indirect, competitor. The intercoppice areas are small, and as the adjacent vegetation is converted from shrubs to annuals conditions change. Fires become more frequent, altering the character of the soil's surface, causing siltation onto the slick spots. The fires and siltation also destroy the crust of microphytic plants. In Montana, Lesica and Shelly (1992) determined that Arabis fecunda Rollins, another rare mustard, was positively associated with the growth of microphytic plants. The cumulative effects of these changes permit invasion of exotic annual plants into the slick spots.





CONCLUSIONS

Throughout the Intermountain West, native plants, both rare and common, are reduced in number and genetic diversity where exotic annuals become dominant. This change in community structure is not a temporary situation, but rather a shift in successional patterns to a self-perpetuating annual community. This change in species composition promotes an increased fire frequency that concomitantly reduces structural diversity and patchiness of the landscape.

The loss of structural diversity, once provided by shrubs and perennial bunchgrasses, modifies abiotic conditions in the community. The new community of exotic annuals competes both directly and indirectly with native plants. Indirect competition includes the increase in fire frequency, stochastic distribution of exotic seeds, increased litter accumulation, increased siltation, and loss of microphytic plants.

Most native species can tolerate moderate amounts of grazing. However, even one season of misuse may cause degradation and subsequently invasion by exotic annuals, thus predisposing the site to fire. After one or more burns, the diverse native plant community is converted to an impoverished community of exotic annuals. Maintaining healthy native communities, the suppression of fire, and the prevention of rangeland wildfires is needed to retain rare and common native plant communities.

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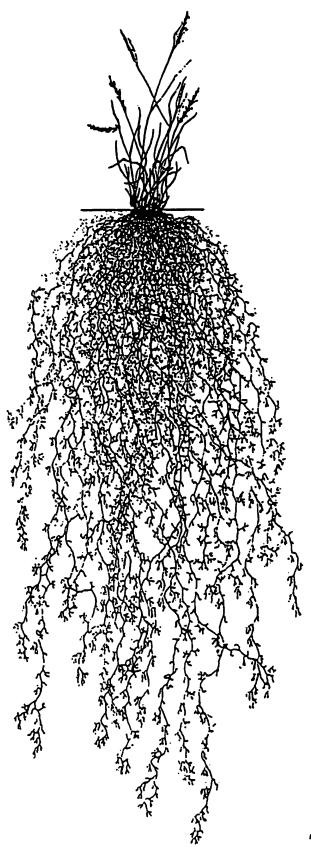
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Restoration: Weed Control



Stipa lettermanii

POTENTIAL ROLE OF CRYPTOBIOTIC SOIL CRUSTS IN SEMIARID RANGELANDS

Jayne Belnap

ABSTRACT

The role of cryptobiotic soil crusts in the functioning of semiarid and arid ecosystems is discussed. These roles include microstructuring of soils in cold-desert ecosystems, influencing soil nutrient levels, and influencing the nutrient status, germination, and establishment of vascular plants in crusted areas when compared to uncrusted areas. For these reasons, re-establishment of these crusts should be an important part of reclamation efforts. Natural recovery rates and the effectiveness of inoculation efforts are discussed.

INTRODUCTION

It has long been reported in the literature that cryptobiotic soil crusts, consisting of cyanobacteria, mosses, and lichens, are an important component of ecosystems in semiarid areas. These crusts may represent up to 70 percent of the living cover in some of these systems. Many roles have been ascribed to these crusts, including effects on soil stability (Anantani and Marathe 1974; Anderson and Rushforth 1976; Anderson and others 1982a.b; Belnap and Gardner 1992; Campbell 1979; Fletcher and Martin 1948; Harper and Marble 1990; Kleiner and Harper 1972, 1977; Loope and Gifford 1972; Marathe 1972; Metting and Rayburn 1983; Shields and Durrell 1964), soil moisture and nutrient status of soils (Belnap and Harper 1992: Brotherson and Rushforth 1983; Campbell 1979; Harper and Belnap, unpublished data; Shields and Durrell 1964), contribution of fixed nitrogen (Belnap 1991; Evans and Ehlringer 1992; Skujins and Klubek 1978), and enhancement of seedling establishment (Harper, unpublished data). Data suggest that these crusts are slow to recover from severe disturbance, requiring 40 years or more to recolonize even small areas (Belnap 1992).

This paper discusses the ecological role of cryptobiotic soil crusts, including their structure, effects on the nutrient status of plants, and effects on seedling establishment and success, as well as ways to hasten their recovery from disturbance. Data are drawn from several different studies conducted over the past 5 years by Belnap (1991, 1992), Belnap and Gardner (1992), Belnap and Harper (1992), Harper and Belnap (1992) and Harper (unpublished).

METHODS

Cyanobacterial soil crusts from sandstone- and gypsumderived soils were collected from Arches and Canyonlands National Parks located in southeastern Utah near Moab. For scanning electron microscopy (SEM) work, samples were either directly gold coated or were prepared by freeze substitution, and then examined with a JEOL 840A scanning electron microscope.

The presence of chlorophyll a was used to estimate the biomass of living cyanobacteria and green algae in the crusts found on the sandy and gypsiferous soils from Arches National Park. Chlorophyll a was extracted from collected samples with dimethyl sulfoxide (DMSO). The DMSO extraction samples were centrifuged and spectrally analyzed on a diode array spectrophotometer at 665 nm to obtain relative values for the amount chlorophyll a present (Belnap 1991).

Plant tissue of the native annual grass, Festuca octoflora, and the native perennial dicotyledonous herb, Mentzelia multiflora, was chosen to compare nutrient status of plants on and off crusted surfaces. Festuca octoflora was collected from a site approximately 20 miles (33 km) southwest of Moab, UT. Mentzelia multiflora was collected from Arches National Park, 10 miles (17 km) northeast of Moab. Both areas have been protected from domestic livestock grazing for over 10 years. Plants were collected from two immediately adjacent sandy sites; one area had well-developed cyanobacterial-Collema lichen crusts, while the other lacked such a crust. At Arches, windblown sand accounted for the lack of crust: at the F. octoflora site, the lack of crust was due to repeated trampling by people over a period of years. Composite samples of at least five individuals (or 2.0 g tissue for the tiny Festuca plants) were collected at each of five locations for each soil surface condition class at each site. Two composite samples of the surface 3.0 cm of the soil profile were collected from each soil surface class at each site.

Soils were analyzed for percent sand using a hydrometer procedure (Bouyoucous 1936). Soil reaction was determined with a glass electrode on a saturated soil/distilled water slurry. Organic matter was determined by wet digestion in 1.0N potassium dichromate (Moodie and others 1963). Total nitrogen in soils was estimated using a micro-kjeldahl procedure (Association of Official Analytical Chemists 1980). "Available" phosphorus was extracted in 0.2N acetic acid, and determined using the iron-TCA-molybdate method (Goldenberg and Fernandez 1966). Exchangeable bases were displaced from the soil with 1.0N ammonium chloride

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and concentrations in the extractable solution were determined using an atomic absorption unit (David 1960). Airdried plant samples (whole plants including major roots remaining when individual plants were pulled up) were cleaned of adherent sand and ground through a 40-mesh sieve using a rotating mill. Samples were stored until analyzed in capped plastic vials. Nitrogen was determined by micro-kjeldahl procedures. A single 1.0-g sample of each specimen was fully digested using a sulfuric acid-nitric acid procedure (1:5 parts respectively of the concentrated acids). Elemental content of essential minerals was determined on aliquots of the digestate using an atomic absorption unit and appropriate analytical procedures (Association of Official Analytical Chemists 1980). Results of tissue analyses for individual elements were compared using an unpaired t-test model.

Seedling germination and establishment were measured over a period of 4 years. Seeds were planted through a template into permanent plots. Seedling establishment and success were measured after germination and after 4 years using a 0.25-m² quadrat frame and Daubenmire cover classes.

RESULTS AND DISCUSSION

The structure of soil crusts from the Colorado Plateau region of Utah was studied by Belnap (1992) using a scanning electron microscope. The crusts in this region are dominated by the cyanobacterium *Microcoleus vaginatus*

(Anderson and Rushforth 1976; Campbell and others 1989; Johansen and Rushforth 1985), which often represents up to 95 percent of the biomass in the soil (Belnap, personal observation). Figures 1-3 show M. vaginatus and M. vaginatus-dominated crusts in sandstone-derived soils. M. vaginatus has a large, distinct, sticky extracellular sheath that surrounds groups of living filaments (fig. 1). When wetted, this sheath material swells, and filaments within are mechanically extruded through the soil. As the substrate dries, the exposed filaments secrete additional sheath material. Rewetting repeats this cycle, resulting in sheath material that winds among the sand particles much like fibers in fiberglass (fig. 2). Even when dry, the sheath material can be seen firmly adhering to soil particles (fig. 3). These connections appear to reduce wind and water erosion, as well as holding the otherwise loose material on slopes well beyond the angle of repose. When wetted, the sheath material swells and covers the soil surface even more extensively than when dry. Sheath material can absorb up to eight times its weight in water, thus absorbing precipitation quickly and increasing the waterholding capacity of sandy soils (Brock 1975; Campbell 1979; Campbell and others 1989). Even when swollen, there is space for rainwater and vascular plant roots to penetrate into the soil between sheaths (fig. 4).

Cyanobacteria and cyanobacterial components of soil lichens fix atmospheric nitrogen most of the year (Belnap 1992; Fuller and others 1960; Skujins and Klubek 1978; Terry and Burns 1987; West and Skujins 1977). Studies

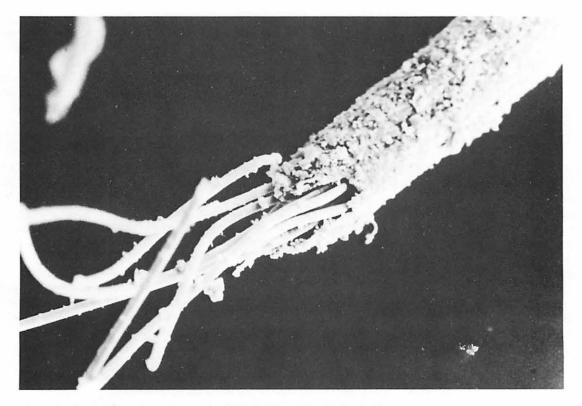


Figure 1—Scanning electron micrograph of *Microcoleus vaginatus*, the dominant cyanobacterium in soil crusts of the Colorado Plateau. Note the living filaments extruded from the sticky extracellular sheath (magnification x 700), as occurs when the organism is wetted.



Figure 2—Scanning electron micrograph of dry cyanobacterial sheaths winding through sandy soils from Moab, UT. Note firm attachment of sheath material to the individual sand grains, even though sheath material is dry (magnification x 90).



Figure 3—Scanning electron micrograph of a sand grain wrapped by cyanobacterial sheaths (magnification x 400).



Figure 4—Scanning electron micrograph of wet cyanobacteria on the surface of a moistened sandy soil from Moab, UT. Note the swollen, rounded sheaths "net" the surface, keeping fine soil particles in place (magnification x100).

utilizing radioactive isotopes of nitrogen have demonstrated that nitrogen fixed by cyanobacteria in the crusts is available to neighboring vascular plants (Mayland and McIntosh 1966; Mayland and others 1966). In some desert systems, these crusts have been demonstrated to be the dominant source of this often-limiting element for associated seed plants (Evans and Ehlringer 1992).

Elemental levels of vascular plants are affected by the presence of these crusts. Levels of N, P, K, Fe, Ca, and Mg were higher in the annual grass Festuca octoflora growing on crusted soils than in plants growing on comparable noncrusted soils. Levels of N, Fe, Ca, Mg, and Mn were higher in the native perennial forb Mentzelia multiflora (Belnap and Harper 1992). Essential nutrient concentrations were also shown to be higher in the tissue of the biennial plant Lepidium montanum growing on soils covered by cyanobacterial-rich crusts than on paired plots where the surface 1.0 cm of crust had been stripped from around the plants 3 months prior to tissue nutrient analyses (Harper and Marble, in preparation). Experiments in the greenhouse show levels of nitrogen in sorghum and rape higher in pots with cyanobacteria when compared to pots without cyanobacteria. Dry weight of plants in pots with cyanobacteria were up to four times greater than in pots without cyanobacteria (Harper and Belnap, unpublished).

Several mechanisms have been postulated to explain this effect. Fletcher and Martin (1948) reported that crusts trapped soil fine particles, which are more nutrient-rich than sand (Black 1968). Lange (1974) demonstrated that compounds in the gelatinous sheath material of half the cyanobacteria species studied were able to chelate elements essential for their growth (for example, iron, copper, molybdenum, zinc, cobalt, and manganese). Four of the five genera shown to possess this ability (*Anabaena, Anacystis, Lyngbya*, and *Nostoc*) are represented by common species in the cryptobiotic crusts of western North American deserts (Shields and Durrell 1964). Belnap (1992) showed that cyanobacterial sheath material was often coated with negatively charged clay particles, providing a mechanism for holding positively charged macronutrients against leaching from the soil profile. It is also possible that nutrient differences are a result of a thermal effect, as dark crusts would be warmer that lighter uncrusted soils, and uptake of nutrients would occur at a higher rate.

The presence of soil crusts can also affect seedling establishment and survival. Experiments done by K. Harper (unpublished) at sites with both fine and coarsely textured soils demonstrate that seedling establishment was much higher for both forbs and grasses in crusted areas when compared to areas where the crust had been removed (table 1). Survival over a 3-year period was enhanced in the four species (grasses and forbs) measured at these sites as well (table 2). Other studies have reported similar enhancement of seedling germination and establishment in crusted areas when compared to noncrusted surfaces (Harper and St. Clair 1985; St. Clair and others 1984).

Trampling negatively affects the cohesion and coverage of cyanobacterial crusts, since the filaments are brittle when dry and easily crushed (Campbell 1989; Harper and Marble 1990). Visual examination of undisturbed soil crusts on

 Table 1—Effects of cryptobiotic soil crust on vascular plant seedling establishment. Seedlings were measured 10 months after early winter planting of four species (*Linum perenne*, Oryzopsis hymenoides, Sphaeralcea coccinea, and Elymus junceus) at three different locations in central Utah. Thirty-two seeds of each species were planted through a template at five randomly chosen spots in each of at least 22 plots representing crusted or not crusted soils at each site. For this table, seedlings of all four species were pooled. The "no crust" treatment consisted of scalping the top 1.0 cm of the soil profile

Site	No crust	Crust	р
Tintic Junction	105	165	<0.1
Buckthorn Reservoir	140	389	<.1
BLM-USU pasture	59	198	<.1
All sites pooled	304	753	<.1

sandy soils of the Colorado Plateau shows cyanobacterial sheath material to occur as deep as 10 cm below the surface of the soil. In contrast, heavily trampled areas support only a thin veneer of cyanobacteria and cyanobacterial sheaths (Belnap 1992). Since no chlorophyll a is found below 1 cm (Belnap, unpublished), sheath material below that depth must represent remnants of cyanobacterial crusts once found near or at the soil surface and later buried by sediments. Thus as aeolian and water-borne materials are trapped in the polysaccharide sheaths of M. vaginatus and other cyanobacteria growing on the surface of desert soils, these sheaths are gradually buried, but their ameliorating influences on water-holding capacity, cation exchange capacity, and soil stability may extend far below the depth to which light can penetrate. Any damage to such abandoned sheath material is nonrepairable, since living cyanobacteria are apparently no longer present at these depths to regenerate filament and sheath materials. As a consequence, trampling may not only reduce soil stability, but soil fertility and soil moisture retention as well.

Restoration of these crusts has been studied by several investigators. These studies have examined both natural recovery and the use of inoculants. Recovery rates depend on the type and extent of disturbance and the availability of nearby inoculation material, as well as on the temperature and moisture regimes that follow disturbance events.

Table 2—Effects of cryptobiotic soil crust on vascular plant survival over 3 years (1981-84) at three different sites with 3 different soil textures. The "no crust" treatment consisted of scalping the top 1.0 cm of the soil profile

Site	Species	No crust	Crust
			urvival -
Tintic Junction	Linum perenne	79	88
Tintic pastures	Oryzopsis hymenoides	75	100
	Elymus junceus	0	100
Buckthorn Reservoir	Sphaeralcea coccinea	17	27
	Elymus junceus	14	100

Estimates of time for natural recovery from disturbance of cryptobiotic crusts have varied widely, ranging from a few years to 100 years for full recovery of all components (Anderson and others 1982b; Callison and others 1985; Cole 1991; Jeffries and Klopatek 1987). Belnap (1992) reported that if only visual estimates of cyanobacterial cover are considered, recovery appears quite rapid. In several experiments where the top 2 cm of the soil surface was removed, all plot surfaces, whether inoculated with nearby material or not, appeared completely covered by cyanobacteria, and most showed rudimentary pedicelling after only 1 year. This gave the impression that the cyanobacterial/ green algal components of the crusts were mostly or fully recovered. Chlorophyll a measurements, however, told a different story: dramatic differences in chlorophyll a levels demonstrated that the amount of photosynthetic cryptobiotic tissue present differed greatly among treatments. Uninoculated plots sometimes supported only 2 percent as much chlorophyll a as was found in nearby undisturbed crusts. Estimates for full recovery of the cyanobacterial biomass, using chlorophyll a concentration as the indicator, ranged from 35 to 65 years. Other aspects of crust recovery, including the depth of accumulated cyanobacterial sheath material and lichen and moss species number and cover, were much slower.

Lichens showed some recovery at three of the four sites tested. At observed rates, full recovery at these three sites would take 45 to 85 years. At one site, no recovery was seen, even after 5 years; consequently, time to full recovery is impossible to predict. Moss recovery was even slower than that of the lichens. At two of the three sites where mosses were found in the undisturbed areas, no mosses were found in the disturbed areas. This makes prediction of recovery rates for mosses at these sites impossible, but clearly they are extremely slow. At the third site, where some recovery was seen, full recovery of moss cover would take over 250 years at the observed rate.

Several studies have demonstrated that inoculation can hasten the biological recovery of disturbed crusts (Ashley and Rushforth 1984; Belnap 1992; Lewin 1977; St. Clair and others 1986; Tiedemann and others 1980). In Belnap's 1992 study, inoculated plots had far greater chlorophyll *a* concentrations than uninoculated plots, indicating a larger biomass of cyanobacteria and green algae in inoculated sites. Inoculated plots also had significantly greater lichen species richness and greater lichen and moss cover than uninoculated plots. However, although lichen and moss cover was significantly greater on inoculated than uninoculated plots, recovery for both lichens and mosses was still extremely slow for both treatments.

Inoculation also hastened some aspects of visual recovery of the cyanobacterial/green algal component. Areas that had been inoculated had greater pedicellation sooner than areas that were not inoculated. Apparent coverage of the soil surface by this crustal component, however, was not hastened by inoculation, since all soil surfaces appeared completely covered within 1 year. Inoculation somewhat hastened the visual recovery of the lichens and mosses; however, absolute differences were so small it was difficult to tell treatments apart, even with close examination.

CONCLUSIONS

Cyanobacterial-lichen soil crusts can contribute in many ways to the ecosystems in which they occur. Such crusts can enhance soil stability, reduce water runoff by producing more microcatchments on soil surfaces and adding absorptive organic matter, improve nutrient (nitrogen and some essential mineral elements) relations for at least some vascular plants, and enhance germination and establishment of some vascular plants. These black crusts may also stimulate vascular plant growth and nutrient uptake by producing warmer soil temperatures during cool seasons when free water is most likely to be available in the cold deserts of the western United States.

Until we have a greater understanding of the short- and long-term effects of impacts on the ecology and functioning of these crusts, and how to reestablish them on disturbed arid lands, land managers should minimize activities that may disturb them.

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BIOLOGICAL CONTROL OF ANNUAL GRASS WEEDS

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ABSTRACT

Biological control of weeds is based on the premise that biotic factors have a significant influence on the distribution, abundance, and competitive abilities of plant species. Soil bacteria that selectively suppress grass weed species may alter competition among range plants. The bacteria can function as a direct delivery system for the natural plantsuppressive compounds they produce. Biological control offers alternative means of suppressing annual grass weed growth and establishment in range systems.

BIOLOGICAL CONTROL

Biological control is the use of natural enemies to control pests and has been utilized ever since humans altered the environment for food production. Biological control can be used to control insects, pathogens, and weeds and is defined as "the action of parasites, predators, or pathogens in maintaining another organism's population density at a lower average than would occur in their absence" (DeBach 1964) or alternatively as "the use of natural or modified organisms, genes, or gene products to reduce the effects of undesirable organisms (pests), and to favor desirable organisms such as crops, trees, animals, and beneficial insects and microorganisms" (Cook 1987).

The three main strategies for biological control are:

1. Classical, which is the importation of exotics or natural enemies for release, dissemination, and self perpetuation on target pests,

2. Augmentation, which involves the introduction of a virulent strain to suppress pests, also called the bioherbicide approach, and

3. Integrated pest management, which uses management techniques to conserve or enhance indigenous enemies of various pests.

An effective biological control agent needs to have certain characteristics in order to be effective. First and most important, biological control agents need to have a narrow host specificity or selectively suppress the target organism and not have any adverse effect on the nontarget population. The suppression of the pest does not necessarily have to be 100 percent lethal to be effective. Second, the agent must survive and act in the environment. It is very easy to find antagonistic relationships in the lab, but often these relationships do not exist in the field under varying environmental conditions. Third, the suppressive activity needs to occur at a critical point in the growth of the target organism. The microorganism needs to survive in the soil and be tolerant of low soil moisture. Finally, the biological control procedure needs to be feasible and be combined with other methods of weed control. Biological control will not necessarily be used alone, but rather in concert with cultural practices and herbicides, with the end result being the suppression of the pest.

INSECTS

Weeds are a problem in range establishment and have the potential to be controlled by biological means, either by the use of insects or microorganisms. The greatest emphasis in biological weed control research in the past has been on the use of insects. The first insect release on record for weed control was the release of a moth (*Dactylopius ceylonicus*) in the mid-1800's to control the pricklypear cactus (*Opuntia vulgaris*) in India. The list of insects used to successfully control many different weed pests continues to expand (Julien 1987). Such biological control agents include a beetle to combat St. Johnswort (*Hypericum perforatum*), a gall-forming fly and a gall-forming mite which attack rush skeleton weed (*Chondrilla juncea*), and beetles to control lantana (*Lantana camara*).

MICROBES

Microorganisms can have a profound effect on plant growth. Phytotoxic effects of microorganisms are often plant species and cultivar specific. These plant-microbe interactions can greatly influence distribution, abundance, and competition among plant species. Plant pathogens potentially may be used to regulate the growth of unwanted plant species growing simultaneously with more desirable plants. This would be especially true if competitive weed growth coincided with environmental factors conducive to bacterial growth and weed-suppressive activity.

Fungal pathogens have also been used to control weeds. Most notable is the use of rusts (*Puccinia jaceae* Otth.) for the control of diffuse knapweed (*Centuria diffusa* Lam.) (Mortensen 1986; Watson and Clement 1986) and skeleton weed (*Chondrilla juncea*) control with the use of *Puccinia chondrillina* (Cullen and others 1973). Mycoherbicides, such as the fungal pathogens of weeds sold under the trade names of DevineTM and CollegoTM, are commercially available. Devine is being used to control stranglervine (*Morrenia odorata*) in citrus (Ridings 1986) and Collego is used for the control of northern joint vetch (*Aeschynomene virginica*, Templeton and others 1986) in rice and soybean. The success of these two commercial mycoherbicides indicates the potential of microorganisms for weed control.

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Plant-suppressive bacteria potentially may be used to regulate the growth of unwanted plant species growing simutaneously with more desirable plants. Downy brome is an excellent weed species for this type of investigation.

Bacteria can exert a subtle, yet profound, effect on plant growth. Rhizobacteria that suppress plant growth can impair seed germination and delay plant development by the production of phytotoxic substances (Alstrom 1987; Schippers and others 1987; Suslow and Schroth 1982). Many plantsuppressive bacteria are effective colonizers of roots and residues (Fredrickson and Elliott 1985; Stroo and others 1988; Suslow and Schroth 1982) and subsequent retardation of plant growth is demonstrated in the laboratory.

Our biological weed control research developed from investigations of the early spring growth of winter wheat (Fredrickson and Elliott 1985). Stunted wheat plants were heavily colonized by bacteria that produced plant inhibitory compounds. These compounds specifically inhibited winter wheat and did not injure other small grains or legumes (Bolton and Elliott 1989). Recognizing this specificity, our initial hypothesis for the use of similar bacteria for biological weed control was that other soil bacteria could be found that inhibited only the grass weed downy brome and not the crop or other plant species.

To date, we have found a number of bacteria that specifically inhibit various grass weeds, but do not affect the crop (Kennedy and others 1991). These naturally occurring soil bacteria inhibit plant growth by the production of plantsuppressive compounds. These bacteria are excellent biological control agents because they are aggressive colonizers of the roots and residue. The bacteria can function as a direct delivery system for the natural plant-suppressive compounds they produce. They tend to be fairly tolerant of low soil moisture, although they do not survive well under hot, dry conditions. They survive well at low temperatures with an optimum temperature often below 15 °C. The greatest amount of toxin is produced at these low temperatures. They are most prevalent in the soil in late fall and early spring. Application of these bacteria during seedbed preparation and the resultant suppression of downy brome root growth may allow other plant species to out-compete weeds. thus leading to the establishment of more desirable range species. If this occurs during the seedling stage, the crop may gain a competitive growth advantage. This increase in crop competitive ability may further suppress weed growth at later growth stages.

Downy brome (Bromus tectorum L.), commonly called cheatgrass, was chosen as a biological control target because it is an especially troublesome weed. It has more vigorous root growth in the winter months, and completes its life cycle early in the spring. It is an invader species from Eurasia that germinates in fall or spring, over wide ranges of temperature and moisture. Downy brome was introduced into North America about 100 years ago (Mack 1981) and continues to be unmanageable in winter annual cropland and rangeland (Morrow and Stahlman 1984). It often is considered an important forage species providing early spring grazing; however, its short growth period, fluctuating forage production, and high fire hazard make it less desirable than other species. Downy brome is an effective competitor for space, water, and nutrients because its roots grow at low temperatures. Perennial grass seedings often

fail because downy brome is so competitive. Downy brome is an excellent plant to be used in biological weed control programs. Application of the downy brome-suppressive bacteria and the resultant suppression of root growth may allow another plant species to out-compete the weed.

In a survey of 3,500 naturally occurring soil bacteria, half were inhibitory to downy brome seedling growth in the *in vitro* screening. Two hundred forty isolates inhibited downy brome and not winter wheat in the *in vitro* assay. In greenhouse studies, 14 isolates continued to inhibit downy brome more than 35 percent with no adverse effect on winter wheat (Kennedy and others 1989). Several of these isolates from the initial screenings have proved to be biologically active in field tests.

Most bacterial isolates investigated thus far inhibit root growth, but some, such as *Pseudomonas fluorescens* strain D7 (*P.f.* D7), also reduce weed seed germination. The toxin apparently slows down the root mass accumulation by downy brome and reduces its competitive ability thereby giving wheat the competitive edge. An additional characteristic of the toxin is that it may affect germination and seedling vigor of the weeds, which results in a reduction in stand or population. The toxin will also reduce tiller number and the total number of seeds, with the end result being less plants with fewer tillers and fewer seeds. Thus, in theory we have a good match for a biological control pair.

Field studies were conducted in eastern Washington to evaluate the effects of the inhibitory bacteria on the growth of downy brome (Kennedy and others 1991). In field trials, in which downy brome was planted in rows, bacterial isolates reduced downy brome populations up to 30 percent and shoot dry weight up to 42 percent (fig. 1). In other studies, bacteria were applied to wheat fields infested with natural populations of downy brome. Downy brome and winter wheat growth and development were measured throughout the growing season. Reduction in downy brome growth varied and was dependent on the specific bacterial strain. One strain of inhibitory bacteria, P.f. D7, reduced plant populations and aboveground growth of downy brome 31 and 53 percent, respectively (fig. 2). In the same experiment, seed production of downy brome was reduced 64 percent. Winter wheat yields were increased by 35 percent with the application of the bacteria and subsequent suppression of downy brome growth (fig. 3). This increase in yield is similar to the yield increase expected from the elimination of a moderate infestation of downy brome. Another bacterium, Pseudomonas syringae strain 2V19, suppressed downy brome growth by 25 percent in the same field study with a 27 percent increase in winter wheat yield. In winter wheat field studies conducted in 1988, 1989, and 1990, suppression of downy brome by P.f. D7 at Lind, La Crosse, Ralston, and Pullman, WA, was 34 percent when the bacterium survived (Ogg and others, unpublished). These studies illustrate the potential for inhibitory bacteria to suppress the growth of weeds, resulting in significant increases in winter wheat yields. Even though the bacteria did not control the downy brome 100 percent, it suppressed downy brome growth so that winter wheat was able to out-compete the weed. Root colonization and plant suppressive ability by these bacteria may be sensitive to many soil factors, including soil water content (Fredrickson and Elliott

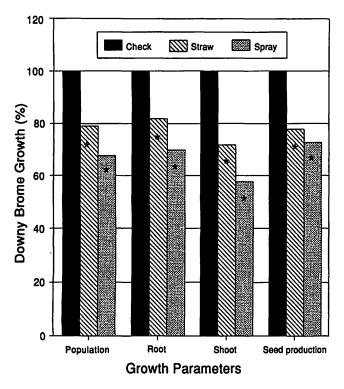


Figure 1—Downy brome growth from seeding field studies inoculated with rhizobacteria directly or spread with straw inoculated with the bacteria. Asterisks indicate significant differences at $p \le 0.05$ (Kennedy and others 1991).

1985; Howie and others 1987; Liddell and Parke 1989; Schippers and others 1987) and soil temperature (Kenerley and Jeger 1990; Loper and others 1985). Root exudate quality or quantity (Van Vuurde and Schippers 1980) or microfloral competition also play a part in bacterial survival (Suslow and Schroth 1982). The production of plant-suppressive compounds and subsequent weed suppression will change with colonization of the root by the bacteria (Bolton and Elliott 1989). In field studies with P.f. D7, time of application was critical to suppression of downy brome. Greatest inhibition of downy brome occurred when the bacterium was applied just prior to a significant rain event, indicating the importance of bacterial survival on biological control efficacy (Kennedy, unpublished).

These rhizobacteria can be compatible with several herbicides for grass control. Compatibility would be advantageous because it would allow for the bacteria to be used to supplement herbicides with poor activity on downy brome. Thus, a combination of the biological control agent and reduced rates of herbicides may reduce significantly the infestations of downy brome and may act synergistically with herbicides to increase activity, selectivity, or spectrum of control.

Microbial weed control, while reducing weed pressures, should significantly reduce costs, the need for tillage, and chemical pesticide usage, thus reduce erosion and water pollution. Microbial amendments, while reducing chemical herbicide rates, could substantially decrease the potential for groundwater contamination from herbicide runoff or

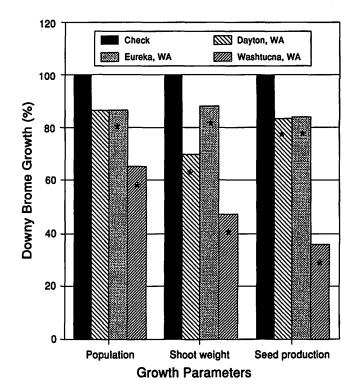


Figure 2—Downy brome growth and seed production from fields inoculated with rhizobacteria and planted to winter wheat at three locations in eastern Washington. Asterisks indicate significant differences at $p \le 0.05$ (Kennedy and others 1991).

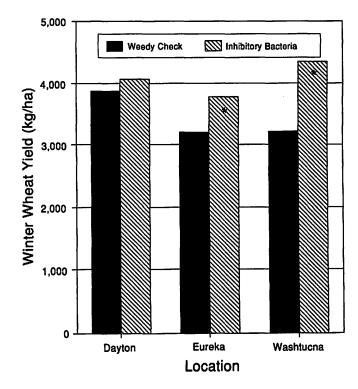


Figure 3—Winter wheat yield from fields inoculated with rhizobacteria and planted to winter wheat at three locations in eastern Washington. Asterisks indicate significant differences at $p \le 0.05$ (Kennedy and others 1991).

seepage into the water table. This new weed control technology has potential for use in rangeland systems.

ACKNOWLEDGMENTS

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MECHANICAL CONTROL OF UNDESIRABLE ANNUALS ON THE BOISE FRONT, IDAHO

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ABSTRACT

Slopes in excess of 40 percent capable of supporting undesirable annual plants have been successfully rehabilitated using mechanical methods of control. Precautions are necessary to reduce the erosion potential of the site and ensure the safety of the equipment operator. Weather, timing of planting, and site preparation can have a large influence on the success or failure of the planting.

INTRODUCTION

Mechanical control of undesirable annuals is an effective method that can be used alone or in combination with other control methods such as burning, chemicals, or grazing. Public opinion will often be the factor determining which method or methods can be used. Mechanical control is limited by topography, rocky soils, soil depth, and type of equipment available. On the Boise Front in Idaho we have been able to work on 40 to 45 percent slopes with varying degrees of success. Often the desired control is achieved, but the weather patterns are not conducive to the seeded species and the site is reinvaded by the undesirable annuals from the surrounding area.

STUDY AREA

The Boise Front elk and mule deer winter range includes the foothill region north and east of Boise, ID. The Boise Front consists of steep canyon slopes; the average slope gradient is nearly 25 percent, with 10 percent of the area having an average of 40 percent, some in excess of 60 percent. Elevations range from 2,800 to 5,906 feet. Average precipitation ranges from 11.8 to 29.5 inches from lower to upper elevations. The majority of the precipitation (65 percent) occurs from November through April in the form of snow at higher elevations and rain below (Johnson and others 1980). Temperature ranges from -23 to 111 °F with average summer and winter temperatures of 71 and 33 °F, respectively (Collett 1977).

The steep terrain and highly erosive granitic soil, plus the weather patterns that result in fast snowmelts or high-intensity storms, often produce 30 to 40 percent of the total sediment yield. Fire suppression, land management practices intended to increase perennial plant cover,

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. and control of off-road vehicle use have improved the watershed in the area. U.S. Department of Agriculture Northwest Watershed Research Center studies show that measured sediment yields from the Boise Front in 1978-79 were only 10 percent of the 1939-40 yields for comparable streamflow rates (Johnson and others 1980).

Big sagebrush (Artemisia tridentata ssp. vaseyana, xericensis, and tridentata) dominates the shrub community. Cheatgrass (Bromus tectorum) and medusahead rye (Toeniatherum asperum) make up a large proportion of the grass species at lower elevations. In the Day clays, Brent-Ludd loam, and other soils containing clays, medusahead rye often comprises 90 percent of the vegetation. Medusahead rye is the most undesirable annual on the Boise Front. It is low in palatability, has low watershed value, and has a high fire hazard. Total control of medusahead would be desirable. Cheatgrass has forage value to both big game and upland game species. Its watershed value is low, and it also has a high fire hazard. We feel, however, that by interseeding perennial grasses and shrubs into annual grass stands we can improve the watershed value, reduce the fire hazard, and improve forage values of the area. Total control of cheatgrass is not our objective.

METHODS

Various types of tillage equipment are available to meet the needs of the sites. Older implements may be found in the "back forty" and, often with a few modifications, can be very effective tools today. Improved implement designs are coming on the market regularly. The target percentage of undesirable plant control will determine if total tillage or interseeder type equipment will be needed. Some equipment that could be used in undesirable plant control projects is:

Moldboard Plow—This implement can be used in rock-free areas, but can be difficult to use in wet clay or sticky soils. It is slow and has a high power requirement. It will generally till deep enough to cover seed and plants. It may have difficulty turning the soil uphill and trailing directly behind the tractor on steep terrain. One-way tilling may be necessary. Three-point, roll-over plows would work best and may be needed in tough sod areas. Generally good control of undesirable plants is achieved with a moldboard plow.

Disk Plow, Wheatland, One-Way Plows—These can be used in lightly rocky areas. Plows should be equipped with 26- to 28-inch disks and will weigh over 3,000

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pounds. The plow has to be set at the maximum angle, usually 40-45 degrees (Hull and others 1952). This equipment will have trouble trailing on steeper slopes, and you may have to plow one-way. Moderate power supplies are needed.

Heavy Off-Set Disk—This is probably the most common implement used to control undesirable grasses. It will handle some rock if care is used. Notched disks will cut better than smooth ones, but break more easily. The maximum angle is necessary to achieve the preferred 4 to 6 inches of penetration. Disk diameter ranges from 28 to 50 inches, and weight is approximately 500 pounds per foot (Larson 1980). A high power supply is needed.

Brushland or Rangeland Plow—This plow was developed by the USDA Forest Service Equipment Development Center at San Dimas, CA. It is based on the Australian Stump-Jumper plow for moderately rocky, uneven terrain. Paired spring-mounted disks, one 24 and one 28 inches at a 4-degree incline, allow each pair to rise over rocks and brush independently of the others. It is 10 feet wide, weighs 6,000 pounds, and cuts 4 inches deep. The draft angle of the plow is adjustable from 30 to 40 degrees. It is heavy and can withstand some abuse (Larson 1980). A moderate power supply is needed.

Disk Chain—A disk chain consists of 24-inch disks bolted to links of anchor chain. A packer-type seeder follows the chain and is used to maintain the disks' distance apart. It prepares a 3- to 4-inch-deep seedbed and plants the area in one pass. It is limited by steep, rocky, or wet soils (Pellant 1990). A moderate power supply is needed.

Pitting Disk Plow—This is a modified one-way or wheatland disk plow with portions of the disks cut out. The disks alternately contact the ground leaving portions of the soil undisturbed. The pitted area traps the runoff, thus increasing forage production. Control of undesirable annuals is limited to the pitted area only. This is a good tool for erosion control on steeper slopes (Larson 1980). A moderate power supply is required.

Chisel Plow and Rippers—These can be used to fracture compacted soil or hardpans. Improved water and nutrient infiltration can increase plant production. They are not effective tools to control undesirable annual plants. They can be used after chemical, fire, or grazing controls to prepare the seedbed. They have a high power requirement.

Interseeders—These are mainly used for short-term control of undesirable plants while desirable species get established. Fair control of undesirable plants in the scalped strip is usually achieved. Interseeders are modified fire plows, bulldozer blades, v-blades, and the South Dakota interseeder. The v-blades and bulldozer blades are used on the Boise Front to interseed shrubs. They have a high power requirement.

Contour Furrower—This implement uses rippers to break up compacted soil, followed by disks to form furrows. The furrows are diked at intervals, and the seed is broadcasted into the furrows. Some control of undesirable plants in the furrows is obtained, but no control occurs in the 5-foot untouched area between the furrows. This implement is best used for erosion control on the contour. Furrows work best on slopes less than 10 percent and rock free. A high power supply is needed.

Rails (A-Frame, Supp, Olson, Monte Cristo)— These are used mainly for shrub control, where there is a desire to limit damage to grasses and forbs. They have a low to moderate power requirement.

Harrows (Self-Cleaning or Pipe), Dixie Drags— These mainly accomplish shrub control with a small amount of disturbance to grass and forbs. They have a low power requirement.

Roto-Beaters—These are used for shrub or heavier vegetation control. They spread litter over the ground and require a low power supply.

Chaining or Cabling—Mainly used for removal of woody material. Some grass and forbs are removed if railroad iron is welded to the anchor chain. This equipment can be used effectively on slopes to 50 percent (Plummer and others 1970). The power requirement is high for chain, moderate for steel cable.

Although most of the equipment mentioned was developed in the past, modification, additions, and some redesigning of older implements can save many dollars in the tight budgets of today.

CONTROL CONSIDERATIONS

Total control of undesirable annuals strictly by mechanical means often requires several tillages, which reduces the roughness of the tilled surface and reduces the amount of surface litter. This increases the potential for erosion. Use of chemicals or fire before tillage will achieve better control with fewer tillages and lessen the erosion potential, especially on slopes over 30 percent. Hull and others (1958) stated that "in general, plowing should not be attempted on slopes steeper than 20 percent because of the potential increase for erosion." We feel that if proper precautions are taken, as described here, 45-percent slopes can be tilled. Chaining has been an effective method for reducing competition from shrubs and trees and to release suppressed plants or seeded plants on slopes as steep as 50 percent in Utah (Plummer and others 1968, 1970). Undesirable annuals on the steep or rocky slopes may not be effectively controlled by the chain, even with rails attached to the links. After chaining, sufficient litter is left on the ground to help protect the soil from erosion.

To reduce the erosion potential, the tillage and seeding must follow the contours. Strip farming or filter strips can also be effectively used to catch run-off if it occurs. Small check dams may be necessary in drainages to help trap sediment. Contour trenches are very effective, but leave a visual scar on the land that may not be accepted by the public. If possible, filter strips, planting sites, and contours should also be made to blend in with the environment to reduce negative visual impacts.

The tillage has to be at least 4 inches deep, with 6 inches preferred, to bury the undesirable plants and seed bank to prevent their growth or germination. On the Boise Front we have found that one tillage has not effectively controlled the undesirable plants, largely because the tillage equipment does not consistently cut deep enough to bury the seed. Improper cutting depth may be caused by equipment failing to trail properly, shallow rocky soil, too dry soil, or equipment improperly adjusted. One-way tilling may be necessary to keep equipment trailing properly.

Tillage must be done at a time when the undesirable plants are most susceptible to control. Spring tillage prior to seed ripe, followed by a fall seeding, is recommended by Plummer and others (1968) and Pellant (1990). For better undesirable plant control, we recommend tilling in the spring prior to seed ripe, followed by a fall tillage after annual seed germination. The seeding should be completed in the late fall just prior to the ground freeze. One must remember that the objective of preparing an area for rehabilitation is to disturb the site as little as possible, remove the competing vegetation, and prepare a good seedbed. Use of fire, chemicals, or grazing could be substituted for the spring tillage followed by the fall seedbed preparation tillage and seeding. The seeding must be completed late enough in the fall so cold temperatures will allow seeds to germinate.

Tillage on steep slopes can generate numerous problems usually not encountered or encountered to a lesser degree on flatter ground. The potential for accidents with the equipment increases, especially with inexperienced equipment operators. The equipment, especially the older types, may not trail properly behind the tractor. Because of improper trailing, some of the slopes may have to be tilled in one direction, which increases the cost considerably. Regarding increased cost for tillage, Plummer and others (1955) stated that "except for watershed protection, it may not be economically feasible to treat and plant slopes in excess of 30 percent." Even on grades above 20 percent, the cost is much greater than on level ground because large equipment cannot be used and you must resort to small machinery. However, in 1961 Plummer and others (1970) were effectively rehabilitating slopes up to 50 percent, which was previously regarded as impossible to do. They used the anchor chain at an approximate cost of \$6 per acre, which was slightly above the average in Utah at that time. In 1987 the modified disk chain used on flat ground in southwestern Idaho had an average cost of \$8.50 per acre. This modified disk chain is also equipped with a seeder (Pellant 1988). Cornering or turning around at ends of rows may present erosion problems especially with older implements without hydraulics. Three-point implements or ones equipped with hydraulics for lifting the tool out of the soil will create less problems on the turns.

We concur with Koehler (1975), A. C. Hull and others (1964), and Plummer and others (1968) that before starting any undesirable plant control or rehabilitation project certain considerations must be met. (1) Is the change in plant cover necessary and desirable? Will it be worth the expense? (2) What are the erosion factors? What steps will have to be taken to keep erosion at a minimum? (3) Can success be expected? Soils, precipitation, timing of planting, and control of competition need to be considered. (4) Does the available equipment match the rehabilitation requirement? (5) Can the area be properly managed after the site is rehabilitated? and (6) What effect will the project have on other uses?

RECOMMENDATIONS

Mechanical control of undesirable plants and rehabilitation of steep slopes (40 to 45 percent) can be accomplished with a minimum of erosion. Precautions for erosion prevention need to be considered in the planning process as well as during implementation of the work. Contour trenching, strip farming, filter strips, check dams, working on the contour, and ripping 6 to 16 inches on the contour are all methods to reduce erosion. The most effective erosion control methods will depend on slope steepness, type of equipment to be used, the amount of soil disturbance, soil type, and expected precipitation.

Working on the contour is highly recommended when using any tillage-type equipment. Chaining and cabling up and down slopes where belowsurface disturbance is minimal and sufficient litter is left to protect the site can be accomplished with a minimal amount of erosion.

One must remember that these ecological systems are fragile and that even when precautions for erosion are being taken there is still a chance that something may go wrong. Combinations of control methods for undesirable plants should be considered. Burning, chemical application, and grazing combined with mechanical control can be used effectively to achieve the project objectives. Projects involving mechanical control of undesirable plants on steep slopes continue to provide new and valuable information. Every project has a different set of problems and with its completion we gain a little more knowledge. Safety considerations are of utmost importance when working on steep slopes. This includes safety for the personnel involved and also for the soil. Steepslope rehabilitation can and will be done to benefit and improve the quality of the land resources.

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A REVIEW OF THE CHEMICAL CONTROL OF DOWNY BROME

Alex G. Ogg, Jr.

ABSTRACT

A review of the herbicides that will control downy brome (Bromus tectorum L.) in wheat, grass seed crops, and Conservation Reserve Program grasses may reveal some potential options for rangelands. Atrazine, chlorsulfuron, diclofop, metribuzin, metsulfuron, paraquat, triallate, and trifluralin will control or suppress downy brome in wheat. Pronamide and glyphosate at low rates will control downy brome selectively in some established grasses. Fluazifop and sethoxydim will control downy brome in fine-leaved fescues. Factors that may limit herbicide use on rangelands include cost, selectivity in mixed species, inactivation by surface litter, weed seed longevity, and environmental concerns.

INTRODUCTION

Downy brome (*Bromus tectorum* L.), also known as cheatgrass, is a winter annual grass weed that was introduced into the United States in the late 1800's (Morrow and Stahlman 1984). By 1914 this weed had spread across the United States and now dominates millions of hectares of crop and rangelands (Mack 1981).

Downy brome is troublesome particularly in the Western United States where it is recognized as a common or troublesome weed in alfalfa (*Medicago sativa*), winter wheat (*Triticum aestivum*), winter barley (*Hordeum vulgare*), tree fruits, bluegrass (*Poa pratensis*), and wheatgrasses for seed, forests, pastures, and rangelands (Mitich and Kyser 1987). Downy brome is an annual that reproduces only from seed (Thill and others 1984). Seedlings can establish only from seed that germinates in the top 4 to 5 cm of soil. Seeds are short-lived (less than 3 years) in most situations, and most control strategies for this weed are driven by the principle of depleting the soil seed bank.

CONTROL METHODS

Downy brome can be controlled in many situations with herbicides and currently is listed as a susceptible weed on the labels of 21 different herbicides (table 1). Downy brome in the germinating or seedling stages is killed easily by herbicides and is susceptible to many more herbicides than those listed in table 1. The main challenge to the use of herbicides is to develop methods that control downy brome selectively in desirable crops.

Downy brome is a major weed problem in winter wheat production in the Western United States and now infests an estimated 5.7 million hectares of the crop. Downy brome costs wheat producers \$350 million annually in lost yield and in costs for mechanical and chemical control practices. Before the advent of selective herbicides, downy brome was controlled in wheat lands by deep plowing and the use of spring crops in the crop rotation. Downy brome that emerges at the same time as wheat or within a few days thereafter is the most competitive with the crop. Therefore, control strategies that will delay the emergence of downy brome until 3 weeks or longer after the crop emerges will be effective in reducing weed competition. Triallate is an example of a herbicide that is short lived in the soil and will suppress downy brome selectively in wheat. In conventionally tilled wheat, diclofop has been the most effective, soil-applied herbicide for the control of downy brome. This herbicide kills downy brome as it germinates. It has reduced downy brome populations up to 95 percent and has allowed wheat yields to increase by 30 to 40 percent (Stahlman 1984).

Metribuzin is the only herbicide available currently that when applied postemergence will control downy brome selectively in winter wheat (Swan and Whitesides 1988). To be effective against downy brome, metribuzin must be applied before the weed begins to tiller extensively. The margin of crop safety with metribuzin is narrow and is based on wheat's ability to metabolize metribuzin rapidly and its ability to root deeply early in its life cycle and thus escape injury from the herbicide (Devlin and others 1987). The use of metribuzin in wheat is restricted to finetextured soils with more than 1 percent organic matter.

In the Pacific Northwest, a special formulation of atrazine (Cheatstop[™]) is registered as a preplant surface treatment for downy brome control in winter wheat planted with deep-furrow drills. The deep-furrow drill moves the treated soil away from the small furrow in which the wheat is seeded. Downy brome growing between, but not within, the wheat rows is controlled. This treatment has controlled downy brome effectively and has increased wheat yields significantly (Bolton and Appleby 1992). Trifluralin is another herbicide whose use for downy

Table 1—Herbicides registered for control of downy brome

Amitrole	Hexazinone	Pronamide
Atrazine	Metribuzin	Propham
Bromacil	Napropamide	Sethoxydim
Diuron	Norflurazon	Simazine
Ethofumesate	Oryzalin	Sulforneturon-methyl
Fluazifop-butyl	Paraguat	Terbacil
Glyphosate	Prometon	Trifluralin

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Table 2—	Influence of fall-applied glyphosate + 2,4-D ¹ on forage
	production of wheatgrasses at Fargo, ND

Species	Cultivar	Forage production	
		Percent of nontreated	
Crested	Nordan	76	
	Fairway	129	
	Parkway	91	
	Ruff	127	
	Hycrest	93	
Western	Walsh	90	
	Rodan	68	
Intermediate	Mandan 759R	103	
	Slate	46	
Thickspike	Sodar	135	
•	Critana	68	

'Gipphosate + 2,4-D applied at 0.4 + 0.7 kg/ha on September 19, 1989, at Fargo, ND.

brome control in wheat is based on positional selectively. This herbicide must be incorporated mechanically, as it does not leach into soil. Wheat must be planted with drills that place the wheat seed below the treated zone.

The soil-persistent sulfonylurea herbicides such as chlorsulfuron and metsulfuron applied preemergence to downy brome have suppressed downy brome 30 to 40 percent in winter wheat, but rates used are generally too low to control this weed consistently.

In no-till winter wheat, a granular formulation of triallate plus trifluralin (BuckleTM) applied to the soil surface before planting wheat has controlled downy brome. The granules are not absorbed by surface litter in no-till fields and thus are more effective than liquid formulations of these herbicides. Selective use of this treatment is dependent on some movement of the herbicide away from the wheat row during the planting operation and on placement of the wheat seed at least 3 to 4 cm deep. Diclofop applied to the soil surface after planting wheat no-till has controlled downy brome selectively but can be absorbed by excessive surface residues and requires rain soon after application for activation. Under ideal conditions, weed control and crop yield response to the use of diclofop in no-till systems can be dramatic.

Pronamide applied in late fall will control downy brome selectively in established (1 year or older) slender wheatgrass (*Elymus trachycaulus* ssp. *trachycaulus*), tall wheatgrass (*Elytrigia elongata*), western wheatgrass (*Pascopyrum smithii*), crested wheatgrass (*Agropyron desertorum*), intermediate wheatgrass (*Elytrigia intermedia*), creeping foxtail (*Alopecurus arundinaceus*), and orchardgrass (*Dactylis glomerata*) grown in Conservation Reserve Program (CRP) lands. The current label for pronamide use on CRP lands prohibits the grazing of treated grasses. However, this herbicide may be useful in an integrated rangeland renovation program to prevent downy brome seed production and thus reduce the soil weed seed bank.

Downy brome is very competitive in new seedings of perennial range grasses and as few as 40 plants per m^2 will reduce shoot biomass of crested wheat grass by 62 percent (Evans 1961). In the 1970's an atrazine-based chemical fallow technique was developed to control downy brome during the renovation of rangelands in Nevada (Eckert and others 1974). Atrazine applied at 1.1 kg/ha in late fall controlled downy brome and most other vegetation for 1 year. A significant advantage of this technique was the accumulation of soil moisture that was available for germination and growth of perennial range grasses seeded 1 year after the atrazine was applied. This technique required the use of deep-furrow drills to move the treated soil away from the seeded grasses. The furrows had an added benefit of protecting the new seedlings from drought and coldtemperature stress. Broadleaf weeds such as Russian thistle (Salsola iberica) and mustards (Sisymbrium and Descurainia spp.) were controlled during the year of grass establishment with 2,4-D. Unfortunately, the use of this technique was limited, and atrazine is no longer registered for use on rangelands. Since the early 1970's, several new, highly active herbicides such as hexazinone and sulfonylureas have become available that may be adaptable to the chemical-fallow technique of renovating rangelands.

Glyphosate is a foliage-active herbicide that will control small downy brome at rates as low as 0.3 kg/ha. Research in Wyoming has shown that glyphosate and paraquat applied in May at low rates controlled downy brome with minimum injury to established range grasses (Whitson and others 1991). To be effective, treatments had to be applied after downy brome emergence was complete. In North Dakota, glyphosate applied at 0.2 kg/ha in the spring did not reduce forage production of western wheatgrass, blue grama (Bouteloua gracilis), and Stipa spp., whereas glyphosate applied in the fall reduced forage production of western wheatgrass (Lym and Kirby 1991). Cutlivars of crested, western, intermediate, and thickspike wheatgrasses (Elymus lancerolatus ssp. lanceolatus) differed greatly in response to applications of glyphosate plus 2,4-D (table 2). Therefore, any research on the tolerance of perennial grasses to herbicides such as glyphosate needs to include cultivars with germplasm diversity. Glyphosate may be useful for reducing the downy brome seed bank in rangelands and should be evaluated extensively.

As mentioned earlier, chlorsulfuron and metsulfuron will suppress downy brome in winter wheat. Comes (1985-87), conducting research in the low-rainfall area of Washington, has shown that new seedings of Nordan crested wheatgrass

Table 3—Control of downy brome and Russian thistle in new seedlings of Covar sheep fescue at Lind, WA

Herbicide	Rate	Downy brome	Russian thistle	Cov sheep f	
	kg/ha	/ha Percent control		No./m²	Vigor ²
Nontreated	0.0	0	0	227	2.5
Bromoxynil + COC ²	.28	0	93	235	2.8
Quizalofop + COC	.11	97	0	323	3.5
Quizalofop +bromoxynil + COC	.11 +.28	99	86	253	3.0

'COC = Crop oil concentrate (1 percent v/v).

²Vigor rating: 0 = plants dead; 5 = plants normal and vigorous.

will tolerate preemergence applications of chlorsulfuron applied at up to 0.05 kg/ha. Forage dry weight of crested wheatgrass was similar to the hand-weeded controls during the year of establishment and was increased up to 200 percent during the second year when the controls were not hand weeded. Similar results were achieved with a number of other range grasses. Davison and others (1984) reported that Nordan crested wheatgrass grown in the greenhouse would tolerate 0.16 kg/ha of chlorsulfuron applied either preemergence or postemergence. Additional research on the use of chlorsulfuron in rangelands is needed to determine the full potential of this and related herbicides.

RECENT DEVELOPMENTS

In recent years, a new group of herbicides has been developed that will control most annual grass weeds, including downy brome, in fine-leaved fescues. Quizalofop applied postemergence (1990-91) at 0.1 kg/ha plus crop oil concentrate controlled downy brome selectively in seedling Covar sheep fescue (*Festuca ovina*) (Ogg, unpublished). Similar results were obtained with fluazifop for barnyardgrass (*Echinochloa crus-galli*) control in Durar hard fescue (*Festuca trachyphylla*). When these herbicides were tankmixed with bromoxynil, most seedling broadleaf weeds were controlled also (table 3). The use of these and related herbicides needs to be investigated more fully under rangeland conditions.

Herbicide cost and sprayer efficiency are major economic considerations in most croplands and are important especially in rangeland. Recently, a new sprayer has been developed that uses 2 to 5 L of total volume per ha (0.25 to 0.50 gallons per acre) and may enhance herbicide activity (Hanks and McWhorter 1991). Referred to as air-assist sprayers, these sprayers use compressed air delivered to each nozzle at 28 to 55 k Pa (4 to 9 psi) to propel the spray solution. Herbicides are dissolved in oil instead of water and micro-metering pumps deliver the herbicide-oil mixture to the nozzles. Spray droplet size is maintained at about 250 microns with this system. Because herbicides are dissolved in oil, coverage of leaf surfaces is improved and spray solutions do not dry as rapidly as water-based sprays (McWhorter and Barrentine 1988). These conditions have enhanced the activity of some herbicides. The air-assist sprayer would appear to have excellent applicability to rangeland conditions and should be evaluated thoroughly.

The most significant problems that need to be addressed in the use of herbicides on rangelands include:

- Cost of herbicides.
- Selectivity in mixed species.
- Inactivation of herbicides by surface litter.
- Weed seed longevity.
- Environmental concerns.

It should be emphasized that total reliance on one method of control, for example herbicides, is rarely successful and is never sustainable. An approach that integrates all available methods (cultural, mechanical, biological, and chemical) is much more likely to produce effective weed control. In addition, the weed management system developed must be integrated into a total rangeland system that recognizes biological, economical, and environmental concerns.

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ECOLOGICAL SIGNIFICANCE OF SEED BANKS WITH SPECIAL REFERENCE TO ALIEN ANNUALS

David A. Pyke

ABSTRACT

Any description of a plant's life history is incomplete if it does not include a description of the seed bank dynamics. Such descriptions must include quantification of the temporal variability in the numbers of seeds in the soil and of the spatial variability of the seed bank. Knowledge of the seed bank dynamics can then be related to natural or induced disturbances. These concepts are discussed relative to the management of lands dominated by exotic annuals.

INTRODUCTION

Reproductive strategies of plants can differ widely among species that coexist within the same community. Some may rarely produce viable seeds, yet persist through vegetative propagation. Others may rely exclusively on the yearly production of viable seeds. Another group may only occur as vegetation during years when environmental conditions are conducive to germination yet remain in the seed banks during years when germination conditions are poor. The seed bank is the storage of viable seeds in either litter or soil until conditions for germination are achieved. An understanding of the patterns and processes that regulate seed bank dynamics of desirable and undesirable species is necessary for the development of ecologically sound management strategies to maintain and restore desirable ecosystems.

In this paper, I will provide a brief overview of seed bank ecology. I will address seed banks as being spatially and temporally dynamic. I will discuss seed bank classification and will relate current vegetation on a landscape to its current seed bank. I will conclude with some suggestions of future directions for research on seed banks pertaining to exotic species found in the Intermountain West.

SEED BANK ECOLOGY

As a population of annual plants reaches the end of its growing season, the culmination of its life is the production of seeds that will make up the next generation. For some exotic species like cheatgrass (*Bromus tectorum*), individuals are annually a consistent part of the community. These species have a wide range of environmental conditions for

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. David A. Pyke is Senior Rangeland Ecologist, Bureau of Land Management, Cooperative Research Unit, and Associate Professor, Department of Rangeland Resources, Oregon State University, Corvallis, OR 97331. seed production and germination; other annuals, like pepperweed (*Lepidium perfoliatum*), may be abundant some years and extremely sparse in other years (Duba 1976). Species that are less predictable components of the community often have a narrow range of conditions for successful reproduction, germination, or survival, yet persist in the seed bank.

The presence of an annual species in a community may be regulated by its seed bank dynamics. Once the seeds develop, dispersal may occur immediately or it may be delayed until later in the season. These two types of dispersal mechanisms result in combinations of risks and benefits. Immediate dispersal allows seeds to reach the soil and to move by secondary dispersal to safe sites for germination. However, immediate dispersal places the seeds at risk of predation from ground foraging granivores, or of pathogens.

Delayed dispersal can be caused by the retention of the seed in the inflorescence after seeds mature. Medusahead (*Taeniatherum caput-medusae*) maintains mature seeds in inflorescences for up to a month or until the spikes are disturbed (McKell and others 1962). Sufficient disturbance can be rendered by high winds or by animals moving through a stand. The long awns associated with medusahead seeds may cause the seeds to remain aboveground in the litter.

Aboveground seed banks do not provide seeds with adequate conditions for germination, but allow a persistent seed bank (note this is a broader definition than Parker and others 1989). The aboveground seed bank on semiarid sites of the Intermountain West is susceptible to mortality by fire, in contrast to the aboveground seed banks of conifer forests and chaparral shrublands, which require fire for germination (Archibold 1989; Parker and Kelly 1989). The species found in the aboveground seed banks of the Intermountain West generally require disturbances to move the seed into adequate contact with the soil, thus moving the seed into the soil seed bank where imbibition, germination, and establishment are improved.

SEED BANK CLASSIFICATION AND PERSISTENCE

Before 1970 many studies investigated the physiological mechanisms associated with germination (see review by Baskin and Baskin 1989), but attempts to incorporate these mechanisms into a general classification of the seed production, persistence, and germination have been few (Grime 1981; Roberts 1981, 1986; Thompson and Grime 1979). For the purposes of this paper, I will use the Thompson and Grime (1979) classification to relate the dynamics of annual seeds in soils of the Intermountain West.

Table 1—Seed bank classification of Thompson and Grime (1979) based on germination time and on persistence of the seed bank

Seed bank type	Germination time	Persistence time
1	Autumn	Summer only
ti	Spring	Winter only
111	When dispersed	Small and persistent
iV	Continuous, but gradual	Large and persistent

The Thompson and Grime (1979) classification is a combination of seed dispersal time, the period of seed bank persistence, and the time of germination (table 1). Exotic annuals with Type I through Type III seed banks are susceptible to management strategies intended to reduce the seed bank population size by reducing the current year's seed crop (for example, prescribed burns after seed maturation and before germination).

Medusahead would be considered a hybrid of Type I and III seed banks. It requires a short after-ripening period before the embryo is capable of germinating (Murphy and Turner 1959; Young and others 1968). This period of afterripening maintains a short summer dormancy. About 10 percent of the seed is capable of persisting in litter or soil for more than 1 year (Sharp and others 1957). An additional short-lived dormancy is thought to exist that can be broken by removing medusahead awns (Nelson and Wilson 1969); however, the exact mechanism of this dormancy is unknown. Cheatgrass is a true Type III species. It is capable of germinating when dispersed, yet it maintains a small persistent seed bank (see Pyke and Novak, these proceedings).

For many alien annuals, we are uncertain how long they may persist in the seed bank. Cheatgrass can be stored under laboratory conditions for up to 12 years with 95 percent viability, but in the field there is little or no evidence of persistence (Hulbert 1955; Hull 1973). In conjunction with a study conducted near Snowville, UT (Pyke 1990), I collected 20 random soil samples (10 by 10 by 3 cm) per sample session over a 2-year period. The soil was thinly spread across the surface of sterile sand and kept moist in a heated glasshouse (20/15 °C; day/night) to germinate seeds. After 4 weeks, seedlings were identified and removed. The soil was then turned and allowed two additional weeks for germination. After the sixth week, the soil was sieved and any ungerminated seeds were collected. identified, and tested for viability using a 1 percent solution of 2,3,5-triphenyltetrazolium chloride (Bewley and Black 1982; Woodstock 1973) for 48 h at 20 °C. The peak seed population occurs immediately after dispersal and declines to near zero by late spring (fig. 1). This decline is consistent with declines in seed banks of other exotic annuals in other semiarid environments (Bartolome 1979; Rice 1985, 1989). The high amount of spatial and temporal variability in the cheatgrass seed bank is noteworthy (fig. 1). This is consistent with the findings from other semiarid communities (Coffin and Lauenroth 1989). Spatial variability demonstrates the importance of multiple sampling times during the year and of adequate replication within a sampling session (Gross 1990).

Annuals with Type IV seed banks are more difficult to control, because large portions of the population remain dormant. They will require more complex prescriptions involving multiple treatments and application times to attack different life stages of the plant. For example, prescribed fire during early summer may kill recently produced seeds while herbicides after germination kill seedlings that emerged from seeds that escaped the fire.

DORMANCY

Seeds are dispersed into heterogenous and sometimes unpredictable environments. Dormancy is an adaptation that some species have evolved to prevent germination, of at least some individuals, until conditions are suitable for successful germination and establishment.

Two dormancy classifications have been proposed. Each has its advantages and disadvantages. Harper (1977) proposed a phenological classification based on the time to germination and on the environmental conditions provided to the seed. There are three categories under his classification: enforced, induced, and innate dormancy. Enforced dormancy is viewed by many as a nondormant condition where the requirements for germination, such as sufficient moisture, have not been experienced by the seed. Induced dormancy occurs when a nondormant seed is exposed to environmental conditions that cause the seed to become physiologically dormant. Cheatgrass has the potential for this dormancy type (Kelrick 1991; Young and Evans 1975). Innate dormancy occurs when seeds are incapable of germinating immediately after they disperse. The seed is either morphologically or physiologically incapable of germinating or due to a physical barrier (a thick seed coat) is

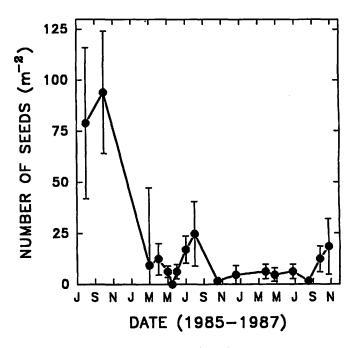


Figure 1—Mean number of viable seeds of cheatgrass found in the litter and upper 3 cm of soil over 2 years. Bars represent ± 1 S.E. of the mean.

Table 2—The types, causes, and characteristics of seed dormancy from the dormancy classification system of Baskin and Baskin (1989) relative to the system of Harper (1977)

Baskin and Baskins' system			Harper's system	
Туре	Causes	Characteristics	Туре	
Physiological	Embryo chemicals inhibit germination.	Fully developed, but dormant.	Innate or induced	
Physical	Seed coat is impermeable to water and inhibits imbibition.	Fully developed and capable of germination.	Innate	
Combinational	Impermeable seed coat and chemicals in embryo inhibit germination.	Fully developed, but dormant.	Innate or induced	
Morphological	Underdeveloped embryo.	Underdeveloped and nondormant.	Innate	
Morphophysiological	Underdeveloped embryo with chemicals in the embryo that inhibit germination.	Underdeveloped and dormant.	Innate or induced	
None		Fully developed.	Enforced	

unable to germinate. Baskin and Baskin (1989) subdivide innate dormancy into five categories of seed dormancy (table 2).

Some species disperse seeds with two dormancy types from the same plant. One type is capable of immediate germination and the other type is physiologically dormant. Jointed goatgrass (Aegilops cylindrica) reportedly contains this combination of dormancy known as heteromorphic seeds (Donald and Ogg 1991). Heteromorphic seeds allow a species to spread germination over two or more seasons, thereby reducing the risk of unpredictable environmentally induced catastrophes that may reduce population sizes. This type of strategy is most common in Gramineae, Compositae, and Chenopodiaceae (Fenner 1985). Venable and Lawlor (1980) have proposed that reproduction is maximized when species with dimorphic seeds have correlated dimorphic dispersal mechanisms. They proposed that seeds with high dispersability should germinate quickly and those with low dispersability should contain some form of dormancy. Of the 27 species examined, 25 complied with their proposed model.

GRANIVORY

Granivory can have an appreciable impact on the population sizes of some plants (see review by Louda 1989). In the California annual grasslands, rodent seed predation can significantly reduce populations of exotic annuals (Borchert and Jain 1978; Marshall and Jain 1970). In the Intermountain West, the exotic annuals tend to be avoided by many granivores if they are given alternative native species (Goebel and Berry 1976; Kelrick and others 1986; McAdoo and others 1983). Therefore, granivores may hasten a compositional change in a community from a dominance of natives to exotics.

Although granivory is a negative impact on plant populations, granivores that cache seed may act as beneficial dispersal agents. Unrecovered seed caches of rodents can act as an effective seed-dispersal mechanism (Price and Jenkins 1987), while adding to the spatial heterogeneity of the seed bank.

Seed predators can be used as biological control agents to reduce the spread of undesirable species. An effective seed predator normally acts as a predispersal agent. One agent is the seed head gall fly (*Urophora quadrifasciata*) that feeds on the knapweed complex (*Centaurea* sp.) (Coombs 1992).

DISTURBANCE

Although prescribed fire is proposed as a technique for reducing seed population sizes, it must be conducted at the appropriate time of year. Slow, hot fires during the seed maturation process of medusahead have been used as an effective tool for reducing population sizes in the following year (Furbish 1953; McKell and others 1962; Murphy and Turner 1959). However, fires during the wrong season (for example, after seed dispersal) are less successful. Repeated fires may favor one exotic annual over another, changing seedbed environments rather than changing the seed bank populations (Young and Evans 1972).

A persistent seed bank is clearly a mechanism for some plants to maintain themselves in environments with regular disturbances. Disturbances may initially reduce the seed bank of a species, but those seeds that remain may be capable of germinating and replenishing the seed bank in a limited amount of time. Cheatgrass is able to respond within the first growing season after a fire with a 50 percent increase in seeds on a burned site relative to an adjacent unburned site (fig. 2). This demonstrates the importance of revegetation following prescribed or wild fires in controlling the spread of exotic annuals.

Revegetating degraded communities with monospecific stands of exotic perennials like crested wheatgrass (Agropyron cristatum) may lead to reductions in the species richness of the seed bank relative to native sites (fig. 3) (Marlette and Anderson 1986). Revegetation of degraded lands by sowing monospecific stands of highly competitive species may be an effective deterrent to annual plant establishment, but it is likely to be a deterrent to the reestablishment of native perennials also (Marlette and Anderson 1986). Similar or possibly more dramatic reductions may occur on sites dominated by exotic annuals, but I am unaware of studies demonstrating this.

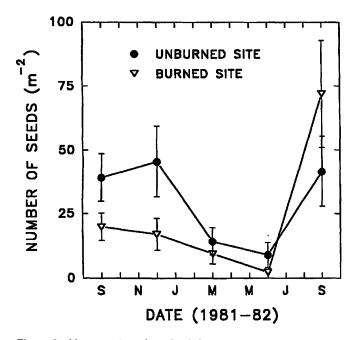


Figure 2—Mean number of seeds of cheatgrass on a burned and unburned site of sagebrush steppe during a single growing season (from Hassan and West 1986). Bars represent ± 1 S.E. of the mean.

QUESTIONS CONCERNING ALIEN ANNUALS

Of all the alien annual species that inhabit the Intermountain West, more is known about the seed and seed bank characteristics of cheatgrass than any other exotic annual. We cannot expect to manage and control the spread of alien annuals without some basic information on postdispersal seed behavior of other exotic species. Studies need to be designed to specifically address this information. We no longer can rely on tangential studies or personal observations to provide the needed information. Studies need to be well designed and replicated in space and in time to provide an adequate picture of the dynamics of seed banks. The following questions should be specifically addressed for each species:

1. Do its seeds persist in the soil or litter, and if they persist, how long will they persist?

2. How quickly does the seed bank decline over a growing season?

3. Does dispersal occur immediately after maturation of seeds or are seeds dispersed over an extended period?

With answers to these questions, managers can begin to prescribe and test various control regimes and to restore native plants across the Intermountain West.

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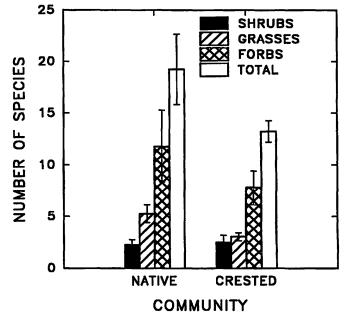


Figure 3—Number of species, partitioned by life form, in a native sagebrush steppe community and on a site revegetated with crested wheatgrass in southern Idaho (from Marlette and Anderson 1986). Bars represent ± 1 S.E. of the mean.

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USE OF LIVESTOCK TO CONTROL CHEATGRASS—A REVIEW

John F. Vallentine Allan R. Stevens

ABSTRACT

Proper grazing management appears urgent in preventing or delaying further encroachment of cheatgrass (Bromus tectorum) into perennial vegetation on western grazing lands and subsequently gaining site dominance. In mixed stands with desirable perennials. livestock grazing might be directed to (1) reducing cheatgrass competition by concentrating grazing of cheatgrass during dough seed stage, providing perennials still have opportunity to complete their life cycles, or (2) basing grazing on the needs of perennials while mostly ignoring cheatgrass. When cheatgrass domination results in a closed community, alternatives appear limited to (1) managing as annual grassland, or (2) revegetation using intensive cultural practices. In conjunction with revegetation, livestock might conceivably be employed for "graze out" in site preparation and /or for selective plant control during germination and emergence of the seeded perennials. However, with these possible limited exceptions, grazing is concluded not to be an effective general tool for cheatgrass control.

INTRODUCTION

Livestock grazing is generally considered a factor in enabling and promoting the establishment and prominence of cheatgrass (*Bromus tectorum*) on western grazing lands. This introduced, aggressive plant species is considered much less desirable than the original perennial vegetation it has commonly replaced; and dry cheatgrass, because of its high flammability, constitutes a fire hazard contributing to repeated wildfires and the further reduction of many less firetolerant native perennials.

Partially redeeming aspects of cheatgrass—these seemingly elevating the species from a classification of worthless to only mediocrity at best—include some forage and site protection potential. Cheatgrass has become the principal forage species on some dry western grazing lands (Fleming and others 1942; Whitson and others 1991); it offers high levels of nutrition for grazing animals during rapid spring growth (Cook and Harris 1952; Murray and others 1978); and has given good animal gains under spring grazing with cattle (Murray and Klemmedson 1968) and sheep (Murray 1971). Although cheatgrass is generally most valuable as spring forage, this is also the time of year when perennial

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. John F. Vallentine is Professor of Range Science and Allan R. Stevens cool-season grasses are most susceptible to damage from grazing (Young and others 1987).

Cheatgrass provides a short period of high palatability in the spring but becomes unattractive to grazing animals as seedheads develop (Hull and Pechanec 1947; Klemmedson and Smith 1964; Vallentine 1989). After the potentially mechanically injurious awns are shed and the herbage has been softened by fall rains, it offers some opportunity for winter grazing on drier areas through curing and reduced weathering on such sites (Deflon 1986; Hull and Pechanec 1947; Young and others 1987). Its major handicaps as a forage producer are its short green forage period, great annual fluctuations in yield (depending on seasonal and annual growing conditions), and rapid weathering and deterioration under moist conditions (Murray 1971; Platt and Jackman 1946; Stewart and Young 1939; Swanson and others 1987). Adjusting animal numbers to properly utilize cheatgrass and optimize animal gains is made particularly difficult by high variability in annual forage yield (Murray and others 1978).

Cheatgrass provides varying levels of protective soil mulch, this favored by reduced levels of herbivory and more biomass being left unburned, and may offer some control against the invasion of even more undesirable green migrant plants. While providing dry, fine fuel to expedite prescribed burns, mature cheatgrass biomass also creates an extreme fire hazard in high herbage production years (Young and others 1984).

A speculative question is whether livestock grazing, in fact, might be used to manipulate cheatgrass stands and help in reducing population levels of this introduced species. This paper explores the interrelationships between cheatgrass and livestock grazing and the opportunities, if any, for using livestock grazing as a biological tool for controlling cheatgrass.

AN AGGRESSIVE INVADER

Cheatgrass is well equipped to be an aggressive invader (Vallentine 1989). It is a prolific seed producer, and seeds normally have high viability. Seeds germinate rapidly when soil conditions become favorable, but adequate numbers of viable seed may stay dormant in the litter and soil to survive 1 or even 2 unfavorable years in a row (Young and others 1987). However, there is a point where reproductive potential in a given year falls below levels where one year's seed production can restock next year's stand; and heavy grazing can potentially reduce the seed stocking ability of a stand (Young and others 1969).

Although typically a winter annual, cheatgrass can germinate in the spring under favorable conditions and still

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produce seed. When seedling density is inadequate to occupy the site to potential, cheatgrass can deplete soil moisture and other resources by growing larger and by prolific tillering (Ganskopp and Bedell 1979). In the more arid portions of the Great Basin, Young and others (1987) found that cheatgrass often fails to germinate in the fall, thereby becoming more dependent upon favorable conditions for spring germination.

A large portion of cheatgrass' competitive ability comes from its ability to germinate and establish in the fall as a typical winter annual and develop rapid root growth (Ganskopp and Bedell 1979). While overwintering in a prostrate rosette form, root growth continues even under low temperatures and reaches nearly its full complement of roots by spring. By the time of active spring top growth, cheatgrass is able to quickly resume growth and effectively remove soil moisture from the upper foot of soil before native perennial grasses can complete their growth, thus providing cheatgrass with a competitive advantage (Swanson and others 1987; Upadhyaya and others 1986; Young and others 1987). This phenomenal ability to consume soil moisture on which perennial seedlings depend and also endure drought enables it to control vast areas for long periods.

INVASION AND SITE DOMINATION

Having first appeared in the Western United States at least by the late 1890's, cheatgrass now occupies large areas in the Intermountain region from the moister part of the blackbrush and shadscale zones, through the sagebrush and juniper zones, and up into the mountain brush zone (Vallentine 1989). Its invasion into the lower, drier sagebrush zone and margins of the salt-desert shrub zone was particularly aggressive and seemingly met with little resistance. It was noted early (Stewart and Young 1939) that cheatgrass usually first established in bare or nearly bare areas where plant cover was deteriorated or absent. Platt and Jackman (1946) promoted the working hypothesis that cheatgrass did not drive out the bunchgrasses but merely followed them.

The rapid invasion and subsequent often near dominance of cheatgrass was expedited if not enabled by the disturbance or loss of the natural perennial cover through cultivation and abandonment, poorly managed cropland, unmanaged grazing, repeated fire, and road construction (Beetle 1954; Klemmedson and Smith 1964; Stewart and Hull 1949). Hull and Pechanec (1947) proposed that it was unlikely that cheatgrass would have invaded unless it had been preceded by disturbances of the previous, original plant cover. In the tallgrass prairies, patchy grazing by cattle has left niches open for the more unpalatable species to inhabit (Collins 1987).

While proposing that the original spread of cheatgrass had little to do with grazing, Beetle (1954) found it apparent that its subsequent local abundance in the West was due to many aspects of mismanagement including grazing. Based on his studies at the Nevada Test Site, Hunter (1991) concluded that the spread of cheatgrass does not require the direct activities of humans and that its spread should be considered a natural phenomena. While pointing to disturbance by humans, including grazing, off-road vehicles, commerce, and recreational use, he also noted the impact of disturbance by burrowing animals, frequent and/or natural fires, and abnormal short-term climatic cycles. Localized big-game impact or disease or insect damage might be added to the latter list.

While Young and others (1987) proposed that cheatgrass moved into sagebrush rangeland largely as a result of the biological vacuum created by excessive grazing, Young and Tipton (1990) considered both this hypothesis and a contrasting hypothesis that cheatgrass may partially grow in environmental potential that native plants never evolved to occupy. They suggested this may have application on the margins of the more arid plant communities within the sagebrush/bunchgrass zone where cheatgrass has been able to insert itself successfully even into climax stands that have been protected from grazing and fire for many years. While concluding that widespread floristic change in the drier parts of the sagebrush zone occurred regardless of grazing use history, Swanson and others (1987) held that cheatgrass is not as well adapted on higher elevation mountain big sagebrush-Idaho fescue sites and gains dominance there only as the result of disturbance.

Young and Evans (1973) investigated succession on six big sagebrush sites of different potential ranging from the edge of the salt-desert shrub to seral communities in the pinyon-juniper. They found that providing a seed source (either artificially or naturally) resulted in establishment and near-total dominance by cheatgrass; and the established populations persisted and continued to dominate the communities. Once cheatgrass becomes well established on its drier adaptation sites, the community is essentially closed to reoccupation by native perennial species (Swanson and others 1987).

After 13 years of livestock grazing exclusion on sagebrush semidesert in west-central Utah, West and others (1984) found that cheatgrass actually increased with no grazing, while it decreased or stayed the same in adjoining grazed areas; they concluded that direct manipulation would be required if rapid return to perennial grass dominance was desired. Robertson (1971) reported on Nevada studies in which sagebrush-grass range was left ungrazed for 30 years; while overall cover increased and bluebunch wheatgrass (*Agropyron spicatum*) minimally reestablished on naturally favored spots, cheatgrass actually increased by 38 percent.

Concern was expressed early that cheatgrass may only be a pause on one of the downward steps on rangeland (Platt and Jackman 1946). Young and others (1972) found in Nevada that continued disturbance pressure on cheatgrass communities caused them to regress even further into Russian thistle (*Salsola iberica*) communities. Tisdale (1986) noted that a major characteristic of annual grassdominated communities in west-central Idaho canyonlands was their instability, as marked by the continued invasion of worthless exotics such as klamathweed (*Hypericum perforatum*), medusahead (*Taeniatherum asperum*), and *Centaurea* species.

Cheatgrass seedling establishment is favored by a rough microtopography (Tisdale and Hironaka 1981; Young and Evans 1973); this favored roughened surface environment along with the planting action of hoof impact with grazing may actually enhance cheatgrass seed germination and emergence. When managed as annual grassland, DeFlon (1986) recommended running sheep over the area in the fall to increase cheatgrass density the following spring. Seeds of cheatgrass are readily distributed mechanically by grazing animals: (1) by having barbed spikelets that attach to the haircoat, and (2) by incomplete digestion and spread through the droppings.

GRAZING AS A CONTROL TOOL

Mechanical defoliation within a week after flowering was found by Finnerty and Klingman (1961) to be effective in preventing seed formation by annual bromes. Laude (1957) found in working with soft brome (Bromus mollis) that removing the terminal buds prevented leaf elongation and seed production. In clipping studies made by Hulbert (1955) on planted cheatgrass plots in the Lewiston, ID, area, clipping at the dough seed stage when purple coloration was just starting caused death of many plants and serious damage to the remainder. When clipped while plants were still green and anthesis was incomplete, few inflorescences subsequently emerged. The potential for plant regeneration decreased as the plants advanced in development through flowering to fruiting. Clipping of plants at a height of 1 cm prior to emergence of the inflorescences reduced the subsequent biomass yield only slightly; progressively later clipping caused progressively greater reduction in subsequent yield. However, Tisdale and Hironaka (1981) found that simultaneous clipping appeared to deleteriously affect the associated perennials even more than cheatgrass.

Stewart and Hull (1949) noted that closely grazing cheatgrass in the early spring with sheep can greatly reduce the height and number of plants or even kill them. Although heavy grazing then reduced the height and numbers of cheatgrass plants, concern was expressed that this level of defoliation would cause loss of soil through erosion. While opting against spring grazing of cheatgrass on low-elevation, saline soils in order to maximize forage production for winter grazing, DeFlon (1986) observed that spring grazing greatly hindered the growth of cheatgrass. Ganskopp and Bedell (1979) reported that utilization or clipping of cheatgrass during the growing period typically reduces total herbage production. However, when moisture is available for subsequent regrowth, production on grazed plants may even exceed that of ungrazed plants.

Young and Tipton (1990) concluded that many individuals, ranchers, land managers, and scientists fail to appreciate that heavy grazing cannot help but partially suppress cheatgrass. They concluded that heavy grazing not only reduces seed production of cheatgrass but also reduces the potential of seedbeds to support the germination of seeds through mulch reduction. However, they concluded that such grazing on a sustained basis is even harder on perennial grasses and does not lead to the eradication of cheatgrass. They further noted that, on the drier cheatgrass habitats on salt-desert ranges, cheatgrass seeds stay in inflorescences much longer than at higher elevation in the sagebrush zone; at these lower elevations cattle readily pick seeds from the plants, thereby directly reducing cheatgrass reproductive potential with minimum consumption of herbage.

Does this suggest any opportunity for imposing selective grazing pressure on cheatgrass in mixed stands with perennial grasses? A rather narrow window of opportunity may exist in early spring for using defoliation by grazing to suppress cheatgrass growth, seed production, and excessive mulch buildup. This would seemingly require high-density grazing for a short duration of time during which time the cheatgrass was closely defoliated and/or seed production was prevented. However, the precise timing would necessarily be when perennial grasses were still dormant or otherwise not selected by grazing livestock or had opportunity later to recover from limited defoliation by regrowing and reaching maturity before the end of the growing season. Sufficient information probably does not presently exist for developing the precise grazing plan needed for exerting biological control, but further research seems warranted.

Heavy grazing of cheatgrass might be beneficially employed in "graze out" just before seed production as part of seedbed preparation for artificial seeding of desirable perennials; or selective suppression of cheatgrass might be exacted during seed germination and emergence of seeded forage species if carefully administered. Launchbaugh (1976) has recommended cattle grazing be used on warmseason, native grass seedings during seed germination, seedling emergence, and initial plant development for weed suppression as well as utilizing the weeds for forage. If this technique were to be effectively applied to enhance establishment of seeded perennials on cheatgrass sites, a high degree of grazing control would be required to prevent damage to the perennial plant seedlings, and this may be a major limitation under practical management situations.

MANAGING CHEATGRASS FOR FULL USE

Where sufficient perennial grasses remain to provide seed or vegetative reproduction, there is some promise of the perennials replacing cheatgrass in mixed stands over time if season and intensity of grazing is based on optimizing the perennial grasses. However, this is likely to be a difficult and slow process even under light grazing (Hull and Pechanec 1947; Pechanec and Stewart 1949) and is apt to constitute inefficient use of the areas involved during the interim period (Cook and Harris 1952). On range with a mix of perennials and cheatgrass, Swanson and others (1987) concluded that dormant-period grazing (late summer, fall, winter, and even early spring if ended while sufficient soil moisture remains to allow the perennial plants to grow) should favor the perennial species on these mixed ranges. When such range is to be managed to prevent further loss of perennials and to enhance their return, Pechanec and Stewart (1949) recommended two-thirds of the bunchgrasses and 40 to 60 percent of associated desirable grasses should remain ungrazed each year. Stewart and Hull (1949) suggested cheatgrass utilization levels of 35 to 40 percent under such management objectives.

Deferment for 2 or 3 successive years is unlikely to benefit bunchgrasses present in minimum stand and may only serve to build up an accumulating mat of dead, ungrazed herbage/mulch and result in a fire hazard. If a rancher has both cheatgrass range and perennial bunchgrass range, it may be more appropriate to defer the bunchgrass area occasionally and fully graze the cheatgrass in early spring (Platt and Jackman 1946). Swanson and others (1987) suggested that spring grazing of cheatgrass may also reduce the fire hazard and provide deferment for seedings of native perennial range in other pastures.

Deferment is not required for perpetuation of annual grass range grazed in the spring—this often results in almost complete waste of the forage crop—and may provide minimal advantage to any remaining perennial plants (Vallentine 1990). Continuous grazing (or repeated seasonal grazing) of annual grasslands during the greengrowth period favors nutrient value, uniform utilization, and animal performance over rotation systems (Heady and Pitt 1979; Murray and Klemmedson 1968; Ratliff 1986).

The breaking up of multiple-permittee allotments into single-permittee allotments in the Intermountain West has permitted fencing and reduced trespassing, thus greatly benefiting range conditions (Young and Tipton 1990). However, Young and others (1987) suggested that the apparent spread of cheatgrass and wildfires onto the margins of the salt deserts and into sand-dune range may be a product of the recent innovations in grazing management. They noted that in recent years many yearlong grazing permits have been changed to 9- or 10-month grazing under some form of deferred management system. This form of grazing management may have permitted cheatgrass to increase and result in hazardous fuel accumulation leading to still further loss of perennials from more frequent wildfires.

Where cheatgrass has gained dominance to the virtual exclusion of more desirable perennial plants, the resulting closed community may be virtually immune to benefits from either nongrazing or prescribed grazing treatment. Protecting from grazing dense stands of competitive annuals such as cheatgrass, medusahead, or tarweed (*Madia glomerata*) is apt to be hopeless unless there is a fair remnant of the original cover remaining (Vallentine 1989).

The resulting management opportunities on cheatgrassdominated range then appear only twofold: (1) manage as annual grassland, or (2) resort to complete seedbed preparation including intensive cheatgrass control and reseeding (Hironaka and others 1983). On low-potential sagebrush sites, either because of soil or rainfall deficiencies, or on shadscale sites, the sole option is apt to be to manage as annual grassland because of difficulty and uncertainty of employing intensive cultural practices in restoring perennials. Here the pristine plant community is no longer the potential, and realistic management goals should reflect this situation (Swanson and others 1987).

Key considerations for managing cheatgrass areas as annual grasslands are adequate seed production, plant litter, and microtopography relief. Being an annual, its forage production annually depends on an adequate seed source, germination, and favorable weather conditions. A roughened soil surface aids in providing more adequate seed coverage and in retaining more favorable moisture and temperature regimes for improved seed germination and emergence (Tisdale and Hironaka 1981; Young and Evans 1973). Leaving 500 lb of herbage residue at the end of the spring-summer grazing season has been recommended for a typical annual grassland site in California (Hooper and Heady 1970), but similar guidelines are not available for the Intermountain annual grasslands.

Even though individual cheatgrass plants will tolerate more severe defoliation than perennial grasses, continued heavy grazing pressure reduces growth rate, size, and density of cheatgrass plants as well. However, because of the importance of leaving adequate plant litter on annual grasslands for soil protection and optimal seedbed conditions, overgrazing should be prevented. Adequate mulch enhances soil moisture and moderates soil temperatures for improved germination of cheatgrass and protects new seedlings through fall and winter. Proper use levels for cheatgrass have been given as 50 percent under spring grazing (Klemmedson and Smith 1964) and 60-70 percent for winter grazing (DeFlon 1986). Continued heavy spring grazing favors the entry and survival of halogeton (*Halogeton glomeratus*) and noxious perennial green migrant species.

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MYCORRHIZAL ECOLOGY OF SHRUB-STEPPE HABITAT

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ABSTRACT

Mycorrhizal associations are present in most plant species on semiarid lands. Within individual root systems, the abundance of mycorrhizal colonization will vary seasonally. Soils in the shrub-steppe habitat in southwestern Idaho tend to be low in organic matter, low in available P and N, and have limited available water. The ecological importance of mycorrhizae in this habitat appears to be related to their role in acquisition of nutrient resources. Following disturbance, these lands are normally invaded by either nonmycorrhizal or facultative mycorrhizal plant species, such as cheatgrass (Bromus tectorum). Studies on revegetation of severely disturbed land indicate that the presence of mycorrhizae improves survival and growth of host plant species.

INTRODUCTION

The term mycorrhizae defines a structural as well as functional association: a mycorrhizae is a mutualistic symbiosis between plant and fungus localized in a root in which energy (carbon compounds) moves primarily from plant to fungus and inorganic resources (principally phosphate) move from fungus to plant.

These mycorrhizal associations are found in a broad range of habitats, including semiarid grasslands. Not only are mycorrhizal associations geographically widespread, but within most communities surveyed, mycorrhizae are abundant both within individual root systems and among the array of plant species present. For example, in semiarid grassland, 95 percent of the dominant plant species have mycorrhizae, and as much as 96 percent of the root length can be colonized (Davidson and Christensen 1977).

Mycorrhizal associations are widespread among plant families, and very few families are nonmycotrophic. Hence, in semiarid grasslands plants belonging to the Compositae, Gramineae, Leguminosae, Rosaceae, Salicaceae, and Solonaceae are usually mycorrhizal. Nonmycotrophy appears to be restricted to a limited number of families such as the Chenopodiaceae, Brassicaceae, Amaranthaceae, and Zygophyllaceae (Trappe 1981).

ASSOCIATION STRUCTURE AND FUNCTION

The principal roots involved in mycorrhizal formation are ephemeral, do not exhibit secondary growth, lack a root cap, and root hairs arise from epidermal cells. Hyphae of vesicular-arbuscular (VA) mycorrhizal fungi enter the young root through the epidermis behind the meristematic region or through root hairs. Infection of plants by VA fungi occurs most commonly in the spring.

Mycorrhizae are classified into three major types based on the physical relationship of the fungus and the root cells. In ectomycorrhizae, the feeder roots are surrounded by a fungus sheath, which may be very thick. Hyphae are abundant in the cortex region of the root, yet rarely penetrate the cortical cells. This is the most common type of mycorrhizae on forest trees of temperate regions. Fungi that form ectomycorrhizae most commonly belong to the classes Basidiomycete and Ascomycete (Trappe 1962).

In endomycorrhizae, following hyphal penetration into the root, the hyphae penetrate the walls of the corticle cells. These types are generally called vesicular-arbuscular mycorrhizae (VAM). The intracellular hyphae produce structures that frequently branch many times within the host cells. These structures are known as arbuscules. Arbuscules are the organs where nutrients and carbon are exchanged between host and fungus. Typically, also formed are vesicles, which are fungal storage units. The hyphae within the cells and older roots are subsequently reabsorbed by the host, and fungal growth is probably controlled in this way. VAM are more widespread than other types and are found in nearly all families of angiosperms and in some ferns, mosses, and liverworts. VAM fungi involved are species of the Endogonaceae (Zygomycetes) (Gerdemann and Trappe 1974).

Ectendomycorrhizae are characterized by having a combination of intracellular hyphae in the cortical cells and a network of hyphae between the cortical cells. These mycorrhizae are not commonly produced; however, when found they are usually in forest trees (Laiho 1965).

Two different types of extramatrical hyphae are produced by VA fungi: runner hyphae and absorbing hyphae. Runner hyphae are thick-walled hyphae that track roots into the soil. The hyphae that penetrate roots are initiated from runner hyphae. An underground network of interconnecting runner hyphae can form between plants of the same species or different species. VAM runner hyphae will be found in the interspace regions typical of sagebrush-grasslands. The absorbing hyphae form a dichotomously branching hyphal network extending into the soil from the runner hyphae. These hyphae appear to be the portions of the fungus that absorb nutrients from the soil for transport to the host (Allen 1991). The fungal hyphae extending into the soil serve as an extension of the root systems; extensions that are both physiologically and geometrically more effective for nutrient absorption than the roots themselves (Read 1984; Read and others 1985).

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Mycorrhizal root systems are of benefit to their respective hosts by increasing the capacity of the roots to absorb nutrients from the soil (Marks and Kozlowski 1973). This is apparently accomplished in several ways: (1) The rootabsorbing surface is markedly increased (measurements have indicated that in some instances total root surface was increased 30 times more than an uninfected root); (2) hyphae radiating from the mycorrhizal root are able to penetrate farther into soil than the root hairs of nonmycorrhizal roots; (3) more phosphate (P) uptake per unit area of mycorrhizal roots than nonmycorrhizal roots.

Mycorrhizae have long been known to affect the P nutrition of host plants, as well as having the ability to absorb other mineral nutrients. Phosphate, the major form of P available for uptake by plants, is relatively insoluble in the soil solution and, therefore, is not readily transported by mass flow. Thus, as mycorrhizal hyphae explore the bulk soil beyond the root hairs, additional P is taken up by the hyphae and transported to the host. Mycorrhizal hyphae, by growing into the soil matrix, can gain access to bulk soil P beyond the depletion zones created by the plant roots (Allen 1991). Soil P concentrations under big sagebrush (Artemisia tridentata) increased with time in a successional shrub desert but declined in the associated interspace regions occupied by mycorrhizae. Hence, mycorrhizae may be involved in the development of these "islands of fertility" that characterize arid regions (M. Allen 1988: Skujins and Allen 1986).

The major limiting factor for both nutrient uptake and productivity is drought. VAM infection has been shown to increase water uptake and to increase drought tolerance of several plant species. A suggested mechanism for enhanced water uptake is that it is P mediated (increased uptake of phosphate by plants results in an increased water uptake and transpiration) (Safir and Nelsen 1985). Allen and Boosalis (1983) demonstrated that two different VAM species (*Glomus fasciculatum* and *G. mosseae*) affected the water relations of wheat (*Triticum aestivum*) differently. *Glomus fasciculatum* improved the drought tolerance of wheat and *G. mosseae* reduced drought tolerance of wheat.

Plant species vary in their dependency on the fungal endophytes. Plant species are defined as to their mycorrhizal dependence: nonmycotrophs, facultative mycotrophs, and obligate mycotrophs (Janos 1980). Many nonmycotrophs are ruderal pioneers of harsh sites. Facultative mycotrophs are susceptible to infection, but may not require it, especially in relatively fertile environments. Some grasses, including cheatgrass (*Bromus tectorum*), may be independent of mycorrhizae. Obligate mycotrophs are those plants which would rarely occur in nature without fungal endophytes and are dependent on mycorrhizae to establish and survive. Many of the shrub species desirable for revegetation are obligate mycotrophs and require VA inoculum.

VAM FUNGAL REPRODUCTION

VAM fungal reproductive structures are in the form of external spores, which are formed either singly or in small masses. These spores, plus hyphal fragments, and root segments represent propagules that can be dispersed and utilized as inoculum for new host plant colonization. The primary vectors for dispersal of mycorrhizal inoculum are wind and animals. VA mycorrhizal fungi have been demonstrated to be wind-blown up to 2 km (Warner and others 1987). A wide range of animals are known to disperse mycorrhizal fungal propagules, and generally, any animal that moves soil can cause the migration of mycorrhizal fungi. Of particular interest in shrub deserts are harvester ants, where they will concentrate mycorrhizal inoculum by lining their seed chambers and tunnels with roots containing a high density of mycorrhizal fungi (Friese and Allen 1988).

MYCORRHIZAE AND LAND DISTURBANCE

In a mycorrhizal association with plants, the fungus is considered as the obligate symbiont, and hence, any disturbance affecting the plant will result in a fungal response (Skujins and Allen 1986). In arid and semiarid regions of Western North America, this relationship between mycorrhizae and land disturbance was initially noted during studies of revegetation of surface mines and mine spoils (Allen and Allen 1980; Call and McKell 1981; Christensen and Williams 1977; Danielson 1985; Loree and Williams 1984). These initial studies, and subsequently others, have shown that only about 1 percent of colonizing plants on a disturbed site are mycorrhizal, whereas on the adjacent, undisturbed sites about 99 percent are mycorrhizal. Studies have shown that most successful pioneers of disturbed sites and new soils are nonmycorrhizal plants, and that many plants may require VA mycorrhizal infection in order to colonize disturbed lands (Miller 1979; Reeves and others 1979).

Disturbance of arid lands significantly reduces the inoculum potential of the soil (propagules or stability of the hyphal network) (Reeves and others 1979). Plants that do not require mycorrhizal infection will be successful on disturbed sites. Nonmycotrophic weeds, such as *Salsola kali* and *Halogeton glomeratus*, can invade disturbed sites rapidly and compete with desired grasses and forbs for water and nutrients. Since many of the invading weed species are nonmycorrhizal, without host plants the VAM fungal propagules in the soil may not be able to persist. Disturbed sites, invaded by and subsequently dominated by weeds, have reported no VAM for up to 10 years. The persistence of communities of these plants will fail to support mycorrhizal populations and thus influence succession of disturbed ecosystems (Allen and Allen 1980).

Various types of disturbances can occur in semiarid grasslands. Examples of some disturbance types include: mining, overgrazing, cultivation, fire, and vehicle use. Land disturbance will have the following impacts on mycorrhizae: (1) lowers mycorrhizal inoculum potential (disturbance of hyphal network and fewer propagules); (2) creates a nutrient pulse available to plants; (3) in early successional stages of recolonization, nonmycorrhizal species will dominate; (4) success of nonmycorrhizal species further reduces the propagules of mycorrhizal fungi; (5) succession is slowed because of the lack of potential mycorrhizal fungi.

RESTORATION OF DISTURBED LANDS

Following disturbance, the processes involved with the restoration of desirable vegetation must also involve the restoration of the mycorrhizal association. The critical phases in restoration of the association are: (1) survival of residuals (spores and mycelial network), (2) migration of plant and fungal propagules to a location where contact can be made, and (3) the environmental characteristics in which establishment occurs.

Restoration of disturbed lands has prompted a greater understanding of recovery of mycorrhizae into the ecosystem. Methods used in the reestablishment of VAM in order to promote recovery of desired plant communities are land management, inoculation, and natural processes.

Land Management

In situations where land is to be disturbed and degradation has not yet occurred, proper land management can be an effective means to preserve VAM and restore desirable plants. Retention of soil organic matter will maintain a soil nutrient supply and will help to promote establishment and persistence of VAM.

Maintenance of a continuous vegetational cover will allow a supply of carbon for fungal survival. Cultivation of land reduces VAM fungal densities and alters their species diversity (Skujins and Allen 1986). Tilling of soil will disrupt hyphal networks and causes VAM spores to decompose more rapidly. The use of minimum tillage (notill) will aid in the maintenance of VAM in the soil. Additionally, inorganic fertilizers, especially superphosphate, should be used with care, since they can drastically inhibit VAM formation.

One of the most successful land management methods has been used following disturbance due to mining. The retention and respreading of topsoil has been used to reestablish VAM and the desirable plant species. Allen and Allen (1980) reported that infection frequency and spore counts were recovered to within 50 percent of undisturbed sites in 3 years after topsoil was respread on disturbed sites. At a site where topsoil was not retained, no infection was observed and non-VAM weeds still predominated 10 years after reclamation efforts began. Even the addition of relatively small amounts of fresh topsoil (2-4 cm in depth) to a site resulted in improved infectivity (Danielson and others 1979; Zak and Parkinson 1983).

Inoculation

Efforts to use VAM fungal inoculum additions to soil or VAM- inoculated plants in outplantings at disturbed areas have had limited success. Lack of techniques for mass production of inocula, introduction of the correct fungal species into the appropriate habitats, and expenses involved with the production and inoculation procedures have limited the effectiveness and use of VAM inoculations.

Natural Succession

Recent studies have encouraged the use of natural successional processes to promote the dispersal and establishment of VAM. In arid soils, shrubs establish themselves in patches or clumps and form "fertile islands." These islands are also sites of highest VAM activity. In disturbed areas, patches composed of shrubs and grasses should be planted. These patches will be inoculum focal points from which vegetation and VAM can spread. With greater shrub establishment, adequate VAM inoculum will be concentrated to initiate mycorrhizae on later successional desirable plants (Allen 1987).

CONCLUSIONS

Vesicular-arbuscular mycorrhizal fungi are essential components of natural semiarid land plant communities. Rehabilitation of disturbed sites should include techniques designed to stimulate reestablishment of VAM symbiosis.

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NEW WEEDY GRASSES ASSOCIATED WITH DOWNY BROME

F. E. Northam R. H. Callihan

The 19th century European settlement and subsequent abuse of Pacific Northwest grasslands made the land susceptible to invasion by alien plants. The introduction and dispersal of downy brome (*Bromus tectorum* L.) brought an aggressive competitor into the region that soon became the dominant species in arid and semiarid grasslands (Branson 1985; Daubenmire 1988; Tisdale 1986). Its dominance has persisted for several decades.

This raises a question as to whether downy brome's invasion and domination of Pacific Northwest lands was a one-time phenomenon. Are those areas now dominated by downy brome closed to invasion by other annual grasses? Do opportunities exist for the establishment of aggressive annual grasses capable of displacing downy brome? Is downy brome's persistent dominance a permanent condition?

This report examines the evidence from five other introduced annual grasses currently established in Idaho to ascertain whether downy brome dominance on Pacific Northwest grasslands is permanent.

METHODS

Identification and distribution records accumulated since 1984 at the University of Idaho weed diagnostic laboratory (Department of Plant, Soil and Entomological Sciences) indicates that the introduction of exotic grasses into the inland Pacific Northwest has not ceased (Northam and others 1988, 1989, 1991).

Five introduced annual grasses were selected as examples of the continuing phenomena of biotic invasions. The historical accounts of interrupted windgrass (Apera interrupta [L.] Beauv.), corn brome (Bromus squarrous L.), little lovegrass (Eragrostis minor Host.), poverty grass (Sporobolus vaginiflorus [Torr. ex Gray] Wood), and ventenata (Ventenata dubia [Leers] Coss & Dur.) in Idaho and Washington were ascertained from the floral literature covering these States (Abrams 1940; Cronquist and others 1977; Davis 1952; Hitchcock 1935, 1950; Hitchcock and Cronquist 1973; Hitchcock and others 1969; Piper 1906; Piper and Beattie 1901, 1914, 1915; St. John 1963). The herbarium records at the University of Idaho (ID) and Washington State University (WSU) and collections by weed diagnostic laboratory personnel were also used to document species distributions.

INTERRUPTED WINDGRASS

This winter annual was first recorded in the Pacific Northwest from British Columbia in 1918 and next near Spokane, WA, in 1922 (Constance and Dillion 1935). Interrupted windgrass is known to occur in eight Idaho and Washington counties.

Winter grain fields are its predominant habitat in these two States, but it is also well established and widely distributed along roadsides in the region (Northam and Callihan 1992a). During a period of 60 to 70 years this alien grass has successfully invaded much of the inland Pacific Northwest agricultural land that is also occupied by downy brome.

CORN BROME

The first known Pacific Northwest record of corn brome was a collection from a reservoir shore in southern Idaho (Elmore County) in 1987; the next record was from a roadside in north-central Idaho (Latah County) in 1988 (Northam and others 1988).

The northern Idaho population was common in a plant community containing downy brome and yellow starthistle (*Centaurea solstitialis* L.). Even though the pest status of corn brome is currently unknown in the Pacific Northwest, this European native has demonstrated that it can thrive in the presence of two extremely weedy species.

LITTLE LOVEGRASS

Not all grass invaders into the Pacific Northwest are winter annuals. Little lovegrass is a summer annual that was collected in north-central Idaho in 1984; and during the next 6 years extensive roadside populations were found in four Idaho and six Washington counties. Each of these counties has extensive infestations of downy brome.

Since little lovegrass was not reported in the last published flora covering both Washington and northern Idaho (Hitchcock and Cronquist 1973), the predominant dispersal of little lovegrass along Pacific Northwest rights-of-way seems to have been during the past 20 years (Northam and Callihan 1992b).

POVERTY DROPSEED

This summer annual grass demonstrated that species native elsewhere on the North American continent have

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invaded the Pacific Northwest. Poverty dropseed is native to the eastern United States, but three roadside populations are known in two Idaho counties (Northam and others 1989). The initial population was discovered in 1981.

The warm-season nature of this species and its drought tolerance (Baskin and Baskin 1973) make it possible for this alien to survive during mid and late summer on sites that have mature downy brome populations.

VENTENATA

Northern Idaho (Kootenai County) was the first Pacific Northwest record for this winter annual weed (Baker 1964). Since the first report in 1956, it has spread along roadsides throughout northern and western Idaho and eastern Washington. This species dispersed and established in 21 Idaho and 13 Washington counties in approximately 35 years.

Infestations have been observed in winter grain fields, pastures, and rangelands. The authors have observed noncultivated sites in which ventenata appears to be replacing medusahead (*Taeniatherum caput-medusae* [L.] Nevski). This species has clearly demonstrated its weedy character in Idaho and Washington and has quickly established in regions that are infested with downy brome.

DISCUSSION

Four overall points have been deduced from the information produced by investigations of these five alien grasses. First, the recent discoveries of previously unreported annual grasses in Idaho and Washington indicate that the introduction of alien species continues. In other words, the introduction of downy brome was not an isolated, one-time occurrence.

The second point results from the frequent occurrence of newly reported grasses along roadsides, indicating that their dispersal has been enhanced by human transportation technology. The third point suggests that alien grasses capable of naturalizing in downy brome-infested areas are present in the Pacific Northwest. The final point is that both winter- and summer-germinating annual grasses are capable of invading downy brome infested areas.

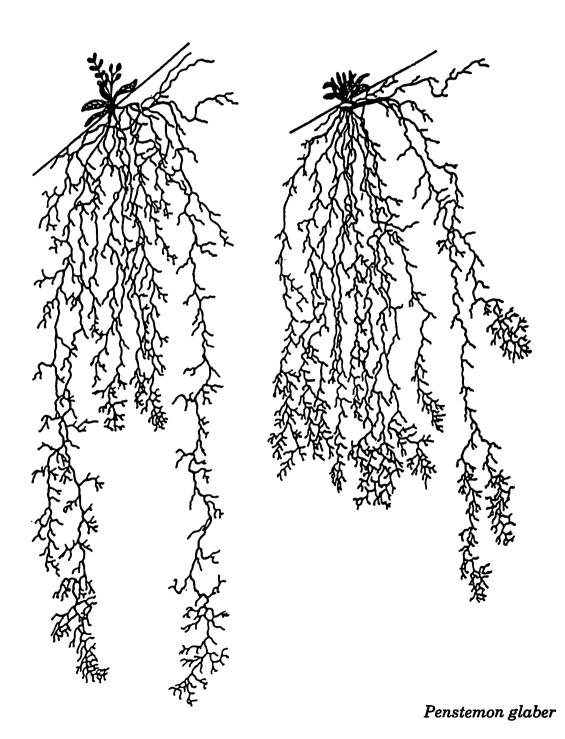
This information supports the following conclusions: (a) The phenomenon of biological invasion by annual grasses still occurs and makes possible the introduction of an annual grass pest that is less desirable than the alien grass weeds that currently infest the Pacific Northwest. (b) Any newly discovered annual grass should be quickly and diligently investigated to determine its distribution, aggressiveness, danger as a pest, and the advisability of initiating control or eradication procedures.

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Restoration: Seed Germination and Establishment



REGULATION OF GERMINATION TIMING IN FACULTATIVELY FALL-EMERGING GRASSES

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ABSTRACT

Seeds of facultatively autumn-emerging grasses germinate in response to autumn rains or postpone germination until the following winter or spring. This research was conducted to determine how germination timing is regulated for seeds of cheatgrass (Bromus tectorum), squirreltail (Elymus elymoides), and bluebunch wheatgrass (Pseudoroegneria spicata), particularly when hydration is interrupted by dehydration episodes of varying duration and severity. For each species, germination rate increased or dormancy levels decreased as a function of time in dry storage, indicating an afterripening requirement. Seeds progressed toward germination with intermittent hydration, but showed significant between- and within-species differences in response to dehydration episodes. Rate of germination was markedly affected, particularly when dehydration occurred just prior to radicle emergence. These findings suggest that germination timing is at least partially regulated by rate and degree of dehydration, which provide a signal regarding adequacy of soil moisture for seedling establishment.

INTRODUCTION

When seeds that are viable and nondormant are provided with adequate water, oxygen, and suitable temperatures, they germinate. Seeds, however, have no control over the external environment to ensure that conditions will remain favorable long enough to complete the germination process. Germination-directed physiology may be interrupted by one to several episodes of conditions unfavorable for germination. Seed response to these episodes mediates their germination behavior during later favorable periods.

Germination interruption due to soil drying is a frequent occurrence for autumn-emerging species in semiarid sagebrush-steppe plant communities, where summer/ autumn precipitation is unpredictable and often followed by periods of rapid surface drying due to high insolation and low atmospheric humidity (Evans and Young 1972; Wight and Hanson 1987). After an autumn precipitation event initiates germination, there is a high probability the seed zone will dry prior to radicle emergence. Therefore, response of germinating seeds to dehydration regimes is an important factor in determining whether autumn germination will occur.

In sagebrush-steppe ecosystems, precipitation is more reliable in winter than summer or autumn, and most species have mechanisms restricting germination to winter or early spring, when drought risk to seedlings is minimal. In contrast, many native and introduced perennial grasses, as well as exotic annual weeds, are facultatively fall-emerging. Seeds mature from midsummer to early autumn and are either nondormant upon dispersal or become nondormant (afterripen) under summer conditions. They either germinate in response to autumn rains, postpone germination until winter or early spring, or, as in the case of exotic annuals like cheatgrass (Bromus tectorum), may carry seeds across years (Hull and Hansen 1974). Seedlings that emerge in autumn have a potential advantage over spring-emerging seedlings because of their headstart in growth, provided they survive risks associated with autumn emergence. These risks include the chance of death by desiccation if germination is triggered by rainfall inadequate to permit establishment. Seeds of facultatively autumn-emerging species would therefore be expected to possess mechanisms for sensing the adequacy of soil moisture associated with autumn precipitation events, and limiting germination to periods with sufficient moisture for establishment.

This study was conducted to determine how germination timing is regulated in seeds of squirreltail (*Elymus elymoides*), bluebunch wheatgrass (*Pseudoroegneria spicata*), and cheatgrass. Multiple ecotypes of squirreltail and cheatgrass were included to determine whether seed response to dry storage and intermittent hydration varies as a function of habitat of origin.

METHODS

Seeds were wild-collected during the summer of 1991 (table 1). Preliminary experiments were conducted with seeds from each collection to determine optimum temperatures for germination and afterripening patterns under contrasting temperature regimes. For experiments involving interjected dehydration episodes, seeds afterripened for at least 6 months were incubated at 20 °C. Control of water potential was achieved using the system of Allen and others (1992), wherein seeds are alternately exposed to liquid ($\psi = 0$) and vapor phase ($\psi =$ negative)

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Table 1-Seed source data for germination experiments

Seedlot	Elevation	January mean temperature	Annual precipitation	 ۲ ₀₀
	m	°C	ст	Hours
Pseudoregnaria spicata				
Provo Overlook	1,970	-1.7	43	108
Elymus elymoides				
South Price	1,250	-4.9	16	84
South Santaguir	n 1,540	-2.2	34	144
Strawberry	2,400	-8.3	65	164
Bromus tectorum				
Green River	1,250	-4.9	16	96
Provo	1,800	-2.0	38	64
Strawberry	2,400	-8.3	65	48

¹T_{co} = time to 90 percent of total germination at 20 °C for each seedlot.

water. This approach facilitated the study of seed response to variations in rate, degree, and timing of dehydration episodes initiated following the onset of imbibition.

Dehydration was timed to occur at an early or late stage of germination, based on the triphasic pattern of water uptake for each species (fig. 1). Early dehydration was initiated near the end of rapid imbibition, which was always 8 or 16 hours following the onset of hydration. Late dehydration was initiated near the end of the lag phase, and varied between 19 and 72 hours depending on species and ecotype. Dehydration episodes were either mild (-4 MPa) or severe (-150 MPa), and lasted for a total of 48 hours.

RESULTS

Continuously Hydrated Seeds—Continuously hydrated seeds germinated most rapidly at constant 15 or 20 °C, or at alternating temperatures with 15 or 20 °C

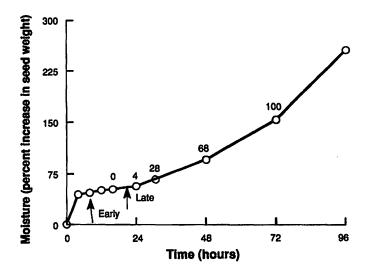


Figure 1—Example of triphasic pattern of water uptake used to determine onset of dehydration episodes. Early = end of imbibition; late = end of lag phase, when first radicle was observed. Data shown are for cheatgrass seeds incubated at 20 °C on saturated blotters in sealed petri dishes. Numbers above data points correspond to percent germination at time indicated.

means. Germination was slower at 10 °C, and was progressively inhibited at temperatures above 20 °C. Although Young and Evans (1977) state that neither squirreltail nor cheatgrass has an afterripening requirement, our data show progressive changes in rate and percentage germination across a range of temperatures when stored under ambient laboratory conditions for a 14-week period (fig. 2). Freshly harvested seedlots contained a fraction conditionally dormant at suboptimal and superoptimal

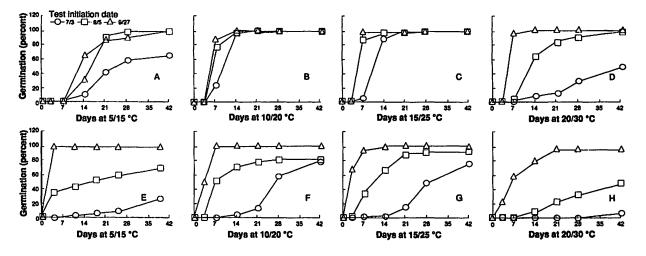


Figure 2—Germination rate curves at four incubation temperatures for squirreltail (A-D) and cheatgrass (E-H) seeds after 2 to 14 weeks of laboratory dry storage. Day 7 differences among test dates within a temperature treatment were significant at p < 0.05 level for both species.

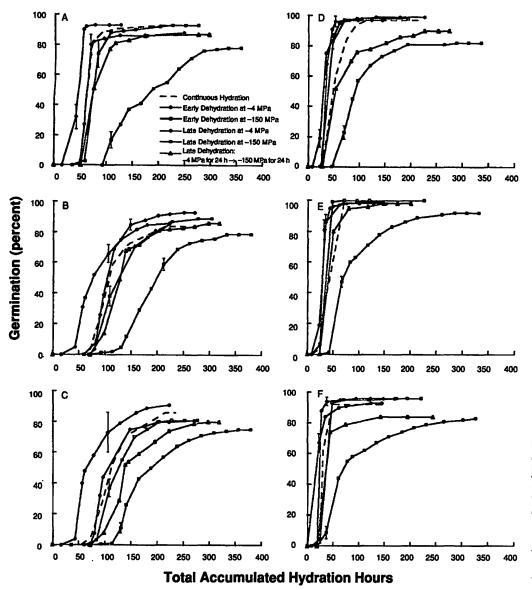


Figure 3—Germination rate curves for squirreltail (A-C) and cheatgrass (D-F) seeds subjected to continuous hydration or an interjected 48- hour dehydration episode early or late during germination. Seeds were from low (A,D), middle (B,E), and high (C,F) elevation sites listed in table 1. Error bars indicate the maximum standard error for each treatment.

temperatures, and germinated slowly at optimal temperatures. Germination rate increased and dormancy levels decreased as a function of time in dry storage.

For afterripened seeds subjected to continuous hydration, time to 90 percent relative germination (T_{90}) (relative germination = percent of total germination for a particular seedlot) varied considerably among species and ecotypes (table 1). Germination of cheatgrass seeds was generally more rapid than for squirreltail or bluebunch wheatgrass. Cheatgrass germination rate increased with collection site elevation, while the rate for squirreltail decreased with collection site elevation.

Seeds Exposed to a Dehydration Episode—Seeds exposed to early dehydration episodes required approximately the same number of hours in contact with liquid water to germinate as did continuously hydrated seeds (fig. 3). Thus, seeds of all species incrementally accumulated progress toward germination during periods when water was not limiting. Early, mild dehydration appears to act as a pause in the germination process, which resumes normally upon rehydration. A slightly faster germination rate with early, mild dehydration suggests that germination-directed physiology can continue to some extent during dehydration episodes that are not too severe.

When dehydration was initiated just prior to radicle emergence, rapid dehydration (-150 MPa) resulted in subsequent germination that was delayed and desynchronized; a mild gradient (-4 MPa) resulted in accumulation of germination processes as with early dehydration. If seeds were exposed to a 24-hour mild dehydration episode prior to exposure to -150 MPa, delayed germination due to severe dehydration was completely or partially avoided (figs. 3, 4).

As with continuously hydrated seeds, there were significant differences in seed response to dehydration episodes depending on species and ecotype. Dehydration at -150 MPa had less of a delaying, desynchronizing effect on subsequent germination of cheatgrass seeds than on squirreltail or bluebunch wheatgrass. Cheatgrass from the low-elevation site had a slower germination rate with

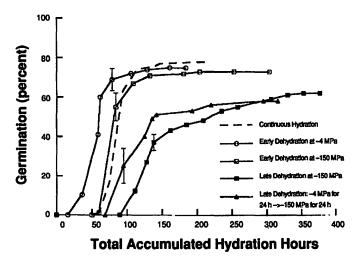


Figure 4—Germination rate curves for bluebunch wheatgrass seeds subjected to continuous hydration or an interjected dehydration episode following an initial hydration period of 16 hours (early) or 69 hours. Error bars indicate the maximum standard error for each treatment.

continuous hydration, and was more strongly delayed/ desynchronized with late, harsh dehydration than seeds of the same species from the high-elevation collection.

In contrast, seeds of squirreltail from the highest elevation source had the slowest germination rate for this species, while seeds from the low-elevation site germinated faster. Still, the high-elevation squirreltail seed was more delayed by dehydration interruptions than was cheatgrass seed, as illustrated by the number of treatments with slower germination than continuously hydrated seeds.

While only one collection of bluebunch was available for this study, its germination response was similar to that of squirreltail. Continuously hydrated seeds had a slow germination rate relative to cheatgrass, and most dehydration treatments slowed germination appreciably. Unlike the other two species, delayed germination of bluebunch seeds due to late, harsh dehydration was only slightly eliminated by a 24-hour pretreatment at -4 MPa.

DISCUSSION

In addition to incubation temperature and degree of seed afterripening, seed response to fluctuating water content is an important variable in determining whether autumn germination will occur. For all grasses included in these studies, seeds progressed incrementally toward germination with intermittent hydration. This is in agreement with findings of Mott (1974), McKeon (1985), and Wilson (1973), who demonstrated that precipitation events inadequate for completing germination can speed subsequent emergence in the field during a later precipitation event. The ecological importance of cyclic wetting and drying in the field has also been emphasized for Chihuahuan desert grassland and Sahel species (Elberse and Bremen 1990; Frasier 1989). While seeds in these studies were subjected to a single dehydration interruption, more extensive research on perennial ryegrass (Lolium perenne) and annual bluegrass (Poa annua) (also facultatively fall emerging) demonstrated that grass seeds can progress toward germination across as many as 16 hydration-dehydration cycles (Allen 1990). With bluegrass, for example, germination could be delayed for more than 200 hours by subjecting seeds to short (8 hour) hydration phases alternating with long (24 hour) dehydration phases at -10 MPa. Under these conditions, bluegrass seeds failed to germinate until exposed to at least 24 hours of continuous hydration. Multiple cycles also had the effect of further synchronizing germination rates, often to the point that all germination would occur during a single hydration period of 16 or 24 hours.

Seed vigor and viability do not appear to be adversely affected by rapid, severe dehydration. In related studies using perennial ryegrass seeds, initiation of harsh dehydration just prior to radicle emergence had a negligible effect on seed viability and vigor as measured by electrolyte leakage and seedling growth rate.

In cold-desert habitats, control of germination timing in the field often operates through dormancy mechanisms that restrict germination until late winter or early spring. This minimizes the risk of seedling death due to inadequate moisture for establishment. However, germination timing of facultatively autumn-emerging grasses is more likely regulated through the rate at which germinationdirected physiology takes place. In contrast with crop seed, where a slow germination rate is often considered to be related to low seed vigor, slow germination in many natural habitats may be adaptive as a deterrent to premature germination at permissive temperatures (Meyer and others 1989). In the case of autumn germination, an afterripening requirement coupled with a slow rate that prolongs the germination process would expand the timeframe over which precipitation events leading to soil moisture replenishment could occur. This would also help limit autumn germination to periods with adequate soil moisture, since a brief period of moisture availability would be insufficient for seeds to complete germination.

Although we do not yet understand the important relationship between afterripening and hydration-dehydration episodes that occur during summer conditions in the field (especially superoptimal temperatures), our data support the hypothesis that seeds can complete germination with a noncontinuous moisture supply. The diurnal wave of solar radiation leads to considerable temperature and moisture fluctuation at the soil surface (Rose 1968), and seeds may progress toward germination over a series of naturally mediated hydration-dehydration cycles. In the case of a precipitation event insufficient to allow completion of germination, seeds at an early or intermediate stage of germination would dehydrate, and progress toward germination would cease. With the following precipitation event, seeds would resume normal progress toward germination or show a slight delay in germination rate (especially for seeds of bluebunch and squirreltail), depending on the rate at which the dehydration event occurred. Seeds that dried rapidly at a late stage in the germination

process would show considerably delayed germination following rehydration, thereby decreasing the probability that autumn germination and emergence would occur.

Within- and between-species variation observed with cheatgrass and squirreltail may provide important clues into seedling establishment strategies. Cheatgrass seeds tend to respond to intermittent moisture with minimal delay in germination rate, especially if collected from a highelevation site. In contrast, squirreltail seeds from the same site required longer to afterripen, were slower to germinate with continuous hydration, and were more substantially delayed following dehydration episodes. Thus, the high-elevation cheatgrass seeds would have a higher probability of germinating in autumn than would squirreltail seeds, given the same seedzone conditions. Cheatgrass seeds from the low-elevation site, presumably with a greater probability of experiencing drought during establishment, are more likely to postpone germination until winter or spring. Again, this prediction is based on a slower rate of afterripening, a slower germination rate, and a greater delay in germination rate with extreme moisture fluctuations. In contrast, the low-elevation squirreltail seeds would have the highest probability for autumn germination for this species.

Field retrieval studies, using both multiple ecotypes and contrasting field site conditions, should make it possible to validate these laboratory-based predictions pertaining to seed behavior of facultatively autumn-emerging species. Currently, fall seedings are usually attempted late enough to preclude the possibility of autumn emergence. For facultatively autumn-emerging species, however, early fall plantings may be advantageous in years with sufficient soil moisture for naturally mediated hydrationdehydration cycles in the seedzone.

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WATER-SOLUBLE CHEMISTRY FOLLOWING SIMULATED BURNING OF SOIL-LITTER OF BIG SAGEBRUSH, SQUIRRELTAIL, CHEATGRASS, AND MEDUSAHEAD

Robert R. Blank Fay L. Allen James A. Young

ABSTRACT

Wildfires induce chemical changes in the soil surface. The magnitude of these chemical changes is influenced by the nature of the vegetative litter being burned. This paper reports on the water-soluble chemistry following simulated burning of soil-litter of big sagebrush (Artemisia tridentata ssp. tridentata), squirreltail (Elymus hystrix), cheatgrass (Bromus tectorum), and medusahead (Taeniatherum caput medusae ssp. asperum). The soil was a fine, montmorillonitic, mesic Typic Chromoxerert collected approximately 20 km east of Susanville, CA. Results indicate that length of simulated burn and temperature of simulated burn interact to generate a particular water-soluble chemistry. Differences in postsimulation inorganic chemistry were noted among the soil-litters, which suggest inherent differences in the soil-litters. The lack of variation in levels of certain organic acids among the soil-litters, however, suggests they were synthesized via pyrolysis of the soil humic fraction, rather than originating from the plant litter itself.

INTRODUCTION

Wildfires considerably influence the water-soluble chemistry of surface soils (DeBano and Conrad 1978; Wright and Bailey 1982). In general, levels of water-soluble nitrate decrease and levels of water-soluble cations increase (Isichei and Sanford 1980; Khanna and Raison 1986; Raison 1979; Smith 1970; White and others 1973). The magnitude of these wildfire-induced changes is influenced by the chemical composition and biomass of the plant community (Wright and Bailey 1982).

Recent work in the sagebrush-steppe of northeastern California showed that high levels of water-soluble organic anions, especially carboxylic acids, formed as a consequence of wildfires in sagebrush subcanopy soils; shrub interspaces, largely occupied by cheatgrass, were unaffected (unpublished research, USDA-ARS, Reno, NV). It was speculated that cheatgrass litter did not contain

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. the raw biochemical materials that when heated would form organic acids. It was unclear, however, if the interspace soils reached elevated temperatures of long enough duration to foster the synthesis of organic anions as temperatures greater than 200 °C apparently are required (unpublished research, USDA-ARS, Reno, NV). This research was thus initiated to determine:

a. If simulated burning of soil-litters dominated by annual grasses yields a different soil chemistry than that of native perennial grasses or shrubs.

b. How the interactive effects of length of burn time and temperature influence water-soluble chemistry among the aforementioned soil-litters.

FIELD WORK

The study area is approximately 20 km east of Susanville, CA. The dominant soil is a fine, montmorillonitic, mesic Typic Chromoxerert (table 1). Vegetation consists of shrubs of big sagebrush (Artemisia tridentata ssp. tridentata) and Lahontan sagebrush (Artemisia arbuscula ssp. longicaulis). Big sagebrush is largely confined to Vertisols; Lahontan sagebrush seems limited to less churning, clayey soils that have a thin, sandy, eolian veneer (E horizon). The most common perennial bunchgrass is squirreltail (Elymus hystrix). Alien annual grasses, cheatgrass (Bromus tectorum) and medusahead (Taeniatherum caput-medusae ssp. asperum), occur in small isolated patches.

Samples were collected in December 1991. Collection areas were limited to places where litter had accumulated to completely cover the soil surface. Depth of collection was essentially the depth of the highly aggregated surface A horizons (table 1). Thus, the material collected is a mixture of soil and litter, which will be referred to as soillitter. Collections of soil-litters were replicated in two nearby areas of similar soil.

LABORATORY ANALYSES

Collected soil-litter was immediately dried at 50 °C, then passed through a 2-mm sieve. Coarse litter was crushed to pass through the sieve. The material was homogenized and stored in paper cartons prior to simulated burning.

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able 1—Selected soil chemical and physical properties of the Typic Chromoxerent soil

orizon	Depth	Sand	Silt	Clay	Organic carbon	Total N	CEC
	cm		Perc	cent		mg/kg	cmol/kg
Α	0-5	30.5	33.0	36.5	0.72	502	31.7
BA	5-20	24.6	24.7	50.7	.51	353	33.0
Bss	20 - 46	23.1	23.8	53.1	.35	243	49.4
Bw1	46 - 86	23.6	28.8	47.5	.35	213	52.0
Bw2	86-122	23.6	28.5	47.9	.29	156	50.8

For simulated burning, 15 g of soil-litter was placed in a 5-mL crucible. The crucibles were placed in a preheated uffle furnace, uncovered, using the following time and emperature matrix: 5 and 15 min exposure time at temeratures of 150, 250, 350, and 450 °C. Previous research as shown that these simulations can produce a wateroluble chemistry closely matching that of a wildfire (un-ublished research, USDA-ARS, Reno, NV).

After simulated burnings, crucibles were cooled and eighed to record weight loss. Material was immediately laced in a 50-mL polypropylene centrifuge tube to which 0-mL of deionized water was added. Tubes were shaken r 30 min on a reciprocating shaker, centrifuged, and filred through 0.22-µm nylon membrane filters. Samples were chemically analyzed within 1 week of the mulated burnings and were kept refrigerated prior to nd between analyses. Samples were chemically analyzed sing high-performance ion exchange chromatography. nions were separated using an Omnipac PAX-500 colmn (Dionex Corp.). The eluant was a 0.75-mM to 50-mM aOH gradient. Detection was by suppressed conductivy and spectrophotometry at 210 nm connected in series. hromatographic peaks were deemed positively identified hen both of the following conditions were met: (1) the tention time of an unknown peak matched a standard eak (all standards reagent grade); and (2) for applicable remical species, the ratio of the conductivity signal to at of the spectrophotometric signal was similar for the nknown peak and the standard. Cations were separated sing a HPIC-CS3 column (Dionex Corp.). The isocratic uant was 27.5-mM HCl, 2.25-mM diaminopropionic acid onohydrochloride, and 2.25-mM histidine monohydroloride. Detection was by suppressed conductivity.

ESULTS

Graphic representation of water-soluble ion concentraon versus temperature-simulated burnings for selected tions and anions is presented in figure 1. When comured with replications (data not presented), several ends can be noted in these data.

At long simulated burning times (15 min), levels of ater-soluble cations, extracted from all soil-litters, exbited a bell-shaped distribution from low to high temratures. Maximum levels occurred at 350 °C for calum and sodium and magnesium (not shown) and at i0 or 350 °C for potassium. At the short simulation time min), however, levels of water-soluble cations increased eadily to 450 °C. Similar trends occurred for the organic ids, formate, acetate, and maleate. There were other commonalties among soil-litters following simulated burning. Levels of water-soluble sulfate increased with increasing temperature reaching the highest levels at 450 °C for both simulated burning times. Nitrate levels generally decreased with increasing simulation temperatures and declined to zero between 250 and 350 °C at the 15-min simulation time.

Heat-induced chemistry for some water-soluable species differed among the soil-litters. Levels of calcium varied considerably among soil-litters. Amounts of watersoluble potassium in unheated samples of big sagebrush were far greater than the other untreated soil-litters and remained high at all simulated burning temperatures.

A most unusual response to simulated burning occurred for water-soluble orthophosphate. At 5-min simulation time, levels of orthophosphate generally decreased with increasing temperature for soil-litters of cheatgrass, squirreltail, and big sagebrush. For medusahead soil-litter, however, levels increased rapidly from 250 to 350 °C, becoming higher than the other soil-litters except for big sagebrush.

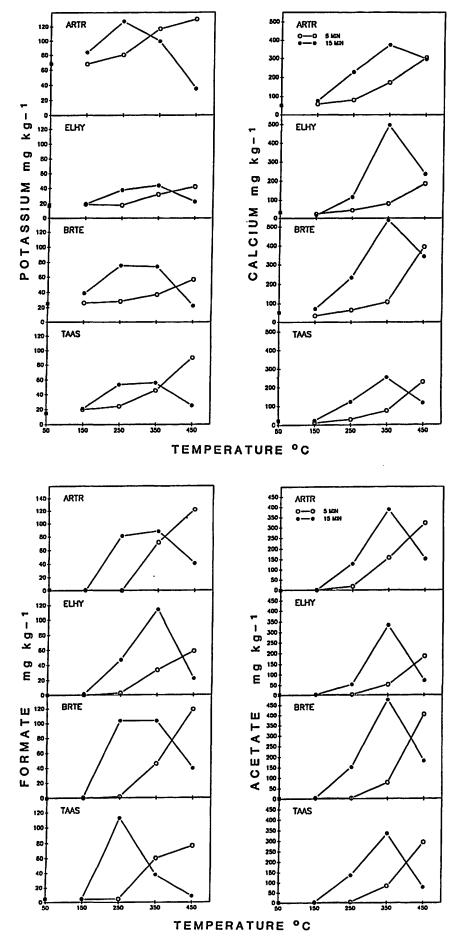
DISCUSSION

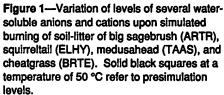
There are both similarities and differences in the response of the various soil-litters to simulated burning. From the data presented in this paper and other simulated burnings we have completed, patterns are evident.

Widely varying levels of water-soluble potassium, magnesium, and calcium, among original untreated soillitters, suggest long-term differential plant cycling. Big sagebrush soil-litter is especially enriched in potassium relative to other soil-litters. Differential elemental cycling among plants and among plant communities is well established (Rodin and Bazilevich 1965). These initial, presimulation, differences in soil elemental content confound interpretation of postsimulation chemistry.

Another pattern is the response of the metal cations sodium, potassium, magnesium, and calcium to the simulated burnings. Levels of these cations decreased substantially at temperatures greater than 350 °C (at 15-minsimulation time). Volatilization temperatures of the metal cations are far above the simulation temperatures used (Raison and others 1984; Wright and Bailey 1982). Alternative explanations of this phenomenon include: (a) at high temperatures additional cation sorption sites are formed, thereby decreasing cation extraction with water, and (b) low-temperature volitization of the cations via metal-ligand complexation.

Levels of most organic anions show a similar trend with temperature as do cations. Unexpectedly, for a given temperature and time, simulated burning produced similar levels of organic acids among all the soil-litters. If these organic anions were derived via pyrolysis of plant litter, then big sagebrush soil-litter, which has a greater proportion of plant litter and is biochemically unique among the soil-litters, would likely respond differently to simulated burning. These data suggest that either (a) the organic anions are derived from raw biochemical building blocks common to all the soil-litters (cellulose for example), or (b) they originate from the soil organic fraction. A clue to the pathway for organic anion synthesis can be gleaned from





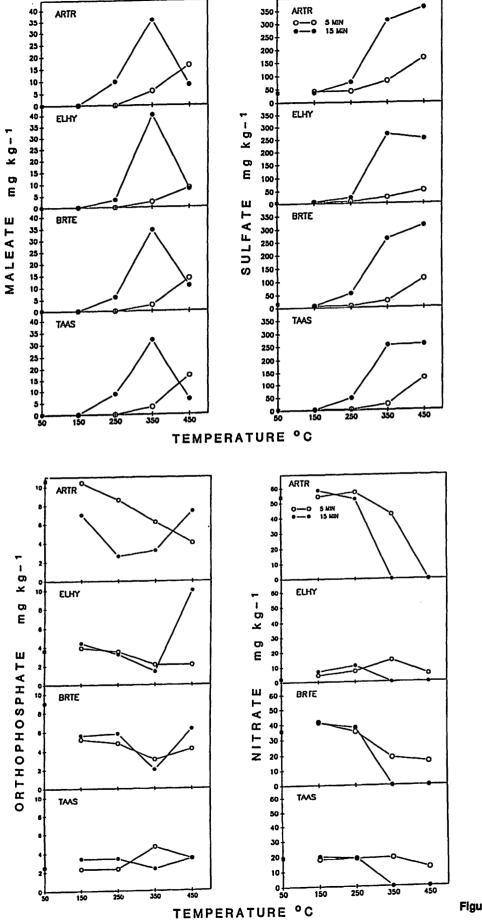


Figure 1 (Con.)

the information on maleic acid; all soil-litters had nearly identical levels of maleic acid. Polymaleic acid has been proposed as a model for fulvic acid (Anderson and Russell 1976). This suggests that pyrolysis of soil humic materials is responsible for the formation of maleate and likely other organic anions.

Our simulations indicate that, given appropriate temperatures and time, all soil-litters tested produced organic anions including the carboxylic acids formate, acetate, and maleate. In contrast, the lack of water-soluble organic anions, postwildfire, in cheatgrass-occupied shrub interspaces (unpublished research, USDA-ARS, Reno, NV) is likely a consequence of insufficient temperatures or exposure times to promote these reactions.

IMPLICATIONS

Pathways of plant succession following wildfires are influenced by many factors including fire intensity, destruction of allelopathic compounds, reduction of competition, release of seed dormancy, seed death, and the production of germination cues—compounds created by wildfire that stimulate certain seeds to germinate (Christensen and Muller 1975; Keeley and others 1985; Moreno and Oechel 1991; Went and others 1952). These research findings pose a question in regard to wildfires in alien annual grass systems as compared with wildfires in native shrubgrass systems.

Is fire intensity significantly less in annual grass wildfires as compared to shrub-grass systems, and if so, does this difference, in part, alter pathways of succession? Available data indicate that annual grass fires will be of lower temperature and shorter duration than sagebrush shrub fires (Gibson and others 1990; McKell and others 1962; Wright and others 1976). Successional pathways on alien annual grasslands in the Intermountain West, subjected to repeated wildfires, lead to an annual grass monoculture, an impoverished ecosystem (Billings 1991). The success of these alien annual grasses is largely due to their plasticity, germination characteristics, and competitiveness (Melgoza and Nowak 1991; Young and others 1987). We speculate, however, that loss of species diversity in these alien annual grasslands occurs, in part, because the cooler and less intense fire regime, as compared with shrub microsites, does not engender qualities in the soil necessary for the germination and establishment of certain species. We will test this hypothesis in future experiments.

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ESTABLISHMENT CHARACTERISTICS OF CHEATGRASS UNDER VARIOUS WET-DRY WATERING SEQUENCES

Gary W. Frasier

ABSTRACT

Water is a major factor in range plant establishment. Greenhouse studies were conducted to evaluate the effect of the first wet-dry watering sequence on establishment of cheatgrass (Bromus tectorum). Cheatgrass has a rapid seed germination, and most seedlings emerge in 4 to 6 days. Many of the seedlings survived dry periods of up to 10 days. These germination and seedling survival characteristics give cheatgrass a competitive advantage in establishment over most desirable range species.

INTRODUCTION

In semiarid regions, water is a critical factor limiting the establishment of most plants, whether desirable or undesirable species. Understanding water requirements for plant establishment provides an insight into which plants may be more easily established in a specific area. Cheatgrass (Bromus tectorum) has become a dominant species in the cold desert regions of the Western United States. It is also a problem as an invader species in wheat areas of the southern-central parts of the northern plains. There is a desire to replace cheatgrass with perennial grass species (Roberts 1991) to improve production and ensure a more dependable forage base. This has proven to be difficult because cheatgrass growth characteristics are better adapted to the existing climatic and edaphic conditions than native species (Daubenmire 1970; Harris 1967; Hull and Hansen 1974; Rummel 1946).

Since water is a major factor in plant establishment, understanding the soil-water requirements for seedling establishment is a first step in developing techniques for replacing cheatgrass with more desirable perennial grass species. Cox and Jordan (1983) found that precipitation frequency in the first few months following seeding was more critical to warm-season perennial grass seedling establishment than the total precipitation quantity. Frasier and others (1984) developed a technique to evaluate the effect of the first wet-dry watering sequence following planting on seedling establishment. Frasier and others (1987) showed that the relative differences in seedling survival as related to water sequences obtained in greenhouse studies were similar to results observed in the field. Frasier and Woolhiser (1988) and Frasier and Lopez (1990) used these data to develop criteria to select plant species adapted to the precipitation patterns of a specific area.

By developing similar information for characterizing the water requirements for seedling establishment of cheatgrass, it may be possible to identify some critical growth periods during seedling establishment or soil-water conditions that can be exploited for establishment of more desirable plant species.

METHODS AND MATERIALS

Greenhouse studies were conducted using the procedure of Frasier and others (1984). Tapered plastic cones, 6.35 cm in diameter by 24.0 cm long, were filled with 660 g of dry, 60-mesh silica sand. Cheatgrass seeds were furnished by James A. Young, USDA Agricultural Research Service, Reno, NV. Ten seeds were placed on the sand surface in each cone and covered with 3 mm of dry sand. Two cones were prepared for each watering sequence.

The treatments were composed of a wet-dry-wet watering sequence conducted over a minimum of 14 days. The lengths of the first wet periods were 2, 3, or 5 days. The lengths of the following dry periods were 5 days, 7 days, or extended (XD) (sufficient time to kill all seedlings and germinated seeds, usually 20 to 30 days). Following the dry period, the cones were wetted daily for 4 to 8 days to determine if there were any viable ungerminated seeds. Each watering sequence was represented by two cones. Cones in the extended dry sequences were wetted for 6 days following the dry period. Included in each watering sequence combination were a set of cones used as a control, which were watered daily for 14 days (14W) (table 1). All cones were initially wetted to field capacity, then watered daily with an overhead reciprocating spray system in a preset watering sequence. During the wet period, the cones were sprinkled daily with sufficient water to bring the average moisture content to field capacity.

One set of studies was conducted during the winter (December-March) and another set in the spring/summer (April-July). The experiments were repeated three to five times in each evaluation period (summer and winter). In the winter, a small electric heater was used to maintain the temperature above 5 °C. During the summer, the greenhouses were evaporatively cooled. The coolers were thermostatically set to come on when the temperature reached 25 °C. Space limitations in the greenhouse made it impractical to evaluate all watering sequences simultaneously. Watering sequences were evaluated in groups using the length of the dry period as a common factor (5D, 7D, and XD dry days). In each group the 14-day wet treatment was

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Wa	tering per	iod		
Initial Final		Replications		
wet	Dry	wet	Summer	Winter
	Days		No.	
2	5	7	5	3
	7	8	3	3
	XD1	6	4	3
3	5	6	5	3
	7	6	3	3
	XD	6	4	3
5	5	4	5	3
	7	6	3	3
	XD	6	4	3
14	0	0	2	2

¹Extended dry of 20 to 30 days.

²Sequence was run with each dry sequence (5, 7, or XD days dry).

included as a common treatment among the separate replications and watering sequence groupings.

The number of live seedlings in the cones for each watering sequence were summed and recorded daily. Data analysis consisted of computing daily means of the seedling counts among replications and calculating the percentages of germinated seeds and surviving seedlings based on the total number of seeds planted. The standard deviations of surviving seedlings among replications were computed to obtain a measure of variability among replications.

RESULTS AND DISCUSSION

The number of seedlings is of major interest in the periods: (1) during and immediately following the initial wet period when the number of seedlings is indicative of the rate of seed germination and initial plant emergence; (2) at the end of the dry period when the plants are most susceptible to and dying from lack of soil moisture; and (3) at the end of the second wet period when there may be new seedlings from seeds that did not germinate in the initial wet period.

After each study was completed, the cones were emptied and the plants inspected for potential root restrictions. These inspections showed that, even with every day wet (14W), the roots did not penetrate to the bottom of the cones. It was concluded that there were no restrictions on seedling survival by root confinement.

The silica sand used as a growing medium had a relatively low water-holding capacity (Frasier and others 1984). Even in the greenhouse environment, the evaporative demand would dry the sand at a rapid rate. In these short-term studies, the seedlings did not reach a vegetative stage that utilized high quantities of water. Most of the water loss from the cones is believed to have occurred by evaporation from the sand surface with lesser amounts lost through the plant transpiration processes.

The daily means of the seedling counts are presented in figures 1 through 4. The standard deviations of seedling counts among replications are shown on selected days representing the periods of major interest (maximum number

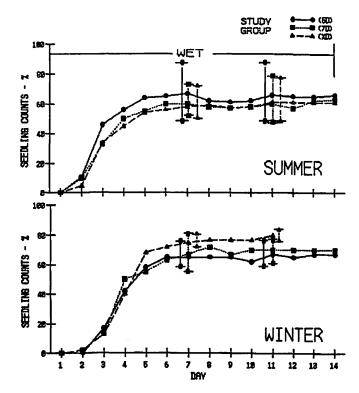


Figure 1—Cheatgrass seedling counts for the every day wet (14W) watering sequence for the three study groupings, 5D, 7D, and XD, for the summer and winter study periods.

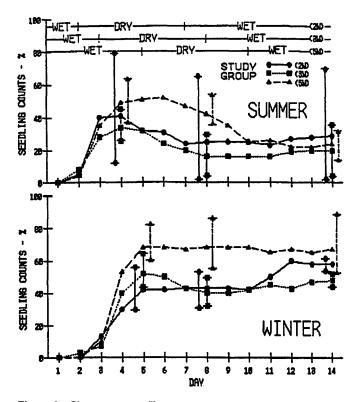


Figure 2—Cheatgrass seedling counts for 2 days, 3 days, and 5 days wet watering sequences followed with 5 days dry for the summer and winter study periods.

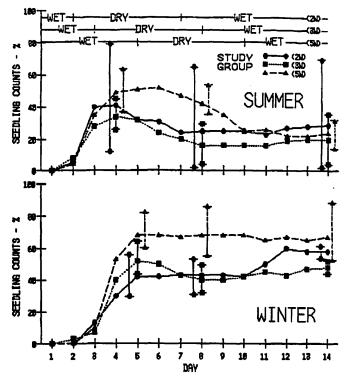


Figure 3—Cheatgrass seedling counts for 2 days, 3 days, and 5 days wet watering sequences followed with 7 days dry for the summer and winter study periods.

of seedlings following the initial wet period, minimum number of surviving seedlings in the dry period, and final seedling counts during the last wet period).

Fourteen-Day Wet Watering Sequence

While there were slight differences in the temperature in the greenhouse during the year (table 2), there were no major differences in the seedling emergence patterns among the various evaluation groupings (5D, 7D, and XD) in either summer or winter (fig. 1). Seedlings began to

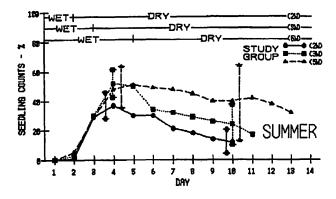


Figure 4—Cheatgrass seedling counts for the summer period with the extended dry (XD) for the 2 days, 3 days, and 5 days wet watering sequence groups.

Table 2-Greenhouse daily temperature range

Period	Maximum	Minimum
	•••••••••••••••••••••••••••••••••••••••	0
Summer	27-30	10-24
Winter	24-30	4-13

emerge on the second day in the summer and the third day in the winter. A total of 55 to 65 percent of the seeds produced seedlings in the summer studies and 65 to 80 percent in the winter studies. Most of the seedlings had emerged by day 6 in the summer and by day 7 in the winter.

Five-, 7-, and Extended-Day Dry Watering Sequences

In the summer periods, maximum seedling counts of 40 to 50 percent occurred on days 4 and 5 (figs. 2, 3, and 4). During the 5- and 7-day dry periods, some seedlings died. With the 3 days wet, there were some ungerminated seeds that later germinated and produced seedlings in the final wet period (figs. 2 and 3).

In the winter, seedling mortality was not a factor in either the 5- or the 7-day dry periods. Approximately 40 to 60 percent of the seeds produced seedlings (figs. 2 and 3). This was the same as the final seedling count in the control (14W) watering sequence. In the 2-day wet watering sequence, some seeds did not germinate in the initial wet period and germinated during the following wet period.

In the extended dry (XD) watering sequences, all seedlings died in 10 to 20 days in the summer and 20 to 30 days in the winter. No seeds germinated in the final wet period following the extended dry periods during either evaluation period.

SUMMARY AND CONCLUSIONS

Cheatgrass has several characteristics with respect to water requirements that make it a competitive plant during seedling establishment. Seed germination is rapid, which provides an advantage over slower germinating species. In addition, cheatgrass seedlings are relatively hardy with respect to surviving drought periods up to 10 days. A replacement plant species for cheatgrass, such as sideoats grama (*Boutaloua curtipendula*) (Frasier and others 1985), must be able to germinate and produce a vigorous seedling in 1 to 2 days of wet soil. The replacement plant seedling must be able to develop a root system and be morphologically adapted to survive drought periods of 10 or more days following a 2-day wet period. Otherwise there is a good chance that the cheatgrass will maintain its dominant position.

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GERMINATION ENHANCEMENT OF PERENNIAL GRASSES NATIVE TO THE INTERMOUNTAIN REGION

Stuart P. Hardegree

ABSTRACT

Seed priming can be used to enhance germination rates of native perennial grasses relative to untreated cheatgrass. A matric-priming technique was used to enhance low-temperature germination rates of seven native perennial grasses. The median germination time at 10 °C was reduced by as much as 8 days. Priming increased germination rates of several species to a level comparable to cheatgrass. Drying back after priming reduced, but did not eliminate, the priming effect.

INTRODUCTION

Native perennial grasses and shrubs have been replaced by cheatgrass (*Bromus tectorum* L.) over large areas of the Intermountain West (Young and others 1987). One of the mechanisms that may contribute to the success of cheatgrass is its ability to germinate and establish a root system at relatively low temperatures early in the spring (Harris and Wilson 1970; Wilson and others 1974; Young and Evans 1982). In an extensive study of germination response to temperature, Young and Evans (1982) predicted that germination advancement of even a few days might make a difference in establishment success of native perennial grasses that are in competition with cheatgrass.

Seed priming is a technique by which seeds are partially hydrated to a point where germination processes begin, but radicle emergence does not occur (Bradford 1986; Heydecker and Coolbear 1977). Seeds that have been primed exhibit more rapid germination and emergence, greater germination uniformity, and sometimes higher total percent germination (Brocklehurst and others 1984; Heydecker and Coolbear 1977). Germination enhancement has been variously attributed to metabolic repair processes (Bray and others 1989; Burgass and Powell 1984), a buildup of germination metabolites (Coolbear and others 1980; Khan and others 1978), osmotic adjustment (Bradford 1986), and to a simple reduction in the lag time for imbibition (Bewley and Black 1982; Brocklehurst and Dearman 1983; Heydecker 1977). The magnitude of germination enhancement depends on the priming medium, priming water potential, priming duration, and whether the seeds are redried after priming (Bradford 1986;

Heydecker 1977; Heydecker and Coolbear 1977). In almost all cases, positive priming effects are expressed to the greatest degree at temperatures normally suboptimal for germination (Heydecker and others 1975). Previous studies on intermountain grass species have shown that prehydration treatments have a beneficial effect on subsequent germination rates (Bleak and Keller 1972; Griswold 1936; Keller and Bleak 1968). These previous studies, however, were not designed to control hydration at subgermination water content.

The purpose of this paper is to outline the development of seed priming treatments for enhancing native-plant germination response to low temperature. These studies include the determination of optimal priming conditions for seed treatment, an evaluation of the effects of drying back primed seeds, and a comparison of native seed germination response to that of untreated cheatgrass.

PLANT MATERIALS

Germination response to priming was determined for bluebunch wheatgrass (Agropyron spicatum [Pursh] Scribn. and Smith), thickspike wheatgrass (Agropyron dasystachyum [Hook.] Scribn.), basin wildrye (Elymus cinereus Scribn. and Merr.), sheep fescue (Festuca ovina L.), canby bluegrass (Poa canbyi Scribn.), Sandberg bluegrass (Poa sandbergii Vasey), and bottlebrush squirreltail (Sitanion hystrix [Nutt.] J.G. Smith). These grasses have been identified by the Bureau of Land Management, U.S. Department of the Interior, as high-priority species for restoring native plant diversity in the Great Basin and on the Columbia River Plateau. Primed seeds were compared to nonprimed seeds of the same species and to nonprimed seeds of three accessions of cheatgrass collected in southwestern Idaho.

PRIMING/GERMINATION SYSTEM

The most common osmotic and solid-matrix seedpriming systems involve intermixture of seeds with the priming medium (Heydecker and Coolbear 1977; Taylor and others 1988). This causes problems for subsequent seed handling, seed water content determination, and oxygen availability during priming (Hardegree and Emmerich 1992). In our experiment, seeds were primed in a priming/germination vial designed for matric-water potential control (Hardegree and Emmerich 1992). In this system, the seeds are separated from an osmotic solution of high molecular weight polymer (polyethylene glycol 8000; PEG) by a cellulose membrane that has a low molecular weight exclusion limit. The membrane excludes

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PEG from contact with the seeds and, therefore, provides a matric-potential control surface for seed equilibration. The matric potential of the membrane surface is determined by the osmotic potential of the solution with which it is in equilibrium. A detailed description of the priming/ germination vial and matric-priming procedure is given by Hardegree and Emmerich (1992).

OPTIMAL PRIMING CONDITIONS

The basis of all seed-priming treatments is to equilibrate seeds at a water potential that allows initiation of positive germination processes but prevents radicle emergence (Heydecker and Coolbear 1977). Optimal priming solutions are usually determined to be at the least negative water potential that does not result in germination during treatment (Dell'Aquila and Tritto 1990; Evans and Pill 1989).

In the current experiment, optimal priming water potential at 25 °C was estimated by determining the germination response of each species to reduced water potential. PEG was mixed with water to yield seven solutions over the water potential range of 0 to -2.5 MPa using equation 4 of Michel (1983) as suggested by Hardegree and Emmerich (1990). Seeds were deposited on the membrane surface in individual germination/priming vials and allowed to equilibrate for 14 days. Seeds were considered germinated and were removed and counted when they exhibited radicle extension of ≥ 2 mm. Germination vials were maintained in a controlled temperature room at 25 °C under both fluorescent and incandescent light for 12 h/day. The cellulose membranes were treated with a light dusting of fungicide powder (Daconil) at the beginning of the experiment. Thirty-five seeds comprised each treatment replicate for the relatively small Poa and Festuca species. Thirty seeds per replicate sample were used for all other species. Each treatment was replicated six times with each vial in a different randomized block within the controlled temperature room.

Priming water potential was estimated to be the least negative water potential that did not result in germination after 14 days. Figure 1 represents the germination response for canby bluegrass and thickspike wheatgrass. Table 1 lists the total germination percent and estimated optimal priming water potentials for each species.

PRIMING EFFECTS

Seeds were primed for 2, 4, 6, or 8 days at 25 °C at the estimated optimal priming water potentials listed in table 1. Date of priming initiation was staggered so that all priming treatments terminated on the same day. Primed seeds were switched to priming/germination vials containing pure water and subsequent germination response at 10 °C was monitored for 21 days. A set of nonprimed control treatments were initiated at the same time that primed seeds were switched to pure water. These control treatments also included three cheatgrass seed lots collected in July 1991 from three sites in southwestern Idaho: Ada County, near Orchard, Ten-Mile Creek, and Kuna Butte. Priming and control treatments were

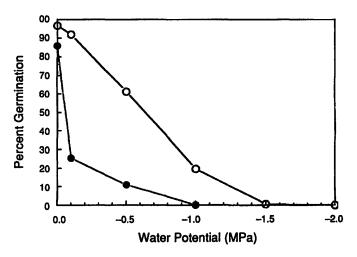


Figure 1—Total percent germination for canby bluegrass (•) and thickspike wheatgrass (o) as a function of water potential. Optimal priming water potential was estimated to be the least negative water potential that resulted in zero germination after 14 days at 25 °C.

Table 1—Estimated optimal priming water potentials determine	ned
from seeds germinated for 14 days at 25 °C, and to	Ital
percent germination in the 0 MPa water potential	
treatments	

Species	Priming water potential (MPa)	Total percent germination	
Agropyron spicatum	-2.5	90	
Agropyron dasystachyum	-2.0	97	
Elymus cinereus	-2.5	63	
Festuca ovina	-2.0	92	
Poa canbyi	-1.0	86	
Poa sandbergii	-1.0	71	
Sitanion hystrix	-1.5	65	

replicated five times for the native species and 10 times for each cheatgrass accession. The priming experiment was carried out in November 1991.

Days to 50 percent of total germination (D_{50}) was determined for each germination vial as an index of germination rate. Means and standard error values of the optimal-priming treatments are listed in table 2. Primed seeds germinated as much as 8 days sooner than nonprimed seeds at 10 °C (table 2). Nonprimed native seeds germinated more slowly than cheatgrass at 10 °C, but several species germinated at a rate comparable to cheatgrass after priming (table 2).

DRYING AFTER PRIMING

Germination response of freshly primed seeds is dependent on seedbed conditions at the time of planting. Germination advancement of the magnitude found in the current experiment assumes optimal field conditions at

Table 2—Days to 50 percent of total germination for optimal
duration treatments and for conrol treatments of native
grasses and cheatgrass (standard error in parentheses)

Species	Treatment duration (days)	Control seeds (D ₅₀)	Primed seeds (D _{so})
A. spicatum	8	7.8 (2.1)	3.2 (0.2)
A. dasystachyum	6	7.9 (0.8)	4.0 (0.5)
E. cinereus	8	14.8 (2.4)	11.4 (2.0)
F. ovina	8	8.7 (1.1)	4.2 (0.3)
P. canbyi	6	11.6 (1.8)	6.8 (1.4)
P. sandbergii	4	13.6 (1.1)	5.4 (0.3)
S. hystrix	8	13.2 (1.6)	5.6 (0.5)
B. tectorum			
Kuna		4.0 (0.3)	
Orchard		3.6 (0.3)	
Tenmile		4.0 (0.8)	

the time of planting. Since primed seeds are metabolically active, it is not feasible to store them for long periods of time if seedbed conditions are not suitable for rapid germination. It is, therefore, desirable to determine whether primed seeds can be dried back without losing the priming effect.

Seeds of each species were primed as before except that only a 7-day priming duration was used. One set of seeds was switched to pure water immediately and monitored for germination for 21 days. A second set was air-dried for 1 week and then switched to pure water for a determination of germination response. A control set of nonprimed seeds was initiated at the start of each germination run and each treatment was replicated nine times. This experiment was carried out in April 1992.

Figure 2 shows the cumulative germination response of freshly primed, primed/dried back, and control treatments

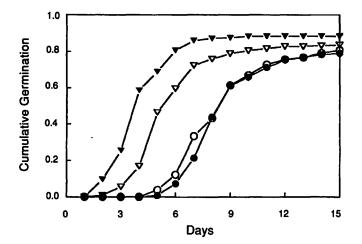


Figure 2—Cumulative germination percent as a function of time for primed (∇) , primed/dried (∇) , and nonprimed control treatments (\bullet ,o) of thickspike wheatgrass germinated at 10 °C. Seeds were primed for 7 days at 25 °C.

for thickspike wheatgrass. Drying back resulted in an average loss of 35 percent of the priming effect on D_{50} . This loss of priming effect ranged from 20 percent for bluebunch wheatgrass to 65 percent for basin wildrye. Some of the priming effect results from a reduction in the lag time of imbibition, which is lost when the seeds are dried back. Germination advancement of primed and dried-back seeds over nonprimed control seeds, however, indicates that metabolic seed processes are responsible for the bulk of the priming effect.

DISCUSSION

Matric-priming has been shown to advance germination in laboratory experiments, but development of a practical application requires further study. One limitation of matric-priming is that the technique as described by Hardegree and Emmerich (1992) is unsuitable for scaling up to handle bulk seed quantities. Matric-priming, however, is thermodynamically equivalent to simple water addition to subgermination water content (Heydecker and Coolbear 1977). We anticipate that matric-priming will be used only to establish the optimal priming conditions of water potential, temperature, and treatment duration. The appropriate seed water content for optimal priming response can then be achieved by gravimetric techniques such as those described by Gray and others (1990) and Heydecker and Coolbear (1977). We predict that our current results do not necessarily reflect the maximum obtainable level of germination enhancement for these species. Other combinations of priming temperature, water potential, and duration may yield better results, as our treatment conditions were semiarbitrary.

Seed priming of native perennial grasses may reduce, somewhat, the competitive advantage of cheatgrass during early spring establishment. All of the experiments described here, however, are limited by the artificial nature of the laboratory procedure. We have not yet determined germination response under field conditions of variable temperature and moisture. Germination rate is also only one of many environmental factors affecting establishment success of native grasses. Measurable benefits from seed treatment may be possible only in conjunction with appropriate seedbed preparation. The most important requirement of any priming system will be to coordinate planting with appropriate conditions of seedbed microclimate. Planting under optimal conditions for germination may not be possible as these conditions may preclude the use of heavy planting equipment. Field application of priming treatments may, therefore, be limited to use of seeds that have been redried before planting.

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SEED USE BY DESERT GRANIVORES

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ABSTRACT

Three western Great Basin study areas that have undergone extensive disturbance were monitored for species composition of granivorous rodents. Disturbed habitats at two of these sites (Red Rock and Flanigan) recovered with native or introduced perennial plants and were dominated by heteromyid rodent species, which are important seeddispersal agents for many desert plants. At one of these sites, Indian ricegrass—a native perennial grass—rapidly dominated the disturbed area, perhaps because of strong interactions between this grass and local heteromyid rodents. The third site (Noble), which lacks heteromyids, has become infested with an introduced annual weed (medusahead). The seed dispersal activities of heteromyids may be important in obtaining desirable responses to disturbance on desert rangelands.

INTRODUCTION

Granivorous, or seed-eating, animals are the most abundant and diverse herbivores in North American deserts. This high abundance and diversity is probably due to the generally greater availability and suitability of seeds as food compared to other types of plant materials in deserts. Desert plants produce large seasonal flushes of seeds, which remain dormant and retain their nutritional quality for substantially longer periods than other aboveground plant parts (Janzen 1971). Even with the seasonal nature of desert seed production, seeds are available to desert granivores in the soil seed pool year-round; this is well illustrated by occasional spring flushes of annual plants from seeds lying dormant in the soil over one or more winters. These properties of desert plant seeds (seasonal production in massive quantities and nutritional retention over time) also make them an ideal food for storing for future use. As a consequence, granivorous diets have been adopted by various groups of desert animals, and desert plants, having coevolved with these granivores, often exhibit adaptations that either reduce levels of seed predation or allow them to capitalize on granivore activities for dispersing their seeds. Here, I concentrate on the latter coevolutionary relationship—seed dispersal.

Various groups of rodents, birds, and seed-harvester ants comprise the granivore guild in North American deserts (Brown and others 1979). Birds and ants are to a large extent seasonal granivores, especially in northern

and high-elevation deserts, because most bird species are resident only from spring through fall, and they eat insects during much of this time, while ants are relatively inactive above ground when temperatures are cold. By contrast, nonhibernating rodent species are active foragers for seeds all year. Furthermore, birds and ants glean seeds largely from the soil surface; rodents dig for buried seeds as well (Johnson and Jorgensen 1981). Thus, rodents are often the main consumers of desert plant seeds. In addition to consuming seeds, though, large numbers of seeds are cached by desert rodent species in three families (Heteromyidae-the kangaroo rats, kangaroo mice, and pocket mice; Muridae-the New World mice, voles, and woodrats; and Sciuridae-the ground squirrels and chipmunks). The heteromyids are a diverse group that is well represented in most desert localities.

Heteromyids and other arid-land rodents can harvest substantial fractions of a given plant species' seed production. The degree of granivory probably depends both on seed density and on desirability of particular seed types. Thus, seeds of some plant species are greatly reduced by rodents, while others may be barely touched (table 1). From a plant's perspective, it is what the rodent does with the harvested seed that is important.

After seeds are harvested, rodents may consume them or cache them in one of two ways (Price and Jenkins 1986). "Larderhoarding"—practiced by most desert rodents refers to placing large caches in a centrally located burrow or nest. "Scatterhoarding"—practiced mainly by heteromyids and to a lesser degree by sciurids—refers instead to placing numerous smaller caches in shallow depressions on the ground surface and covering them with soil.

Table 1—Previous studies documenting percentages of plant seed production harvested by rodents

Plant type (site)	Seeds harvested	Source
	Percent	
Annual grasses (California Central Valley)	93	Pearson 1964
Annual grasses (Southern California)	30-65	Borchert and Jain 1978
Erodium cicutarium (Mojave Desert)	95	Soholt 1973
Larrea tridentata (Chihuahuan Desert)	87	Chew and Chew 1970
Oryzopsis hymenoides (Great Basin Desert)	46	McAdoo and others 1983
Desert plants (Mojave Desert, NV)	30-80	Nelson and Chew 1977
Forbs (Arizona grassland)	<1	Pulliam and Brand 1975

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It is through scatterhoarding activities that desert rodents are most likely to have a positive effect on seedling recruitment; larderhoards are generally placed too deep underground for seedlings to successfully emerge if they germinate. Thus, the net effect of rodents on seedling recruitment of a particular plant species is largely determined by numbers of seeds that are removed from the germinable seed pool by consumption and larderhoarding versus numbers that persist in scatterhoards for later germination (Price and Jenkins 1986). Scatterhoards that are not recovered for future consumption may benefit seeds in three different ways: (1) buried seeds may have a higher probability of germination and establishment than unburied seeds (Vander Wall 1990), (2) buried seeds are not vulnerable to consumption by nonscatterhoarding granivores (birds and ants) that harvest seeds only from the soil surface (Price and Jenkins 1986), and (3) seeds of certain desert plant species may have enhanced germinability when they have been handled by scatterhoarding rodents (La Tourette and others 1971; McAdoo and others 1983; Reynolds and Glendening 1949). In this regard, heteromyid rodents, being very common and avid scatterhoarders in North American deserts, are very important components of arid rangeland communities. Although heteromyids have been known to have important effects on range vegetation for some time (for example, Reynolds 1950), results of long-term experiments in the Chihuahuan Desert have recently highlighted the ecological significance of these "keystone" granivores; rodent exclusion experiments have shown that heteromyids directly affect the species composition and physiognomy of the local plant community (Brown and Heske 1990).

Table 2 lists a sample of plant species that have been found germinating from rodent scatterhoards; this list includes grasses, shrubs, and trees and both native and introduced species. The native species listed appear to be dependent on harvesting by animals for dispersal since their seeds lack external appendages that could facilitate dispersal by other means (for example, wind or adhesion to fur), while the introduced species (cheatgrass) has such appendages to facilitate dispersal. This is to be expected, since native plant species have coevolved with local granivores, while successful invasions of exotics are most likely with species that do not need to rely for dispersal on a granivore guild that is unfamiliar with them.

In this paper, I present data on the species composition of granivorous rodent communities at three disturbed study sites in the western Great Basin Desert. I show that for two of these sites, where native plants have recovered well from disturbance, rodents include mainly scatterhoarding

 Table 2—Previous studies documenting germination of desert plant

 seeds from rodent scatterhoards

Plant species	Location	Source
Velvet mesquite	Arizona	Reynolds and Glendening 1949
Indian ricegrass	Nevada	McAdoo and others 1983
Antelope bitterbrush	California	Hormay 1943
	Oregon	West 1968
	Nevada	Vander Wall 1990
Palo Verde	Arizona	McAuliffe 1990
Cheatgrass	Nevada	La Tourrette and others 1971

heteromyid species, while at the third site, which is dominated by an introduced annual weed species, heteromyids and other scatterhoarders are rare. I also discuss data from two experiments: (1) a field study illustrating strong interactions between heteromyids and a native animaldispersed grass species, and (2) laboratory seed preference tests with captive heteromyids showing that these rodents prefer seeds of this native grass to those of two introduced annual grasses. My aim is to illustrate the potential importance of scatterhoarding granivores for desert rangelands by showing examples of desirable successional responses to disturbance where these animals are common and undesirable responses where they are lacking. Certainly, numerous ecological and historical factors combine to determine such responses, but plant/animal interactions involving native granivores are one such factor that has received little attention.

METHODS

Field studies were conducted at two northwestern Nevada sites (Red Rock, Washoe Co., Reno NW Quad.: T21N.R18E.S14; and Flanigan, Washoe Co., Flanigan Quad. T27N.R18E.S2) and a northeastern California site (Noble, Lassen Co., Shaffer Mtn. Quad. T30N.R15E.S27). The Red Rock and Flanigan sites were burned in 1985 and 1988, respectively, while the Noble site was disturbed by extensive grazing of sheep over several decades preceding this study. Prefire vegetation at Red Rock consisted of big sagebrush (Artemisia tridentata), Mormon tea (Ephedra viridis), desert peach (Prunus andersonii), and various herbaceous species seeded after a previous fire, especially crested wheatgrass (Agropyron desertorum), which dominates the postfire vegetation. Prefire vegetation at Flanigan consisted largely of big sagebrush, scattered shrubs of other native species, and infrequent bunches of Indian ricegrass (Oryzopsis hymenoides); Indian ricegrass dominates the postfire community at Flanigan. The Noble site was dominated by low sagebrush (Artemisia arbuscula) before disturbance and remains so in adjacent undisturbed areas; the disturbed site has been dominated by an invasion of medusahead wildrye (Taeniatherum caput-medusae) but also has squirreltail (Sitanion hystrix) and rare Indian ricegrass bunches. Medusahead and cheatgrass (Bromus tectorum) have invaded undisturbed areas at Noble as well. but to a lesser extent. Soils are sand at Flanigan, heavy loam at Red Rock, and clay at Noble.

I censused rodent populations by livetrapping twice monthly at Red Rock since the 1988 fire, and at irregular intervals at Flanigan and Noble since 1988 and 1991, respectively. I trapped in the disturbed areas and in adjacent undisturbed (or less disturbed) areas at all three sites.

At Flanigan, I conducted experiments from 1989 to 1991 to quantify numbers of Indian ricegrass seeds harvested and cached by heteromyids. Seed harvest was quantified by planting single seeds and groups of 2, 10, and 100 seeds at various depths (0, 1, 2, 4, or 6 cm) in randomly determined locations, which were checked after 7 days to determine if they had been removed by rodents. Seed caching was quantified by placing petri dishes with 40 g of Indian ricegrass seeds labeled with fluorescent dye on the ground and locating dye spots left at scatterhoards under UV light the following night. I tested for rodent preferences for Indian ricegrass, cheatgrass, and medusahead by offering food-deprived captive rodents from Noble 1.0 g of each seed type in separate petri dishes. Trials were videotaped in the laboratory. The seed types chosen first and eaten in the largest quantities were determined by replaying videos and used as criteria to assess potential preferences.

RESULTS AND DISCUSSION

Proportions of various rodent species captured at the three study sites are shown in table 3. Four rodent species were captured at both the Red Rock and Noble study sites. Only one of the species occurring at Noble is a heteromyid (Great Basin pocket mouse—Perognathus parvus), and this species was rare in the disturbed (medusahead) habitat. By contrast, a nonheteromyid species (deer mouse-Peromyscus maniculatus) was caught significantly (P < 0.05) more frequently in the medusahead than in the sagebrush habitat at Noble. Heteromyids occurred in similar proportions in disturbed and undisturbed habitats at Red Rock, and were represented by two species (Great Basin pocket mouse and Panamint kangaroo rat— Dipodomys panamintinus) in both habitats. These two species were the earliest colonizers of the burned area after the 1988 fire at Red Rock. Six rodent species occurred at Flanigan, and all but one of them (white-tailed antelope ground squirrel—Ammospermophilus leucurus) were heteromyids. While only one of the heteromyid species (Merriam's kangaroo rat-D. merriami) was common in unburned sagebrush habitat at Flanigan, three were quite common in the burned (Indian ricegrass) habitat (Merriam's kangaroo rat, Panamint kangaroo rat, and Ord's kangaroo rat-D. ordii) and two others (desert

kangaroo rat—D. deserti—and little pocket mouse—P. longimembris) were present as well (table 3).

Heteromyids were equally or more abundant in disturbed habitats during early stages of plant succession as in undisturbed habitats at Red Rock and Flanigan, and at the latter site there was actually a pronounced increase in heteromyid species diversity during this recovery. By contrast, the only heteromyid species occurring at Noble was less common in disturbed than in undisturbed habitat. Although a cause-and-effect relationship cannot be inferred from these data, it is interesting to note that the disturbed habitat at Noble, where native perennial plants have been mostly replaced by a medusahead monoculture, is also depauperate in the scatterhoarding rodents that disperse the seeds of many native plant species. Heteromyids are generally able colonizers of disturbed areas, as indicated by the Flanigan and Red Rock data (table 3) and by an ongoing field experiment at Red Rock (USDA-ARS, unpublished data). In this experiment, I first demonstrated that three plots in the burned habitat had similar densities of three rodent species (Great Basin pocket mouse, Panamint kangaroo rat, and deer mouse), after which I removed vegetation on two of these plots by mowing. Heteromyids remained on the control and mowed plots in similar densities, but on the latter plots the nonheteromyid species (deer mouse) disappeared after vegetation removal. This suggests that the lack of heteromyids at Noble is not simply attributable to past disturbance.

The impressive abundance and diversity of heteromyid rodents in the burned habitat at Flanigan is probably due to the dominance of Indian ricegrass in this area. This perennial grass species appears to have evolved a very close interaction with heteromyids. Its seed is highly preferred by these rodents; seeds of other plant species have been

Table 3-Relative abundances (percent) of various rodent species occurring in disturbed
and undisturbed habitats at three western Great Basin study sites. Fire caused
the disturbance at the Red Rock and Flanigan sites; extensive use by domes-
tic sheep disturbed the Noble site. Heteromyid rodents, the primary scatter-
hoarding species at these sites, include species in the genera Dipodomys and
Perognathus

		Percentage of captures		
Study site	Rodent species	Undisturbed habitat	Disturbed habitat	
Flanigan:		Sagebrush	Indian ricegrass	
	Dipodomys merriami	89	54	
	Dipodomys ordii	2	27	
	Dipodomys panamintinus	1	12	
	Dipodomys deserti	0	3	
	Perognathus longimembris	1	3	
	Ammospermophilus leucurus	7	1	
Red Rock:		Agropyron/shrub	Agropyron	
	Dipodomys panamintinus	2	16	
	Perognathus parvus	55	67	
	Peromyscus maniculatus	14	17	
	Reithrodontomys megalotis	29	0	
Noble:	1101011000011011190110901009	Sagebrush	Medusahead	
110010.	Perognathus parvus	23	2	
	Peromyscus maniculatus	50	95	
	Reithrodontomys megalotis	23	2	
	Spemophilus lateralis	4	0	

found to drop out of heteromyid diets in nature when Indian ricegrass produces seeds (McAdoo and others 1983). Indian ricegrass has a classical animal-dispersed seed morphology, and seedlings appear to come mainly from heteromyid scatterhoards, which generally persist longer after germination than single seedlings (personal observation). Seeds in these scatterhoards often have 100 percent germination, partly because heteromyids discriminate against empty and nonviable seeds when harvesting Indian ricegrass (McAdoo and others 1983). Finally, the germinability of Indian ricegrass is enhanced when the seeds have been handled by heteromyids; this may be due in part to breaking mechanical dormancy of the seed by removal of its coat by rodents, but even unshelled seeds that have been handled by heteromyids have improved germinability (McAdoo and others 1983).

Results of field experiments at Flanigan indicated that up to 50 percent of Indian ricegrass seeds were harvested by heteromyids over a 7-day period. Depth of seeds in the sand had a significant effect on harvest rate (P < 0.05); seeds on or near the surface were harvested in the greatest quantities. Seed density, however, had no effect on harvest rate. Single seeds or pairs were harvested at rates similar to groups of 10 or 100, illustrating the efficiency of heteromyids at locating even low-density soil seed reserves. By locating caches containing seeds labeled with fluorescent dyes. I found that up to 25-35 percent of Indian ricegrass seeds harvested by heteromyids were initially cached in scatterhoards, and that scatterhoards contained about 250 seeds on average. The largest scatterhoard found had 1,427 seeds. Although the scatterhoarding rates I have found at Flanigan are fairly high, it was also apparent from dye traces around rodent burrows and from large amounts of dyed seeds that I could not locate that many seeds were being larderhoarded or consumed. While it is not yet possible to determine net effects of heteromyids at this site on the Indian ricegrass population, it is clear from the rapid domination of Indian ricegrass in response to removal of shrubs by fire that a large soil seed reserve was in place even though this grass was uncommon in the prefire plant community. Because most of the Indian ricegrass population at Flanigan consists of clumps of two or more sameaged individuals, it is likely that this rapid postfire response was due to rodent scatterhoards providing this seed reserve.

In laboratory seed preference experiments, the only rodent species that was common in medusahead habitat at Noble (deer mouse) exhibited a significant (P < 0.05) preference for medusahead and Indian ricegrass over cheatgrass. Great Basin pocket mice, the only heteromyid species at Noble, also preferred Indian ricegrass, but avoided medusahead seed. At Noble, established Indian ricegrass plants thrive quite well, but new recruits are seldom found. Although Indian ricegrass may show some promise for being established in areas vulnerable to medusahead infestation, the heteromyids which prefer Indian ricegrass seeds and act as its dispersal agents may be lacking, thus limiting the persistence of an Indian ricegrass population. Other rodents, such as deer mice, may occur commonly in medusahead habitats, but their activities will not promote the establishment of native, animal-dispersed plant species. This may explain why squirreltail, which has seed appendages for dispersal by wind or adhesion to

fur, is more common in the medusahead habitat at Noble than other native plants dependent on animal dispersal vectors.

In conclusion, I suggest that a stronger understanding of granivores' effects on native and introduced plant species may be an important element in understanding successional processes in desert rangeland plant communities. Such information may simply allow prediction of plant species responses following disturbance based on knowledge of granivore species composition in a given area. Eventually though, arid-land restoration efforts may include active management for granivores that play important roles in maintaining native plant communities. Although range restoration efforts involving active human intervention, such as artificial seeding, may produce more rapid results than "natural restoration" by native fauna, the latter carries the advantages of reduced financial expenditure, of not being logistically restricted by spatial scale, and of ultimately resulting in more "pristine" plant communities.

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TEMPERATURE PROFILES FOR GERMINATION OF CHEATGRASS VERSUS NATIVE PERENNIAL BUNCHGRASSES

Ellen Martens Debra Palmquist James A. Young

ABSTRACT

Profiles for germination in relation to temperature were developed for seeds of cheatgrass (Bromus tectorum), other introduced brome species (B. mollis, B. japonicus, B. brizaeformis, B. rubens, and B. diandrus), and three native bunchgrass species (Stipa thurberiana, Festuca idahoensis, and Elytrigia spicata). Seeds were incubated at 55 constant or alternating temperatures from 0 °C to 40 °C. Cheatgrass seeds were highly germinable over a wide range of constant and alternating incubation temperatures. The germination of seeds of other brome species and of the native bunchgrasses was much more limited.

INTRODUCTION

Seeds (caryopses) and germination are obviously a key portion of the ecology of an annual such as cheatgrass (*Bromus tectorum* L.). There are three aspects of the seed ecology of this species that are critical. These factors are simultaneous and continuous germination and soil-litter seedbanks.

The inherent potential of the physiologic systems of cheatgrass seeds to support germination must interact with the potential of seedbeds to support germination. Cheatgrass is very plastic phenotypically. The species is established over an immense expanse of diverse habitats in North America. Ecotypic variation has been demonstrated for the species. Variable habitats and perhaps genotypes have led to conflicts in interpreting the seed ecology of the species. Most of these conflicts can be easily accounted for and interpreted if genetic and environmental differences are understood.

In the western Great Basin, cheatgrass only germinates in the fall once every 5 years. Germination normally occurs in very early spring when seedbed temperatures are at or near freezing during a portion of each diurnal fluctuation (Evans and others 1970). Competition in such seedbeds is

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. primarily for available soil moisture. A method of partially escaping this competition would be to germinate when temperatures are extremely low during the winter. In the Great Basin environment most precipitation occurs during the midwinter months, almost completely out of phase with temperatures that permit growth (Houghton and others 1972). Considering the limited potential of Intermountain area seedbeds to support germination and establishment of seedlings, it has long been noted that species that have seeds that germinate simultaneously and at the earliest possible time have the highest and most consistent opportunity for success.

Simultaneous germination is apparently a great advantage for cheatgrass, but the extreme variability in the frequency of moisture events in temperate desert environments presents the risk that all the seeds would germinate in one flush and then die due to drought. The reciprocal of simultaneous germination is continuous germination. Cheatgrass accomplishes continuous germination through seeds acquiring dormancy in the field (Young and others 1969). The duration of this acquired dormancy can be influenced by the duration of moist incubation and gibberellin enrichment of the substrate.

Remember that cheatgrass seeds are only going to acquire dormancy if they are not in a seedbed environment that permits simultaneous germination. The position of cheatgrass seeds in seedbeds in relation to litter and microtopography largely controls simultaneous germination. Litter and microtopography influence extremes in temperature and relative humidity. Therefore, temperatures at which cheatgrass seeds will or will not germinate become important in defining simultaneous germination and partially in the induction of acquired dormancy and continuous germination. A second aspect of this research is how germination of seeds of native perennial species and other annual grasses compares to germination of cheatgrass seeds.

Our purpose was to compare germination temperature profiles for various sources of cheatgrass and other perennial and annual species adapted to similar environments.

METHODS AND MATERIALS

We compared the germination of collections of seeds of cheatgrass from Pyramid Lake and Edwards Creek Valley, NV. Germination-temperature profiles were also obtained

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Table 1—Definition and explanation of parameters calculated from germination profiles

Germination parameter	Calculation	Purpose
1. Mean germination	<u>Σ germination</u> 55	Simple, single-factor parameter that can be compared statistically.
2. Mean germination of temperature regimes with some germination	Σ germination No. regimes with germination	High value compared with overall mean germination restricted to specific temperature regimes.
3. Regimes with some germination	No. regimes with germination 55	Indicates breadth of response in relation to temperature.
4. Regimes with optimum germination	No. regimes with optimum germination 55	By itself, this is a difficult parameter to interpret. A large number of regimes with optimum germination is ideal, if the mean germination of the optima is high.
5. Optimum germination	max germination – (confidence interval + 2)	This definition of optimum relates statistically, through the confidence interval, to means associated with the maximum observed germination. We use the narrow definition of one-half the confidence interval to limit the number of optima.
6. Mean of optima	optima No. of optima	Provides measure of temperature regimes that support highest germination not markedly different from maximum.
7. Maximum germination	Mean with highest germination	Gives measure of ultimate potential to germinate under ideal conditions.
8. Frequency of optima	No. times temp. reg. supports optimum germ. No. sources tested	Gives a precise measure of what is optimum temperature for germination of cultivar or group of cultivars.

for the annual brome species, rattlesnake grass (B. brizaeformis [F. & M.]), Japanese chess (B. japonicus Thurb.), foxtail chess (B. rubens L.), ripgut (B. diandrus Roth.), and soft chess (B. mollis L.). These annual grass seed germination profiles were compared to those of bluebunch wheatgrass (Elytrigia spicata [Pursh] D.R. Dewey), Idaho fescue (Festuca idahoensis Elmer) and Thurber's needlegrass (Stipa thurberiana Piper) from previously published sources. Seeds of the brome species were collected from naturalized stands and stored in the laboratory until tested.

Seeds of each source were placed on one thickness of germination paper (blotter paper without germicides) in closed petri dishes and kept moist with tap water during incubation in dark germinators. The seeds were considered germinated when the radicle emerged 2 mm. Germination counts were made after 1, 2, and 4 weeks of incubation. We used four replications of 25 seeds each, arranged in a randomized block design. Seeds were incubated at 0, 2, 5, and 5 °C increments through 40 °C, and at alternating temperature regimes consisting of 16 hours at each cooler temperature and 8 hours at each warmer temperature daily. For example, 0 °C alternated with 2, 5, 10, 15, 20, 25, 30, 35, and 40 °C, but 35 °C alternated with 40 °C only (Young and Evans 1973). Where multiple collections were available, we have taken the mean of the data for each species.

To present a broader spectrum, for the last section on frequency of optima, we used published and unpublished data from our files on other collections of each of the species discussed in this paper. We used a total of 24 collections of *Bromus* and 19 other grasses.

Quadratic response surface analysis was used to analyze seed germination data in relation to constant and alternating temperatures (Evans and others 1982). Several parameters were calculated from the response surfaces to help interpret the germination response (table 1). Response surface comparisons, among species or collections, were made using procedures developed by Palmquist and others (1987). The response surfaces were compared at different categories of seedbed temperatures (fig. 1), which were derived from microenvironmental monitoring of seedbed conditions in the early spring in the western Great Basin (Evans and Young 1970).

CHEATGRASS GERMINATION PROFILE

The seeds of both collections of cheatgrass were highly germinable at a wide range of constant and alternating

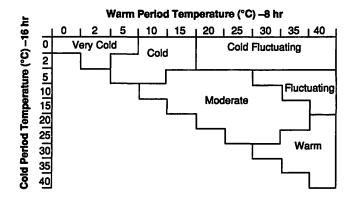


Figure 1—Average germination (percent) for general categories of seedbed temperatures.

Table 2—Temperature-germination profile of estimated percent germination for cheatgrass from Pyramid Lake, 1989¹

Cold period					Warm per	riod 8 h °C				
16 h °C	0	2	5	10	15	20	25	30	35	40
0	² 81(5)	83(4)	85(4)	87(3)	87(4)	85(4)	82(4)	76(3)	69(4)	59(6)
2		86(4)	89(3)	91(3)	92(3)	91(3)	88(3)	83(3)	77(3)	68(5)
5		.,	92(4)	96(2)	98(2)	98(3)	96(3)	92(2)	86(3)	79(4)
10				97(4)	100(3)	100(2)	100(3)	100(2)	96(3)	90(4)
15				•••	97(4)	100(3)	100(3)	100(3)	99(3)	95(4)
20					• • •	90(4)	93(3)	94(3)	94(3)	91(4)
25						.,	78(4)	80(3)	82(3)	81(4)
30							. ,	59(4)	62(3)	63(4)
35								.,	35(5)	37(5)
40									Λ -γ	4(7)

¹Temperature-germination profile for Edwards Creek was very similar.

² Numbers in parentheses are one-half the confidence interval for the germination estimate (p = 0.05).

Species	Optimum germination	Temp. with some germ.	Temp. with opt. germ.	Mean of optima
		Percer	nt	
Cheatgrass	¹ 97	100	22	96
Bluebunch wheatgrass	90	95	13	86
Idaho fescue	81	87	7	77
Thurber's needlegrass	25	80	5	24

Table 3-Germination of cheatgrass and three other native perennial bunchgrasses

¹Mean of two sources (Pyramid Lake and Edwards Creek).

incubation temperatures (table 2). The Pyramid Lake and Edwards Creek Valley collections of cheatgrass had maximum germination of 100 and 94 percent, respectively (table 3). For seeds produced under semiarid wildland conditions these are both highly viable seed collections. Some germination occurred at 100 percent of the 55 temperatures tested for the two collections. Optimum germination (see table 1 for definition of optimum) occurred at 22 percent of the temperature regimes of both sources. The mean germination of the optima temperature regimes for cheatgrass was 96 percent.

PERENNIAL GRASS GERMINATION PROFILES

The germination profiles of bluebunch wheatgrass and Idaho fescue showed a maximum germination of 90 and 81 percent, respectively, with some germination at 95 and 87 percent of the 55 temperature combinations (table 3). The mean of the optimum temperature regimes for germination was 96 percent for the cheatgrass selections and 86 and 77 for bluebunch wheatgrass and Idaho fescue, respectively. The number of temperature regimes supporting optimum germination dropped to 13 and 7 percent as compared to the 22 percent for cheatgrass. Thurber's needlegrass was the lowest germinator of the group tested, having a maximum germination of 25 percent. Although 80 percent of the temperature combinations showed some germination, only 5 percent of the temperature regimes supported optimum germination, with a mean of optima of 24 percent.

CHEATGRASS VERSUS NATIVE BUNCHGRASSES

In all categories of seedbed temperatures the cheatgrass collections had markedly higher estimated germination than the three native perennial bunchgrasses (table 4). The only statistical overlap occurred at moderate temperatures where the germination of seeds of bluebunch was not significantly (p = 0.05 percent) lower than the cheatgrass collections. At very cold, cold, cold fluctuating, fluctuating, and warm temperatures the estimated germination of seeds of the native bunchgrasses is significantly lower (p = 0.05) than the cheatgrass collections.

OTHER BROMUS SPECIES PROFILES

Rattlesnake grass and Japanese chess collections produced the highest maximum germination of the *Bromus* species tested (table 5). The maximum observed germination for both the rattlesnake grass and Japanese chess was 100 percent for all collections tested and optimum germination occurred in 45 percent of the temperature regimes for rattlesnake grass and 35 percent of the temperature regimes for seeds of the Japanese chess collections. Some germination occurred at 98 and 97 percent of all temperature regimes tested. The mean of optima for both was 99 percent.

Germination profiles for seeds of foxtail chess were similar to those for collections of cheatgrass seeds (table 5).

Table 4—Comparison of response surfaces for germination-temperatures for seed of two collections of cheatgrass and three native perennial bunchgrass¹

	Seedbed temperature category									
Collection	Very cold	Cold	Cold fluctuating	Fluctuating	Moderate	Warm				
Cheatgrass										
Pyramid Lake	84a	91a	78a	90a	95a	57b				
Edwards Creek	70a	79b	76a	83a	90a	73a				
Bluebunch wheatgrass	13b	46c	34b	50b	78ab	31c				
Idaho fescue	7b	32c	17b	18c	60b	19c				
Thurber's needlegrass	4b	9d	3c	2d	16c	4d				

¹Estimated germination means followed by the same letter within columns are not significantly different at the 0.05 level of probability as determined by overlap of the confidence intervals.

Table 5—Germination of cheatgrass and five other annual brome species	
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Species	Optimum germination	Temp. with some germ.	Temp. with opt. germ.	Mean of optima
		Percer	nt	
Cheatgrass	¹ 97	100	22	96
Rattlesnake grass	100	98	45	99
Japanese chess	¹ 100	97	35	99
Foxtail chess	¹ 98	97	18	97
Ripgut	81	84	18	77
Soft chess	66	100	25	63

Values are means of multiple collections.

Foxtail chess seeds had a maximum germination of 98 percent. There was some germination at 97 percent of the 55 temperature regimes tested, but only 18 percent of the temperatures regimes supported the optimum germination. The mean germination for the optimum temperature regimes was 97 percent. In comparison, the cheatgrass collections tested had an average maximum germination of 97 percent, with 22 percent of the temperature regimes supporting optimum germination. The mean of the optima was 96 percent.

Ripgut had maximum germination of 81 percent with 18 percent of the temperature regimes supporting optimum germination (table 5). Some seeds germinated at 84 percent of the temperatures tested. The mean optimum germination was 77 percent. The poorest germinator of the *Bromus* species tested was soft chess. The maximum germination was 66 percent with 25 percent of the temperature regimes supporting optimum germination. The mean optimum germination was 63 percent. Some germination occurred at 100 percent of the temperature regimes tested.

RESPONSE SURFACE COMPARISONS

Over all seedbed temperature categories, estimated germination of rattlesnake grass seed was not significantly (p = 0.05) different from that of cheatgrass. There was no significant difference between Japanese chess and cheatgrass at five of the six categories. Significant differences occurred only under the fluctuating temperature regime category, with cheatgrass higher. Seeds of foxtail chess had no significant differences in germination at very cold, cold, and moderate categories of seedbed temperatures compared to cheatgrass. Estimated germination of seeds of ripgut and soft chess was not significantly different from cheatgrass at only one temperature category each. Ripgut did comparably well at the cold and soft chess did comparably well at the warm category of seedbed temperature as compared to the cheatgrass collection (table 6).

OPTIMUM TEMPERATURE REGIMES

The most frequent optimum germination temperature regimes, those regimes where optimum germination occurred 80 percent of the time, for all the plant material tested (15 collections) were 10/20 and 15/20 °C (table 7). For the two collections of cheatgrass tested for this paper, the most frequent temperatures (occurring 100 percent of the time) for optimum germination were 10/15 through 10/30 and 15/15 through 15/35 °C. For a broader spectrum of cheatgrass collections (10 collections), the most frequent optima, occurring 80 percent of the time, occurred at 10/20, 10/25, and 15/20 °C (table 8).

The species of *Bromus* besides cheatgrass (14 collections) had most frequent optimum germination, occurring 93 percent of the time, at 10/20 and 15/20 °C temperatures (table 9).

One collection of each of the native perennial grasses was tested. The most frequent temperatures for optimum germination from these data were: bluebunch wheatgrass 10/20, 10/25, 15/20 through 15/30, 20/25, and 20/30 °C; Idaho fescue 15/15, 15/20, 20/20, and 20/25 °C; and for Thurber's needlegrass 15/15, 20/20, and 25/25 °C (table 10). Bluebunch wheatgrass and Idaho fescue had an optima of 15/20 and 20/25 in common, and Thurber's needlegrass and

Table 6—Comparison of response surfaces for biological areas of germination-temperatures for seed of two collections of cheatgrass and five other *Bromus* species¹

	Seedbed temperature category									
Collection	Very cold	Cold	Cold fluctuating	Fluctuating	Moderate	Warm				
Cheatgrass										
Pyramid Lake	84a	91a	78a	90a	95ab	57b				
Edwards Creek	70ab	79bc	76a	83ab	90ab	73a				
Rattlesnake grass	87a	99a	75ab	74bc	96a	49bc				
Japanese chess	51bc	86ab	63abc	63cd	96ab	51bc				
Foxtail chess	84a	95a	58bc	52d	85bc	34c				
Ripgut	18cd	58cd	43c	21e	65cd	9d				
Soft chess	11d	36d	49c	52d	61d	45bc				

¹Estimated germination means followed by the same letter within columns are not significantly different at the 0.05 level of probability as determined by overlap of the confidence intervals.

Table 7---Frequency of optima (percent) for 15 collections of plant material tested

Cold period					Warm pe	riod 8 h °	C			
16 h °C	0	2	5	10	15	20	25	30	35	40
0				27	53	47	7			
2			7	33	60	53	33			
5			7	27	67	67	40			
10				13	67	80	73	53		
15					53	80	73	60	20	
20						60	67	40		
25							7	· 7		
30										
35										
40										

Table 8—Frequency of optima (percent) for 10 collections of cheatgrass

Cold period	l	Warm period 8 h °C												
16 h °C	0	2	5	10	15	20	25	30	35	40				
0	10	10	10	20	20	10								
2		10		20	30	10	30	10						
5				20	40	50	30	10						
10				20	50	80	80	60	10					
15					40	80	70	70	40					
20						40	60	40	10					
25							10	10	10					
30														
35														
40														

Table 9-Frequency of optima (percent) for 14 collections of Bromus, excluding cheatgrass

Cold period	Warm period 8 h °C												
16 h °C	0	2	5	10	15	20	25	30	35	40			
0				36	64	57	14	7	7	7			
2			7	50	79	64	43	7	7	7			
5			7	36	86	86	50	7	7	7			
10				7	79	93	86	57	7	7			
15					43	93	86	64	21	14			
20						86	50	36	14	7			
25							14	14	7				
30								7	7				
35													
40													

Table 10—Optimum germination for bluebunch wheatgrass, Idaho fescue, and Thurber's needlegrass
(1 = Bluebunch wheatgrass, 2 = Idaho fescue, 3 = Thurber's needlegrass)

Cold period					Warm pe	riod 8 h °	C			
16 h °C	0	2	5	10	15	20	25	30	35	4
0	-									
2										
5										
10						1	1			
15					2,3	1,2	1	1		
20						2,3	1,2	1		
25							3			
30										
35										
40										

Table 11—Frequency of optima (percent) for seven collections of bluebunch wheatgrass and 11 collections of Idaho fescue (in bold)

Cold period	Warm period 8 h °C												
16 h °C	0	2	5	10	15	20	25	30	35	40			
0								_					
2													
5													
10				18	14 27	43 18	57 9						
15					57 91	100 1 00	100 91	100 45	18				
20						86 91	100 100	100 36	18				
25							57 55	43					
30													
35													
40													

Idaho fescue had 15/15 and 20/20 in common, but there were no temperature regimes that gave optimum germination for all three collections.

With data from our earlier files, we compared seven collections of bluebunch wheatgrass and found 100 percent of them gave an optimum germination at five temperature regimes: 15/20 through 15/30, 20/25, and 20/30 °C. For Idaho fescue, we found 100 percent of the 11 collections gave optimum germination at the 15/20 and 20/25 °C temperature regimes. The most frequent optimum incubation temperatures for bluebunch wheatgrass and Idaho fescue are 15/20 and 20/25 °C (table 11).

CONCLUSIONS

The only temperature regime that seems to be the best for all *Bromus* species as well as bluebunch wheatgrass and Idaho fescue is 15/20 °C. All of the above species had optimum germination occurring in one or more other temperature regimes, but not the same ones. Cheatgrass does germinate at a wider range of temperatures than the other plants and at a greater percent germination within that range.

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GERMINATION AND ESTABLISHMENT ECOLOGY OF BIG SAGEBRUSH: IMPLICATIONS FOR COMMUNITY RESTORATION

Susan E. Meyer

ABSTRACT

Big sagebrush (Artemisia tridentata) seedling recruitment is limited by seed production and dispersal in space and time, by genetic constraints of specific ecotypes, and by environmental factors that include weather, microsite attributes, soil microbiota, herbivory, and inter- and intraspecific competition. Establishing this species from seed on degraded wildlands requires use of site-adapted ecotypes, manipulation of seedbed conditions to provide favorable microsites, and reduction of early competition from both annual grass weeds and seeded species.

INTRODUCTION

Big sagebrush (Artemisia tridentata) is the regionally dominant shrub on millions of acres of steppe shrubgrassland in the Intermountain West (West 1983). Abusive grazing practices have resulted in the depletion of native perennial bunchgrasses from the shrub-grassland understory over large areas, opening the way for establishment of annual grass weeds such as cheatgrass (Bromus tectorum) (Billings 1990). This in turn has set the stage for massive conversion through repeated cycles of wildfire to annual grasslands dominated by exotic species (D'Antonio and Vitousek 1992).

Any effort to restore shrub steppe plant communities now dominated by exotic annual grasses to the structurally complex and species-rich communities that existed in presettlement times must include ecologically sound and effective techniques for reestablishing big sagebrush through direct seeding. By examining factors that affect big sagebrush recruitment in wildland stands as well as in artificial seedings, this paper provides a synthesis of the information currently available to address sagebrushrelated restoration problems in shrub-steppe ecosystems.

FACTORS LIMITING RECRUITMENT

Seed Production and Seed Bank Dynamics—The potential annual achene (dry single-seeded fruit hereafter referred to as a seed) production of a single big sagebrush plant may be in the range of 500,000 seeds (Welch and

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Site differences and between-year differences in resource availability (especially water) also play a role in seed production (Young and others 1989). Basin big sagebrush populations in bottoms that receive run-on moisture often set large seed crops every year. Xeric upland Wyoming big sagebush stands may set very little seed except in wet years. High-elevation mountain big sagebrush stands usually set seed every year, but seed production per plant is not necessarily high.

Intraspecific competition within a stand may also affect flowering intensity and seed set, especially in dry years. Young and others (1989) found that big sagebrush individuals in weeded, spaced plantings set more seed than plants of in situ populations at five arid sites in northwestern Nevada. Seed production was one to two orders of magnitude lower in the Nevada plantings than in a seed orchard on a mountain big sagebrush site in northern Utah (Welch and others 1990).

Because it is partially self-fertile, isolated plants of big sagebrush can set seed in the absence of any nearby source of pollen (McArthur and others 1988). Thus seed set is probably not strongly pollen-limited in this windpollinated species even in years when flowering is sparse. Seed production variation between individuals is also seen in field cultivation where resource limitation is not a factor (Welch and others 1990).

Plant disease can affect flowering or seed set. Stem rust fungi may reduce seed yield in field cultivation and probably play a similar role in native stands (Nelson 1992). Insect predispersal seed predators and herbivores like thrips that feed on flower parts may also reduce effective seed set. Disease or parasitic insect agents responsible for gradual dieback and ultimate death of individual plants may lower whole-plant vigor so that flowering is reduced or eliminated, resulting in senescent or decadent stands.

Excessive browsing by ungulates can have a major effect on seed stalk production. This impact may be especially great for remnant individuals on heavily used mule deer winter ranges. On a mountain big sagebrush site near Hobble Creek, UT, protection from browsing for a

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single winter resulted in a 20-fold increase in number of seed stalks the following fall, and successive years of protection resulted in a progressive increase in seed production for 6 years (Wagstaff and Welch 1990, 1991).

Seed Dispersal in Space and Time-Sagebrush seeds are very small (average weight 0.018 g/100 seeds for ssp. tridentata, 0.025 g/100 seeds for ssp. vaseyana and wyomingensis; Meyer and others 1987). They are dispersed by wind over some distance, even though they possess no special adaptations for wind dispersal. Maximum reported dispersal distances are in the range of 30 m, but most seeds (85-90 percent) fall within 1 m of the canopy edge (Wagstaff and Welch 1990; Young and Evans 1989a). Seedling recruitment studies showing concentrations of seedlings farther out from the mother plant on the windward side illustrated the effect of wind direction in dispersal (Wagstaff and Welch 1990). Mueggler (1956), Frischknecht and Bleak (1957), and Johnson and Payne (1968) all emphasized the ineffectiveness of long-distance dispersal by wind as a means of recolonization on large forage grass seedings or burns. The importance of residual plants not killed at the time of treatment as a source of seeds for reinvasion of forage grass seedings by big sagebrush has been clearly established (Frischknecht and Bleak 1957; Johnson and Pavne 1968).

Most big sagebrush seeds produced in a given autumn are gone from the soil seed bank by late spring of the following year (Young and Evans 1989a). Seed retrieval and emergence studies have shown that the great majority of seeds are lost from the seed bank through germination in winter or spring (Meyer 1990; Young and Evans 1989a). Postdispersal loss to rodents appears minimal, possibly because of small seed size (Latourette and others 1971).

A small fraction of big sagebrush seeds may sometimes persist over the summer following dispersal, as evidenced by second-year emergence in artificial seedings (Monsen and Richardson 1986; Welch 1993) and the presence of small quantities of seeds in summer seed bank samples. Hassan and West (1986) found a small fraction of viable big sagebrush seeds in seed bank samples even after a summer burn, lending credence to the conclusion of Mueggler (1956) that postburn establishment was from an in situ seed bank. Young and others (1989) were unable to detect viable seeds in postburn seed bank samples but reported seedling establishment at very low densities (1 plant/1,000 m²) on the burn.

Neither Hassan and West (1986) nor Young and Evans (1975) detected a winter peak in seed numbers, presumably because seed production was very low or absent on site in the years of sampling in their studies. In a later study, Young and Evans (1989a) found that seed bank numbers peaked in January a few weeks after the initiation of dispersal.

The fraction of seed that enters the persistent seed bank is probably much less than 1 percent, but given the sometimes prodigious seed production, this tiny fraction is potentially significant. Because of the germination ecology of the species, persistence over more than a single summer is extremely unlikely. Big sagebrush seed is relatively short-lived in warehouse storage, a characteristic often associated with formation of transient or only weakly persistent soil seed banks (Stevens and others 1981).

Another contributor to loss from the effective seed bank is dispersal to microsites where successful emergence is impossible, as into the deep duff under juniper trees. Because of their small size and limited reserves, placement of seeds at depths exceeding 5 mm during artificial seeding probably effectively removes them from the seed bank (Jacobson and Welch 1987). Natural processes such as freeze-thaw and wet-dry cycles may also sometimes result in deep burial.

SEEDLING ESTABLISHMENT AND SURVIVAL

Genetic Factors—There are major genetically based differences among subspecies and ecotypes of big sagebrush with regard to both seed germination and seedling establishment traits. These differences are correlated with the selection pressures of different habitats and with a variable life history strategy.

Using a community composition approach, Bonham and others (1991) found evidence to support the idea that the three major subspecies represent different life history strategies in spite of their basic similarity in habit and reproductive biology. Using the classification system of Grime (1977, 1984), they determined that for populations in the Piceance Basin of western Colorado, basin big sagebrush should have a more ruderal or colonizing strategy, mountain big sagebrush should have a more competitionbased strategy, and Wyoming big sagebrush should have a strategy based on the ability to tolerate abiotic stress. The prolific seed production and smaller seeds of basin big sagebrush do seem to be the attributes of a colonizing taxon. The regular, but not necessarily large, seed production of mountain big sagebrush could be based on the predictable need to invest a high proportion of energy into vegetative growth in the face of competition. The sporadic seed production of Wyoming big sagebrush populations could be interpreted to mean that resources fluctuate unpredictably. In high-stress years, all resources are needed to maintain vegetative growth; in low-stress years the extra may be allocated to sexual reproduction.

Growth rates of the three subspecies also tend to support this life history strategy interpretation. Mountain big sagebrush growth rates are faster than those of Wyoming big sagebrush but slower than those of basin big sagebrush when even-aged plants are grown in a common garden setting (McArthur and Welch 1982). These differences in growth rates parallel differences in absolute size at maturity.

Growth rate differences are present even in the early seedling stages. Welch and colleagues (Booth and others 1990; Welch and Jacobson 1988) found that Wyoming big sagebrush seedlings had the lowest maximum growth rates and reached this maximum earliest. Their relatively rapid early shoot growth was accompanied by more rapid root elongation than in the other two subspecies. The seedlings showed no further increase in shoot height after 15 weeks in the greenhouse, even though resources were not limiting. This seedling strategy appears to be an adaptation for sites that dry quickly in the spring, xeric upland sites where abiotic drought stress is the most serious threat to seedlings.

Basin big sagebrush seedlings had the most rapid shoot growth rate at 7 weeks and continued to have a positive growth rate for the full 24 weeks of the experiment, reaching heights three times the heights of Wyoming big sagebrush seedlings. But their rate of early root elongation was less than that of Wyoming big sagebrush. They invested in shoot growth at the expense of root growth at least in the early stages and showed a highly plastic response to the continued availability of resources. This strategy appears to be an adaptation to relatively resource-rich and frequently disturbed environments such as floodplains, where opportunistic growth patterns permit continued growth as long as conditions remain favorable, increasing the probability of seed production early in life. Floodplain sites would also dry out more slowly, allowing the seedlings to harden gradually.

Mountain big sagebrush seedlings showed a third pattern of growth. Early root elongation was slowest and root length at 24 weeks was least of the three subspecies; shoot growth rate was intermediate. This seedling strategy appears to be an adaptation to relatively mesic but densely vegetated sites, where competition may be for some belowground resource other than water. Maximum root length may not be as important as root proliferation in the shallow soil layers where nutrients are concentrated. Shoot growth rate must be fast enough to permit survival in an environment that could become light limited in summer, but there is no advantage to an extremely plastic response in an environment where resources are predictably limited.

These seedling studies (Booth and others 1990; Welch and Jacobson 1988) described differences at the subspecies level; each subspecies was represented by four to five accessions from throughout the range. While betweenpopulation differences within a subspecies were not discussed, one can infer from the experimental error structure that these differences must have been minimal. Harniss and McDonough (1975), in work with a single accession of each subspecies, failed to detect any subspecies difference, possibly because of small container size and overwatering (Welch 1993).

Patterns of variation in big sagebrush seed germination traits, on the other hand, are much more strongly correlated with habitat attributes at the population level than they are with subspecies identity (Meyer and Monsen 1991, 1992; Meyer and others 1990; Young and Evans 1989b). Big sagebrush seed germination biology at the species and subspecies level has been characterized by several workers (Harniss and McDonough 1976; McDonough and Harniss 1974a,b; Payne 1957; Weldon and others 1959; Young and Evans 1991). The seeds are usually nondormant at harvest though they often require light. Primary dormancy that is removed by moist chilling has been reported mostly for montane populations of mountain big sagebrush (McDonough and Harniss 1974b; Meyer and Monsen 1991). The light requirement of nondormant seeds may be removed through chilling or dryafterripening (Meyer and others 1990). The seeds germinate over a wide array of temperatures, including many

in the higher range. As pointed out by Young and Evans (1991), germination of big sagebrush seeds by early spring is virtually certain in this fall-seeding species, so that germination response at higher temperatures is largely irrelevant ecologically. Differences among subspecies and ecotypes that are ecologically relevant have to do with responses to conditions likely to be encountered by the seeds between the time of dispersal and the optimum time for germination in a given habitat.

The mortality risk to seedlings when autumn-produced seeds germinate prior to spring is likely to vary as a function of climate. Seeds from populations at cold winter sites are produced early in the fall and require mechanisms to reduce the probability of germination under both fall and early winter conditions. Mechanisms to limit autumn germination include dormancy that is not removed by short moist chilling, slow germination (requiring more than 10 days to reach 50 percent) at autumn temperatures, and a light requirement that limits germination under the more favorable moisture regime of the shallow subsurface. These mechanisms are found in highelevation mountain big sagebrush populations, on sites where autumn storms are the norm (Meyer and Monsen 1991, 1992; Meyer and others 1990). High-elevation Wyoming big sagebrush seeds lack dormancy and slow rate mechanisms but have a light requirement; their sites are generally autumn-dry, so surface emergence is unlikely (Meyer and Monsen 1992; Meyer and others 1990).

The likelihood of germination during winter at montane sites is controlled by germination behavior under snowpack. Germination rate at near-freezing temperatures is slow (more than 100 days required to reach 50 percent) in seeds from long-winter sites for all three subspecies, especially in the dark (Meyer and Monsen 1991, 1992; Meyer and others 1990). Its rate accelerates when the snow thins enough to become translucent, signaling the approach of the optimum time for emergence. In this way germination takes place just before or just as the snow is melting.

The germination timing scenario for big sagebrush seeds at mild winter, warm desert fringe sites is quite different. Seeds are dispersed in early winter. Winter conditions are optimal for seedling establishment; early emergence is an advantage in a habitat where snowpack does not persist and the risk of early spring drought exceeds risks associated with freezing. Seeds from all subspecies on these kinds of sites are nondormant and have rapid germination rates at both cool and near-freezing temperatures (Meyer and Monsen 1992). Fifty percent may germinate under near-freezing conditions in as few as 10 days. They also tend to be less light requiring (Meyer and others 1990).

These studies with seeds from 70 populations of big sagebrush from a wide geographic range show that germination regulation functions predictively to time germination to immediately precede or coincide with conditions that are optimal for seedling establishment. Field emergence studies indicate that most emergence takes place immediately in the wake of spring snowmelt (Meyer and Monsen 1990b; Wagstaff and Welch 1990; Young and others 1990). Emergence studies may not be able to demonstrate that between-population differences in germination traits are related to different fitness consequences at a particular site in a given year (Meyer and Monsen 1990a,b; Young and others 1990). Risks to seedlings are stochastic in nature; sometimes the weather events that germination timing mechanisms have evolved to contravene may not take place. And the optimization of timing does not by any means guarantee success every year, even on the native site.

Big sagebrush seeds have no clear mechanism for between-year carryover of any major seed fraction, but a few seeds may retain their light requirement even after chilling (Meyer and others 1990). Shallowly buried seeds with a light requirement probably account for the small amount of carryover that sometimes takes place.

Environmental Factors—Even though ecotypes of big sagebrush have seed germination and seedling growth patterns that are site-adapted to maximize the chances of seedling establishment, the vast majority of sagebrush seedlings that emerge are not recruited into the population. Many environmental factors, both abiotic and biotic, act to restrict recruitment.

A primary factor in seedling mortality is undoubtedly the weather. Any weather event or sequence that pushes seedling-zone environmental conditions beyond the range of tolerance can cause mortality. Newly emerged seedlings are remarkably frost tolerant, as they must be to survive emergence in the very early spring, but late spring frosts, when the seedlings are no longer hardy, may be a significant cause of mortality (Meyer and Monsen 1990a). Many seedling deaths attributed to frost may actually be a result of damping-off diseases or mechanical damage associated with frost heaving.

Drought is a principal cause of seedling mortality. Again, timing is important. Especially on xeric Wyoming big sagebrush sites, seedlings must be able to survive summer drought to establish, regardless of the year. But they need sufficient time to become drought hardy. Early or protracted drought can cause mortality. Sagebrush seedlings established on mine sites where there is little competition may have remarkably high first-year survival rates through summer drought periods (Monsen and Meyer 1990; Monsen and Richardson 1986).

Another key weather variable is amount and timing of winter snowfall. In a seeding experiment on a series of semiarid mine sites, a single late-winter snowfall made the difference between zero emergence at one site and emergence as high as 80 percent of seeds sown at another similar site (Monsen and Meyer 1990). It appears that emergence is rarely achieved except when winter snow cover is present. Early spring watering on part of the unsuccessful seeding did not result in emergence, and there was no emergence the following year, which had adequate winter snowpack.

Artificial big sagebrush seedings on large disturbances such as burns sometimes fail even when natural recruitment takes place in adjacent native stands (Monsen 1992). This is true even when good seedbed conditions are created and competition is controlled. It may be that extra snow accumulation in the lee of adult shrubs accounts for much of the difference in recruitment success (Sturges and Tabler 1981).

Monsen and others (1992) tested the idea of enhancing big sagebrush establishment using snow harvesting. The study, which was carried out at three semiarid mine sites, included a factorial combination of snowfencing and crimped straw mulch treatments. Seedling emergence was increased by a factor of six in the snowfence treatments at a site with average winter precipitation; up to 60 percent of sown seed emerged. At a site with record high winter precipitation, there was no effect from either snowfencing or mulch, and emergence averaged 30 percent of sown seed. At a site with below-average precipitation, maximum emergence (10 percent of sown seed) was observed in snowfencing treatments with or without straw mulch, with a lower percentage (7 percent) on the straw mulch only treatment. On this site there was no emergence at all without some form of snow harvesting. These results strongly suggest that snow harvesting, whether by in situ vegetation or by structures, can increase big sagebrush emergence in years of average or below-average winter precipitation. It also supports the idea that successful emergence is dependent on snow cover.

Because they are surface or near-surface emerging, big sagebrush seeds are very sensitive to microsite conditions. The pericarp wall that is somewhat gelatinous when wet and the hypocotyl hairs help fix the germinating seed to the surface and permit the radicle to penetrate the soil (Young and Martens 1991).

Young and others (1990) showed, through the use of an elaborate experimental design that involved reciprocal soil transport among five sites on an elevational gradient, that soil surface characteristics are sometimes as important as winter precipitation for big sagebrush seedling emergence. The best soil for emergence was one that combined silts and clays in the top 2-mm fraction with a high gravel content; more uniformly sandy granitic soils were generally not as favorable. The authors hypothesized that the surface characteristics of the most favorable soil, which was from a site at the extreme dry end for big sagebrush, might be the key factors that made establishment possible on this site. Surface characteristics changed during the course of the winter, and surface features when the plots were broadcast seeded in the fall had more effect on emergence than spring surface features. The idea of a gravel mulch to improve water relations for establishment was also supported in an earlier study, where a surface mulch of glass marbles also increased emergence (Young and Evans 1986).

Application of topsoil often improves seedling success on semiarid mine spoils. In a study at the Beacon Pit Mine in central Nevada, Monsen and Richardson (1984) seeded shrubs, grasses, and forbs onto a rock waste dump with and without topsoil. Most species established better on topsoiled sites, but big sagebrush results were unequivocal—no seedlings established unless topsoil was present. In a no-topsoil area that was seeded to grasses and forbs only, the seeding failed, and the area was subsequently colonized by rubber rabbitbrush (*Chrysothamnus nauseosus*). Ten years after the initial seeding, size class distributions for rubber rabbitbrush and big sagebrush were obtained from this area (Meyer and Monsen 1990b). Over 60 percent of the rubber rabbitbrush individuals were in adult size classes (height >30 cm), and less than 1 percent were <10 cm. About 70 percent of the big sagebrush plants, on the other hand, were in the <30-cm size classes. This suggests that, after initial invasion by rubber rabbitbrush, site conditions were ameliorated, permitting subsequent colonization by big sagebrush. The rabbitbrush plants formed coppices of finer textured windborne material and organic matter, improving the seedbed microenvironment for sagebrush emergence and establishment. The presence of topsoil microbiota, such as vesicular arbuscular mycorrhizae and free-living nitrogen fixers, may also be important for big sagebrush recruitment (Cundell 1977).

Probably the most-researched aspect of big sagebrush seedling recruitment is the role of interplant competition. Few of these studies have taken place in established big sagebrush stands, however. Within-species competition is probably important in restricting seedling recruitment in closed stands, though the interaction may be as much between adults at the flowering and seed production stage as between adults and seedlings. Stand thinning using chaining resulted in an exponential increase in seed production by surviving Wyoming big sagebrush plants under drought conditions in a pinyon-juniper woodland in eastern Utah (Davis 1992).

Reichenberger and Pyke (1990) reported on a study using hollow tubes of varying depth to give establishing seedlings varying degrees of protection from matrix vegetation root competition. They found that establishing Wyoming big sagebrush seedlings on a dry site and mountain big sagebrush seedlings on a more mesic site were both more negatively impacted by competition from a matrix of adult big sagebrush plants than by competition from either native bluebunch wheatgrass or introduced crested wheatgrass vegetation. Owens and Norton (1989) found that postseedling juvenile survival was a function both of initial plant size and gap size. Shelter from the canopy of an adult individual increased survival as long as gap size was large.

Because of high seed densities and synchronous germination, intense competition between big sagebrush seedlings probably accounts for much of the initial mortality as the soil dries out in late spring. In a study with different pieces of seeding equipment on a mine disturbance, Monsen and Meyer (1990) found that survival of emerged seedlings was significantly higher in seeding treatments that resulted in greater spatial dispersion of seeds. This suggests that a major cause of mortality was intraspecific mortality or self-thinning in treatments where seedlings tended to be more closely spaced. Owens and Norton (1990) found that cohort density up to 30 individuals/m² had no effect on survival rates for postseedling juveniles, perhaps because initial self-thinning had already taken place. Mortality was concentrated in the smaller size classes, however.

Most of the work on interspecific competition effects on big sagebrush establishment was undertaken to understand how to prevent establishment. The useful life of a forage grass seeding on sagebrush range is determined in part by the rate of reestablishment of the eradicated shrub species (Blaisdell 1949; Pechanec and others 1944). A great deal of useful knowledge about big sagebrush establishment ecology was generated.

One of the first generalizations to emerge was that if eradication took place too late in the fall, the effect was to plant big sagebrush along with the seeded grass species (Bleak and Miller 1955; Frischknecht and Bleak 1957; Johnson and Payne 1968). This showed that big sagebrush (basin big sagebrush in most of these cases) could establish along with created wheatgrass in years when late-season precipitation was above average. Once the created wheatgrass was well established, it could effectively exclude further big sagebrush recruitment even in the face of seed production by residual plants. If the created wheatgrass stand was thin because of poor initial emergence or heavily grazed, sagebrush recruitment would continue.

In their study in Ruby Valley, NV, Frischknecht and Bleak (1957) found that seeded bluebunch wheatgrass stands in good condition were more likely to permit big sagebrush recruitment than crested wheatgrass stands in similar condition. This result parallels the experimental results of Reichenberger and Pyke (1990) at Curlew Valley, the Wyoming big sagebrush site. At the mountain big sagebrush site, however, their experimental results indicated that competition from bluebunch wheatgrass was more severe than from crested wheatgrass, although both had a significant negative effect on survival.

Johnson and Payne (1968) found no relationship between grass density and sagebrush reestablishment rates on a series of forage grass seedings in southwestern Montana. They gave no indication of grazing intensity. Date of treatment and presence of residual plants not initially killed were the main factors affecting seedling recruitment. They found increased recruitment rates on finer textured (silty) soils and on more mesic northwest slopes in some cases.

Owens and Norton (1990) found that juvenile survival was higher in short-duration grazing pastures than under continuous spring grazing. Richardson and others (1986) compared grazed and ungrazed treatments 7 years after seeding mountain big sagebrush with grasses and forbs on a mid-elevation mine site in southeastern Idaho. They found significantly lower big sagebrush plant densities in the grazed treatment, an effect they attributed at least partially to trampling.

Richardson and others (1986) also examined the effect of different grass mix seeding rates on shrub establishment. Mountain big sagebrush was better able to establish in competition with a mix dominated by crested and intermediate wheatgrass than was antelope bitterbrush, but was unable to establish when grass mix seeding rates exceeded 12 lb/acre. Recruitment increased dramatically when shrubs were seeded alone.

The effect of exotic annual grasses such as cheatgrass in limiting field recruitment of big sagebrush (and most other native shrubs) has been observed countless times, but few quantitative studies have documented this effect. Young and Evans (1989a) reported no new recruitment of big sagebrush over a 4-year period at five sites with cheatgrass-dominated understories in northwestern Nevada, in spite of the fact that some emergence took place every year. Wagstaff and Welch (1990) carried out an experimental study that examined the effects of tillage and protection from browsing on natural recruitment of mountain big sagebrush around remnant maternal plants on heavily disturbed mule deer winter range on the Wasatch Front. They found that no tillage and early tillage treatments resulted in a total lack of recruitment, while late fall tillage (after cheatgrass emergence) resulted in seedling densities that were directly correlated with maternal plant seedstalk production. Seedling survival through the first summer was very high. These studies, as well as numerous observations from throughout the cheatgrass problem area in the Intermountain West, demonstrate the futility of seeding big sagebrush onto cheatgrass-infested wildlands without some strategy for cheatgrass control.

IMPLICATIONS FOR COMMUNITY RESTORATION

Some argue the feasibility or even the desirability of restoring semiarid shrub-grasslands that have been converted to exotic annual grassland. It is true that the millions of acres in the Intermountain West that have undergone this conversion or are on the brink of conversion through wildfire present a daunting spectacle to the restorationist. Any method that is likely to be used over an area of significant size must be inexpensive on a peracre basis. This limits the practical options to direct seeding.

In reestablishing big sagebrush from seed, the first choice is of a source of seed to plant. It is of paramount importance not only to plant the correct subspecies, the same one that was native onsite predisturbance, but also to match seed collection site and seeding site habitat characteristics as closely as possible. This means collection of the seed from a known wildland stand, preferably one not far from the seeding site. On large disturbances, onsite collection of seed is usually not possible, but it might be possible to collect from remnant plants and use the seed to start a seed production field (Welch and others 1990). Another possibility is to manage wildland stands in situ to increase seed production, perhaps through stand thinning.

The seed should be spot checked for quality prior to large-scale harvest, harvested when fully ripe, carefully cleaned (excessive heat or handling can damage the seed), and stored under cold dry conditions (<10 °C, 6-8 percent moisture content) until use. Purity of commercial lots of big sagebrush seed averages 10 to 20 percent. Because of its small size, it is usually seeded with a carrier, so cleaning to any higher purity may not be cost-effective or necessary. Viability of recently harvested seed should be in the 85 to 95 percent range. Properly stored seed should remain viable for at least 5 years if it was initially of high viability. Viability should be rechecked with a germination test immediately before seeding to determine seeding rates on a pure live seed (PLS) basis. Seeding rates in the range of 0.25 to 0.5 lb/acre PLS are appropriate.

Big sagebrush seed should be surface planted or planted with very light coverage on a firm (not hard or compacted) seedbed. Broadcast seeding is usually as effective as any other method. Site preparation or planting methods that create a loose, sloughing seedbed should be avoided, as they can result in poor soil-seed contact or planting too deep. But some surface roughness to create a variety of microsites is encouraged. Sagebrush seed should not be drill seeded.

The best season for planting is late fall, just before the first winter snowfall, when big sagebrush would naturally be dispersing onsite. Broadcast seeding onto snow in winter may be very successful. Spring seeding should be avoided.

If the sagebrush is to be seeded in a mix with other species, it may be helpful to separate different components, as in different drop boxes on the seeder, especially if the mix includes fast-growing perennial grass species. This may be less necessary when seeding with native grasses rather than introduced forage grasses bred for rapid seedling growth rate. Seeding rates for the more competitive species should be kept relatively low, especially if spatial segregation is not possible, as in aerial broadcast seeding.

Soil fertility may affect the outcome of a seeding. Higher fertility favors faster growing species more plastic in their response to nutrient supply. Shrub seedlings have more opportunity to obtain the water they need to survive the first summer when low fertility keeps competing seedlings smaller.

No truly satisfactory method for controlling weed competition on large-scale big sagebrush plantings has been developed. Methods currently in use include summer burning while weed seed heads are still on the plants, tillage or herbicide treatment after fall greenup, and scalping to remove weed seed-infested soil from the immediate vicinity of the planted seeds. These methods may or may not create a good seedbed for big sagebrush.

Not all weeds are equally damaging to big sagebrush seedling survival. Russian thistle (*Salsola pestifer*) can actually act as a nurse plant. Annual grasses such as cheatgrass inevitably have a negative effect, as mentioned earlier.

Another more long-term strategy for big sagebrush establishment is the idea of first establishing early seral species, such as squirreltail (*Elymus elymoides*, formerly *Sitanion hystrix*), that appear to be better able to compete with exotic annual grasses. Once early seral natives take hold and dominate the site, big sagebrush could then be seeded along with late-seral understory species.

The use of snow harvesting techniques to increase odds of big sagebrush establishment may be justified if the site is in a precipitation zone where winter snowpack is unlikely to be sufficient without manipulation. The sagebrush could be spot-seeded near snow-trapping structures or in topographic positions where extra snow is likely to accumulate naturally. Once a small stand is established, the shrubs themselves will act as snow traps and seed sources that enhance shrub recruitment downwind in subsequent years. As long as the matrix vegetation is made up of species that permit some recuitment, and other factors such as browsing by deer are not limiting, the shrub population should continue to extend itself through time. Other possibilities are seedbed manipulation such as contour furrowing to increase snow accumulation or an annual cover crop (preferably one not capable of persisting on the site) to create snow-trapping stubble.

The art and science of ecological restoration are still in their infancy. But much of the information acquired over the last 80 years in the name of range improvement can be utilized and reinterpreted in the light of a new set of public land management goals that place the health and diversity of natural ecosystems at the top of the list of priorities. The opportunity and responsibility we have to take part in this redirection of research efforts is truly exciting and challenging.

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SPINY HOPSAGE SEED GERMINATION AND SEEDLING ESTABLISHMENT

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ABSTRACT

Reestablishment of spiny hopsage (Grayia spinosa [Hook.] Moq.) on disturbed native sites improves shrub diversity, contributing to development of subcanopy soils, vegetation, and associated ecosystem stability. Spiny hopsage may be established by fall or winter planting of seeds or bracted utricles at a depth of 0.5 cm using drills or seeder-packers. Seeds of Mojave Desert populations germinate in response to fall or winter rains of at least 160 mm; those from southeastern Oregon and southwestern Idaho germinate in early spring following overwinter exposure to cool, moist seedbed microenvironments. Germination, emergence, and seedling establishment are episodic; success depends on availability of soil water. Survival may be enhanced by site preparation and planting techniques that reduce vegetative competition and improve water catchment.

INTRODUCTION

Endemic to the Intermountain West, spiny hopsage (Grayia spinosa [Hook.] Moq.) occurs in Wyoming big sagebrush (Artemisia tridentata Nutt. ssp. wyomingensis Beetle & A. Young), pinyon-juniper (Pinus L.-Juniperus L.), salt-desert shrub, and Mojave Desert communities (Daubenmire 1970). The species provides cover for birds and other small animals, spring and early summer forage for big game and livestock, and soil stabilization on gentle to moderate slopes (Gullion 1964; McCullough 1969; USDA-SCS 1968). Growth and nutrient content of vegetation growing near spiny hopsage are enhanced by accumulation of litter rich in potassium and other cations (Rickard and Keough 1968).

Areas within the native range of spiny hopsage have been depleted or damaged by livestock grazing, wildfires, invasions of weedy annuals, mining, off-road vehicle use, road and pipeline construction, and other human activities (Blaisdell and Holmgren 1984). Reestablishment of the species on these sites is often desirable. Billings (1949), Dayton (1931), Monsen and Christensen (1975), and Plummer (1966), encouraged development of spiny hopsage as a revegetation species. Plummer and others (1968) evaluated its revegetation attributes, assigning high ratings for persistence and resistance to insects and disease and low ratings for initial establishment and natural spread. They recommended spiny hopsage for use in pinyon-juniper, basin big sagebrush (Artemisia tridentata Nutt. var. tridentata), Wyoming big sagebrush, shadscale (Atriplex confertifolia [Torr. and Frem.] Wats.), and blackbrush (Coleogyne ramosissima Torr.) vegetation types.

An understanding of requirements for natural or artificial establishment of spiny hopsage seedlings is needed to permit development of direct seeding techniques for the species. This paper summarizes current knowledge of spiny hopsage seed germination, seedbed ecology, and seedling establishment.

Northern Shrub Steppe and Great Basin—Spiny hopsage plants may remain dormant during dry years, but large quantities of new branches, leaves, and fruits (bracted utricles) are usually produced during years with good spring rainfall (Rickard and Warren 1981; Shaw 1992). Seed quality varies widely with weather conditions, insect infestations, and other factors (Shaw 1992). Filled utricles ripen from late spring to mid-summer. Many utricles normally fail to develop; large numbers of fruiting bracts are normally empty. Consequently, the quantity of viable seeds contributed to the soil seed bank and the potential for seedling establishment may vary considerably from year to year.

Establishment of spiny hopsage is episodic with germination, emergence, and survival dependent on local environmental conditions, particularly precipitation. In southeastern Oregon and southwestern Idaho, emerging seedlings were observed only in years with above-average spring rainfall (Shaw 1992; Shaw and Haferkamp 1990). Seedlings emerged in early spring from litter accumulations beneath nurse plant canopies or from shrub interspaces slightly downwind. In addition to female spiny hopsage plants, greasewood (Sarcobatus vermiculatus [Hook.] Torr.), Wyoming big sagebrush, and male spiny hopsage plants growing near seed sources also acted as nurse plants. Compared to interspaces, shrub clumps provide more favorable water, temperature, light, soil texture, organic matter, and nutrient conditions for establishment of many species (Pierson and Wight 1991; Rickard and others 1988; Wallace and Romney 1972; Wallace and others 1980). Maturation of these seedlings, however, occurs only in canopy openings.

In contrast to the observations of early spring germination, Glazebrook (1941) reported spiny hopsage seedlings emerged in fall immediately after seeds reached maturity. Although he collected seeds in eastern Washington, he did not specify the site of this observation nor did he comment on the late date of seed maturation.

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The episodic nature of seedling establishment may partially explain seemingly contradictory reports of native spiny hopsage seedling occurrence. For example, the USDA-SCS (1968) reported spiny hopsage establishes rapidly in eastern Washington bluebunch wheatgrass (Agropyron spicatum [Pursh] Scribn. & Smith) or needleand-thread (Stipa comata Trin. & Rupr.) communities depleted by overgrazing or other disturbances. By contrast, Daubenmire (1970) found no spiny hopsage plants with fewer than 16 xylem rings after extensive searches in eastern Washington.

Natural recovery of spiny hopsage on disturbed sites was studied at the U.S. Atomic Energy Commission, Nuclear Test Site (USAEC-NTS) in the southern Great Basin. Shrub recovery was monitored at Pahute Mesa following nuclear testing in 1965. Elevation of the site is 1,800 to 1,890 m and mean annual precipitation 119 to 279 mm. Following testing, no spiny hopsage seedlings remained in the totally killed area (Wallace and others 1977, 1980). Shrub recovery began rather quickly, even though the totally killed area was dominated by Russian thistle (Salsola iberica Sennen and Pau) and the partially killed area by grasses during the first 5 years. In an unusually good precipitation year, a large number of spiny hopsage seedlings emerged and grew to heights of 0.3 to 0.4 m (Wallace and Romney 1972). By 1976, spiny hopsage and total shrub seedling density had increased to the point that shrub recruitment appeared adequate for replenishing the site. Density of new spiny hopsage seedlings was 34 per hectare in the totally killed area, 55 per hectare in the partially killed plot, and 14 per hectare in the control area. Seedlings in the totally killed area presumably established from external seed sources.

Mojave Desert—Manning and Groeneveld (1990) found that spiny hopsage seedlings in the Transition Zone between the Great Basin and Mojave Desert in Owens Valley, CA, also developed beneath nurse plants, particularly in heavily grazed areas. Beatley (1979/80) made a similar observation for the northern Mojave Desert.

Wallace and Romney (1972) reported Mojave Desert populations of spiny hopsage produced nondormant seeds capable of germinating rapidly when adequate water was available. Ackerman (1979) found seeds of 11 common Mojave Desert shrubs including spiny hopsage germinated following fall or winter rains (October to March) of at least 160 mm. Establishment of these species was considered episodic as only one of 201 seedlings emerging on study plots between 1971 and 1975 survived until spring 1977. Of 63 spiny hopsage seedlings emerging, 62 succumbed the first year and one the second year.

Further evidence for episodic seedling establishment was provided by El-Ghonemy and others (1980) who examined size-class distributions of spiny hopsage and nine other perennial species in undisturbed areas of Rock Valley in the northern Mojave Desert. Size classes were defined on the basis of plant biomass. Frequency histograms for size-class distribution on a natural log basis showed a somewhat negatively skewed distribution for spiny hopsage, resulting from segregation of the numerous smaller, and presumably younger, individuals into many size classes. The mean dry weight of spiny hopsage plants was 74.3 ± 85.8 g. Approximately 66 percent of the plants weighed less than the modal size class (24.4 to 64.6 g) and 17 percent weighed more, again indicating an abundance of small (young) plants. They concluded this distribution possibly reflected emergence and survival of many seedlings in response to good rainfall 2 years prior to sampling.

The impact of supplemental water on seedling emergence and establishment in a community dominated by goldenhead (Acamptopappus shockleyi Gray) and bursage (Ambrosia dumosa [Gray] Payne) was examined near Mercury, NV, in the northern Mojave Desert (Hunter and others 1980). Plots of native vegetation were sprinkler irrigated to maintain soil water content above 5 percent, increasing annual water input from an average of 100 to 150 mm to about 350 to 450 mm (Wallace and Romney 1972). After 3 years of irrigation followed by 4 years of natural rainfall, spiny hopsage density increased from 288 to 438 plants/ha and biomass from 41 to 241 kg/ha. On nonirrigated plots density increased from 356 to 465 plants/ha and biomass from 59 to 109 kg/ha. Possible reasons for the increase on nonirrigated plots were not discussed.

Wallace and Romney (1972) studied seedling emergence in disturbed creosote bush (*Larrea tridentata* [DC.] Cov.) communities of the Mojave Desert within the USAEC-NTS. They found few spiny hopsage seedlings emerged unless artificial irrigation was applied.

GERMINATION STUDIES

Threshed seeds and northern shrub steppe and Great Basin seed sources have been utilized in most studies of spiny hopsage seed germination and in full-scale plantings. Work with bracted utricles and Mojave Desert populations is more limited.

Dry afterripening reduces seed dormancy of several shrubby chenopods (Ansley and Abernethy 1985; Pendleton and Meyer 1990; Springfield 1969, 1972). Shaw and others (in press), found no consistent differences between laboratory germination or field seedling establishment of 2- and 4-year-old spiny hopsage seed collections from one southwestern Idaho and one southeastern Oregon site. King (1947) found germination of a 6-year-old seed lot from eastern Washington was enhanced by a 2-week moist prechill at 5 °C, but a 12-week moist prechill was required for a 4-year-old seed lot from the same area. He suggested the differences might be attributed to duration of dry afterripening.

Laboratory studies by Glazebrook (1941) indicated light had no influence on germination when 1-year-old spiny hopsage seeds harvested in eastern Washington were incubated at 22 to 26 °C. The positive response (92 percent germination in 35 days) of this seed lot to an alternating temperature regime of 30/20 °C (8 h/16 h) and work indicating seedlings could be "frozen solid while still very young and yet survive" led him to recommend early spring or late fall sowing for nursery production. Smith (1974) reported moist prechilling for 60 or 90 days at 4 °C improved the rate of spiny hopsage germination. Germination of prechilled seeds incubated at 22 °C or 30/ 20 °C (day/night) was complete in 8 or fewer days compared to 30 days for controls. Both moist prechilling periods were also effective in increasing total germination of seeds incubated at 22 °C (maximum of 36 percent compared to 21 percent for controls); only the 90-day moist prechill improved total germination (29 compared to 25 percent) when seeds were incubated at 30/20 °C.

Shaw (1992) found a 45-day moist prechill at 3 to 5 °C improved both total germination and germination rate of bracted utricles and seeds of one southwestern Idaho and one southeastern Oregon seed source. For the incubation temperatures tested (10, 15, 20, 25, 30, 15/5, and 10/2 °C [8/16-h alterations]), germination increased from 9 to 64 percent with moist prechilling. Days to 50 percent germination declined from 24 to 11.

Wood and others (1976) examined the germination response of four Nevada (Great Basin) and one California (Mojave Desert) spiny hopsage seed sources to 55 constant and alternating temperatures. All seed sources were nondormant. Highest constant temperature germination percentages were obtained at 10 and 15 °C (66 to 74 percent). A 5 °C low temperature alternating with high temperatures between 0 and 30 °C, inclusive, provided the highest germination percentages (70 to 90 percent) for all five seed lots. After 1 week, greatest seedling elongation of a Dayton, NV, seed lot occurred at 5, 15/20, 20, and 5/25 °C.

Shaw (1992) found total germination of moist-prechilled (45 days) bracted utricles and seeds from southwestern Idaho and southeastern Oregon incubated at 5/15 °C was similar to constant temperature germination over the 20to 30-°C range, but the rate was slower. The findings of Shaw (1992), Smith (1974), and Wood and others (1976) may be typical of species adapted to germinate in late fall or early spring when soil water content is most likely to be favorable for seedling establishment.

Wood and others (1976) suggested the drifts of spiny hopsage fruiting bracts that sometimes accumulate under and around shrubs, mixing with leaves and other debris to form a thick mulch, may modify the seedbed environment. They found that air-dried bracted utricles are highly hygroscopic, increasing 41 percent by weight when placed over water in a desiccator. Bracted utricles of a Mojave Desert seed source were highly tolerant of osmotic stress. When incubated in polyethylene glycol solutions of -0.8 to -1.2 MPa, their germination was not reduced compared to controls incubated in water, suggesting bracts might function to regulate the osmotic potential of the utricles, enabling them to attain the osmotic potential required for germination. Germination of bracted Mojave Desert utricles incubated in NaCl solutions occurred only at water potentials greater (less negative) than -1.3 MPa, suggesting ion toxicity might be occurring at lower potentials.

Wood and others (1976) found constant temperature germination of bracted utricles and seeds of a Mojave Desert seed source did not differ over the 2- to 40-°C range. In contrast, Shaw (1992) reported bracts reduced germination of moist-prechilled southwestern Idaho and southeastern Oregon seed sources incubated at several constant and alternating temperatures. Bracts did not decrease water uptake by the seed or provide mechanical restraint to embryo emergence, consequently inhibition of oxygen uptake was suggested as a possible mechanism for their action. Whether bracts remain intact in the field through winter has not been investigated.

Differences in seed dormancy noted by Glazebrook (1941), Shaw (1992), and Wood and others (1976) may have resulted from genetic variation, seed cleaning procedures, or both. Lack of a moist-prechill requirement might be expected for Mojave Desert populations. Shaw (1992) found southwestern Idaho and southeastern Oregon seeds were rendered germinable by partial or complete removal of the testa. Both normal and abnormal germination were increased by threshing techniques that disrupted the testa.

DIRECT SEEDING

Stark (1966) and Plummer and others (1968) recommended use of local spiny hopsage seed sources for rangeland plantings. Few data on population differences have been reported. Shaw and others (in press) found germination and establishment of seed lots collected from similar environments in southwestern Idaho and southeastern Oregon and planted at two southern Idaho sites did not differ consistently. Wood and others (1976) found bracted utricles and seeds of a Mojave Desert seed source from California germinated at higher temperatures than did four Great Basin sources from Nevada. Common garden studies of spiny hopsage were recently initiated in southeastern Idaho by the USDA-SCS (Hoag 1992) and should provide considerable information on variability among populations and site requirements for their establishment.

Failures of early spiny hopsage plantings in Utah were attributed to planting the small seeds (869 to 932/g) at excessive depths (Plummer 1984; Smith 1974). Glazebrook (1941) recommended seeds be surface broadcast, while Kay and others (1977) recommended a seeding depth of 10 mm. Wood and others (1976) found few or no seedlings established when seeds were broadcast on smooth or packed surfaces in a greenhouse study. Broadcasting bracted utricles on a rough soil surface resulted in 18 percent seedling establishment. Establishment of 48 percent from seeds and 51 percent from bracted utricles was obtained by planting at a depth of 5 mm.

Recommended seeding rates range from 0.6 to 4.4 kg/ha (Anderson and Shumar 1989; Rosentreter and Jorgenson 1986). Shaw and others (in press) reported first-year establishment ranged from 0 to 23.5 percent of viable seeds planted in late fall at two southern Idaho sites during 2 years. Seeds were direct seeded or broadcast and covered. Planting depth in both cases was about 5 mm.

Planting spiny hopsage seeds in late fall or winter in southern Idaho exposed seeds to cool, moist seedbed environments, permitting early spring emergence when soil water conditions were favorable for growth prior to the onset of summer drought (Shaw and others, in press). During 1 year, seeds at two sites began germinating in late February and early March when maximum and minimum air temperatures averaged 8 and 0 °C and surface soil temperatures averaged 4 and -2 °C. Seedlings emerged in March and early April when maximum and minimum air and surface soil temperatures averaged 12 and 0 °C.

Shaw (1992) reported field emergence from southwestern Idaho plantings was severely limited if soil water was low. The possibility that some nongerminating seeds may have entered secondary dormancy was indicated by high viability and low to moderate laboratory germination of seeds recovered from late fall or winter plantings in early summer. Early and late-spring plantings did not provide temperature or moisture conditions necessary to permit germination and emergence. Longevity of field-planted seeds in primary or secondary dormancy was not examined, but limited second and third year emergence was noted.

Shaw and Haferkamp (1990) reported developing seedlings produced a single shoot and a taproot system with few lateral roots during the first growing season. They found some seedlings in southwestern Idaho plantings were damaged or destroyed by seed harvester ants (*Pogonomyrmex salinus* Olsen) and nymphs of an unidentified plant bug (*Melanotrichus* spp.). Wallace and Romney (1972) recommended control of herbivores and competing vegetation for establishment of spiny hopsage and other desert shrubs.

DISCUSSION

Until additional research is completed, general guidelines for reestablishing shrubs should be followed when direct seeding spiny hopsage. In the absence of seed transfer guidelines, seeds from local sources should be planted. Bracted utricles and seeds can be drilled or planted through seeder-packers. Large fruiting bracts may clog some drill drops, but bracted utricles must be threshed carefully to avoid embryo damage. Bracted utricles and seeds should be planted about 0.5 cm deep. As the ability of spiny hopsage seedlings to compete with herbaceous species is poorly known, the species should be planted separately or in mixtures with other shrubs. Shrub seeds with different planting depth requirements must be planted through separate drill drops; seeds of most shrubs can be mixed together for planting through seeder-packers. Spiny hopsage may be mixed with other grass, forb, and shrub seeds for aerial seeding, but seeds should be covered. A rate of 66 seeds/m² is frequently used for planting shrub mixes. The planting rate for spiny hopsage often may be dictated by seed availability.

Late fall or winter planting is required for spiny hopsage in southwestern Idaho and southeastern Oregon to permit exposure of bracted utricles or seeds to cool, moist seedbed conditions. Fall planting may also be required in the Mojave Desert to permit germination and emergence following fall or winter precipitation.

Microenvironmental conditions in prepared seedbeds differ sharply from those in natural seedbeds beneath nurse plants. Consequently, spiny hopsage establishment may be enhanced by mulching or water catchment techniques that moderate soil water, temperature, or nutrient conditions.

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RANGELAND SPECIES GERMINATION THROUGH 25 AND UP TO 40 YEARS OF WAREHOUSE STORAGE

Richard Stevens Kent R. Jorgensen

ABSTRACT

Germination results are presented from seed stored in an open warehouse in Sanpete County, UT, for 19 shrub, 16 forb, and three grass species for 25 years, and 12 shrub, 20 forb, and 29 grass species for 0 to 40 years. Germination, longevity, and afterripening are discussed for each species and group of species through various periods of storage. Each species exhibited its own unique germination characteristics that varied with source and age of seed. Some species' viability increased with increasing age while others decreased with age.

INTRODUCTION

In 1981 Stevens and others published seed germination data for 32 shrub and forb species stored in an open warehouse through 15 years. These data along with 20 and 25 years germination data for seed of the same species and sources and six additional species are included in this report. In addition, germination results are given for 61 shrub, forb, and grass species with 0 to 40 years of storage.

A limiting factor to range rehabilitation can be the availability of quality seed of desired species at affordable prices. With most wildland species good seed crops are not produced every season: seed needs to be obtained in good years and stored until needed. It is not uncommon to store commercially produced seed. Seed may have to be stored for a few months to many years. Utah State law requires that marketed grass seed be tested every 18 months, and forb and shrub seed every 9 months. These requirements can differ by State. Rules and procedures for testing seed have been established for many wildland species (Stevens and Meyer 1990). Stored seed is generally not tested on a regular basis or prior to seeding when used by the person or agency storing it. Some species possess considerable afterripening, with maximum germinability not reached for a number of years following collection. Some species do not retain viability well, while others experience little change over long periods of storage. To obtain maximum seeding results and maximum return of dollars spent, it becomes imperative to know germinability over years and how long a species can or should

be stored. Germinability of each species will affect the seeding rate.

Germination data of some range grasses stored a number of years have been reported (Hafenrichter and others 1965; Little 1937; Tiedemann and Pond 1967). However, longevity germination studies of wildland shrubs and forbs have been somewhat limited. Springfield (1968, 1970, 1973, 1974) worked with germination and longevity of stored winterfat (*Ceratoides lanata*) and fourwing saltbush (*Atriplex canescens*) seed. Longevity reports on germination of stored winterfat (Stevens and others 1977) and antelope bitterbrush (*Purshia tridentata*) seed (Giunta and others 1978) have been made.

Plummer and others (1968) listed the duration of good viability for 44 shrubs, 24 forbs, and five grasses. Plummer and others (1970) also reported germination results after relatively short periods of storage on seed of a number of native shrubs and forbs. Two works from the U.S. Department of Agriculture, Forest Service (1948, 1974) included information on germination and longevity studies for native trees and shrubs. Van Haverbeke (1989) reported on viability of 20-year-old ponderosa pine (*Pinus ponderosa*) seed. Kay and others (1984) reported on germination of seed of 22 Mojave desert shrub species following 9 years of storage. Kay and others (1988) ran germination tests on seed of 115 desert grasses, forbs, and shrubs that had been stored for up to 14 years.

Seed of rangeland species in the Intermountain West are commonly stored in open, unheated, and uncooled warehouses and granaries, sometimes for extended periods. Little information is available as to the length of life of many warehouse-stored rangeland seeds.

METHODS

Study 1: Germination Through 25 Years of the Same Seed Sources—During the fall of 1963, current seed of 19 shrub, 16 forb, and three grass species (table 1) were hand-collected from native stands or purchased from commercial sources. Seed was commercially or handcleaned to 85 percent purity or higher, placed in cotton bags, and deposited in metal file cabinets in an open warehouse in Ephraim, Sanpete County, UT, for the duration of the study. Over 25 years (1963-88), temperature in the warehouse ranged from a low of -29.9 to a high of 38.3 °C. Mean daily temperatures during winter, spring, summer, and fall periods were -3.3, 6.7, 20, and 7.2 °C, respectively.

Germination tests on the stored seed were conducted in February of 1965, 1966, 1967, 1968, 1970, 1973, 1978, 1983, and 1988. These dates marked the beginning of the

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Species					Ye	ars of sto	rage			
Common name	Source	2	3	4	5	7	10	15	20	25
					Percei	nt germina	tion1		• • • • • • • •	
Shrubs:										
Amelanchier alnifolia Saskatoon serviceberry	Spring City Canyon, UT	91	80		91	²85 —	72	76 -	1	0.3
Amelanchier utahensis Utah serviceberry	Henrieville, UT	97	99		99	96	9 0 —	67 —	5	0
Artemisia nova	Manti,	81 —	66	55 —	34 -	5	1	0	0	0
Black sagebrush Artemisia tridentata ssp. tridentata	UT Ephraim,	73	82	67	70 -	24	1	0	0	0
Basin big sagebrush Atriplex canescens	UT Panaca,	32	47	40	40	50	43	37 –	18	11
Fourwing saltbush	NV					•••		•		
Ceanothus martinii Martin ceanothus	Manti Canyon, UT	3	5	5	12	³10 +	40	36 -	5	6
Ceratoides lanata Winterfat	Corona, NM	90	83	74 –	18	7	0	0	0	0
Cercocarpus ledifolius	Mayfield,	67	63		80	76	69	64	44	28
Curlieaf mountain-mahogany Cercocarpus montanus	UT Ephraim Canyon,	63	65	61	68 -	46 -	25 -	3	0	0
True mountain-mahogany Chrysothamnus nauseosus ssp.	ÚT									
hololeucus	Richfield,	80 —	65 —	34	14	11 -	7	0	0	0
White rubber rabbitbrush Cowania stansburiana	UT American Fork,	480*+		89	89	84	89	91 —	66	63
Cliffrose Ephedra nevadensis	UT Wah-Wah Valley,	90	93	91	85	89	91	85	79	77
Nevada ephedra	UT	90			65	03		00 -	19	
<i>Ephedra viridis</i> Green ephedra	Manti, UT	88	92	92	84	80	82	88 —	24	2
Grayia brandegei	Escalante, UT	87	92	86 —	57 —	13	6	0	0	0
Spineless hopsage Peraphyllum ramosissimum	Ephraim Canyon,	42	42	42	37	39 -	21	10	-	0
Squawapple Purshia giandulosa	UT Bishop,	78	86	80	80	69	73	65	61	60
Desert bitterbrush	CA	70	00	00	80	69	73	05	01	00
Purshia tridentata	Mt. Dell,	79* +	86	87	94	88	88	85	84	74
Antelope bitterbrush	UT									
Ribes aureum	Manti,	48			28 -		27	6	2	0
Golden currant	UT									
Symphoricarpos oreophilus Mountain snowberry	Spanish Fork Canyon, UT	80	64		92	80	44	8	10	8
Forbs:										
Balsamorhiza macrophylla	Bountiful,	35	28 -	17	20 -	4	0	0	0	0
Cutleaf balsamroot	UT									
Balsamorhiza sagittata Arrowleaf balsamroot	Paradise Valley, NV	40	42		37 –	20	1	0	0	0
Eriogonum heracleoides	Brigham City,	51 *+	87		90 —	64 -	16 —	5	-	0
Wyeth eriogonum Hedysarum boreale	UT Orem.	59	67	58	55 -	25	40	10		04
Utah sweetvetch	UT	99	07	30	- 55	25	40	16	11	21
Heracleum lanatum	Pleasant Creek	7	8 –	2	1	0	0	0	0	0
Cowparsnip	Canyon, UT									
Ligusticum porteri	Ephraim Canyon,	41	28	24	36 -	13	0	0	0	0
Porter ligusticum Linum perenne	UT Ephraim,	66 *	701.	05	00		70	05	-	-
Lowis flax	Ephraim, UT	00 -	72*+	85	93	83	70	25	8	0
Lomatium kingii	Ephraim Canyon,	69	73		73 –	37 -	8	2	0	0
Nuttall Iomatium	UT				/0-	57 -	0	2	U	U

Table 1—Mean percentage germination of seed from 38 shrub, forb, and grass species after 2, 3, 4, 5, 7, 10, 15, 20, and 25 years in storage in an open, unheated, and uncooled warehouse

Table 1 (Con.)

Species					Ye	ars of sto	rage			
Common name	Source	2	3	4	5	7	10	15	20	25
					Percen	t germina	tion1			
Forbs: (Con.)						•				
Lupinus alpestris Mountain lupine	Ephraim Canyon, UT	58	77	69	60	26	28	13	6	1
Lupinus sericeus Silky lupine	Ephraim Canyon, UT	97	99	100	99 —	86	85	92 -	75	76
Penstemon palmeri Palmer penstemon	Ephraim Canyon, UT	83	81		79	65	50		-	0
Medicago sativa Alfalfa 'Rambler'	Canada	69	76	75	75	70	77	66	73	67
same + hard seed		92	95	94	92	79	86 —	71	78	71
Sanguisorba minor Small burnet	Ephraim, UT	88*+	93	91	96 -	82	87	88	69 +	83
Sphaeralcea grossulariifolia Gooseberry globemallow	Benmore, UT	7	7	6	9	6	7	6	-	2
Tragopogon porrifolius Vegetable oyster salsify	Mt. Pleasant, UT	65	65	66	66	46	31 –	13	0	0
Viguiera multifiora Showy goldeneye	Ephraim Canyon, UT	18	17	11	13	13 -	1	0	0	0
Grasses:										
Agropyron intermedium Intermediate wheatgrass	Washington	95	96	93	94	80	78 –	63	13	1
Bromus inermis Smooth brome	Colorado	70	71 –	52	39 -	15	11	3	1	0
Secale cereale Winter rye	Idaho	89	88	82	75 -	56	48	32	2	0

Results based on four samples of 100 seeds each at 100 percent purity.

Indicates significant decrease in germination between adjoining years at (p < 0.05).</p>

*+Indicates significant increase in germination between adjoining years at (p < 0.05).

**Indicates significant afterripening at (p < 0.05).

second, third, fourth, fifth, seventh, 10th, 15th, 20th, and 25th year of storage following harvest. For each species in each year of sampling, four random samples of 100 seeds each were selected and individually placed between damp papers, wrapped in plastic, and placed in a refrigerator. Temperature in the refrigerator ranged between 1.1 and 3.3 °C. Care was taken to ensure that only undamaged seed with good fill was selected and used. Results are based on 98 percent fill and 100 percent purity for all species except fourwing saltbush (52 percent fill) and Martin ceanothus (Ceanothus martinii) (59 percent fill). Seed samples were checked at 14-day intervals. All germinated seeds were removed and the number that had germinated was recorded. Seed samples remained in an unlighted refrigerator for the duration of the study. Germination checks were made on schedule for up to 16 months. Seeds were considered germinated when the hypocotyl length reached 5 mm. Data were subjected to analysis of variance with SAS (SAS 1982).

Study 2: Germination of the Same Seed Source Following Collection and 5 to 15 Years Later—For six shrub, 12 forb, and nine grass species (table 2), two 100-seed samples were taken from freshly collected seed and from seed of the same lots 5 to 15 years later. Seed storage, selection, germination tests, and data analysis were made as described in study 1. Study 3: Germination of Various Seed Sources over 17 Years—Seeds of six shrub, eight forb, and 20 grass species (table 3) were placed in paper bags and stored for 1 to 40 years in the open warehouse described in study 1. Some species had various sources of seed with various years of storage. Seed selection and germination tests were carried out as described in study 1, with the exception that a few sources had sufficient seed for only two 100-seed samples.

STUDY 1 RESULTS

Germination and retention of viability varied between species, sources within a species, and years of storage (table 1). Two species, desert bitterbrush (*Purshia glandulosa*) and 'Rambler' alfalfa (*Medicago sativa*), did not significantly (P < 0.05) lose any germinability with 25 years of storage. Working with desert bitterbrush, Kay and others (1988) had little loss of germination in 6 years. Antelope bitterbrush seed germination did not decrease significantly for 20 years and only dropped to 74 percent between 20 and 25 years. Nevada ephedra (*Ephedra nevadensis*) had a significant loss between 15 and 20 years but retained acceptable germination of 77 percent

Species						Years o	f storage					
Common name	0	5	6	7	8	9	10	11	12	13	14	15
			•••••	•••••		Percent g	ermination	2 ¹		• • • • • • • • •		
Shrubs:												
Berberis repens	25									23		
Oregon-grape												
Caragana arborescens	88		85									
Siberian peashrub												
Lonicera tatarica	57		۹						31			
Honeysuckle												
Peraphyllum ramosissimum	67				49							
Squawapple												
Peraphyllum ramosissimum	58			58								
Squawapple												
Shepherdia argentea	85					88						
Silver buffaloberry												
Forbs:												
Astragalus cicer	^{\$} 51*		4+	89								
Cicer milkvetch												
Astragalus cicer	73				65							
Cicer milkvetch												
Astragalus galegiformis	88			89								
Giant astragalus												
Coronilla varia	41*		+		70							
Crownvetch												
Osmorhiza occidentalis	94		_							44		
Sweetanise												
Penstemon eatonii	71*		+							87		
Eaton penstemon												
Penstemon eatonii	63*		+							82		
Eaton penstemon												
Penstemon palmeri	89									82		
Palmer penstemon												
Penstemon platyphyllus	74										68	
Thickleaf penstemon												
Penstemon spectabilis	30*		+					+	+	75		
Showy penstemon												
Viguiera multiflora	44		_									1
Showy goldeneye												
Viguiera multiflora	39		_							0		
Showy goldeneye												
Grasses:												
Agropyron elongatum	72*		+			91						
Tall wheatgrass			т									
Agropyron elongatum	85					87						
Tall wheatgrass	•••											
Agropyron elongatum	85					92						
Tall wheatgrass	•••					-						
Bromus inermus	91	94										
Smooth brome	••											
Festuca elatior	69*		+		99							
Meadow fescue			•									
Muhlenbergia wrightii	14*		+	62								
Spike muhly			•									
Oryzopsis hymenoides	9*		+									49
Indian ricegrass												
Oryzopsis hymenoides	55						63					
Indian ricegrass												
Stipa comata	88				63							
Needle-and-thread	-		-									

Table 2-Percentage germination of the same seed source for shrubs, forbs, and grass seed, comparing freshly collected seed and seed with various years of storage in an open warehouse

¹Results based on two samples of 100 seeds each at 100 percent purity. ²-Indicates significant decrease in germination between germination years at (p < 0.05). ^{3*}Indicates significant afterripening at (p < 0.05). ⁴+Indicates significant increase in germination between germination years at (p < 0.05).

Table 3-Seed germination of selected species with 0 to 40 years of storage. Seed of the same species may not be from the same source

Species							ars of sto						
Common name	1	2	5	6	7	8	9	10	13	14	15	16	17
						Perce	ent germi	nation ¹					
Shrubs:							-						
Atriplex hymenelytra Desert holly			57										
Atriplex lentiformis Big saltbush										92			
Caragana pygmaea				85				67					
Pygmy peashrub <i>Ceanothus cuneatus</i> Wedgeleaf ceanothus						63							
Ceanothus fendleri										27			
Fendler ceanothus													
Colutea arborescens Bladdersenna	45							37					
Forbs:													
<i>Erodium cicutarium</i> Alfileria										(40) years, §) 0)	
Medicago sativa Alfalfa	95										86		
Melilotus officinalis	84									59			
Yellow sweetclover Onobrychis sativa	92								27				
Sainfoin Osmorhiza occidentalis	52								34 A				
Sweetanise									0477				
Penstemon eatonii Eaton penstemon	88										86		
Penstemon platyphyllus Hillside penstemon										68	58		
Pentstemon subglaber Smooth penstemon											52	41	40
Grasses:													
<i>Agropyron cristatum</i> Fairway wheatgrass	95				39								
Agropyron desertorum Crested wheatgrass	96			91							8		
Agropyron sibiricum	95									38			
Siberian wheatgrass Agropyron spicatum	94			86									
Bluebunch wheatgrass	97								47				
Agropyron trichophorum Pubescent wheatgrass	9/								4/				
Alopecurus arundinaceus Reed foxtail				86									
Alopecurus pratensis Meadow foxtail								91					
Bromus erectus	96					91							
Meadow brome Dactylis glomerata			89		82				(30 ye	ears, 44)			
Orchardgrass Festuca elatior					73		69						
Meadow fescue							~~						
Festuca ovina Sheep fescue				82	63								
Festuca rubra Red fescue					72					41			
Koeleria cristata								40					
Prairie junegrass <i>Lolium perenne</i>		95		93									
Perennial ryegrass				30									

Table 3 (Con.)

Species						Ye	ars of st	orage					
Common name	1	2	5	6.	7	8	9	10	13	14	15	16	17
• · · · · · · · · · · · · · · · · · · ·						Perc	ent germ	ination ¹ -					
Grasses: (Con.)							-						
Phleum pratense								98					6
Timothy													
Poa bulbosa					99								
Bulbous bluegrass							•						
Psathyrostachys junceus					82						23		
Russian wildrye													
Secale montanum	88												50
Mountain rye													
Sporobolus airoides					99								
Alkali sacaton													
Sporobolus columbiana							63						
Subalpine needlegrass													

'Results based on two or four samples of 100 seeds each.

with 25 years. Nevada ephedra seed stored in a warehouse in California lost significant germination after the first year, but seed stored at -15 °C did not lose germination with 14 years of storage (Kay and others 1988). Silky lupine (*Lupinus sericeus*) and small burnet (*Sanquisorba minor*) germination decreased significantly between 5 and 7 years. However, they had 76 and 83 percent germination, respectively, after 25 years.

Cliffrose (Cowania stansburiana), curlleaf mountainmahogany (Cercocarpus ledifolius), fourwing saltbush, green ephedra (Ephedra viridis), Nevada ephedra, and gooseberry globemallow (Sphaeralcea grossulariifolia) exhibited a significant loss in germination between 15 and 20 years. In work in California with cliffrose and green ephedra, Kay and others (1988) obtained results similar to the above. Springfield (1970), working with fourwing saltbush, had a 50 percent loss of germination over 15 years. Utah serviceberry (Amelanchier utahensis), Lewis flax (Linum perenne), and intermediate wheatgrass (Agropyron intermedium) retained acceptable germination for 10 to 15 years.

Mountain snowberry (Symphoricarpos oreophilus), Saskatoon serviceberry (Amelanchier alnifolia), true mountain-mahogany (Cercocarpus montanus), squawapple (Peraphyllum ramosissimum), and showy goldeneye (Viguiera multiflora) had a significant loss in germination between the seventh and 10th year of storage.

Basin big sagebrush (Artemisia tridentata ssp. tridentata), arrowleaf balsamroot (Balsamorhiza sagittata), silky and mountain lupine (Lupinus alpestris), Nuttall lomatium (Lomatium nuttallii), Palmer penstemon (Penstemon palmeri), Porter ligusticum (Ligusticum porteri), small burnet, Utah sweetvetch (Hedysarum boreale), vegetable oyster salsify (Tragopogon porrifolius), Wyeth eriogonum (Eriogonum heracleoides), and winter rye (Secale cereale) retained consistent germination for 5 to 7 years. Duration of good viability was listed by Plummer and others (1968) as 5 years for arrowleaf balsamroot, Palmer penstemon, Porter ligusticum, Nuttall lomatium, and Utah sweetvetch and 3 years for Lewis flax and vegetable oyster salsify. Kay and others (1988) reported Palmer penstemon had slightly longer viability.

Golden currant (*Ribes aureum*), spineless hopsage (*Grayia brandegei*), and winterfat germination dropped significantly after 4 years of storage; cowparsnip (*Heracleum lanatum*), cutleaf balsamroot (*Balsamorhiza macrophylla*), and smooth brome (*Bromus inermis*) after 3 years; black sagebrush (*Artemesia nova*) and white rubber rabbitbrush (*Chrysothamnus nauseosus* ssp. *hololeucus*) after only 2 years. Kay and others (1988), working with Mojave desert accessions, had similar results with white rubber rabbitbrush but less retention of viability with winterfat. Stevens and others (1977) reported similar results with winterfat. Springfield, (1968, 1973, 1974), working in New Mexico, found that winterfat would lose viability rapidly unless it was stored in a cold environment.

Alfalfa viability is a combination of hard and germinated seed. Hard seed is viable seed that does not absorb water nor germinate during the germination test. 'Rambler' alfalfa seed germination percentage did not significantly change over 25 years. However, germination percentage of hard seed did significantly decrease between the 10th and 15th year of storage.

Five species showed considerable afterripening by demonstrating a significant increase in germination with age. Antelope bitterbrush, cliffrose, small burnet, and Wyeth eriogonum germinability increased to the third year and Lewis flax to the fourth year after harvest. Kay and others (1988) demonstrated a similar increase in cliffrose germination over the first 3 years.

STUDY 2 RESULTS

Germination tests of new and several-year-old seed of 20 species, six of which had more than one accession, produced variable results (table 2). Eight species exhibited considerable afterripening. One source of tall wheatgrass (Agropyron elongatum) had 19 percent more germination

with 9-year-old seed than from new seed. However, two other sources had no significant change in germination over 9 years. New seed of meadow fescue (Festuca elatior) exhibited 69 percent germination and 8 years later, 99 percent. Spike muhly (Muhlenbergia wrightii) germination went from 14 to 62 percent in 7 years. For one source of Indian ricegrass (Oryzopsis hymenoides), 14 years after harvest, germination increased from 9 to 49 percent. Another source with only 10 years storage had no significant change in germination. One source of cicer milkvetch (Astragalus cicer) went from 51 to 89 percent germination in 7 years. A second source, however, had no significant change in germination with 8 years of storage. Crownvetch (Coronilla varia) seed showed a significant increase in germination from 41 to 70 percent in 8 years. In two accessions of Eaton penstemon (Penstemon eatonii), germination significantly increased over 13 years. One went from 71 to 87 percent and the second from 63 to 82 percent. Showy penstemon (P. spectabilis) exhibited a significant increase in germination from 30 to 75 percent in 10 years.

Germination percentage did not significantly change in accessions of 11 species: Oregon-grape (Berberis repens) (25 to 23 percent in 13 years), Siberian peashrub (Caragana arborescens) (88 to 85 percent in 6 years), one source of squawapple (no change in 7 years), silver buffaloberry (Shepherdia argentea) (85 to 88 percent in 9 years), cicer milkvetch (72 to 85 percent in 9 years), Astragalus galegiformis (88 to 89 percent in 7 years), Palmer penstemon (89 to 82 percent in 13 years), thickleaf penstemon (Penstemon platyphyllus) (74 to 68 percent in 14 years), tall wheatgrass from two sources (85 to 87 percent and 85 to 92 percent in 9 years), smooth brome (91 to 94 percent in 5 years), and Indian ricegrass (55 to 63 percent in 10 years).

Only five species exhibited significant loss in germination percentage over their individual storage periods: honeysuckle (Lonicera tatarica) (57 to 49 percent in 12 years), squawapple (67 to 49 percent in 8 years), sweetanise (Osmorhiza occidentalis) (94 to 44 percent in 13 years), showy goldeneye from two sources (44 to 1 percent in 15 years, 39 to 0 percent in 13 years), and needle-and-thread (Stipa comata) (88 to 63 percent in 8 years).

STUDY 3 RESULTS

Even though the source of seed is not the same for most species, results (table 3) can be used as a general guide in estimating longevity for many species. For a good number of the species in this study, there are no other available extended longevity data.

Retention of germinability with years of storage varied considerably with the shrubs. Big saltbush (Atriplex lentiformis) expressed more longevity (92 percent in 14 years) than did desert holly saltbush (A. hymenelytra) (57 percent in 2 years). Five-year-old seed of pygmy peashrub (Caragana pygmaea) germinated at 85 percent and 10 year-old seed at 67 percent. Wedgeleaf ceanothus (Ceanothus cuneatus) had considerably more germination (63 percent) with 10-year-old seed than did Fendler ceanothus (C. fendleri) (27 percent) with 14-year-old seed. Bladdersenna (Colutea arborescens) showed little difference in germination with 1-year-old (45 percent) and 10-year-old (38 percent) seed.

All of the tested forb seed showed considerable longevity. Forty-year-old seed of alfileria (*Erodium cicutarium*) exhibited 90 percent germination, alfalfa 86 percent with 15-year-old seed, and yellow sweetclover (*Melilotus officinalis*) 59 percent with 13-year-old seed. The penstemons— Eaton, hillside, and smooth (*Penstemon subglaber*) had 86, 58, and 52 percent, respectively, with 15-year-old seed. The forbs, sweetanise and sainfoin (*Onobrychis sativa*), expressed 34 and 27 percent germination with 10-year-old seed.

A majority of the grass species had good germination after 7 to 9 years. The wheatgrasses (Agropyron ssp.), in general, exhibited high germination for 7 to 8 years. Sixyear-old Reed foxtail (Alopecurus arundinaceus) seed germinated at 86 percent, while meadow foxtail germinated at 91 percent after 13 years. Meadow brome (Bromus erectus) showed 96 percent germination with 2-year-old seed and 91 percent with 9-year-old seed. Orchardgrass (Dactylis glomerata) germination with 5-, 7-, and 30-yearold seed was 89, 82, and 44 percent, respectively. Germination of 82 percent after 7 years and 23 percent after 15 years was obtained with Russian wildrye (Psathyrostachys junceas) seed. The fescues-meadow, sheep (Festuca ovina), and red (F. rubra)-all had germination of over 63 percent with 7-year-old seed. Prairie junegrass (Koeleria cristata) showed 40 percent germination 10 years after harvest. Perennial ryegrass (Lolium perenne) had 93 percent with 6-year-old seed. Of the grasses tested, timothy (Phleum pratense) exhibited considerable longevity with 98 percent germination from 10-year-old seed. Bulbous bluegrass (Poa bulbosa) and alkali sacaton (Sporobolus airoides) exhibited identical germination (99 percent) with 7-year-old seed. Nine-year-old subalpine needlegrass (Stipa columbiana) seed germinated at 63 percent. Mountain rye (Secale montanum) had 80 percent germination from new seed and 50 percent with 17-year-old seed.

VARIATION IN GERMINATION

In these studies, difference in germination between sources of a number of shrub, forb, and grass species was found. Comparing results from more than one seed source per species in study 1 (table 1) and additional sources of the same species in study 2 (table 2) demonstrated variations in germination between sources. Two sources of squawapple, one in study 1 and the other in study 2, both held germination for 7 years. A third source in study 2, however, had significantly less germination in the eighth year. Considerable variation between various shrub species' seed sources, especially sources from differing environmental conditions, has been reported for fourwing saltbush, winterfat, rubber rabbitbrush, big sagebrush, and bitterbrush (Meyer 1989, 1990; Meyer and Monsen 1990; Meyer and others 1987; Meyer and Pendleton 1990; Stevens and others 1977).

After 13 years, germination of one Palmer penstemon seed source (study 2) did not change significantly (89 to 82 percent). An additional source of Palmer penstemon in study 1 held its germination for only 5 years (83 to 79 percent) and then dropped to 65 percent by the seventh year. Kitchen and Meyer (1991, 1992) reported considerable variation in germination between sources of Palmer penstemon and other Intermountain penstemons. Some variations were found between cicer milkvetch sources. One source in study 2 had 51 percent germination the year of harvest and significantly increased to 89 percent in 7 years. The second source showed a slight decrease (73 to 65 percent) over 8 years.

Young and Evans (1982) worked with a number of coolseason range grasses and found variation between varieties and sources within the same species. In our studies we had one source of smooth brome whose germination did not significantly change in 5 years (91 to 94 percent) (study 2), and one that showed 70 percent germination with 2-year-old seed and significantly dropped to 52 percent with 4 years of storage. There were three sources of tall wheatgrass in study 2. One source demonstrated afterripening by increasing its germination between the first and ninth year (72 to 91 percent). Germination increased slightly but not significantly in 9 years (85 to 87 percent and 85 to 92 percent) for the two other sources. Two sources of Indian ricegrass in study 2 demonstrated somewhat differing results. The first source started out with 9 percent germination and 14 years later had increased to 49 percent. The second source started out at 55 percent and increased slightly to 63 percent in 10 years.

SUMMARY

Each species exhibited its own unique germination characteristics that varied with source and age. Seed of many species can be obtained and stored for various lengths of time and still retain acceptable germinability. Some species' germination increased with age; others' decreased with age. Because percentage germination is a measure of the number of seed per 100 that will germinate and have the potential to produce a seedling, all new seed and seed that has been in storage should be tested by an official seed laboratory (Stevens and Meyer 1990) prior to purchase and seeding. Purchase price and seeding rate should be adjusted to the most recent germination test.

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ENHANCED PERFORMANCE OF GRASS SEED BY MATRICONDITIONING

J. D. Maguire E. S. Maring W. J. Johnston C. D. Burrows

Preplant conditioning with moist solid carriers, a technique termed matriconditioning, has proved effective in improving germination and early seedling emergence. Matriconditioning grass seed with Micro-Cel E (MCE), a synthetic calcium silicate, produced rapid, uniform emergence and greater seedling growth under environmental stress conditions.

As indicated in figure 1, water uptake by germinating seed follows a triphasic pattern (Bewley and Black 1985). By maintaining high negative water potential the MCE, which has negligible osmotic effects, controlled imbibition of the seed to a level that allowed pregermination without radicle protrusion. The objectives of this study were to develop seed preconditioning techniques via matriconditioning to improve grass seed germination, emergence and stand establishment.

MATERIALS AND METHODS

Grass seeds used were Kentucky bluegrass (Poa pratensis), big bluegrass (Poa secunda), Idaho fescue (Festuca

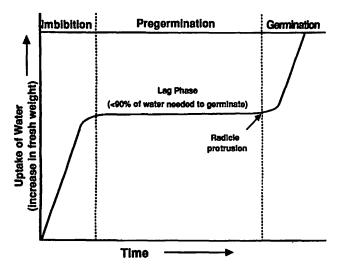


Figure 1—Imbibition of water by seed during germination. (Adapted from Bewley and Black 1985).

Grass species	Seed:carrier: water	Duration	Water content	Water potential
	Weight ratio	Days	Percent	MPa
Bluebunch				
wheatgrass	16:8:24.0	4	66	-1.90
Wildrye	16:8:28.8	4	53	-1.28
Idaho fescue	16:8:17.6	2	65	-2.15
Kentucky				
bluegrass	16:8:18.0	7	50	-2.10
Big bluegrass	16:8:20.8	4	52	-2.33

Table 1—Ratio of seed:carrier:water, duration, water content, and water potential of matriconditioned grass seed

idahoensis), bluebunch wheatgrass (Pseudoroegneria spicata ssp. spicata), and wildrye (Leymus giganteus). MCE, a hydrated synthetic calcium silicate, was used as the solid carrier in conditioning seed. Seeds were matriconditioned at 15 °C in glass jars with lids loosened to allow oxygen exchange according to methods outlined by Khan and others (1990). The ratios of seed to carrier to water were as indicated in table 1. After conditioning, seeds were placed on a fine-meshed strainer and MCE was washed off with deionized water. Seeds were air dried under ambient laboratory conditions for 2 days. Seeds were germinated on blotters in petri dishes at 25/15 °C (12 h light-12 h dark) or planted in field soil for emergence. Ambient average temperatures ranged from 7.5 to 14.5 °C during field studies.

The matric potentials (the water retentive force) of the MCE and the various grass seed species were determined with a thermocouple psychrometer (model SC-10, Decagon Devices, Pullman, WA) connected to a nanovoltmeter (model NT-3, Decagon Devices). Table 1 shows the water content and water potential of seeds at end of matriconditioning.

RESULTS

The effects of matriconditioning on the germination of the grass species evaluated are shown in table 2. Matriconditioning enhanced germination rate and percent germination of bluebunch wheatgrass. Time to 50 percent of total germination (T-50) for matriconditioned seed was 2.5 days vs. 3.9 days for untreated seed. Total germination was 96 percent and 89 percent for matriconditioned and untreated seed, respectively. Kentucky bluegrass

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Table 2—The effect of matriconditioning on the germination of for	ur
grass species at 25-15 °C (12 h light-12 h dark)	

	Matrice	ondition	ned seed	Untreated seed				
Grass species	۲-10 ^י	²T-50	Germi- nation	T-10	T-50	Germi- nation		
	Da	ays	Percent	Da	ys	Percen		
Bluebunch								
wheatgrass	1.5a ³	2.5a	96a	3.0b	3.9b	89b		
Wildrye	3.3a	5.0a	90a	4.1b	5.6b	84a		
Idaho fescue Kentucky	3.6a	5.0a	73a	5.1b	6.9b	62a		
bluegrass	3.4a	5.0a	91a	5.5b	7.0b	91a		
Big bluegrass	2.8a	4.0a	93a	3.8b	5.1a	86a		

¹Time to 10 percent of total germination.

²Time to 50 percent of total germination.

³Mean separation between respective columns (T-10, T-50, percent germination) by LSD (P = 0.05).

germination rate was enhanced by matriconditioning, T-50 was 5 days vs. 7 days. Wildrye and Idaho fescue germination rates were also enhanced. For these species, T-50 for matriconditioned seed compared to untreated seed was 5 days vs. 5.6 days and 5 days vs. 6.9 days, respectively.

Bluebunch wheatgrass time to 50 percent field emergence was 17 days for matriconditioned seed vs. 20 days for untreated seed (fig. 2). Total emergence was 75 percent vs. 65 percent, respectively, 28 days after planting. Total Kentucky bluegrass emergence was the same (35 percent) for matriconditioned and untreated seed, apparently due to favorable temperatures; however, earlier emergence was obtained by matriconditioning the seed (fig. 3). Time to 10 percent emergence for MCEconditioned bluegrass seed was attained at 16 days vs. 20 days for untreated seed. Unpublished data (Burrows) indicate that MCE improved overall performance of

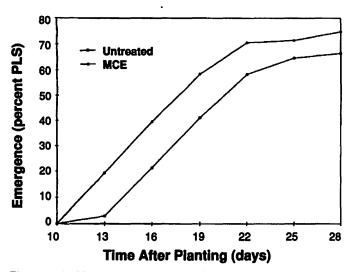


Figure 2—Field emergence of matriconditioned bluebunch wheatgrass compared to untreated seed, based on pure live seed (PLS) percentage. Planted March 11, 1992. Temperatures ranged from 7.5 to 14.5 °C.

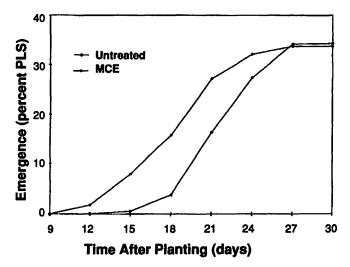


Figure 3—Field emergence of matriconditioned Kentucky bluegrass compared to untreated seed, based on pure live seed (PLS) percentage. Planted March 11, 1992. Temperatures ranged from 7.5 to 14.5 °C.

Kentucky bluegrass in wet soil under cool temperatures. Field trials are continuing to evaluate biomass production and suppression of grassy weeds.

CONCLUSIONS

Preplant conditioning of grass seed with solid carriers such as Micro-Cel E enhanced germination and early emergence under environmental stress and may improve overall stand establishment. This seed-priming technique has potential for biological suppression of annual grassy weeds in pastures and rangelands.

ACKNOWLEDGMENTS

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REPRODUCTIVE BIOLOGY OF BITTERBRUSH: INTERACCESSIONAL HYBRIDIZATION OF PLANTS GROWN IN A COMMON GARDEN

R. L. Pendleton E. D. McArthur

Bitterbrush (*Purshia* spp.) and cliffrose (*Cowania* spp.) comprise a widespread western North American species complex, a complex capable of interspecific gene exchange. Various species of this group are important in landscape dominance, wildlife habitat, browse for wild and domestic ungulates, contribution to the rare species flora, and wildland nitrogen fixation. Antelope bitterbrush (*P. tridentata*) and Stansbury cliffrose (*C. stansburiana*) are the most common and widespread members of this species complex.

This study looks at the reproductive system of antelope bitterbrush, testing whether individual plants of this species are self-incompatible and whether pollination is facilitated by insect vectors. We also examine intra- and interpopulation compatibility of four core antelope bitterbrush accessions in a diallelic crossing design supplemented by additional antelope bitterbrush and Stansbury cliffrose pollen donor accessions. One of the four core accessions is of hybrid origin (*P. tridentata* x *C. stansburiana*).

Specific questions addressed by this study are:

1. Are individual plants of *Purshia* self-incompatible? What role does wind play in the pollination of this species?

2. What fruiting characteristics are attributable to maternal or paternal effects? Are there differences among populations?

3. Are crosses using within-accession pollen more successful than crosses between accessions? What are the characteristics of interspecific crosses?

METHODS

Four core antelope bitterbrush populations (Bryce Canyon, UT; Canyon Mountains, UT; Fairview, UT; Thoreau, NM) are among some 60 antelope bitterbrush and Stansbury cliffrose accessions growing in a Springville, UT, uniform garden. The Thoreau accession is of hybrid origin. In May 1989, we applied the following treatments to separate branches on six individuals of each of the four populations: control (open pollination), bagged (self pollination), bagged and emasculated, bagged with self pollen added, and bagged with nylon net (wind pollination). In May 1990, treatments consisted of reciprocal hybridization among the four core populations (two separate donor bushes for each recipient bush), one self pollination, one open pollination, one nearby random antelope bitterbrush pollen donor, one 'Lassen' (Shaw and Monsen 1986) antelope bitterbrush pollen donor, and two Stansbury cliffrose (from St. George and Provo Canyon, UT) pollen donors for a total of 12 treated branches per bush for each of six bushes per accession.

Except for open- and wind-pollination treatments, mass pollination was accomplished at anthesis in white paper sacks, which were used to isolate the treated branches. Cloth net bags replaced the paper sacks and were added to the open pollination treatments to protect the developing fruits from insect predation and to collect ripening fruits. After harvest, receptacles and fruits were counted and sorted into three developmental classes. Fruit and seed size measurements were also recorded. Data were analyzed using the General Linear Models procedure on SAS.

POLLINATION

Bitterbrush is highly self-incompatible. In year 1 of the study, 1.06 percent of the flowers on branches that were bagged to exclude pollinators set fruit. Similar results were recorded in year 2, with self pollination producing a 1.59 percent fruit set. In contrast, an average 82.9 percent of open-pollinated flowers produced fruit.

Wind pollination within the high-density common garden was nearly as effective as open pollination (77 percent fruit set). Fruit set in the hybridization treatments averaged less than 70 percent. The reduction in fruit set with treatment is likely due to a "bag effect" (not all flowers were open or accessible to pollen introduced to the bag).

MATERNAL AND PATERNAL EFFECTS ON FRUITING CHARACTERISTICS

Differences between the four maternal populations were tested using individual plants as the error term of the model. Significant differences were found in seed weight,

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Table 1-Attained significance values from ANOVAs for maternal and paternal effects. NS = nonsignificant

	Mean seed weight	Mean fruit length	Percent fruit initiated	Percent fruit developed	Percent fruit matured	Percent fruit aborted
Maternal population	0.0007	0.0009	0.0039	0.0047	0.0113	0.0018
Maternal parent	.0001	.0001	.0001	.0001	.0001	NS
Paternal population	NS	.0135	NS	.0433	.0559	NS
Paternal parent	NS	.0008	NS	NS	NS	NS

fruit length, percent fruit initiated, percent fruit developed, percent fruit matured, and percent fruit aborted (table 1). The Thoreau population, which contains introgressed *Cowania* genes, was significantly different from other populations in all variables. The smaller seeds, multiple seeds per receptacle, and longer tails on the fruits, traits it shares in common with *Cowania*, attest to its hybrid origin. The Bryce Canyon population had significantly less fruit abortion than either West Fairview or Canyon Mountain populations.

Maternal parent plant had a profound effect on fruiting characteristics, being highly significant for all variables except fruit abortion. For nonintrogressed populations (Thoreau omitted), seed weight is almost exclusively determined by the maternal parent. Maternal-parent effects include both genetic and environmental components.

Three variables show some effect attributable to paternal-parent population. The strongest effect is observed in fruit length. Fruits developing from cliffrose (*Cowania*) pollen tended to be longer than other sources. Cliffrose crosses also tended to produce a lower percent seed set than other pollen treatments. West Fairview produced the highest percent fruit set.

Individual pollen parent effects were highly significant for the fruit length variable. Again, cliffrose pollen sired the longest fruits. The two Canyon Mountain pollen sources were significantly different from each other, one plant siring fruits nearly as long as those produced by cliffrose pollen, the other siring short fruits.

INTRA- VS. INTERPOPULATION CROSSES

Although significant only at the p = 0.1 level, intra- and interpopulational comparisons demonstrate an interesting trend that may be worthy of more detailed investigation. Within-population crosses initiate (82.5 percent vs. 74.0 percent) and develop (60.0 percent vs. 50.6 percent) a higher percentage of fruit, but also abort (16.5 percent vs. 12.0 percent) a higher percentage of developing fruit before reaching final maturity. Intra- and interpopulational crosses did not differ in the percent of mature fruit produced.

CONCLUSIONS

1. Bitterbrush is self-incompatible but widely fertile on an intra- and interpopulational basis, including hybridization with cliffrose. Cross-fertilization and hybridization for breeding purposes can be accomplished with relative ease. Where plants are closely spaced, wind may play a significant role in effecting pollination. Pollen limitation should not pose a significant problem to fruit production in an orchard setting.

2. The maternal parent has the greatest effect on fruiting characteristics, being highly significant for nearly all variables examined in this study. The maternal parent largely determines seed weight, which in turn affects seedling survival and performance. Mean seed weight in a given lot can likely be increased through selective propagation of large-seeded mother plants in a garden setting or, alternatively, by selective field harvesting.

3. Paternal effects, though less substantive, are also important in fruit development. This study demonstrates morphologic effects attributable to pollen source. Studies are now planned that will examine possible paternal and maternal effects on seed germination and seedling establishment. The demonstration of maternal (at least some of which is due to genetics) and paternal (all of which is due to genetics) effects on seed development and morphology confirms the presence of a large genetic pool amenable to breeding programs.

4. Intra- and interpopulational crosses mature the same proportion of seed, albeit through different means. Within-population crosses initiate more fruit, but also abort a higher proportion. This further supports the conclusion that fruit production in bitterbrush is largely a function of resource availability, rather than pollen limitation.

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THE (CERTIFIED) SEEDS OF REVEGETATION

Stanford A. Young

The goal of any revegetation project is to have a healthy stand of desirable plants growing in the proper place. Using high-quality seed of known origin and genetic identity will help attain the project goal by (1) ensuring that plants of the desired species and variety or ecotype are introduced, (2) avoiding the introduction of unwanted species, and (3) avoiding costs of reseeding.

The best way to obtain such seed is to specify that it be certified. A named variety of a plant species is usually available as **CERTIFIED SEED** (blue tag). FOUNDA-**TION**.**SEED** (white tag) and **REGISTERED SEED** (purple tag) are utilized by seed growers to produce the Certified class. Such seed has been field inspected and laboratory tested to ensure varietal identity, genetic purity, and high quality standards (high seed purity and germination, and strictly limited amounts of other crop seed, weed seed, inert matter, and diseased or insectdamaged seed).

Seed of a plant species for which there are no released varieties (or there are ecotypes of interest that are distinctly different from any released varieties) may also be obtained as officially certified seed. SOURCE IDENTI-FIED CLASS (yellow tag) indicates verification by a seed certification agency of State, county, and elevation from which the seed lot was collected. SELECTED CLASS (green tag) indicates seed of an ecotype or germplasm that has been compared (using specified criteria and methods) with other ecotypes or germplasm selection of a species and is shown to have unique characteristics. TESTED CLASS (blue tag) indicates seed of an ecotype or germplasm selection that has been selected and also progeny tested to prove that unique traits are heritable.

With certified seed you can be assured that the seed in the bag is the variety or ecotype claimed. Otherwise, there is no easy way to confirm whether someone is selling Hycrest or Ephraim crested wheatgrass versus common wheatgrass, or Immigrant prostrate kochia versus the weedy *Kochia scoparia*. Similarly, verification of origin of fourwing saltbush seed lots has been a problem in the industry, as has differentiating between seed of subspecies and ecotypes of *Artemesia tridentata*. A seed laboratory analysis listing a variety name or origin of collection is not proof of variety or germplasm identity it reflects only the unsubstantiated claim of the person sending in the sample.

Seed is NOT certified unless there is a tag of the designated color attached to the bag, that states the class (CERTIFIED or SOURCE IDENTIFIED, for example) of certified seed in large block letters and has the insignia of the specific State certifying agency that attached the tag. The legally mandated presence of an analysis tag on the bag is not an indication of certification status, though close inspection of the analysis tag becomes extremely important if certified seed is not obtainable for a certain variety or ecotype. Don't be misled by someone who says that the seed "came from a certified field," "we don't have the tags yet," or "it's just as good as certified."

Seed certification offers an avenue of upgrading quality and genetic identity and purity of seed available to plant managers so that the goals of the revegetation project are met. If buyers ask for and are willing to pay a fair premium for this seed, the seed industry will respond with adequate supplies.

Following is a list of those reported to have current interest and experience in growing, collecting, or conditioning certified seed of reclamation species for wholesale and retail markets. However, this list is **NOT** inclusive of all companies where certified seed or other high-quality seed or plants for revegetation may be obtained. Contact the seed certification agency in your State for further information.

Tom Adsit Box 17 Decker, MT 59025 (406) 757-2223

Arkansas Valley Seed Co. 4333 Hwy 66 Longmont, CO 80501 (303) 320-7500

Big Sky Wholesale Seeds P.O. Box 852 Shelby, MT 59474 (406) 434-5011

Blue Mountain Seeds, Inc. P.O. Box 185 Imbler, OR 97841

Bruce Seed Farm 91 Lower Deep Creek Townsend, MT 59644 Carhart Feed & Seed Box 55 Dove Creek, CO 81234 (303) 677-2233

Cenex/Land O'Lakes Seed P.O. Box 155 Williston, ND 58802-0155 (701) 572-5180

Conservaseed P.O. Box 455 Rio Vista, CA 94571

Etheridge Seed Farms 2028 Lane 11 Powell, WY 82435 (307) 754-2366

Don Faxon 598 Road 11 Powell, WY 82435 (307) 754-3287

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Garrison Seed Co. 923 D Street Box 1604 Greeley, CO 80632 (303) 356-7002

Globe Seed & Feed P.O. Box 445 Twin Falls, ID 83303-0445 (208) 733-1373

Gooding Seed Co. P.O. Box 57 Gooding, ID 83330 (208) 934-8441

Grassland West Co. P.O. Box 489 Clarkston, WA 99403 (509) 758-9100

Great Western Seed Co. P.O. Box 387 Albany, OR 97321

Homan Brothers Seed, Inc. 101 N. 55th St., Ste. 1 Phoenix, AZ 85034 (602) 244-1650 Idaho Grimm Growers P.O. Box 276 Blackfoot, ID 83321 (208) 785-0830

Charles Inouye & Sons P.O. Box 937 Gunnison, UT 84634 (801) 528-7863

Intermountain Seed P.O. Box 62 Ephraim, UT 84627 (801) 283-4383

Jacklin Seed Co. W. 5300 River Bend Ave. Post Falls, ID 83854-9499 (208) 773-7581

Maple Leaf Industries P.O. Box 9-6 Ephraim, UT 84627 (801) 283-4701

Northrup King Company 418 Albert St. Billings, MT 59102 (406) 252-0568 Plummer Plant & Seed Co. P.O. Box 70 Ephraim, UT 84627 (801) 283-4844

Round Butte Seed Growers P.O. Box 117 Culver, OR 97734

Smith Seed Service P.O. Box 195 Halsey, OR 97348

Southwest Seed 13260 Rd. 29 Dolores, CO 81323 (303) 565-8722

Sharp Bros. Seed 101 E. 4th St. Rd. Greeley, CO 80631 (303) 356-4710

Kelly Spiering 71170 Road 19 Powell, WY 82435 (307) 754-4349 Stevenson Intermountain Seed P.O. Box 2 Ephraim, UT 84627 (801) 283-6639

Dean Swift Seed Co. P.O. Box B Jaroso, CO 81138 (719) 672-3739

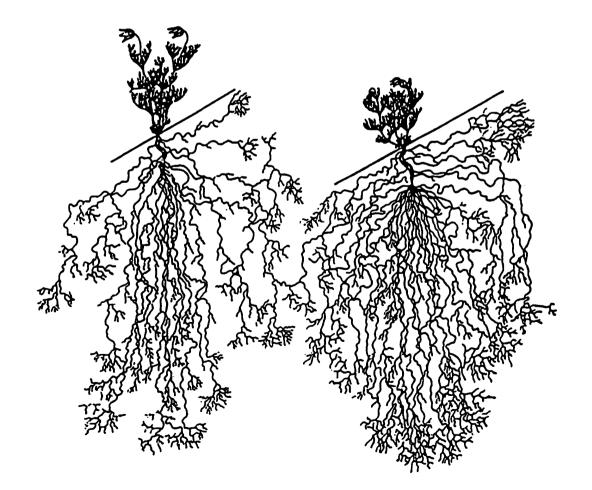
Wheatland Seeds, Inc. P.O. Box 513 Brigham City, UT 84302 (801) 734-9191

Willamette Seed Co. P.O. Box 791 Albany, OR 97321

Willamette Valley Plant 36100 Highway 228 Brownsville, OR 97327

Wind River Seeds Rt. 1, Box 97 Manderson, WY 82432 (307) 568-3325

Restoration: Seedbed Preparation and Seeding



Clematis hirsutissima

EFFECTS OF POLYACRYLAMIDE ON ESTABLISHMENT AND GROWTH OF CRESTED WHEATGRASS SEEDLINGS AND SAGEBRUSH TUBELINGS

Saud L. Al-Rowaily Neil E. West

ABSTRACT

Experiments employing two forms (cross-linked and noncross-linked) of polyacrylamide (PAM) at 0.2 percent, mixed with a silt loam Xerollic Calciorthid top soil, were performed in 1991. Larger cracks and lower mean penetrometer resistance occurred in the two PAM treatments compared to the untreated control. The two kinds of PAM failed to produce significant differences in soil moisture or crested wheatgrass (Agropyron desertorum) germination. Oneyear-old tubelings of big sagebrush (Artemisia tridentata) did not grow significantly faster or flower significantly sooner or more abundantly than the untreated controls.

INTRODUCTION

Arid or semiarid rangeland environments are characterized by limited soil moisture, poor water-holding capacity, high evaporation, and low soil organic matter (Stoddart and others 1975). Besides lack of rainfall, crust formation, vesicular structure, physical degradation of the soil surface, and high erodibility and runoff are also some of the main problems limiting rangeland production (Singer 1991; Wood 1988).

Crust formation on soil surfaces is due to a combination of three primary mechanisms (Agassi and others 1981, 1985; Paul and Clark 1989): (1) loss of soil organic matter; (2) the effect of raindrop impact energy, which causes a disintegration of the soil aggregates and compaction; and (3) the dispersion of clay particles at the soil surface. Taylor (1962) reported that in semiarid or arid environments, rapid and highly rigid crust development is enhanced by high evaporation demand, and rapid drying of the soil surface. Crusts impair seedling emergence and plant establishment (Shainberg and others 1990; Wood and others 1982). Crusting also leads to increased runoff and erosion, followed by a reduction in infiltration (Agassi and others 1985; Morin and others 1981; Shainberg and others 1990).

Water and wind erosion are another serious problem in rangeland environments (Singer 1991). Poor structure, low organic matter content, and the presence of salts

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Saud L. Al-Rowaily and Neil E. West are Graduate Student and Professor, respectively, Department of Range Science, Utah State University, Logan, UT 84322-5230. (especially Na) lead to some of the common problems in arid environments such as high wind and water erodibility (Singer 1991). The soil surfaces in arid environments are easily moved by wind because of lack of surface soil moisture and sparse or nonexistent vegetation protection (Singer 1991).

One possible solution to overcome these rangeland limitations is the use of soil conditioners. Following some initial enthusiasm for soil conditioners in the early 1950's when the Monsanto Chemical Company marketed a patented chemical compound named "Krilium," interest declined because of the uncertainty of the outcome of costbenefit analysis over a wide range of crops and climates. Recently, two symposia were held, one in Ghent, Belgium, in 1975 (De Boodt 1975), and one in Las Vegas, NV, U.S.A., in 1973 (Gardner and Moldenhauer 1975). Also, an entire issue of "Soil Science" was recently devoted to the subject in 1986 (Volume 141). These events occurred after improved formulations of more appropriate polymers invited reexamination of their utility.

Newer soil conditioners have been shown to improve seedling emergence, establishment, growth, and survival (Callaghan and others 1988; Cook and Nelson 1986; Helalia and Letey 1989; Rubio and others 1989, 1990; Wallace and Wallace 1986a, b; Woodhouse and Johnson 1991). However, Hamilton and Lowe (1982) reported decreased germination of tobacco with high levels of polymer application because of crusting. Synthetic conditioners have also been shown to reduce penetrometer resistance (Cook and Nelson 1986; De Boodt 1975; Helalia and Letev 1989; Rubio and others 1989, 1990; Steinberger and West 1991; Terry and Nelson 1986; Wallace and Wallace 1986b), and evaporation, especially in soils with coarse textures (De Boodt 1975; Rubio and others 1990; Woodhouse and Johnson 1991). They also improve some important soil physical properties such as bulk density and aggregate stability (Terry and Nelson 1986), and improve infiltration (Ben-Hur and others 1989; Mitchell 1986; Shainberg and others 1990; Smith and others 1990; Terry and Nelson 1986), leading, in some cases, to reduced soil erosion (De Boodt 1975; Gabriels and De Boodt 1975; Smith and others 1990; Wallace and Wallace 1986c). Some of these soil conditioners are capable of absorbing large amounts of water (Johnson 1984a; Woodhouse and Johnson 1991). Callaghan and others (1988) reported that a synthetic soil conditioner called polyvinyl alcohol almost doubled the field capacity of sandy soil when added at a concentration of 0.5 percent.

Most of the work done with soil conditioners has concentrated on agronomic and horticultural soils (Ben-Hur and others 1989; Cook and Nelson 1986; Terry and Nelson 1986; Wallace and Wallace 1986a). There are very few studies on the use of soil conditioners in rangeland soils (Rubio and others 1989, 1990; Steinberger and West 1991). Even if conditioners stay expensive, there are good possibilities in using them in appropriate rangeland contexts such as mined land reclamation, campgrounds, snow or sand barriers, and roadside revegetation.

The objectives of these studies were to investigate during the 1991 growing season the effects of two kinds of polyacrylamide (cross-linked and non-cross-linked) on crested wheatgrass (Agropyron desertorum) germination, big sagebrush (Artemisia tridentata) tubeling growth, and soil cracking, soil crusting, and soil moisture.

MATERIALS AND METHODS

Polyacrylamide (PAM) is a synthetic soil conditioner that is prepared by acrylamide polymerization (Azzam 1980). The unit structure of PAM is:

Non-cross-linked PAM, (hereafter designated as NC-PAM), trade named "Complete Green" (CG), is an anionic (relatively lower charged) polyacrylamide with a molecular weight of $10-15 \times 10^6$ g/mol (Aly and Letey 1988). This polyacrylamide was obtained from Complete Green Company (Los Angeles, CA).

Cross-linked PAM (hereafter designated CL-PAM) is a very persistent conditioner with a high salt-buffering capacity. It can absorb water up to 40 and 500 times its own weight (Johnson 1984b). This polyacrylamide is also anionic and possesses relatively higher charges. It was obtained from Western Polyacrylamide Inc. (Castle Rock, CO).

Experiment 1

The purpose of this study was to evaluate the effects of PAM on seedling emergence, growth, and survival of crested wheatgrass. Topsoil from a silt loam Xerollic Calciorthid from a Curlew Valley site (Bjerregaard and others 1983) was thoroughly mixed with PAM (0.2 percent by weight) in a cement mixer for 40 minutes. The mixture was then applied in trenches (10 cm wide, 11 cm deep, 270 cm long) on which the seeded furrow was centered. Four replications of each treatment were used. Some furrows received 0.0 PAM (controls). The same numbers of pure live seed of crested wheatgrass were sown in each furrow on June 9. The plot was then sprinkled with well water to saturation on June 9. Germination (percentage of pure live seed emerging) and growth and survival (percentage of plants surviving by the end of the experiment) were monitored daily for the first 2 weeks and less

frequently for the remainder of the growing season. Growth rate was monitored by counting new leaves and height progression of the plants. Weeds on these beds were eliminated weekly through hand cultivation.

Soil moisture was monitored by using time-domain reflectometry (TDR) (Topp and others 1984). Twenty conductors (25 cm long and 5 cm apart) were randomly placed horizontally throughout each trench. Readings of soil water content were taken at times of initiation and the dates listed in table 1.

Volumetric water content (Θ) was calculated following Topp and others (1984):

 $\Theta = -0.053 + 0.0292 \text{ Ka} - 5.5 \times 10^{-4} \text{ Ka}^2 + 4.3 \times 10^{-6} \text{ Ka}^3$

where Ka is the apparent dielectric constant.

 $\mathbf{K}\mathbf{a} = (ctL)^2$

where L is the length of the conductor (mm), c is the velocity of an electromagnetic signal in free space (300 mm/nsec), and t is the travel time of the voltage pulse as measured by TDR (nsec).

The strength of soil crust was measured in the field by a hand-held penetrometer (Brandfort 1986) at 19 random points on each furrow. Soil cracking was quantified following the techniques used by Steinberger and West (1991). Two random sections (10 by 32 cm) in each furrow were photographed using a Polaroid Spectrum System camera. Photographs were analyzed using a digitized image computer analysis program (Sigma-Scan). Length and area of each crack was calculated, then the area was divided by the length to get a comparison between treatments.

Experiment 2

This study was carried out to evaluate the effects of PAM on shrub tubeling growth and survival. Two raised beds (2.4 by 1.8 m and 0.6 m deep) were constructed using railroad ties and filled with the soil from Curlew Valley. PAM (0.2 percent by weight) was mixed with the soil for 40 minutes in a cement mixer and deposited in an augured hole (10 cm wide and between 10 and 50 cm deep). The remainder of the hole and all the control holes were filled with untreated soil and then compacted to densities similar to those in the beds as a whole. Beds were sprinkled with well water on May 7, 1991, before transplanting, to start with a saturated soil.

Table 1Dates at which the soil moisture
readings were taken via TDR
methods for both experiments
1 and 2

Reading number	Date taken		
	June 10, 1991		
2	June 30, 1991		
3	July 5, 1991		
4	Aug. 22, 1991		
5	Aug. 28, 1991		
6	Sept. 4, 1991		
7	Sept. 12, 1991		
8	Sept. 15, 1991		

One-year-old shrub tubelings of big sagebrush were transplanted to equidistant points on a grid having PAM or control soils underneath in both beds on May 12, 1991. Tubelings were grouped into similar size and vigor classes, and then one of each class was randomly assigned to each bed and location within the bed. Each plant received 1,000 ml of water at the time of planting. Nine replications of each treatment were started, but some died or were consumed by insects. Weeds on these beds were eliminated weekly through cultivation. The growth rate, phenological progression, and survival of the shrubs were monitored weekly throughout the growing season.

Soil moisture was monitored under each plant in each bed using TDR. Four conductors (two 25 cm and two 45 cm long and 5 cm apart) were placed vertically under each shrub. Moisture readings were taken by TDR periodically throughout the experiment (table 1). At the end of the experiment, the shrubs were harvested to obtain dry biomass. Cut portions of shrubs were placed in an oven for 24 hours under 48 °C. The roots were also extracted by washing the soil and root mass between the depth of 25 cm and 45 cm using a sieve (4 mm in diameter). The extracted roots were ovendried at 48 °C for 24 hours.

EXPERIMENT 1 RESULTS

Effect of Two PAM Conditioners on Cracking and Penetrometer Resistance—Detailed data on the area/ length cracking ratio and penetrometer resistance on the soil surface are shown in table 2. The area/length cracking ratio on the soil surface in CL-PAM treatments was significantly (99 percent confidence level) greater than that of the control and NC-PAM treatments. However, there was no significant difference between NC-PAM and control treatments. The CL-PAM amendment involves crystals that absorb water and swell. As evaporation takes place, soil surface shrinks back, leading to a greater chance of cracking.

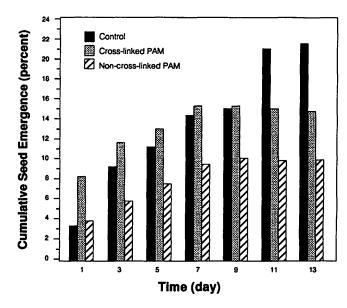


Figure 1—Cumulative seedling emergence of crested wheatgrass as influenced by two PAM conditioners.

The mean penetrometer resistance data show that the surface of the soil crust in the controls had the greatest soil strength (table 2). Both CL and NC-PAM treatments yielded similar less-strong crusts.

Effects of Two Soil Conditioners on Seeding Emergence and Soil Moisture—Seeding emergence of crested wheatgrass was recorded over a 2-week period (fig. 1). Crested wheatgrass seedlings emerged well, both with and without PAM applications, and no significant differences were found among treatments. An invasion of grasshoppers prevented us from following further grass growth past August 2, 1991.

	Replications					
	Treatment	1	2	3	4	Меал
Penetrometer Resistance (kg/cm ²)	Control	2.969 (0.877)	2.201 (0.713)	1.856 (1.117)	2.125 (0.753)	2.288
	Cross-linked PAM	0.739 (0.36)	1.062 (0.547)	1.291 (0.607)	1.154 (0.575)	1.062
	Non-cross- linked PAM	1.335 (0.238)	1.724 (0.537)	l.796 (0.531)	l.604 (0.513)	1.615
Cracking Area/length ratio	Control	0.345 (0.115)	0.245 (0.314)	0.538 (0.312)	0.432 (0.302)	0.390
	Cross-linked PAM	0.447 (0.321)	0.808 (0.464)	0.896 (0.307)	0.758 (0.369)	0.735
	Non-cross- linked PAM	0.434 (0.171)	0.658 (0.229)	0.436 (0.311)	0.467 (0.153)	0.499

Table 2—The influence of two PAM conditioners on penetrometer resistance (kg/cm²) and cracking (numbers within parentheses are standard deviations from the mean¹

LSD (0.01) = 0.159 mean treatment for penetrometer resistance; LSD (0.01 = 0.211 mean treatment, for cracking.

In view of the pronounced soil crusting in the control soil, it was surprising that there was no significant difference in crested wheatgrass seedling emergence among treatments. Contrary to the expectation, seedling emergence was higher on controls (but not significantly) than PAM-treated plots.

Soil moisture content data are presented in figure 2. There were no overall significant differences among treatments in terms of soil moisture. There were, however, fluctuations of moisture level in soils during the 3 months because there were rainfall events on certain days, particularly August 28 and September 12. For this reason, significant differences in soil moisture level were observed among days on all treatments. In view of the pronounced soil cracking on CL-PAM plots, it was surprising that there were no significant differences in soil moisture or water availability among treatments.

EXPERIMENT 2 RESULTS

Effect of Two PAM Conditioners on Soil Moisture— Soil moisture content over 3 months decreased from the first day of measurement to the last day of measurement (fig. 3). There were no significant differences in soil moisture among treatments.

Effect of Two PAM Conditioners on Biomass—Dry big sagebrush aboveground biomass data (table 3) and belowground biomass (table 4) showed no significant differences among treatments. Phenological progression and flower and seed production (data not shown) were also not different between treatments.

SUMMARY AND CONCLUSIONS

Effects of two PAM amendments at one level of concentration (0.2 percent) on one rangeland soil and two plant species were investigated. Soil cracking, penetrometer resistance, and moisture levels were investigated in the field. In addition, root density of big sagebrush and phenological progression, flowering, and fruiting were quantified.

Contrary to expectations from literature, the two PAM treatments did not improve total emergence of crested wheatgrass. Larger soil cracks were present in the two PAM treatments compared to the controls. The two PAM treatments also had lower penetrometer readings than the controls, showing the effect of these conditioners in ameliorating crusting. Both field experiments showed,

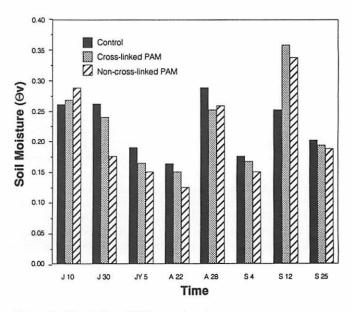


Figure 2—Effect of two PAM amendments on soil moisture content. (J = June; JY = July; A = August; S = September).

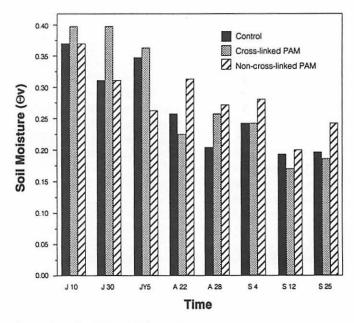


Figure 3—Effect of two PAM conditioners on soil moisture at 25 to 45 cm of depth. (J = June; JY = July; A = August; S = September).

Table 3—The effect of two PAM conditioners on sagebrus	sh dry aboveground biomass (gm)	
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Treatments	Replications						
	1	2	3	4	5	6	7
Control	27.7	43.6	5.8	25.8	15.6	28.4	40.8
Cross-linked PAM	6.4	47.8	0.6	42.5	9.5	9.1	57.3
Non-cross-linked PAM	32.6	42.0	14.6	4.4	12.6	56.7	50.7

Table 4-The effect of two PAM conditioners on sagebrush dry root biomass (gm)

•				R	eplications				
Treatments	1	2	3	4	5	6	7	8	Mean
Control	1.4	0.8	1.1	1.9	0.3	0.3	0.97	(')	0.97
Cross-linked PAM	0.1	0.3	0.6	1.1	2.8	0.7	2.8	2.9	1.41
Non-cross-linked PAM	2.8	3.1	0.4	0.05	0.6	2.9	2.8	1.8	1.81

¹Missing data; plant defoliated by harvester ants on June 24, 1991.

however, that the two PAM conditioners did not improve soil moisture or have any significant effect on sagebrush tubeling growth, phenological progression, flowering, seed production, and root density. Sample sizes in both experiments were small and variances high, and thus, Type II errors may have been incurred.

Any future studies of PAM conditioners should employ increased sample sizes and take into consideration different application rates of these synthetic conditioners. Further chemical properties of soil also should be tested for interactions with PAM.

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FACTORS INFLUENCING POSTFIRE SAGEBRUSH REGENERATION IN SOUTH-CENTRAL IDAHO

Mike Boltz

ABSTRACT

Sagebrush seedling establishment appeared to be strongly related to moisture availability as influenced by ecological site, soil surface texture, herbaceous competition, microtopography, seedling year precipitation, exposure, position on slope, etc. Many of the same factors influence seed source availability following wildfire and likelihood of reburn prior to maturity. Compaction planting methods show promise for enhancing seedling establishment.

INTRODUCTION

Like many portions of the Intermountain region, the Jarbidge Resource Area (JRA) of the Boise District, Idaho, Bureau of Land Management (BLM), has experienced a major vegetation conversion from big sagebrush (Artemisia tridentata) communities to herbaceous communities. Since 1973, wildfires have converted over 740,000 acres of the 1,690,473 acres of public land within the JRA from shrub to herbaceous vegetation. From 1971 to 1986, over 9 percent of the previously burned areas reburned, with additional large reburns in 1987. About 343,000 acres were reseeded for Emergency Fire Rehabilitation (EFR) during this period, primarily to herbaceous species. Some shrubs, particularly fourwing saltbush (Atriplex canescens). were included in these seed mixes, but generally did not establish in sufficient densities to mitigate the ongoing shrub loss. Large fires and accelerated fire frequencies in previously burned areas suggested that natural redevelopment of sagebrush communities on burned lands might not meet Jarbidge Resource Management Plan wildlife habitat objectives. Large-scale loss of shrub habitats and attendant public controversy regarding land treatment proposals in the Jarbidge Resource Management Plan prompted a 1987 reevaluation of JRA EFR practices as a component of the Jarbidge Sagebrush Management Plan. The Jarbidge Sagebrush Management Plan, consisting of a Normal Fire Rehabilitation Plan and a Greenstripping Plan, was designed to maintain sagebrush communities on newly burned sites and reduce the rate of conversion to herbaceous communities by fire.

To evaluate the need for large-scale replanting of big sagebrush, it was necessary to assess the natural regeneration potential of big sagebrush within the JRA. A 1985 attempt to use bioassay of soil samples from a recently burned area did not provide a reliable indication of sagebrush regeneration potential. Consequently, ecological site-based predictors were developed based on observed responses following fires to assess the need for inclusion of big sagebrush in EFR seed mixes. Degree of annual infestation, soil and climatic conditions, and the influence of reburns were also examined. Sagebrush reinvasion following fires was compared to that following other types of sagebrush control treatments to evaluate the premise that sagebrush would reinvade large burns as reliably as on other types of treatments.

In 1986, duplicate big sagebrush planting trials were established at two sites representative of the major ecological sites that are most vulnerable to wildfires. The trials were established by the Boise District in conjunction with Steve Monsen of the Forest Service, Intermountain Research Station, Shrub Sciences Lab and Marshall Haferkamp of the Agricultural Research Service. Evaluation of the trials was completed at the Shrub Sciences Lab. The results of these trials were integrated with the site-based predictors and the Jarbidge Resource Management Plan objectives in developing the EFR prescriptions in the Jarbidge Sagebrush Management Plan.

The 1986 trials indicated that standard reseeding equipment (drills) would not dispense big sagebrush seeds consistently at an adequate rate due to inadequate agitation, small aperture size, and seed tube blockage. At that time, results of the few aerial applications had been poor or were difficult to differentiate from natural regeneration. The 1986 trials also suggested that sagebrush establishment was enhanced by cultipacking into the soil surface. Consequently, the Boise District developed a sagebrush seeder that incorporated a fertilizer spreader, anchor chain or tire drags, and a vine-roller cultipacker.

STUDY AREA AND METHODS

The Jarbidge Resource Area is located in south-central Idaho in Elmore, Owyhee, and Twin Falls Counties. The JRA is subdivided into a number of historic grazing administrative units, such as the Saylor Creek Unit. The majority of the JRA is located south of the Snake River between the Bruneau River, Salmon Falls Creek, and the Humboldt National Forest boundary to the south in Nevada, with a smaller portion located north of the Snake River between King Hill and Bennett Creeks. The plant communities and associated ecological sites within the JRA are shown in table 1.

Salt desert shrub (SDS) communities, which include the shadscale (Atriplex confertifolia), winterfat (Ceratoides

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Table 1—Plant communities and associated ecological sites in the Jarbidge Resource Area.	Site abbreviations are used in the figures in this
paper. Other abbreviations used in the figures are defined in text	

Plant community	Ecological site	Abbreviation CL7-10	
Shadscale/Indian ricegrass	Calcareous Loam 7-10		
Winterfat/Indian ricegrass	Silty 7-10	S7-10	
Nuttall saltbush/Indian ricegrass	Saline Silty 7-10	SS7-10	
Greasewood/basin wildrye	Saline Bottom 8-12	SB8-12	
Wyoming big sagebrush/Thurber needlegrass	Saline Upland 7-12	SU7-12	
Basin big sagebrush/Indian ricegrass	Sand 8-12	S8-12	
Wyoming big sagebrush/Indian ricegrass	Sandy Loam 8-12	SL8-12	
Wyoming big sagebrush/Sandberg bluegrass	Loamy 7-10	L7-10	
Wyoming big sagebrush/Thurber needlegrass	Loamy 8-10	L8-10	
Wyoming big sagebrush/bluebunch wheatgrass	Stony Loam 8-12	SL8-12	
Wyoming big sagebrush/bluebunch wheatgrass	Loamy 10-12	L10-12	
Wyoming big sagebrush/bluebunch wheatgrass	Loamy 10-13	L10-13	
Mountain big sagebrush/bluebunch wheatgrass	Loamy 12-16	L12-16	
Mountain big sagebrush/bluebunch wheatgrass	South Slope 12-16	SS12-16	
Basin big sagebrush/basin wildrve	Loamy Bottom 12-16	LB12-16	
Basin big sagebrush/Idaho fescue	Loamy Upland 12-16	LU12-16	
Black sagebrush/bluebunch wheatgrass	Shallow Calcareous Loam 10-16	SCL10-16	
Low sagebrush/Idaho fescue	Shallow Claypan 12-16	SC12-16	
Mountain big sagebrush/bluebunch-fescue	Loamy 13-16	L13-16	
Mountain big sagebrush/Idaho fescue	Loamy 16+	L16+	

lanata), Nuttall saltbush (Atriplex nuttallii), and greasewood (Sarcobatus vermiculatus) communities, comprise only a small portion of the JRA, and are localized on the Bruneau Arm and along the Snake River Canyon. The low (Artemisia arbuscula), black (Artemisia nova), and mountain big (Artemisia tridentata ssp. vaseyana) sagebrush communities occur at higher elevations on Bennett Mountain and near the Nevada border.

Each Site Writeup Area (SWA) defined by the 1981-83 inventory was classified into present plant communities based on the overstory and understory dominants based on composition by weight. SWA's normally include only one seral community of one ecological condition class of one ecological site. However, some SWA's are complexes of single seral plant community/condition class/ecological site units. Seedings were classified by the composition by weight of annual grasses and seeded species. Vegetation that was predominantly cheatgrass (*Bromus tectorum*) or medusahead (*Taeniatherum asperum*) was classified as annual communities.

The ecological site classification was plotted on a half inch per mile scale base map and overlays of the present plant communities (1981-83), post-1971 fires, and land treatment projects were prepared. The project/fire segment was the sampling unit for evaluating (1) frequency of sagebrush reinvasion, (2) percent reburn, and (3) percent shrub survival within exterior fire and/or land treatment project boundaries. Each project/fire segment included (1) only one ecological site or complex of ecological sites, (2) only one uniform pretreatment community, (3) only one uniform sagebrush control or reseeding treatment, which was applied at only one point in time, and (4) only one posttreatment plant community or plant community complex (SWA). The boundaries of these project/fire segments were determined by the overlap of the fire, project, and plant community overlays and the base map so that the conditions were met simultaneously.

The plant communities from the 1963 Saylor Creek Unit inventory were plotted on a half inch per mile scale overlay to evaluate the conversion of sagebrush to herbaceous vegetation between 1963 and 1981. The Saylor Creek Unit has had the most extensive sagebrush losses to wildfire in the JRA and therefore lends itself to analysis of landscape changes through wildfire. The location, extent, and dominant species composition of the plant communities were contrasted for the 1963 and 1981 overlays. All other old (1955-65) inventory plats were compared with the JRA fire map, project files, and the 1981-83 inventory overlay to determine the extent of wildfires and dominant species composition of prefire communities in other administrative units prior to 1971. Comparison of this information indicated that there were few major range fires prior to 1971 in all administrative units except Saylor Creek. Most fires that did occur prior to 1971 in the other administrative units were documented by project files. The widespread conversion of sagebrush to herbaceous vegetation in the other administrative units after 1971 could therefore be evaluated without significant bias. (No fire maps were made prior to 1971.)

The area of mature shrub communities surviving each fire expressed as a percentage of the total area within exterior fire boundaries was determined from: (1) previous calculations by the inventory within burned SWA's; (2) digitizer measurements of the overlays for each ecological site within fire boundaries; or (3) ocular estimates of relative cover on the overlays for each ecological site within fire boundaries.

The post-1963 and post-1971 reburn statistics were derived from an overlay of fire frequency for fires between 1971 and 1985. The percent reburn for all areas burned prior to 1963 was estimated ocularly as a percent of the total area within exterior fire boundaries for each post-1971 fire within the Saylor Creek Unit. Ocular estimates were based upon the midpoints of three cover classes (0-25 percent, 26-75 percent, 76-100 percent), 0, and 100 percent. Evidence of burning prior to 1963 was provided by dominance of nonseeded herbaceous vegetation or by project records. The percent reburn since 1971 for each post-1971 fire in the entire JRA was determined in a similar manner. The database includes all fires after 1971 but prior to the time a given site was inventoried between 1981 and 1983.

Percent reburn, percent shrub survival, fire acreages from the Boise District fire records, and dominant species composition of prefire communities were used to estimate acreage converted from shrub to herbaceous vegetation by each fire. The Site Writeups (descriptions of seral community floristic composition by weight) were used to determine sagebrush composition by weight for each burned, plowed, sprayed, or chained SWA. Personal knowledge also tempered evaluation of sagebrush reinvasion based solely on the Site Writeups, particularly for projects that were relatively new at the time of the inventory.

The 1986 planting trials were conducted on previously sagebrush-dominated sites near Wintercamp (Crows Nest) and Three Creek Well in Owyhee County, ID, which had initially burned in 1985. Crows Nest, a Loamy 8-10 site on Purdam-Power-Elijah silt loams (Noe 1991), was previously in poor ecological condition. Three Creek Well, a Loamy 10-13 site on Heckison-Big Flat-Inside Desert silt loams (Harkness 1992), was previously in fair to good ecological condition. Both sites were reburned with a propane field flamer to control cheatgrass competition, recreate newly burned conditions, and facilitate identification of planted sagebrush seedlings. This was done at Crows Nest in May 1986 and at Three Creek Well in September 1986. Half of each of the two sites was disked by a diskchain to compare burned/plowed and burned pretreatments. The replicated planting treatments were: broadcast/anchor chained, disk-chained/broadcast, broadcast/imprinted, cultipack seeder, rangeland drill, and broadcast without coverage. In November 1986, Wyoming big sagebrush (Artemisia tridentata ssp. wyomingensis) and Nordan crested wheatgrass (Agropyron desertorum) were planted at average rates as shown in table 2.

Every effort was made to dispense the seed at equivalent rates with all reseeding equipment. Soil conditions were moist to wet at planting at Three Creek Well and moist to surface dry at Crows Nest. These trials applied variable treatments to relatively uniform sites. Cheatgrass cover and frequency and density of seeded and native species were measured in 40 randomly placed one square meter quadrats in each replication (two per site) of each treatment at both sites. Measurements were made in May 1987.

The Poison Springs, Solosabal, and Pothole Reservoir sites are located near Glenns Ferry, ID. They were previously sagebrush-dominated, but all burned initially in June 1987. Poison Springs is a Loamy 10-12 site on Trosi-Chilcott-Tenmile gravelly loams; Solosabal is a Loamy 8-10 site on Owsel-Purdam silt loams (with inclusions of

Table 2—Average seeding rates	at Crows	Nest and	Three C	Creek
Well sites				

	Low ra	ate	High rate			
Study site	Artrw(PLS)	Agde	Artrw(PLS)	Agde		
	Lb/acre					
Crows Nest	0.38	13.96	1.18	9.36		
Three Creek Well	.58	21.42	1.14	11.16		

Sandy Loam 8-12 on Xeric Torriorthents); Pothole Reservoir is a Loamy 8-10 site on Colthorp-Chilcott-Elijah-Purdam-Scism silt loams (Noe 1991). All three sites were previously in poor ecological condition. In December 1987 and January 1988, mixed Wyoming, mountain, and basin (Artemisia tridentata ssp. tridentata) big sagebrush seed lots were applied at the Poison Springs site and mixed basin and Wyoming big sagebrush seed lots were applied at the Solosabal and Pothole Reservoir sites. All seed lots were sold as Wyoming big sagebrush, but were contaminated with other subspecies. The overall application rate was 6.2 lb/acre bulk (0.7 lb PLS/acre). The sagebrush was applied directly with the Jarbidge Sagebrush Seeder (anchor chain drag) to moist or frozen seedbeds that had been drilled earlier under dry conditions. These plantings applied a relatively uniform treatment to varied microsites.

The Solosabal and Poison Springs sites were intensively evaluated in June 1988. Five 50-m transects were established at each of three subareas at the two sites. Understory and seeded species were rated by frequency, density, and percent ground cover in 30 1-square-meter plots along the first 10-m, third 10-m, and fifth 10-m intervals of each 50-m transect. Sagebrush seedling density was measured using a rating system to expedite counting of individuals. Consequently, the estimated densities may be higher than the actual densities.

Studies on plowed greenstrips used a 100-foot baseline transect running parallel to the seeding treatment. One 50-foot-long belt was randomly selected and permanently marked within each 20-foot interval along the baseline, running at a 45-degree angle to the baseline. Nested plot frequency and plot density were sampled at 5-foot intervals along the belts within a 50- by 50-cm nested plot frequency frame. Point cover was sampled on the four tips of the frame. Finally, densities of shrubs were counted in five 1/100-acre plots.

Statistical analysis included complete factorial analysis for sagebrush seedling densities, and ANOVA for 1986 trial seeding rates and sagebrush survival among ecological sites. Frequency of sagebrush reinvasion by ecological site, control treatment, and pretreatment vegetation and sagebrush seedling frequency by plot were analyzed by chi-square tests of independence.

RESULTS AND DISCUSSION

The average yearly reburn rate of previous fires for each major ecological site or similar group of sites is shown in figure 1. The percent reburn was estimated for

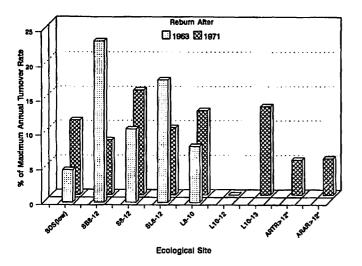


Figure 1—Average reburn of previous fires in the JRA as a percent of the maximum annual turnover rate (6.67 percent) for replacement of mature sagebrush stands in 15 years. Abbreviations for ecological sites are as shown in table 1 and in the text.

each fire as a whole rather than independently for each included ecological site within exterior fire boundaries. However, only fires that included the ecological site in question were included in the average. Although there is considerable separation among ecological sites among geographical groups of fires, the lack of independence in the data among ecological sites does not permit statistical analysis. The ecological sites are arranged in the approximate relative order of moisture availability and phenological development considering soil depth, texture, and precipitation zone. Both factors influence both the length of the fire season and the pattern of burning, which, in turn, influence probability of reburn and amount of sagebrush survival as islands and as individuals. The average yearly reburn rate shown in figure 1 is calculated as a percentage of 6.67 percent to compare the different time periods and magnitude of reburn. An annual reburn rate of 6.67 percent of a given area assuming no overlap of successive reburns would completely reburn the area by the end of 15 years. Since it takes a minimum of 15 years to redevelop a mature stand of sagebrush, a reburn rate much over 6.67 percent would probably prevent mature stands from redeveloping even if seedling establishment occurred.

In the Saylor Creek Unit, the average yearly reburn rate between 1963 and 1981 apparently differed among ecological sites. The probability of reburn was higher on the Sandy Loam 8-12 and Saline Bottom 8-12 ecological sites. Shrub communities on these ecological sites and on the Sand 8-12 site were already highly disturbed and invaded by cheatgrass, and a relatively large portion of them had already burned in 1963. The probability of reburn was relatively low on salt desert shrub (SDS-low) sites, which occur primarily on steep slopes and broad, very coarse-soiled ridgetops and support less fine fuel than the other ecological sites (Noe 1991). These include Nuttall saltbush, winterfat, and shadscale communities. Few of these had burned prior to 1963. The Loamy 8-10 sites were less highly disturbed, and had experienced relatively few fires prior to 1963. None of the other ecological sites are found in the Saylor Creek Unit.

In the JRA as a whole, no strong differences were observed in the average yearly reburn rate among ecological sites from 1971 to the date of inventory. This partially reflects the lack of independence in the data in that many of the same large fires were included in the statistics for each ecological site in the 7- to 13-inch precipitation zone. However, the fire frequency overlay indicated that the probability of reburn tended to increase after initial conversion of large areas of sagebrush to herbaceous vegetation, and geographically separated reburn "hotspots" developed. This is somewhat evident for the SDS-low group of ecological sites, and the Sand 8-12, the Loamy 8-10, and the Loamy 10-13 ecological sites in figure 1.

The probability of reburn tends to be lower than average for mountain and basin big sagebrush sites (ARTR>12"), which receive over 12 inches of annual precipitation. The black and low sagebrush sites(ARAR>12") also have a lower than average probability of reburn. These low sagebrush and low-black sagebrush intergrade sites generally have low productivity, particularly of fine fuel (Harkness 1992; Noe 1991), and are in better ecological condition than lower precipitation ecological sites, with little cheatgrass invasion. The low incidence of reburn on the Loamy 10-12 site is attributed to the small area occupied by the site and the good road access and availability of fuel breaks where it occurs. In general, sagebrush regeneration potential based on reburn probability is relatively poor on the Sand 8-12, Sandy Loam 8-12, Loamy 8-10, and Loamy 10-13 ecological sites, and relatively good on low and big sagebrush sites that receive over 12 inches of annual precipitation.

The average percent of the area within fire boundaries occupied by unburned fingers and islands of mature sagebrush communities (black bars) or mature mixed big sagebrush/salt desert shrub communities (dotted bar) at inventory is shown in figure 2. Sparse fuels and broken topography tend to retard fire spread on most of the salt desert shrub (SDS) sites, and to promote patchy burning. The relatively low survival of mature sagebrush communities on the Sandy Loam and Sand ecological sites in the 8- to 12-inch precipitation zone reflects the same factors influencing the probability of reburn there; namely, low moisture availability, accelerated phenological maturity, and greater annual grass invasion. However, the higher incidence of reburn alone did not account for lower survival, as the majority of the initial burns in sagebrush on these two sites did not reburn prior to the inventory. The greater survival of sagebrush within fire boundaries on the Loamy 7-10, 8-10, and 10-13 ecological sites reflects less continuous fuels (less cheatgrass) (Whisenant 1990), a generally lower frequency of reburn, and a somewhat longer green period. Site conditions are somewhat cooler and moister, and the soils have higher available water capacity (AWC), lower permeability, or both (Harkness 1992; Noe 1991). The Loamy 10-12 site has a greater than average cheatgrass composition due to its location in a highly disturbed setting.

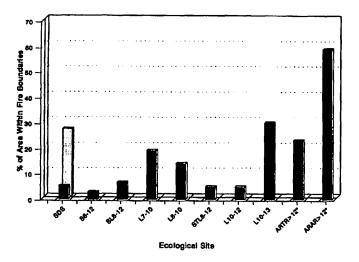


Figure 2—Average sagebrush survival as average percent of total area within exterior fire boundaries that was mature sagebrush at inventory. Abbreviations for ecological sites are as shown in table 1 and in the text. Means were significantly different ($F = 6.42^{\circ}$, P = 0.00).

Incidence of reburn was low on big and low/black sagebrush sites receiving over 12 inches of annual precipitation, except around Cedar Butte. Cheatgrass is relatively insignificant on these sites, which include the bulk of the fair or better ecological condition communities in the JRA. Survival of substantial areas of sagebrush within fire boundaries reflects the relatively long green period, less continuous fine fuels, and interspersion of the two types of ecological sites. The low/black sagebrush sites tend to serve as fuel breaks in all but the most extreme burning conditions.

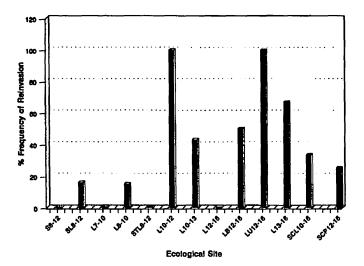


Figure 3—Frequency of occurrence of sagebrush composition exceeding 5 percent by weight for burned and reseeded project segments. All segments were previously sagebrush-dominated and did not reburn. Abbreviations for ecological sites are as shown in table 1. Frequencies were significantly different among sites ($\chi^2 = 22.74^*$, P = 0.05).

Figure 3 is based on the Site Writeups for burned and seeded project segments that did not reburn prior to the inventory. Sagebrush reinvasion/survival as individuals was considered absent for segments that lacked sagebrush or had less than 5 percent sagebrush composition by weight. Since the same Site Writeups were often used for both reburned and nonreburned communities, or reflected only the earliest stages of postfire succession, personal knowledge of the vegetation was also used to determine whether significant sagebrush reinvasion had occurred.

Natural sagebrush survival as individuals/reinvasion by seed was poorest on the driest sites, evidently reflecting more uniform burning and lower seed survival and availability (Bunting 1985; Young and Evans 1987), or harsher growing conditions for seedlings (Britton and Clark 1985). Poor interspersion of surviving sagebrush plants on cleanly burned areas further retards reinvasion by seed. Since the sandy big sagebrush sites have the lowest, most erratic precipitation, the lowest AWC, and most rapid surface soil permeability (Noe 1991), the availability of surface soil moisture is relatively brief and undependable. The loamy big sagebrush sites in the 7- to 10-inch precipitation zone also had a low frequency of survival/reinvasion in spite of more favorable soil/climatic characteristics. The loamy big sagebrush sites in the 10- to 13-inch and 12- to 16-inch precipitation zones and the low and black sagebrush sites in the 10- to 16-inch precipitation zone had a higher frequency of survival/ reinvasion. These big sagebrush sites have a moderate to high AWC and moderately slow to slow permeability, while the low and black sagebrush sites have a very low to moderate AWC and slow permeability (Harkness 1992; Noe 1991). Surface soil moisture availability to seedlings is relatively dependable on these sites. This pattern is reasonable in light of the fact that big sagebrush seeds require saturation of the surface soil for germination (Weldon 1956).

Figure 4 is based on the frequency of occurrence of sagebrush composition by weight within the specified composition limits in Site Writeups for burned areas. The pattern is similar to figure 3, but excludes noninventory information and includes Site Writeup data for reburned areas and for both seeded and unseeded burns. There is no significant difference in the frequency of nonreinvasion of seeded and nonseeded burns by ecological site (p = 0.05). The drier ecological sites generally have less sagebrush survival/reinvasion on burned sites than the moister ecological sites, with the exceptions of the Saline Upland 7-12 and the Calcareous Loam 7-10 sites. Fires on these two ecological sites probably burned less completely due to low continuity and production of herbaceous fuels, and the sagebrush may represent plants that survived the fires. Big sagebrush survival/reinvasion comprising over 25 percent of total production was not observed on sandy sites, salt desert shrub sites, or loamy big sagebrush sites averaging below 9 inches of annual precipitation. Sagebrush must regenerate from soil seed reserves on sites without significant survival of mature plants (Johnson and Payne 1968; Mueggler 1956). The harsher the site conditions, the more unlikely is the establishment of adequate stands of shrubs from the soil seed reserves alone (Britton and Clark 1985).

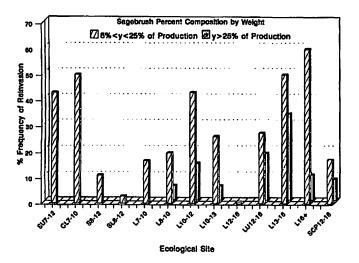


Figure 4—Frequency of occurrence of sagebrush composition by weight in specified composition classes from Site Writeups for burned areas, both seeded and unseeded. Abbreviations for ecological sites are as shown in table 1. Frequencies were significantly different among sites ($\chi^2 = 48.87^*$, P = 0.05).

Figure 5, like figure 3, represents burned and seeded project segments. Prefire sagebrush communities with predominantly bare ground or perennial grass understories were considered to have low cheatgrass levels, while prefire sagebrush communities with predominantly cheatgrass understories (particularly in the interspaces) were

considered to have moderate cheatgrass levels. Previously burned or plowed areas dominated by cheatgrass and lacking a significant sagebrush overstory were considered to have high cheatgrass levels. The frequency of sagebrush reinvasion following fire was significantly higher for sagebrush communities with a minimal cheatgrass component than for sagebrush communities with a cheatgrass understory or for previously burned areas dominated by cheatgrass. This could reflect (1) cleaner burns and poor interspersion of surviving sagebrush plants due to more continuous fuels on infested sites, (2) a much greater number of safe sites on and slower cheatgrass occupation of previously uninfested burned communities, and (3) typically lower cheatgrass levels on ecological sites receiving over 10 inches of annual precipitation.

Figure 6, like figures 3 and 5, represents reseeding project segments that did not reburn. The sandy and loamy Wyoming big sagebrush sites in the 7- to 13-inch precipitation zone received most of these treatments. The burned treatment had significant (≥5 percent of composition by weight) sagebrush reinvasion significantly less often, while the plowed treatment had significant sagebrush reinvasion significantly more often than expected. Reinvasion on the chained and sprayed treatments was not significantly different from the expected. While the chained treatments (11 years), sprayed treatments (13 to 26 years), and plowed treatments (11 to 28 years) were considerably older than the burned treatments (1 to 26 years) at the time of the inventory, most of the burned treatments still lacked a detectable sagebrush component in 1987-89 (over 5 to 9 years after the fire). Project segments that developed a significant sagebrush component

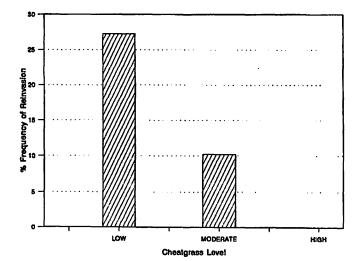


Figure 5—Frequency of occurrence of sagebrush composition exceeding 5 percent by weight for burned and reseeded project segments. All segments were previously sagebrushdominated and did not reburn. Cheatgrass levels are defined in the text. Frequencies were significantly different among levels ($\chi^2 = 8.45^*$, P = 0.05).

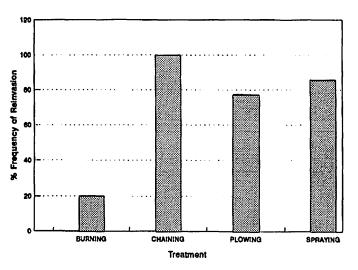


Figure 6—Frequency of occurrence of sagebrush composition exceeding 5 percent by weight for reseeded project segments. All segments were previously sagebrush-dominated and did not reburn. Frequencies were significantly different among sagebrush control treatments ($\chi^2 = 49.32^{**}$, P = 0.05).

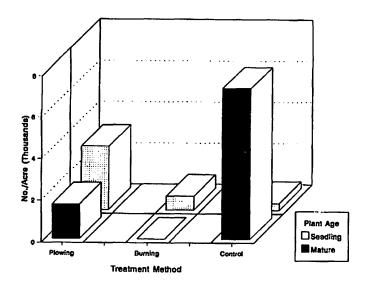


Figure 7—Average densities of mature and seedling Wyoming big sagebrush plants. Treatment means were significantly different ($F = 27.06^{\circ}$, P = 0.00) for mature plants and did not differ (F = 0.75, P = 0.48) significantly for seedlings.

after the inventory were classified as reinvaded based on these later inspections. The relatively low threshold (5 percent) used in the analysis also tended to minimize differences between treatment ages. Chaining, spraying, and plowing tend to have lower sagebrush mortality (Marquiss 1967; Taha 1972) and better interspersion of surviving plants than burning, and those control treatments or the subsequent reseeding operation may even plant whatever sagebrush seed is present, especially if done in the fall (Bleak and Miller 1955). The lack of a significant seed source on site during the first year after disturbance when the site is relatively open would appear to be a major factor retarding sagebrush reinvasion of treated sites (Bartolome and Heady 1978; Bunting 1985; Mueggler 1956).

Figure 7 shows mature and seedling big sagebrush densities on plowed/seeded, burned/seeded, and untreated Loamy 8-10 and Loamy 10-12 sites that had low and moderate cheatgrass levels prior to treatment. Figure 7 illustrates the differences in degree of sagebrush mortality and seedling density between plowed and burned treatments, even though seedling densities are not significantly different among treatments. These results support those shown in figure 6.

To sum up figures 1 through 7, burned big sagebrush sites receiving less than 10 inches of annual precipitation, particularly if the understory was cheatgrass-dominated, have an unsatisfactory probability of sufficient natural regeneration to restore prefire sagebrush cover and structure in a timely manner. This is due to: (1) inadequate soil seed reserves and poor survival of well-distributed mature plants to serve as a seed source; (2) the combined impacts of erratic and low precipitation, soil texture and depth, and herbaceous competition on moisture availability to sagebrush seeds and seedlings; and (3) higher loss of young sagebrush plants to subsequent reburns.

Figure 8 shows the results of the fall 1986 seeding trials at the Crows Nest study site (Loamy 8-10). Permeability was moderately slow to slow, and the AWC was moderate at both sites. The burned pretreatment resulted in very low levels (2.2 percent average cover) of cheatgrass competition during the seedling year. The disk-chained pretreatment and planting treatments tended to have higher cheatgrass cover (6.0 percent average cover), but neither level interfered with establishment of the seeded species. March and May 1987 each received slightly over 1 inch of moisture, but the 4.99 inches of precipitation received was only half of the average at the nearby Horse Butte weather station. It appears that the unusually low precipitation and the effects of the planting treatments themselves on seeding rate, planting depth, and seedbed moisture characteristics were responsible for the low and erratic densities of big sagebrush seedlings.

The low densities of sagebrush seedlings on the diskchain and rangeland drill treatments could be partially explained by the significantly lower than average seeding rates achieved by these treatments (p = 0.10). Planting depths were probably more variable for the drill, disk-chain, and anchor chain treatments. The average planting depth was potentially greatest with the rangeland drill, since the other treatments used surface broadcasting. The relatively high soil disruption of the disk-chain treatment may have allowed deeper penetration/burial of part of the seed. The anchor chain coverage treatment also had the potential to bury at least some of the sagebrush seed rather deeply by dragging dirt over it under the dry surface soil conditions. These effects may have been magnified on the relatively

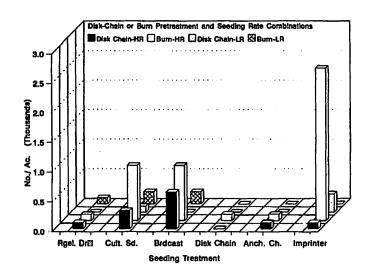


Figure 8—Average densities of Wyoming big sagebrush seedlings by seeding treatment, pretreatment, and seeding rate for fall 1986 at the Crows Nest site. The imprinter treatment mean was significantly higher than for other treatments, the burned pretreatment mean was significantly higher than the disk-chain pretreatment mean, and the high seeding rate (HR) mean was significantly higher than the low seeding rate (LR) mean (p < 0.05 for all). The seeding rate and pretreatment effects were primarily due to the imprinter treatment. loose disk-chained pretreatment, particularly under relatively dry conditions during treatment. Big sagebrush seedlings emerge poorly from soil depths over one-fourth inch (Plummer and others 1968).

The broadcast only, anchor chain, and drill treatments relied in concept much more on overwinter settling to provide good soil-seed contact than did the cultipacker, imprinter, or disk-chain treatments. Soil moisture was adequate at treatment to allow formation of depressions by these compaction treatments, which helped store and concentrate the available moisture through the seedling year. The imprinter and cultipacker were especially effective on the burned pretreatment, which required less pressure for creation of stable depressions. In reality, the disk-chained seedbed was looser than that of the other two compaction treatments, and much of the seed fell behind the roller bar and did not receive compaction planting. Good soil-seed contact should promote germination by prolonging saturated soil conditions around the seeds. This should become more important as seedling-year precipitation declines or as surface soil permeability increases. Lack of seed coverage could hinder good soil-seed contact, but excessive planting depth could prevent emergence.

The broadcast-only treatment yielded substantial numbers of seedlings on both the burned and disk-chained pretreatments. The disk-chained pretreatment offered many depressions to trap the seed and concentrate the available moisture, and the relative looseness probably promoted seed coverage by overwinter sloughing. The majority of the seed broadcast on the burned pretreatment remained on the soil surface in absence of a coverage treatment. Some of it undoubtedly fell into soil cracks at planting or over the course of the dry winter. Moisture accumulation around playettes may have played a role in promoting germination.

Figure 9 shows the results of the fall 1986 seeding trials at the Three Creek Well study site (Loamy 10-13). The Wyoming big sagebrush seedling densities at this site were lower, the average cheatgrass cover was very low (0.5 percent), and competition from native perennial species was much higher than at Crows Nest. This site had been in better ecological condition and had higher site potential, resulting in much greater natural recovery of perennial herbaceous species than at Crows Nest. There were no significant differences between the disked and burned pretreatments, or the seeding rates, or among the planting treatments. However, the disk-chain pretreatment tended to have higher big sagebrush seedling densities, probably reflecting some reduction in herbaceous competition. This was particularly true for the broadcastonly treatment. The actual seeding rate for the drill and disk-chain treatments (low rate only) was significantly lower (p = 0.10) than for the other treatments. Few of the planted seedlings were in evidence the second year, probably because of excessive herbaceous competition. The results suggest that high herbaceous competition for moisture can offset the benefits of more favorable ecological site characteristics for sagebrush seedling establishment.

For the fall 1987 plantings, the Loamy 8-10 ecological site (Solosabal) had a considerably lower frequency of occurrence of big sagebrush seedlings than the Loamy 10-12 site (Poison Springs), but there was high variability

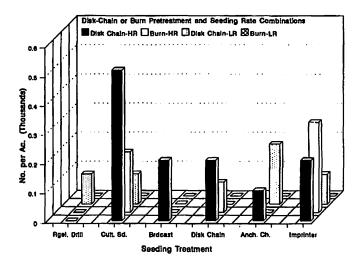


Figure 9—Average densities of Wyoming big sagebrush seedlings by seeding treatment, pretreatment, and seeding rate for fall 1986 plantings at the Three Creek Well site. There were no significant differences (p < 0.05) between disk-chain and burn pretreatments, seeding rates, or seeding treatments. Seeding rate abbreviations are the same as in figure 8.

among subareas at both locations (fig. 10). Precipitation was slightly above average for March, April, and May of the seedling year, but overall averaged only 78 percent of normal. The soils at the Loamy 8-10 site are deep and have a high AWC and moderately slow permeability, with the exception of Sandy Loam 8-12 inclusions on the steep

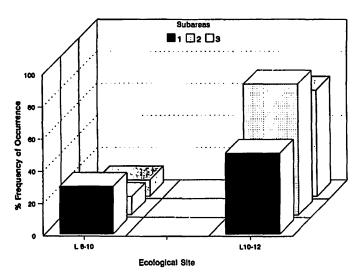


Figure 10—Frequency of occurrence of sagebrush seedlings by plot on two burned sites replanted in fall 1987 with the Jarbidge Sagebrush Seeder. Both sites were previously sagebrushdominated. The 0.7-lb/acre PLS seeding rate was between the low and high seeding rates of the 1986 plantings. Frequencies by plot were significantly different among subareas ($\chi^2 =$ 29.66*, P < 0.05).

slopes (Noe 1991). The subarea with the highest seedling frequency on the Loamy 8-10 site was at the base of a northeasterly slope. The other two subareas were located on a level bench with a slight easterly slope and high on the steep northeasterly slope, respectively. Inclusions of the Sandy Loam 8-12 site with their lower AWC and moderately rapid permeability had few or no seedlings, as did well-drained ridgetops and southerly exposures of the Loamy 8-10 site. In some portions of the project, the only seedlings that established were in drainage channels. Seedling year cheatgrass cover was much higher (38.3 percent), but more typical of burned sites than at Crows Nest or Three Creek Well. Perennial cover averaged 7.8 percent. There was still no significant correlation between the numbers of big sagebrush seedlings and understory composition. Natural regeneration was absent.

The general exposure at the Loamy 10-12 site is to the southwest. Rock outcrops and stone nets are frequent, the topography is more broken, and the soils are shallower than on the Loamy 8-10 site. Many of the narrow ridgetops have a gravelly surface layer, which supports relatively little herbaceous growth. The gravelly areas are interspersed with pockets of loam, sandy loam, and sand surface texture. The AWC of the soils is low to moderate with slow to very slow permeability due to depth or surface texture (Noe 1991). The subarea with the highest seedling frequency was on a southwesterly ridgetop with a loamy surface soil well interspersed with gravelly loam and stone nets in the drainages. The subarea with the second-highest seedling frequency was in a pocket of loamy surface soil at the base of a northerly exposure. The other subarea was on a broad loamy ridgetop with few pockets of gravelly loam. Some plants also became established on gravelly ridgetops, on pockets of sandy soil, and even among the stone nets, but establishment was highly variable from place to place, even on the loamy soil type. Natural regeneration was minimal. Cheatgrass cover averaged 17.2 percent and perennial cover averaged 18.4 percent, but again, there was no significant correlation between numbers of big sagebrush seedlings and understory composition. This may reflect the depletion of perennials in poor-condition big sagebrush communities and temporary suppression of the annuals by the intensity of the fire. The greater variability in soils and habitats may have provided more "safe sites" than at the Loamy 8-10 site, in addition to the greater, more reliable precipitation. The Pothole Reservoir site did not receive enough seedling-year precipitation to allow full establishment and growth of the seeded species, including Wyoming big sagebrush.

The pattern of average seedling densities on the Loamy 8-10 and Loamy 10-12 sites corresponds exactly to that of the frequency of occurrence (fig. 11). Seedling densities were much higher on the 1987 plantings than on the 1986 plantings, reflecting a more normal level of precipitation and, apparently, favorable seedbed moisture characteristics and planting depth. The results tend to support the patterns of reinvasion in figures 3 and 4. On all but Area 1 at the Loamy 10-12 site, the wet soil was frozen to a shallow depth at application. Only the tops of the sidecast hummocks were dry enough to be easily moved by the anchor chain drag. This loose soil was available for covering

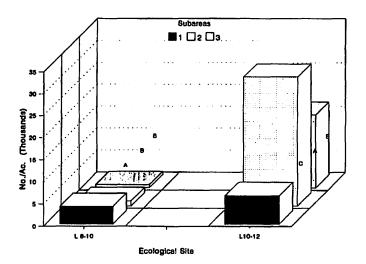


Figure 11—Average densities of sagebrush seedlings on two burned sites replanted in fall 1987 with the Jarbidge Sagebrush Seeder. Both sites were previously sagebrush-dominated. The 0.7-lb/acre PLS seeding rate was between the low and high seeding rates of the 1986 plantings. Mean densities with different letters at each site are significantly different (P < 0.05). Mean densities were not compared between sites.

the seed. The cultipacker firmed the loosened soil into a fairly level puddled surface with shallow furrows, which was stable during the seedling year. The seedbed resembled an imprinted seedbed, but with fewer, shallower, more widely spaced depressions. The furrows still concentrated the moisture, and seed-soil contact was probably good. It appeared that cultipacking enhanced the natural settling and puddling from overwinter precipitation, and that the anchor chain covered much of the seed. The Jarbidge Sagebrush Seeder apparently provided good coverage and firming for most soils under the planting conditions, except for the gravelly and stony areas, which had little loose soil from the drilling operation. It combined some of the best features of equipment used in the 1986 plantings. However, sagebrush seedling establishment still appeared to be strongly related to moisture availability as influenced by ecological site, soil surface texture, herbaceous competition, microtopography, seedling year precipitation, exposure, position on slope, and other factors, even when effective planting methods are used.

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AN INTERNATIONAL APPROACH FOR SELECTING SEEDING SITES: A CASE STUDY

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ABSTRACT

Climatic and edaphic data were collected at 210 buffelgrass (Cenchrus ciliaris) seeding sites in North America and at 30 sites in Kenya. Site selection in North America was based on three survival categories: (1) where the grass persisted and spread outside the seeding site; (2) where the grass persisted but did not spread; and (3) where the grass persisted for 10 years before disappearing. Sites in Kenya were near the original seed collection site. Of the climatic and edaphic characteristics evaluated, only organic carbon and total nitrogen can be used to select sites where buffelgrass can be expected to establish, persist, and spread. This approach may aid revegetation specialists in the Western United States who wish to reestablish native plants.

INTRODUCTION

Buffelgrass (*Cenchrus ciliaris*), a perennial, warm-season bunchgrass is native to Africa, Asia, and the Middle East (Bogdan 1961; Holt 1985; Khan and Zarif 1982). The species predominates where surface soils are sandy and annual precipitation varies from 200 to 1,200 mm (Cox and others 1988).

Buffelgrass seed collected in the Turkana Desert, northcentral Kenya, was sown and evaluated for seedling establishment, forage production, and long-term persistence in Texas during the 1940's (Holt 1985). Seedlings from seed sown in summer were easily established and mature plants survived winter in south Texas. In 1949 the Soil Conservation Service informally released T-4464 buffelgrass.

T-4464 plants initially persisted at most planting sites in south Texas, and between 1949 and 1985 the grass was established on over 4 million ha (Cox and others 1988). Seed were transported south to Mexico and successfully established along the eastern and western coasts (Agostini and others 1981; Cota and Johnson 1975; Hanselka 1985; Molina and others 1976). Land managers assumed that the plant would persist under a wide variety of climatic and edaphic conditions. Established populations, however, spread to nonplanted sites only at a few locations in south Texas and northwestern Mexico. At other seeded sites, plant populations have either persisted but not spread or disappeared.

Because T-4464 was originally collected in north-central Kenya, and spreads most frequently in southern Texas and northwestern Mexico, we believe climatic and edaphic conditions around the original collection site and where the plant spreads in North America to be more similar than where the plant fails to spread or dies. If this hypothesis is true, then climatic and edaphic information from southern Texas, northwestern Mexico, and north-central Kenya can be used to select high-potential buffelgrass seeding sites in the Northern and Southern Hemispheres. Information that defines the relationship among climate and soils, and plant germination, emergence, persistence, and reproduction will reduce the failures associated with rangeland revegetation attempts.

STUDY SITES

Two hundred and ten buffelgrass seeding sites were selected subjectively in North America, and 30 sites were selected where T-4464 seed were originally collected in northcentral Kenya. In southern Texas and Mexico soils were collected at: (1) 60 sites where the grass persisted and spread outside the seeding site; (2) 100 sites where the grass persisted but failed to spread; and (3) 50 sites where the grass persisted for 10 years or more before disappearing.

Site elevations vary from 20 to 700 m in North America, and from 15 to 580 m in Kenya. Slopes range from 2 to 10 percent. Precipitation ranges from 200 to 1,200 mm in North America, and is bimodally distributed in either spring and summer or winter and summer. In Kenya precipitation ranges from 200 to 400 mm, and is bimodally distributed in early and late summer.

From more than 300 weather stations we selected: (1) 25 in southern Texas and eastern Mexico; (2) 10 in southern Mexico; and (3) 17 in western Mexico (Climatography of the United States 1985; Climatography of Mexico 1982). Seven stations were selected in north-central Kenya (Agroclimatological Data for Africa 1984). Station selection was based on: (1) records in excess of 20 years; (2) less than 10 km from a seeding or collection site; and (3) elevational similarities between weather stations and either seeding or collection sites.

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WEATHER PARAMETERS

Weather categories were (1) precipitation, and (2) maximum and (3) minimum temperatures. Site parameters were summed by month and divided by record length.

SOIL SAMPLING

Soils were collected to 10-cm depths near the crown of three buffelgrass plants or in open areas where buffelgrass plants persisted 10 or more years before disappearing. Composited samples (three) were air-dried, passed through a 2-mm sieve, and thoroughly mixed. Duplicate subsamples from each composite were analyzed for particle-size distribution (Day 1950), pH (saturated paste), electrical conductivity (EC) of the saturated extract, and cation exchange capacity (CEC) (U.S. Salinity Laboratory Staff 1954), ammonium acetate-soluble cations including calcium (Ca), potassium (K), sodium (Na), and magnesium (Mg), total nitrogen (TN), organic carbon (OC) (Jackson 1958), and available phosphorus (P) (Olsen and Sommers 1982).

EXPERIMENTAL DESIGN

Because site selection is not random, and sites within treatments were unequal, the treatment variances are compared. For each soil component a Hartley test was used to determine differences ($P \le 0.05$) among treatment variances.

RESULTS AND DISCUSSION

Weather Parameters

Total mean annual precipitation where buffelgrass spreads $(\bar{x} = 440 \text{ mm})$ is approximately 35 percent less than where the species persists but does not spread $(\bar{x} = 675 \text{ mm})$, and 45 percent less than where the species dies (fig. 1). Adult buffelgrass plants may be more drought tolerant than anticipated since precipitation in northeastern Kenya ($\bar{x} = 300 \text{ mm}$) is about 30 percent less than that recorded where the species spreads in North America.

In North America precipitation amounts (fig. 1) and temperature extremes (figs. 2 and 3) are variable in summer, but where buffelgrass spreads summer precipitation ranges from 330 to 550 mm. In contrast, the plant persists but does not spread or dies when growing season precipitation ranges from 600 to 1,200 mm. When summer precipitation exceeds 600 mm, spittlebug (*Aeneolamia albofasciata*) populations rise, and nymphs and adults extract fluids from buffelgrass leaves and shoots (Flores and Velazco 1974). When spittlebug populations exceed 100 per plant, buffelgrass plants may die (Cazares and others 1985).

Fall and winter precipitation amounts are similar at African and North American sites (fig. 1), but temperature extremes differ within and between continents (figs. 2 and 3). In southern Mexico winter temperatures are mild and buffelgrass seed germinate when soil moisture is available, but seedlings almost always die because winter rains occur infrequently (Molina and others 1976; Oquendo and others 1983). Along the coastal areas of southern Texas and eastern Mexico winter temperatures are similar to southern

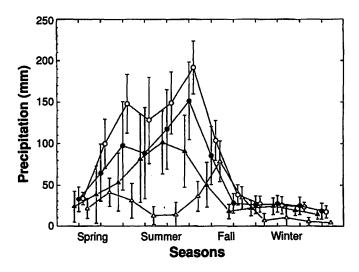


Figure 1—The variation in mean monthly precipitation distribution at buffelgrass seeding sites in North America and where seed were originally collected in Africa. Lines represent sites where the plant persists and spreads from a seeding (\bigstar), persists but does not spread from a seeding (\blacklozenge), dies (\circlearrowright), and where seed were originally collected in north-central Kenya (ձ).

Mexico in 1 of 5 years, and buffelgrass seed may germinate in winter. In most years, however, summer-produced seed survive until the following summer. At sites where buffelgrass spreads, cool maximum winter temperatures limit germination when soils are moist. Under cool-dry and cool-wet conditions buffelgrass seed remain viable for 3 or more years (Winkworth 1963).

Mean spring precipitation amounts where buffelgrass persists but does not spread or dies are 1.5 to 2.5 times greater

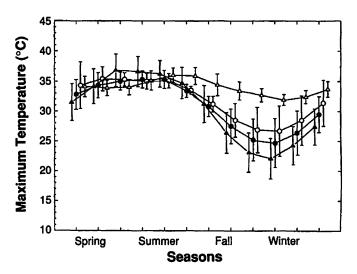


Figure 2—The variation in mean monthly maximum temperatures at buffelgrass seeding sites in North America and where seed were originally collected in Africa. Lines represent sites where the plant persists and spreads from a seeding (\blacktriangle), persists but does not spread from a seeding (\blacklozenge), dies (\circlearrowright), and where seed were originally collected in north-central Kenya (\vartriangle).

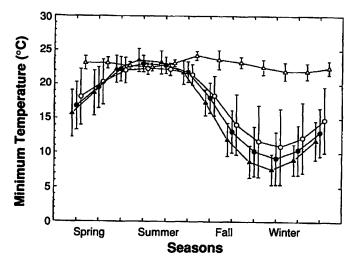


Figure 3—The variation in mean monthly minimum temperatures at buffelgrass seeding sites in North America and where seed were originally collected in Africa. Lines represent sites where the plant persists and spreads from a seeding (\blacktriangle), persists but does not spread from a seeding (\blacklozenge), dies (\circlearrowright), and where seed were originally collected in north-central Kenya (△).

than where the species persists and spreads (fig. 1). Abundant spring rains along the Texas and eastern and southern Mexico coast enhance the production of established buffelgrass stands, and forage quality and quantity exceeds that of existing perennial grasses (Hanselka 1985; Molina and others 1976). However, seedlings from seed germinating in spring usually die during the midsummer drought (Oquendo and others 1983). Spring precipitation occurs less frequently where buffelgrass spreads at inland sites in southern Texas (Crystal City to Laredo) and in northwestern Mexico.

Soil Physical and Chemical Properties

Where buffelgrass spreads, soils are generally coarse textured and low in total nitrogen and organic carbon (table 1). At inland sites in southern Texas and northwestern Mexico, buffelgrass was found on alluvial fans. At these sites, geologically young acidic granitic soils developing at higher elevations were deposited by water over geologically old alkaline sedimentary soils at lower elevations (Hausenbuiller 1978; Hendricks 1985). Geologically young granitic soils are usually acid if they have undergone little leaching and weathering (Birkeland 1974).

When buffelgrass either persists but does not spread or dies, the combined fine soil particles (clay plus silt) usually exceed 50 percent, and total nitrogen and organic carbon are 2 to 3 times greater than where the plant spreads (table 1). Under high-precipitation regimes, water leaches exchangeable cations beneath the rooting zone, and acidity increases when hydrogen and aluminum ions accumulate (Brady 1974). This process does not occur at buffelgrass seeding sites in southern Mexico because a hardpan limits downward nutrient movement (Mac Vicar and others 1977). However, seasonal flooding saturates these soils, and poor soil aeration is known to limit buffelgrass growth and persistence (Humphreys 1967).

Of the measured edaphic properties, only total nitrogen and organic carbon variances differed ($P \le 0.05$) among treatments (table 1). Total nitrogen and organic carbon quantities were least where the species spread, intermediate where the species persisted but did not spread, and greatest where the species died. Under moist tropical conditions bacterial, fungal, and nematode populations in soils supporting buffelgrass are 10 to 50 times greater than in arid soils (Khan and Zarif 1982; Nada 1985; Rees 1972; Van den Berg 1985). As buffelgrass stands disappear at tropical seeding sites they are replaced by deep-rooted bunchgrasses that require additional water and nutrients (Winkworth 1963).

North-central Kenya soils are more coarse and in our opinion less fertile than those where the species has been

Table 1—Means and standard deviations for particle-size distribution and selected chemical properties at sites where buffelgrass either spreads, does not spread, or dies at planting sites in south Texas and Mexico, and where the seed of the plant was originally collected in north-central Kenya. An asterisk (*) indicates a significant difference (P ≤ 0.05) among variances in the three survival categories

		Survival categories			
Property	Persists and spreads	Persists but does not spread	Dies	Hartley test	Kenya
Sand (%)	61.1 ± 20.2	44.9 ± 24.6	35.3 ± 15.4	NS	82.0 ±14.8
Silt (%)	17.5 ± 10.8	24.1 ± 13.2	32.3 ± 7.2	NS	11.9 ± 9.2
Clay (%)	21.5 ± 11.6	31.0 ± 15.3	32.4 ± 11.2	NS	6.1 ± 6.1
Silt + Clay (%)	39.0 ± 18.7	55.1 ± 24.3	64.7 ± 16.2	NS	18.0 ±14.8
pH	[•] 7.8 ± .5	7.6 ± .6	7.5 ± .4	NS	8.1 ± .5
EC (ds m ⁻¹)	.3 ± .2	.3 ± .1	.3 ± .1	NS	.2 ± .1
TN (%)	.1 ± .1	.3 ± .2	.5 ± .3	•	.1 ± .1
OC (%)	.9 ± .7	2.6 ± 2.9	4.4 ± 3.6	•	.3 ± .2
P (mg kg ⁻¹)	10.6 ± 11.9	12.9 ± 12.7	10.0 ± 22.3	NS	17.2 ± 9.2
CEC (cmol kg ⁻¹)	22.5 ± 13.4	38.1 ± 24.4	61.8 ± 24.9	NS	15.6 ±13.7
Na (cmol kg ⁻¹)	.4 ± .6	.4 ± .4	.4 ± .2	NS	.2 ± .2
K (cmol kg ⁻¹)	1.1 ± .7	1.9 ± 1.3	1.8 ± .9	NS	1.0 ± .9
Ca (cmol kg ⁻¹)	35.9 ± 26.5	42.0 ± 23.0	47.8 ± 16.6	NS	12.4 ±13.5
Mg (cmol kg ⁻¹)	1.9 ± 1.5	3.2 ± 2.2	3.7 ± 2.5	NS	2.1 ± 1.6

seeded in North America (table 1). Nevertheless, soils at sites where the species spreads are generally equivalent to those in Kenya, with the exception of phosphorus.

CONCLUSIONS

For more than 100 years revegetation specialists have tried to artificially improve western rangelands (Cox and others 1988). The procedures most widely used were to: (1) chemically or mechanically reduce competition; (2) prepare a seedbed; (3) plant seeds of as many species, accessions, or cultivars as possible; and (4) pray for rain. In about one of every 10 attempts the planting was a success, but it was not possible to predict future planting success because plant establishment and persistence were not correlated with site climatic and edaphic conditions.

To determine the importance of climate and soil on longterm buffelgrass persistence we classified 210 buffelgrass seeding sites in three survival categories. Our evaluations indicate that a planting success (persists and spreads) or planting failure (dies) can be predicted with measurements of soil organic carbon and total nitrogen. High variability in our second survival category (persists but does not spread) occurs because we were unable to assess long-term management impact. For example, if grazing management was altered or implemented, sites in the second survival category might be reclassified under persists and spreads. Conversely, sites in the second survival category might be reclassified under dies if management were removed.

To obtain a regional estimate of buffelgrass adaptability the land manager might use local, regional, and global climatic and soils maps. Precise seeding site definition may be aided by satellite imagery if a correlation exists between soil color and either soil organic carbon or total nitrogen.

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RELATING SEEDBED ENVIRONMENTAL CONDITIONS TO SEEDLING ESTABLISHMENT

Bruce A. Roundy

ABSTRACT

Most revegetation studies measure only precipitation and seedling density, cover, or forage production. Concurrent and continuous measurement of seedbed water and temperature conditions and seedling emergence may help explain why certain species and seedbed treatments are successful, while others are not. Seedbed environmental data may help construct laboratory experiments that are more representative of field conditions for evaluating successful establishment characteristics. A challenge for revegetation scientists is to construct seedling establishment models to predict responses under different climatic and weather conditions.

INTRODUCTION

The current emphasis on using native species for revegetation necessitates an understanding of their establishment requirements. Traditionally, revegetation studies have been empirical, evaluating the density, cover, and production of different species and plant materials on different seedbeds, soils, and years. This empirical testing has produced revegetation guidelines, principles, and specific site recommendations for revegetation of semiarid rangelands (Roundy and Call 1985). However, this approach has usually not provided the information necessary to understand why certain plant materials and techniques succeed or fail on different sites or in different years (Call and Roundy 1991). Consequently, we still do not know why many native plants are hard to establish and what environmental conditions are required for their successful establishment.

Plant improvement scientists have emphasized the importance of characterizing the establishment environment and selecting for adaptive establishment characteristics (Johnson and others 1981; Wright 1975). However, it has been difficult to identify morphological and physiological characteristics that can be consistently used to develop selection criteria for improved plant establishment (Johnson and others 1981). These researchers have attempted to evaluate plant materials under simulated drought conditions using specialized techniques and growth chambers. Although the plant materials have often shown differential response to these simulated drought conditions, it has often been difficult to show that superior plant materials in the laboratory also have superior establishment in the field. Laboratory evaluations of germination and seedling growth are often conducted under static environmental conditions, such as static temperature and water potential. However, these responses are difficult to interpret in terms of field establishment due to the dynamic environmental conditions of field seedbeds. Concurrent measurement of field environmental conditions and biologic responses (such as germination, root growth, seedling survival) may be necessary to fully understand why seedings succeed or fail, what the establishment requirements are for different plant materials, and what biological characteristics are adaptive for establishment under certain environmental conditions.

MEASURING SEEDBED ENVIRONMENT

An important first step is to quantify the environmental conditions such as the soil moisture and temperature conditions of the seedbed. Only a few of the hundreds of revegetation studies have concurrently measured soil moisture and temperature conditions during seedling establishment. Most of these studies have sought to determine the benefits of seedbed modification for revegetation.

McGinnies (1959) sampled surface soil moisture gravimetrically every 2 to 4 days in April and May to determine the benefit of different furrow depths for maintaining available soil water for germination on a silt-loam soil. Herbel (1972) measured temperature and soil water potential at 1-3 cm to show advantages of pitting, furrowing, and mulching in New Mexico during summer rainfall. Springfield (1972) reported decreased soil temperature and increased time of soil water availability under various mulches in New Mexico. Evans and Young (1987) pioneered studies of seedbed environmental conditions, as modified by microtopography and plant litter, in relation to the establishment of cheatgrass (Bromus tectorum) and other weedy range plants. They used large equipment and strip-chart recorders to continuously measure soil moisture, temperature, and humidity.

Electronic microloggers are now available to continuously read a variety of sensors. Data can be easily transferred to a computer and handled with spreadsheet or data base software. Pin-point soil temperatures can be easily measured by small thermistors or thermocouples, but the measurement of soil water content or potential at the microscale of most seeds and seedlings is not possible due to the large size of the sensors. Gypsum blocks and fiberglass soil cells are commonly 2 cm in width or diameter. Gypsum blocks are sensitive from -0.1 to -1.5 MPa of matric potential while fiberglass soil cells are sensitive

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to water contents from saturation to air dry. Soil cells should be individually calibrated for greatest accuracy. Fiberglass cells and gypsum blocks can be continuously read by electronic microloggers and are either less expensive, more reliable, or measure a smaller volume than psychrometers, neutron probes, or the promising timedomain reflectrometry (TDR) technology (Call and Roundy 1991).

Smaller soil water sensors are needed to best determine seed-soil water relations relative to germination and seedling growth. Most seeds are appropriately buried 0.5 to 1.5 cm deep, but most moisture sensors are difficult to bury more shallow than a 1-cm depth where they sense a 1- to 3-cm interval. Small changes in soil water conditions near seeds on the surface or buried at a shallow depth may be difficult to detect with current sensors or sampling methods but could greatly affect germination responses (Harper and others 1965; Winkel and others 1991).

An advantage of continuously measuring soil moisture and temperature conditions is that it may help to quantify how effective certain seedbed modifications are under different weather conditions. Jackson and others (1991) used thermocouples and gypsum blocks to determine the effects of mulch and catchment berms for establishment of desert saltbush (*Atriplex polycarpa*) on an abandoned farmland site in the Sonoran desert. After spring rains, mulch reduced 1-cm temperature peaks by 9 °C and resulted in continuously available soil water at 1- to 3-cm depths for 20 days, while nonmulched plots had intermittently available water (fig. 1). Berms and mulch also lengthened the period of subsurface water availability that was associated with higher establishment and vigor of desert saltbush.

Continuous monitoring of soil water content using fiberglass cells has shown that seedbed disturbances such as cattle trampling and land imprinting may lengthen the available water period enough to improve seedling establishment during moderately wet, but not dry, summer rainy seasons in the Southwest (Roundy and others 1992). Disturbed seedbeds in 1988 were associated with a shorter period when soil water was unavailable and also higher seedling emergence than undisturbed seedbeds (fig. 2). In 1989, available water periods were too short for all treatments to permit successful seedling establishment. This study suggests that the period and timing of available soil water (water content above some corresponding matric potential) may be more critical to seedling establishment and of more interpretive value than the actual soil matric potential at a given time.

Monitoring of soil moisture and temperature along with specific canopy manipulations allowed Sumrall and others (1991) to determine that increased seedling recruitment of Lehmann lovegrass (*Eragrostis lehmanniana*) after burning was due to modification of the microenvironment associated with canopy removal. Removal of the lovegrass canopy resulted in increased diurnal temperature fluctuations and presumably red light at the seedbed, both of which stimulate Lehmann lovegrass germination (Roundy and others 1992a, c). Increased emergence of lovegrass on burned and mowed plots was not associated with greater soil water availability since these plots dried out

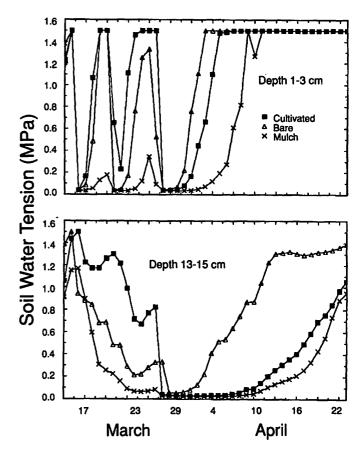


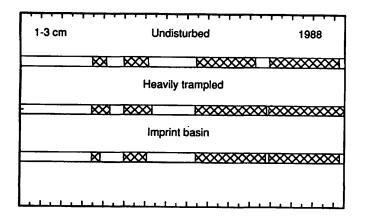
Figure 1–Soil water tension (MPa) at 6 a.m. at 1-3 cm (top) and 13-15 cm (bottom) depths above catchment berms on abandoned farmland in the Sonoran desert. Cultivation and especially mulching delayed increases in water tension after rain and increased establishment of desert saltbush (Jackson and others 1991).

more quickly than those with an intact canopy. This information is valuable because it suggests strategies for replacing this exotic grass with shade-tolerant native grasses. The lovegrass could be killed with an herbicide and used as a mulch to inhibit its own germination and conserve soil water for native grass establishment.

BIOLOGICAL RESPONSES TO ENVIRONMENT

Microenvironmental monitoring may allow us to define most probable soil temperature and moisture scenarios. This may allow us to not only conduct laboratory tests of germination and seedling growth under more representative environmental conditions, but also to determine what biological responses are most likely to succeed under particular seedbed conditions.

For example, laboratory germination responses under actual field temperature curves may be more representative of field germination responses for some species, compared to responses under constant or abruptly alternating temperatures (fig. 3). This may be especially true for germination tests under cooler temperatures.



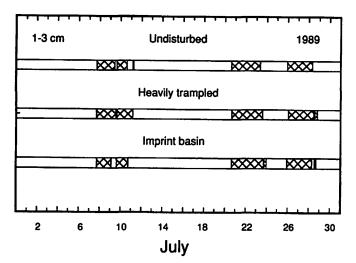


Figure 2–Periods of available water (volumetric water content greater than a corresponding matric potential of –0.1 MPa) at a 1-3 cm depth as indicated by crosshatching, for different seedbed treatments on a loarny upland range site in southern Arizona during two summer rainy seasons. Seedbed disturbance slightly increased the period of available water and was associated with greater seedling emergence in 1988 but not 1989 (Roundy and others 1992b).

Abrupt temperature alternations between maximum and minimum temperatures may result in a longer time above a given threshold temperature in a 24-hour period than would occur under field temperature alternations between the maximum and minimum. Abruptly alternating temperature tests could result in higher germination estimations in the laboratory for cooler or widely fluctuating temperature extremes than would actually occur in the field. On the other hand, abrupt temperature alternations may help to break dormancy of some species and increase germination compared to gradual alternations.

Continuous concurrent measurement of soil temperature and moisture permits determination of actual diurnal temperature curves when water is available in the seedbed. These curves can easily be programmed into "ramping" growth chambers to permit germination testing under actual field temperature conditions. The effects of

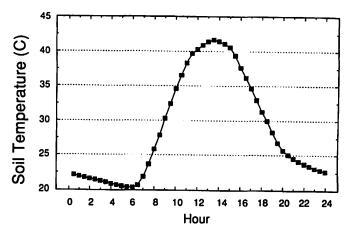


Figure 3–Diurnal bare soil temperatures at 1 cm in the semidesert grassland in southern Arizona. Data are from means of two sites when the soil was wet (matric potential > -0.1 MPa) during the summer rainy season (Roundy and others 1992b, c; Sumrall and others 1991).

actual field temperature conditions on breaking of dormancy and germination responses as determined in the laboratory may provide important clues to the establishment requirements of some species and may have enhanced interpretive value for explaining field emergence.

An understanding of actual seedbed temperature and moisture dynamics is necessary to determine biological responses that result in successful establishment in certain environments. For example, ability to germinate and develop roots under cool temperatures has been identified as a major reason that cheatgrass is successful on Intermountain rangelands (Harris and Wilson 1970). Researchers have concluded that successful perennial grass competitors would also need to germinate and develop roots during the winter and early spring to be able to compete with cheatgrass for stored soil moisture during the spring growth period (Aguirre and Johnson 1991).

However, rapid root growth may not necessarily be most associated with ability of warm-season grasses to establish during the summer rainy season in the semidesert grassland in southern Arizona. In fact, introduced grasses such as Cochise (Eragrostis lehmanniana x E. tricophera) and Lehmann lovegrass are more easily established in revegetation projects, but have less and slower root growth than other grasses such as sideoats grama (Bouteloua curtipendula) and blue panicgrass (Panicum antedotale) (Simanton and Jordan 1986). These warmseason grasses elongate their subcoleoptile internodes to produce adventitious roots at the soil surface (Hyder and others 1971; Winkel 1990). They generally require 9 to 11 days of continuously available soil moisture to develop adventitious roots (Winkel 1990). This suggests that prolonged available moisture after germination or the ability to tolerate drought until consistent rainfall occurs is necessary for these species to successfully establish.

Laboratory root growth studies (Winkel 1990) and field moisture measurements (Roundy and others 1992b) suggest that if germinating rains are not followed by subsequent rains, the soil drying front will proceed faster than seminal root growth and seedlings will desiccate (fig. 4). Although sideoats grama seminal roots grow faster than those of Cochise lovegrass, they are not fast enough to stay ahead of the soil drying front in the absence of rain.

Just why the exotic lovegrasses are more easily established than native grasses in the semidesert grassland is the subject of an ongoing "seed fate" study where we are trying to determine field germination and seedling survival responses in relation to specific rainfall events and subsequent dry periods. Frasier and others (1985, 1987) have shown that sideoats grama may germinate rapidly under a short wet period and thereby be vulnerable to seedling desiccation during the subsequent dry period. The introduced lovegrasses may be slower to germinate under a short wet period (Frasier and others 1985, 1987) and more likely to survive by requiring a longer wet period to germinate. They may avoid the initial summer rainstorms in July, which are usually followed by a dry period, and save their germination for more consistent rainfall in late July and August.

ESTABLISHMENT MODELS

This example illustrates the need to relate meteorological conditions and actual field temperature-moisture conditions to biological establishment responses. Because of all the different possible meteorological scenarios, this problem should be addressed by development of seedling

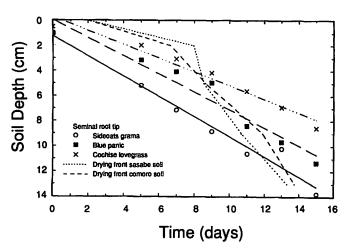


Figure 4–Maximum seminal root depth as a function of time since seed wetting for three warmseason grasses (Winkel 1990). Small dashed lines represent the time that soil matric potentials decrease to ≤ -1.5 MPa at a given depth after the end of a 2-day rainstorm on two typical sandy loam soils during the summer rainy season in southern Arizona (data from study of Roundy and others 1992b and unpublished data, University of Arizona, Tucson). In the absence of subsequent rain, the soil drying front may exceed the rate of seminal root elongation.

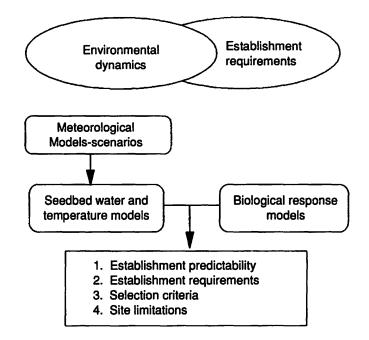


Figure 5–Relating seedbed environmental dynamics to plant establishment requirements through construction of seedling establishment models could advance the predictability of revegetation science.

establishment models. These models have not been developed, but would have three basic parts (fig. 5): (1) a meteorological model to determine and set weather conditions of known probabilities; (2) an environmental model to estimate seedbed water and temperature conditions as a function of soil characteristics and meteorological inputs; and (3) a biological response model to estimate establishment responses such as germination, root and shoot growth, and seedling survival in relation to temperature and moisture dynamics and thresholds.

Meteorological models and weather generators are available. Probabilities of different weather patterns over different relevant time scales need to be determined. A number of temperature and moisture models are available (Chung and Horton 1987; Lascano and van Bavel 1983) but most have not been evaluated or validated with rangeland seedbed environmental data, which have been lacking in the past (Wight and Hanson 1987). Biological response data must be developed under more representative sets of field temperature and moisture dynamics to determine representative germination and growth rates and appropriate thresholds.

Using environmental models to drive biological response models necessitates a greater understanding of the relationship between temperature and moisture dynamics and germination and seedling growth than we now have for most species. However, development of revegetation science in this direction may allow us to be much more realistic and predictive of revegetation success, without years of extensive trial-and-error field testing. We should be able to better determine plant requirements for establishment, site suitability for different plant materials, appropriate selection criteria for enhanced establishment, and the value and necessity of various seedbed modifications for different climates and weather conditions (fig. 5). This mechanistic approach may also be helpful in determining compatible species for establishment of more diverse plant communities.

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INTERSEEDING AND TRANSPLANTING TO ENHANCE SPECIES COMPOSITION

Richard Stevens

ABSTRACT

Shrub, forb, and grass species can be interseeded and transplanted into annual and perennial grass and forb communities to improve the nutritional quality of forage and lengthen the season of grazing use. The addition of shrubs and forbs by interseeding and transplanting to grass and forb communities increases plant community diversity, which should increase the diversity of animals as well. Herbicides or scalping can be used to eliminate competing plants in and near the seeding and transplanting area. When transplanting, proper handling of plant materials is essential to success.

INTRODUCTION

Within the Intermountain West, vast areas are dominated by fairway crested wheatgrass (*Agropyron cristatum*), standard crested wheatgrass (*A. desertorum*), cheatgrass (*Bromus tectorum*), and other introduced and native perennial and annual grasses. Hundreds of thousands of acres are also occupied by various shrub and forb communities with low productivity.

Shrub, forb, and grass species have been successfully established through interseeding and transplanting in perennial and annual communities and on prepared and disturbed sites.

Interseeding and transplanting adapted palatable and useful shrubs and forbs into less-productive communities or monocultures can improve the nutritional quality of forage and lengthen the season of grazing use, especially later in the year when grasses are dry and crude protein values are low (Rumbaugh and others 1981; Van Epps and McKell 1978). Additional benefits include improved species richness, community diversity, esthetics, cover, forage production, and soil stability. Because monocultures of any species are poor habitat for most wildlife, improved diversity will result in an increase in the diversity of birds, mammals, reptiles, and insects found in the community (Reynolds 1980).

Selecting plant materials adapted to the planting site is important for any successful revegetation program (Penrose and Hansen 1981; Rehfeldt and Hoff 1976; Stevens 1981). Selected species must be able to establish, persist, and maintain themselves and produce seed. This does not mean that the transplant or seed needs to come from or near the proposed treatment area, but it does mean that they need to be adapted to site conditions.

INTERSEEDING

Interseeding of compatible shrubs, forbs, and grasses into plant communities with low productivity or little diversity can provide a means for improving habitat, forage production, forage quality, species richness, community diversity, and soil stabilization. A number of shrubs have been successfully interseeded to improve big game, small game and nongame, and livestock ranges (Barnes and Nelson 1950; Monsen 1980a, 1980b; Plummer and others 1968; Stevens and others 1981). Interseeding has been used to establish desirable species in closed communities of cheatgrass (fig. 1) and mountain tarweed (*Madia glomerata*) (Arizona IRTS 1969; Giunta and others 1975), and other annual and perennial communities (Derscheid and Rumbaugh 1970; Lang 1962; Nyren and others 1980).

Interseeding can provide an attractive alternative to complete community alteration caused by seedbed preparation or when the purpose is to modify rather than replace a plant community (Jordan 1981; Vallentine 1989). To effectively interseed into existing annual and perennial communities, competitive plant material within or near the seeded area has to be temporarily eliminated. Interseeding can also occur in conjunction with other seeding on prepared seedbeds.

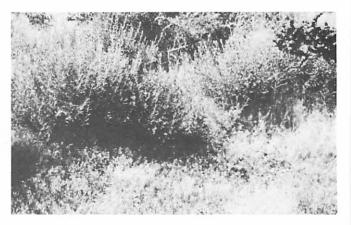


Figure 1—Six-year-old fourwing saltbush plants that were interseeded into a cheatgrass community.

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Interseeding in Conjunction With Removal of Existing Vegetation—Two economically effective methods of removing competitive vegetation are use of herbicides or scalping. These methods have to: (1) be wide, and in the case of scalping, deep enough to remove or kill all seeds and rhizomes of competing vegetation; (2) allow seeded species to become established before competing vegetation reinvades; and (3) result in scalps with shapes and sizes that will collect moisture (Jordan 1981; Stevens and others 1981).

Competing vegetation can be killed in strips or in spots with appropriate herbicides (fig. 2A) (Eckert 1979; Nyren and others 1980; Stevens 1985a). The sprayed strips or spots can be seeded with fall drill or broadcast seedings (fig. 2B). These techniques allow seeding to occur in the most fertile soil and in association with litter that can help protect seedlings from temperature and moisture extremes (Stevens 1985b).

Competing vegetation can be mechanically removed with various types of pitters, scalpers (Giunta and others 1975; Jordan 1981; Larson 1980; Monsen 1980a,b; Nyren and others 1978; Schumacher 1964; Stevens 1979; Vallentine 1989; Wright and others 1978), and with rototillers (Smoliak and Feldman 1978). The Sieco fire plow and Hansen Scalper are the most commonly used scalpers (Larson 1980).

The width of the scalp or pit depends on the density, vigor, and growth form of major species in the existing vegetation, the species being interseeded, and site conditions. Care must be taken to ensure that the most fertile surface soil is not removed (Stevens 1985b). Drier sites require wider scalps because of increased competition for moisture. On arid sites, summer fallowing may be required to minimize competition and maximize moisture availability (Bement and others 1965). Scalps made on the contour with cross dams can catch and hold additional moisture from snow and rain (Branson and others 1962; Stevens 1978). The additional moisture enhances chances of seedling establishment and subsequent plant growth. Interseeding shrubs into cheatgrass brome, Giunta and others (1975) found that shrub seedling establishment was superior in 61-cm (24-inch)-wide scalps as opposed to 10-cm (4-inch), 20-cm (8-inch), and 42-cm (16-inch)-wide scalps. When interseeding native shrubs into established crested wheatgrass, Van Epps and McKell (1978) found that the best scalps should be 101 cm (40 inches) wide, with optimum spacing being 152 cm (60 inches). This study also monitored seedling establishment in intermediate wheatgrass (Agropyron intermedium) 1, 2, 3, and 4 years after seeding. The widest scalps, 76 cm (30 inches) wide and 29 cm (9 inches) deep, resulted in the most plants per 30 cm (12 inches) of scalp. Established plants in the wider scalps also were the most vigorous and largest. They also began flowering sooner than plants in the narrower scalps.

Seeding generally occurs in conjunction with scalping. This can be accomplished with a Hansen Browse Seeder or Thimble Seeder attached following the scalper.

Interseeding in Conjunction With Other Seeding Techniques—Shrubs, forbs, and grasses can be seeded separately, in conjunction with, and simultaneously with other species. Interseeded species can be seeded with



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Figure 2—Strip of intermediate wheatgrass sprayed with Roundup (A) and seeded (B) to various shrubs and forbs.

seed dribblers and thimble seeders (Larson 1980) mounted on crawler tractor tracks at the same time broadcast or drill seeding is occurring (fig. 3). As the tractor track moves forward, seeds are dropped onto soil ahead of the moving track. The tractor presses the seed into the soil, making a firm seedbed. This technique can leave rows of seeded species wherever the tractor travels.



Figure 3—Fourwing saltbush plants seeded through seed dribbler mounted on crawler tractor that was chaining pinyon and juniper trees.

It is important to only seed compatible species next to each other. Species that are more aggressive in establishment should be kept away from species that do not establish well with competition. Where compatible species are kept separate, all seeded species can become established and do well (fig. 4).

Seeding equipment that includes a seedbox (such as drills or disk-chains) can be modified to segregate seed of various species. Seed of selected species can be separated from each other with partitions within the seedbox or by being placed in different seedboxes and seeded through separate seed drops. Most shrub and many forb seedlings do not establish or compete well when planted in close proximity to most perennial grasses. This is especially true for the more aggressive grass species such as standard crested, fairway crested, Siberian wheatgrass (Agropyron sibiricum), intermediate wheatgrass, smooth brome (Bromus inermis), and Russian wildrye (Psathyrostachys juncea).

Variations in seed mixing procedures of multispecies mixtures can provide greater landscape patchiness, diversity, and appearance. Several variations can result by mixing only a portion of the seed prior to seeding and putting the mix and bags of single species into the seed bin (broadcast) or drill box at random. As a result there will be areas where all species are seeded simultaneously, areas with only one or a few species, and all gradations in between. This can result in excellent foraging areas adjacent to various types of habitat. The esthetic effect is a more natural appearance with vertical and horizontal variation rather than an even unnatural appearance.

It is important to seed species that are adapted to site conditions. Early and mid-seral species generally do best in the disturbed scalps or pits and are generally successful in spreading naturally into existing perennial and annual communities. Species that have performed well when interseeded include big sagebrush (Artemisia tridentata), rubber rabbitbrush (Chrysothamnus nauseosus), fourwing saltbush (Atriplex canescens), forage kochia (Kochia prostrata), antelope bitterbrush (Purshia tridentata), alfalfa (Medicago sativa), small burnet (Sanguisorba minor), Lewis flax (Linum perenne), Palmer penstemon (*Penstemon palmerii*), yellow sweetclover (*Melilotus officinalis*), western yarrow (*Achillea millefolium*), globemallow (*Sphaeralcea* spp.), and mountain rye (*Secale montanum*).

TRANSPLANTING

A number of shrubs (fig. 5) and forbs have been successfully transplanted into established grass stands to enhance species composition, stabilize soil, increase the quality and quantity of forage, and improve cover value (McArthur and others 1974; Monsen 1974; Shaw 1981; Stevens 1981; Stevens and others 1981; Tiedemann and others 1976). When transplanting into competitive grass, forb, or shrub communities success can be increased by opening spots or strips with an effective herbicide or by scalping the soil and existing plant material. Scalps perpendicular to the prevailing storm direction can collect considerable snow. Scalping too deep can remove the most fertile portion of the soil and reduce plant growth (Stevens 1985b). Scalping and transplanting are generally done simultaneously with the scalper attached in front of the transplanter.

There are a number of important procedures that must be followed when transplanting. General rules for wildings, bareroot, and container-grown stock are: (1) never allow roots to become dry, (2) keep plants cool and out of direct sunlight, (3) compact soil well around the roots at planting time, and (4) plant during cool periods with adequate soil moisture (Ferguson and Monsen 1974; Penrose and Hansen 1981; Ryker 1976; Stevens 1981).

Proper handling of plant materials will usually make the difference between success and failure. Exposed roots of bareroot stock can dry out in as little as 5 seconds on windy days, and in 15 seconds or less on overcast days. Roots of container stock will tolerate somewhat longer periods of exposure than will bareroot stock roots. Roots need to be kept damp and cool at all times (fig. 6). Roots may become heated or dry when plants are moved from shipment containers to the transplanter holding bin. However, mishandling most commonly occurs just before



Figure 4—Wyoming big sagebrush drill seeded in conjunction with and separated from crested wheatgrass.

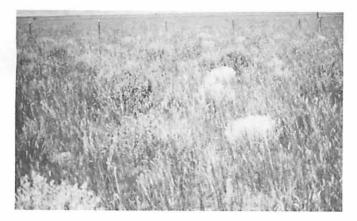


Figure 5—Fourwing saltbush, winterfat, antelope bitterbrush, white rubber rabbitbrush and Wyoming big sagebrush transplanted into an established stand of crested wheatgrass.

placing the transplant in the soil. Transplants must to be moved rapidly from the protected holding area into the soil to minimize root exposure.

Transplant stock is generally stored, wrapped, and shipped in plastic or cardboard boxes. Excessive destructive heat can build up quickly in these containers when they are placed in direct sunlight for short periods of time.

Proper placement of transplants in the soil is critical. Planting holes and openings should be deep enough to allow all roots to be straight and the root collar to be at ground level when buried. Plants will die if they are planted too deeply. Roots should be completely vertical, with no "J" or "S" root placement; otherwise, the plant could be stunted or die. Soil should be firmly compacted around all roots. Air pockets must be eliminated. Air pockets and loose soil will result in poor anchoring, drying of roots, poor uptake of water and nutrients and, ultimately, the death of the plant.

Within the Intermountain West, transplanting should be done in the early spring. Advantages of planting at this time include: (1) plants are still dormant; (2) the chance of severe frost heaving has passed; (3) soil moisture from winter snow will likely be high; (4) two or three spring storms are likely to follow; and (5) temperatures are low. In the sagebrush and pinyon-juniper types of central Utah, transplanting usually has to occur before mid-March to meet all these requirements. The latest allowable date will vary with elevation, vegetative type, latitude, storm patterns, and the arrival of spring.

The size and proportion of root and type can affect establishment success. Proper shoot-root ratio is important. For many species the most successful transplanting has resulted with roots from 15 to 30 cm (6 to 12 inches) long and tops at least 33 cm (13 inches) long (McKenzie and others 1980; Stevens and others 1981). Pruning top growth is sometimes necessary to maintain balance. Too much top growth can put great demand on roots for moisture during the establishment period.

Transplanting results will vary among species (table 1) (Everett 1980; Ferguson and Monsen 1974; Stevens 1980; Tiedemann and others 1976). For example, wildings of most sagebrush and rabbitbrush species transplant with 80 to 90 percent success (Stevens and others 1981). About 30 to 40 percent success can be expected with fourwing saltbush bareroot stock with taproots. Success can be increased substantially with this species by using rootpruned transplants with branched root systems.

The intensity and timing of grazing can affect transplanting success. Most transplants need at least 2 years to become well enough rooted and established to endure much use. Grazing pressure should be considered when determining how large an area to transplant and how many plants will be used. Where grazing pressure exists, it is best to cluster transplants rather than scattering them. Based on experience at big game ranges, transplants will be better protected if they are planted as an extension of an existing stand. Mature plants can then absorb a major portion of use.

Successful and rapid transplanting can be accomplished with a tractor-mounted reinforced tree transplanter that requires hand placing of transplants. A hand-fed transplanter can plant from 10 to 18 bareroot stock plants per minute (Stevens and others 1981). Rate varies with the species being planted, soil type, moisture conditions, and spacing between transplants. Rocky ground should be avoided. The automatic pickup and planting system found on some tree transplanters cannot be used successfully with most shrub bareroot, wilding, or container stock. Most transplantable shrubs have multiplebranched, fibrous, or fairly long root systems that tangle in the fingers and chains of the automatic planting device.

Transplants of many species are available as containergrown or bareroot stock. Container-grown stock may have several advantages over bareroot stock. Roots of container-grown stock are established in a growth medium and are less likely to dry. Container stock is usually available when needed. Bareroot stock cannot be lifted until the frost is out of the soil and may not be available when site conditions are ideal for transplanting. Bareroot stock has several advantages over container-grown stock. When properly planted, bareroot stock generally has a higher rate of survival (Croft and Parkin 1979), establishes more

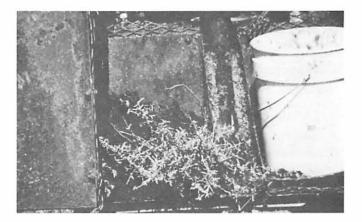


Figure 6—Transplants in holding bin on transplanter. Roots of transplants must be kept damp and cool at all times.

Table 1—Expected transplanting establishment success from various shrub, forb and grass species, bareroot, wilding and container grown stock¹

Species	Common name	Bareroot and wilding stock	Container- grown stock
Shrubs:			
Amelanchier alnifolia	Saskatoon serviceberry	6	4
Artemisia abrotanum	Oldman wormwood	-	10
Artemisia nova	Black sagebrush	10	10
Artemisia tridentata ssp. tridentata	Basin big sagebrush	10	10
Artemisia tridentata ssp. vaseyana	Mountain big sagebrush	10	10
Artemisia tridentata ssp. wyomingensis	Wyoming big sagebrush	8	8
Atriplex canescens	Fourwing saltbush	3	1
Ceratoides lanata	Winterfat	6	2
Cercocarpus ledifolius	Curlleaf mountain-mahogany	5	2
Cercocarpus montanus	True mountain-mahogany	5	2
Chrysothamnus nauseosus ssp.	White rubber rabbitbrush	8	7
albicaulis and ssp. hololeucus			
Chrysothamnus viscidiflorus	Low mountain rabbitbrush	7	7
Colutea arborescens	Bladdersenna	5	4
Cowania stansburiana	Cliffrose	5	4
Ephedra viridis	Green ephedra	4	1
Kochia prostrata	Forage kochia	8	8
Peraphyllum ramosissimum	Squawapple	5	4
Purshia tridentata	Antelope bitterbrush	6	4
Quercus gambelii	Gambel oak	5	2
Rhus trilobata	Skunkbush sumac	5	
Rhus glabra	Rocky Mountain sumac	5	
Ribes aureum	Golden currant	8	8
Rosa woodsii	Woods rose	8	8
Sambucus caerulea	Blueberry elder	5	4
Sarcobatus vermiculatus	Black greasewood	3	1
Symphoricarpos spp.	Snowberry	9	9
Forbs:			
Achillea millefolium	Western yarrow	10	10
Artemisia ludoviciana	Louisiana sagebrush	10	10
Aster spp.	Aster	10	10
Balsamorhiza sagittata	Arrowleaf balsamroot	1	
Coronilla varia	Crownvetch	10	10
Hedysarum boreale	Utah sweetvetch	5	8
Linum perenne	Lewis flax	8	8
Lupinus spp.	Lupine	2	6
Medicago sativa	Alfalfa	6	8
Sanguisorba minor	Small burnet	6	7
Sphaeralcea spp.	Globernallow	8	8
Viguriera multiflora	Showy goldeneye	6	9
Grasses:			
Bunch grasses		8	10
Sod grasses		10	10

 110 = high percent of establishment can be expected when proper transplanting techniques are used; 1 = low percent of establishment can be expected, even when proper transplanting techniques are followed.

quickly, and is larger and more vigorous (Stevens 1980). Bareroot stock is generally older (1 to 3 years) (Stevens 1981) than container stock (3 to 4 months) (Penrose and Hansen 1981). Bareroot stock generally has woody stems and fibrous root systems. Container stock is generally grown under forced conditions, resulting in young, sometimes weak, spindly plants with only one small taproot. For most shrub species, bareroot stock is less expensive than container stock, considering purchase price and transplant cost for each established plant (Croft 1980).

CONCLUSIONS

To enhance shrub and forb communities in the Intermountain West, both interseeding and transplanting have proven effective methods of increasing diversity. If either is undertaken, I recommend:

1. Temporary elimination of competitive plant material by proper use of scalping or herbicides.

2. Interseeding mixed seed collections to increase chances of success and vary appearance and diversity. However, only compatible species should be seeded next to each other and species need to be adapted to site conditions.

3. When transplanting, never let roots dry out, keep plants cool and shaded, compact soil well around roots. Proper stem/root ratio is important. Plant early in spring when weather is cool and soil is moist.

4. Keep grazing pressure off newly planted or seeded areas for at least 2 years following planting.

5. Since bareroot stock is hardier, older, and more economical, I recommend use of bareroot stock for transplanting unless site conditions are optimum too early in spring when only container-grown stock is available.

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DRILL SEEDING IN WESTERN CANADA

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ABSTRACT

Reports on the degree of success in Saskatchewan of various forage seeding equipment in relation to methods of land preparation prior to seeding. Research sites varied from aspen parkland pastures to semi-arid rangelands. Land preparation included complete and partial cultivation and the use of glyphosate (N-(phosphonomethyl)glycine) for complete or partial vegetation control without cultivation. Seeding equipment included roller-broadcast, disk-opener, and hoe-opener drills. In all cases, seeders that had independent depth control on each opener were best.

CLIMATE AND SOILS IN SASKATCHEWAN

In general, the climatic, soil, and vegetation zones run from southeast to northwest across Saskatchewan (Anon. 1976). Much of the province is in the brown soil zone (Aridic-Typic Borolls), with native vegetation of short-midgrass rangeland, mostly cool-season species except on the sandy soils of the southwest where some warm-season grasses either are or can become a major component. To the northeast are black- and grey-wooded soils (Cryic soils) as the precipitation/evaporation ratio improves.

Average precipitation increases only slightly across the province from 360 mm at Swift Current in the southwest to 400 mm at Melfort in the northeast, with between 25 and 35 percent coming as snow between October and April. The probability of the snow remaining on the ground until spring increases from southwest to northeast. The peak probability and amount of precipitation is in late June over the whole area. The precipitation/evaporation ratio during the growing season improves from 1:5.6 at Swift Current to 1:3.0 in the northeast at Nipawin on the edge of the boreal forest zone. At all places, moisture is usually increasingly deficient as the season progresses.

The best moisture conditions are from the start of the growing season in April or May, through June. Usually there follows hot, dry weather until late August. Frosts increase in frequency and severity from mid-September

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. John Waddington and F. Ben Dyck are Research Scientists, Agriculture Canada Research Station, Swift Current, SK S9H 3X2, Canada. Garry G. Bowes is a Research Scientist, Agriculture Canada Experimental Farm, Indian Head, SK SOG 2K0, Canada. Duane H. McCartney is a Biologist, Agriculture Canada Research Station, Melfort, SK SOE 1A0, Canada. until freezeup in early November. The snowmelt will normally produce a fully saturated soil profile in the northeast, to anywhere from good moisture to near bone dry depending on the year in the southwest.

The best time to seed, because we use cool-season species, is in early spring. The second-best time is into cold soil in late fall for an early spring germination. The worst time is in late spring because of the short interval for seedling growth before the increasingly hot and dry part of the growing season.

SYMMETRIC AND ASYMMETRIC DOUBLE-DISK OPENERS

Each disk of a standard 34-cm diameter double-disk opener was fitted with 2-cm-wide depth control bands attached 2.5 cm from the cutting edge. This opener was compared with an experimental asymmetric double-disk opener designed and built at Swift Current Research Station. The experimental opener has a 38-cm vertical disk and a 28-cm disk angled at 7 degrees to the larger disk. The center for mounting the smaller disk is 5 cm below and 2.5 cm behind the larger disk mounting so that the bottoms of the disks are on the same horizontal plane. A rubber-tired wheel 5 cm wide and 33 cm in diameter is mounted beside the large disk as an adjustable gauge wheel depth controller (Lawrence and Dyck 1990).

The experimental opener proved to be superior to the standard opener for seeding a wide range of forage species (table 1). The asymmetric openers have been fitted to all plot seeding equipment and some field-scale drills at the Research Station, and are giving us excellent forage establishment.

Table 1—Forage seedling emergence after planting with a standard double-disk furrow opener and an experimental asymmetric double-disk opener

Forage species	Standard double-disk opener	Experimental double-disk opener
	Percent	emergence
Altai wild ryegrass	29	46
Russian wild ryegrass	33	52
Intermediate wheatgrass	34	50
Crested wheatgrass	70	94
Tall wheatgrass	30	42

EQUIPMENT TESTED

Swift Current Range Drill—This is a heavy, triple-disk drill, designed and built at the Research Station for seeding in rough northern range conditions. It has large cutting disks that have no trip mechanism, so at least half of the weight of the drill can come to bear on any one disk. The cutting disks are followed by large double-disk assemblies with depth-control bands, and at the back are U-shaped packers, one of which drives the seed metering.

Each seeding and packing run is suspended independently, and can follow quite uneven land contours. Transport wheels at each side are raised when seeding and have only a minor stabilizing function (McLaughlin and Dyck 1986).

John Deere Powertill—This drill has powered rotary disks that cut slots in the soil about an inch wide when the disks are new, and about a quarter of an inch wide when they are badly worn. Seed is dribbled behind the disks and some of it falls in the slots.

Cover is provided by soil thrown up in a spray behind the rotating disks and dismally inadequate packer wheels run over the (hopefully) covered seed. Seeding depth is controlled by a shoe that slides on the ground between pairs of disks.

Moore Unidrill—This drill has single-offset disks that have a shoe on the back through which seed is dropped in the opened slots cut by the disks. A heavy T-section packer wheel runs behind each disk. Seeding depth is controlled by an adjustment on the hitch and trailing land wheels.

Zero-Till Hoe Drill—This drill was designed and built at Swift Current for seeding grain crops directly into standing stubble. It has narrow hoe openers with high and wide clearance for trash. Seeding depth is controlled by a caster wheel in front and steel packer wheels behind the openers.

Swift Current Forage Drill—This drill has the asymmetric disk openers described earlier (Lawrence and Dyck 1990), and was built at Swift Current for seeding forages into fallow or standing stubble. A plastic packer wheel runs behind the disk assemblies. Each opener-packer combination is suspended independently and can follow uneven soil surfaces. Landwheels at each side of the machine provide stability.

Connor-Shea Zero-Till Pasture Drill—Rolling colters cut slots in the ground and are followed by narrow-winged hoes, which open the slots for seed and undercut 2 to 3 inches on either side of the seed placement. Each opener is fixed to the frame by a coil tyne. Depth control is provided by land wheels at each side of the frame.

Oregon Range Drill—This drill has large, steel wheels, each with a V-ridge that presses a furrow into which seed is dropped. A drag chain covers the seed. Each wheel is suspended independently from the frame.

British Columbia Rangeland Drill—This drill uses a Brillion style of opener, where the first set of ridged rollers open a furrow, and the second set are offset enough to split the ridges and cover the seed that has been dropped in the furrows, and pack the soil. The Manitoba Brillion Drill—A front set of ridged rollers open a furrow. A seed box is mounted on the back set of rollers, which are articulated to the front set. Seed is dropped immediately in front of the back rollers and covered by their ridge-splitting action.

EXPERIMENTS CONDUCTED

A Comparison of Mechanical and Chemical Methods for Vegetation Control Prior to Seeding-The Swift Current range drill was used as the seeder in a test to compare the effects of resident vegetation suppression on establishment of bromegrass (Bromus inermis Leyss.)alfalfa (Medicago sativa L.) or crested wheatgrass (Agropyron cristatum [L.] Gaertn.)-alfalfa mixtures in the greywooded soil zone. Glyphosate {N-(phosphonomethyl)glycine} was applied broadcast at the standard rate of 2.5 kg/ha a.i. to the resident vegetation, which was primarily Kentucky bluegrass (Poa pratensis L.) sod. Lesser rates of 2.0 and 1.0 kg/ha were also applied together with 1.7 kg/ha of ammonium sulfate. A fourth treatment was rotavation to control the vegetation. Both alfalfa and grasses were seeded at 80 seeds/m of row. Vegetation control and seeding were carried out in late May or early June in each of 4 years (Bowes and Zentner 1992).

Better establishment of the seeded species was obtained when the resident vegetation was suppressed, but the method used to suppress it was not critical (table 2). The lower rates of glyphosate were equally effective as the standard rate when ammonium sulfate was included in the spray mixture. The alfalfa established satisfactorily with or without suppression of the bluegrass, although establishment and productivity were better after bluegrass suppression. Bromegrass establishment and production were much better if the bluegrass was suppressed before seeding the brome. None of the treatments permanently reduced the bluegrass. It recovered, probably from a seedbank in the soil, and also perhaps from rhizome fragments not killed by the suppression treatment. An economic analysis indicated that over the long term there was no benefit to suppressing the resident bluegrass prior to seeding an alfalfabromegrass mixture.

A Comparison of Three Drills for Direct Seeding After Resident Vegetation Suppression—The site of this experiment is about 100 miles north of the site of the experiment described earlier; the soil and climate are much the same. We wished to replace the resident smooth bromecreeping red fescue (*Festuca rubra* L.)-weed vegetation with meadow bromegrass (*Bromus biebersteinii* R.&S.).

We sprayed the pasture in October 1984 with glyphosate. This was late in the season, but a satisfactory kill of the resident sward should have been obtained. The poor kill was probably a result of inactivation of the glyphosate by clay suspended in the water we used. Consequently, we resprayed the following June and seeded in August. We set up a four-replicate test of the three machines, and measured success by how much of the drill runs were occupied by the desired meadow bromegrass in 1986, 1 year after seeding, and again in 1988.

The Swift Current drill was significantly better on what was mostly dead, untilled sod (table 3) (McCartney 1985).

	Populatio	n in year seeded	D.M. yield		
	Alfalfa	Bromegrass	Alfalfa	Bromegrass	Total
	Plan	nts/m of row		kg/ha	
No suppression	6	5	1,290	91	2,240
Glyphosate 2.5 kg/ha	10	10	1,980	490	3,040
Glyphosate + am. sulf.			• • • •		
2.0 kg + 1.7 kg	10	9	1,600	410	2,780
Glyphosate + am. sulf.					
1.0 kg + 1.7 kg	10	10	1,690	550	2.920
Rotavated	7	8	1,580	610	2,830
Significant contrasts (percent)					
No suppression					
vs. suppression	1	1	1	1	1
Rotavate vs.	,		•	•	•
glyphosate	1	NS	NS	NS	NS

Table 2—Comparison of various glyphosate treat	nents or rotavation with an untreated check for establishment of
bromegrass alfalfa in bluegrass sod	

Table 3—A comparison of three drills for seeding meadow brome-
grass into turf suppressed by glyphosate in northeastern
Saskatchewan

	Percent of drill run occupied by meadow brome			
Drill	September 1986	August 1988		
Swift Current Range				
Seeder (triple-disk)	87	64		
John Deere Powertill				
(powered disk)	¹ 63	¹ 53		
Moore Unidrill				
(single offset disk)	¹ 58	¹ 51		

¹Significantly different ($\rho < 0.05$) from the range drill.

However, in 1991, dry matter production of both the meadow brome and the rest of the vegetation was not significantly different among the three drill treatments.

A Comparison of Six Drills for Seeding Alfalfa Into Untilled Sod—In each of 3 years, 1985-87, we applied glyphosate at 2.2 kg/ha plus 0.5 percent v/v Agsurf (nonylphenoxypolyethoxy ethanol) at several sites throughout Saskatchewan to kill strips of resident vegetation at a time during the growing season when it was actively growing. The width of the killed vegetation strip varied from site to site and from year to year but was within the range 30-100 cm. We seeded alfalfa at 100 seeds/m (1985) or at 200 seeds/m (1986-87) into the dead vegetation late in October, using three or four drills (table 4). A more detailed description of experimental technique can be found in Waddington (1992). The seeds germinated the following spring.

Assuming that an alfalfa content of about 20 percent is needed to provide the optimum benefit to a pasture (Sheehy 1989), about 10 percent or 5 percent of seed needs to establish at these seeding rates. Soil moisture conditions were fair-excellent in 1986 and 1987, but extremely poor in 1988. Establishment success was measured as numbers of seedlings established by late summer of the year following seeding.

The various disk machines performed best (table 4). A satisfactory stand of alfalfa was obtained in 1986 only after using the Swift Current Range Seeder. In 1987, all the disk seeders produced satisfactory stands. In 1988, the very dry conditions prevented the development of any adequate stands. Of the drills tested, the Swift Current Range Seeder was clearly the best under Saskatchewan conditions. The Connor-Shea drill also showed promise. It performed as well as the range drill in a very dry year. These experiments also showed the importance of independent suspension for each drill run so that they can follow the land contours. Otherwise, the seeds are placed either too deep or too shallowly much of the time.

The effect of overall climatic conditions can be seen in table 5. With good seeding equipment, we usually obtained satisfactory stands in the moister areas. In the drier areas

Table 4—Effect of drills on percentage of alfalfa established at the end of the seedling year

Drill	1985-86	1986-87	1987-88
Swift Current Range Drill (triple-disk)	9	10	2
Swift Current Forage Drill (double-disk)	—	6	1
Moore Unidrill (single offset disk)	2		
Connor-Shea Zero-Till			
Pasture Drill (winged hoe)	—		2
Swift Current Zero-			
Till Grain Drill (narrow hoe)	2	—	-
John Deere Powertill (powered disk)	3	5	1

Table 5—Percent of alfalfa seeds established after seeding with the Swift Current Range Drill on several sites in Saskatchewan

	Brown-soil zone			Dark-bro zo		Biack-grey-soil zone	
Year	Swift Current (loam)	Webb (sand)	Crane Valley (clay)	Lanigan (loam)	Scott (loam)	Indian Head (clay)	Pathlow (loam)
1985-86	8	0	_	3	_	_	24
1986-87	0	0	<1	15	13	36	_
1987-88	<1	_	<1	3	2	2	2

of the brown-soil zone, and in a very dry year such as 1988, we usually failed to establish the alfalfa. In more recent experiments at Swift Current, we have established excellent alfalfa stands after spraying and seeding in early spring (Waddington and others, these proceedings).

A Comparison of Heavy Roller Drills—Often in northern pastures, seeding must be done in stony, roughly cultivated land, often with dead branches or roots of trees lying on or near the surface. We compared the Oregon, British Columbia, and Manitoba drills for ability to seed bromegrass-alfalfa in these conditions.

We were unable to make measured comparisons of seedling establishment, but seedling emergence after using the Oregon drill was about 10 days earlier than after the other two. There was a rain immediately after seeding, so germination conditions were good. All three drills drop seeds in the bottom of a furrow made by the roller or wheel ahead of the seed spout. The Oregon seeder leaves the seed there and covers it with a drag chain, so water moving into the furrow during a rain soaks into the soil immediately above the seed. The other two drills split the ridge with a second roller and bury the seed at the bottom of the new ridge. Consequently, water soaks into the soil at the side of the seed rather than directly above it. Establishment was good for all three drills by the end of the growing season.

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DIRECT SEEDING OF ALFALFA INTO NORTHERN PASTURE AND RANGELAND

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ABSTRACT

Controlling resident vegetation in the vicinity of a seedling was essential for successful alfalfa (Medicago sativa L.) establishment. An area about 50 cm wide was optimum: a wider control area was of more benefit to the weeds than to the alfalfa. Different precipitation patterns in 1989 and 1990 probably together with other weather-related factors had a major effect on alfalfa germination and survival during the seedling year.

INTRODUCTION

Southwest Saskatchewan is a semiarid area with erratic winter snows and growing season rains totaling 360 mm per year on average (range: 184-624 mm). Resident vegetation is mid-shortgrass prairie or seeded pasture deficient in nitrogen and with only a minor legume component. The inclusion of alfalfa (*Medicago sativa* L.) in grazing lands can increase productivity as much as 100 percent in some years (Leyshon 1978).

Seedlings need ecological "space" around them to improve their chances of establishment (McConnaughay and Bazzaz 1987). In arid and semiarid areas, this "space" is mainly a need for adequate water at the right times. The usual method of controlling the resident vegetation is to cultivate as needed until the old vegetation is dead, and then seed the desired species. This method is risky because of potential erosion, and failure to establish a new stand because of light, heat, and wind stresses on seedlings. Also, even in the best circumstances, the area may produce well below its potential if the forages are slow to reach mature size (McElgunn 1978). Direct seeding into sod killed by herbicide has worked well in some situations but not in others (Bowes 1978).

The use of glyphosate {*N*-(phosphonomethyl)glycine} to suppress all or part of the resident vegetation, followed by seeding a legume in late fall for germination early the following spring, has met with success in moister areas of

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EXPERIMENTAL PROCEDURES

Experiments were started in 1989 and 1990 in adjacent areas of a 30-year-old crested wheatgrass (Agropyron cristatum [L.] Gaertn.) field. Glyphosate was applied in May of each year at 2.2 kg/ha a.i. in 100 L water/ha. New growth of the crested wheatgrass was about 15 cm high. Sprayed strips were 8 m long and 0 (no glyphosate applied), 25, 50, and 75 cm wide.

Alfalfa was seeded in a single row down the center of each sprayed strip and in the check (not sprayed) in early June at 100 seeds/m. In each experiment, spacing between treated strips was 3 m, and each treatment was replicated four times.

Daily precipitation records were available from a nearby site (fig. 1). Soil moisture was measured in 10-cm increments to 50 cm several times during the growing season using a neutron soil moisture meter with access tubes in the alfalfa row. Alfalfa seedlings were counted in early summer (June-July) and again in early fall (late Augustearly September). Aboveground dry matter was measured at the end of the growing season (mid-September). Alfalfa crowns were dug to a depth of 25 cm in late October 1990 and grown in darkness to estimate root reserves.

RESULTS AND DISCUSSION

Soil moisture at seeding time was consistently above the permanent wilting point, which is about 11 percent water by volume in the soil on which the experiments were conducted (Cutforth and others 1991). But by late July, soil water was well below the permanent wilting point in the near-surface layers of soil, and was close to the permanent wilting point at all depths where the resident vegetation had not been controlled (table 1). Increasing the width of control strip in the crested wheatgrass resulted in more water available for seedling alfalfa growth throughout the soil profile into midsummer.

All aspects of plant growth were positively correlated with the width of the strip of crested wheatgrass controlled (table 2), although only the weeds showed a major benefit from a control width wider than 50 cm. There was a major

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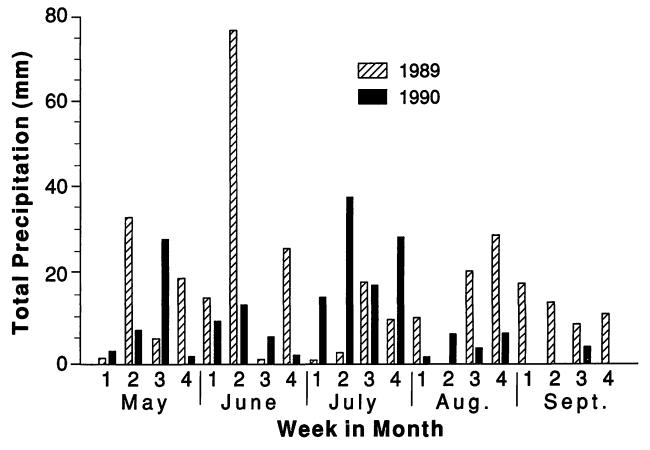


Figure 1—Total weekly precipitation for May 1 to September 30 for 1989 and 1990.

Soil depth	Width of vegetation control										
	July 29, 1989				August 14, 1990						
	0 cm	25 cm	50 cm	75 cm	0 cm	25 cm	50 cm	75 cm			
ст	Percent moisture										
0	5.3	5.6	5.0	6.1	5.6	5.9	9.5	11.6			
10	9.3	12.3	12.6	14.1	9.7	12.8	16.6	16.3			
20	10.0	13.8	14.2	15.4	10.8	14.5	18.0	18.2			
30	10.8	15.2	15.3	16.2	11.4	14.3	18.9	19.0			
40	12.0	16.3	16.4	17.3	11.8	13.6	16.9	18.3			

Table 1-Effect of width of vegetation control area on summer moisture levels (percent) in soil beneath seedling alfalfa¹

¹Permanent wilting point is about 11 percent in this soil.

Table 2-Effect of width of vegetation control on alfalfa and weed establishment and growth characteristics

Plants and characteristics	Width of vegetation control (cm)								
	1989				1990				
	0	25	50	75	0	25	50	75	
Alfalfa									
Pop./m	10	39	44	47	0	8	13	16	
D.M. (g/m)	0.5	5.1	13.3	14.8	0.1	1.6	6.2	10.8	
Regrowth (g/plant)	0.07	0.18	0.30	0.33	0.03	0.3	0.7	0.7	
Weeds									
D.M. (g/m)	1.2	7.4	24.9	43.3	0	0.4	1.0	6.9	

difference between 1989 and 1990 in alfalfa seedling numbers and plant growth in the field. This reflects the heavy rainfall shortly after seeding in 1989 (fig. 1), which resulted in excellent seedling germination and establishment that year.

The benefit did not appear in regrowth ability as measured by growth to exhaustion in the dark (table 2). Perhaps those seedlings that did establish in 1990 had larger root reserves because there was less competition between alfalfa plants than in 1989.

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DISK-CHAIN-DIKER CONSIDERATIONS FOR SEEDBED PREPARATION

Harold T. Wiedemann

ABSTRACT

Equipment to prepare seedbeds on shrub-littered rangeland has been under development by the Texas Agricultural Experiment Station for several years. The disk-chaindiker is a combination of the disk chain and chain diker implements; the combination device shows promise for rangeland seeding. The disk-chain-diker is composed of several components, each of which influences its performance. Drawbar pull as influenced by operating mass, disk blade size, chain size, chain angle, roller configuration, and diking chain attachment is discussed.

BACKGROUND

Equipment to prepare seedbeds on debris-littered rangeland has been under development by the Texas Agricultural Experiment Station for several years. The disk chain and chain diker are two significant advancements that have been combined to form the "disk-chain-diker" implement (fig. 1). This unique tool shows promise for rangeland seeding (Wiedemann and Smallacombe 1989).

The disk chain was developed first, and its purpose was to till land littered with logs and brush debris. Disk blades were welded to alternate links of a large anchor chain and swivels were attached to each end of the chain. When the chain was pulled diagonally, disking action was achieved as it rotated (fig. 1). Early engineering studies on disk chains evaluated pulling characteristics, operating mass, and other engineering indices (Wiedemann and Cross 1982, 1985, 1987). In seeding studies at six locations, grass densities were increased 35 and 92 percent over seedbeds prepared by nonmodified (smooth) chains in loamy sand and clay loam, respectively, in a 20- to 25-inch annual rainfall zone (Wiedemann 1982). We found the disk chain to be well suited for use on extensive acreages of debris-littered rangeland. It can easily be pulled over shrubs like tarbush (Flourensia cernua DC.), creosotebush (Larrea tridentata DC.), sagebrush (Artemisia filifolia Torr.), sand shinnery oak (Quercus havardii Rydb.), and small mesquite (Prosopis glandulosa Torr. var. glandulosa) on undisturbed rangeland; however, it was originally designed to traverse stumps and logs on rootplowed land.

The chain diker was developed by an Australian inventor to reduce runoff from wheat (*Triticum aestivum* L.) fields. This tool uses specially shaped blades welded to a large anchor chain. As it is pulled over tilled land, the chain rotates and the blades leave a broadcast pattern of diamond-shaped basins 4 inches deep. There are about 18,000 basins per acre (fig. 2). Pulling the chain diker behind a disk chain achieves tillage, land smoothing, and basin formation in a single pass, and greatly improves the operation of the disk chain. The chain diker will traverse any size brush debris the disk chain can traverse. Diking increased grass stand densities threefold compared to nondiked treatments the first year when May/June rainfall was 37 percent below normal; however, in years with 25 and 27 percent above-normal rainfall there was no difference in densities between treatments, all were excellent (yr 2 = 1.48 plants/ft²; yr 3 = 2.56 plants/ft²; 25 inches/ yr average rainfall). In a 48 percent lower rainfall zone (13 inches/yr), diking increased grass stands by 50 percent, average stand 0.38 plants/ft². Diking appears to have the best potential when rainfall is limited.

Chain diking has been evaluated for runoff reduction in a 3-year wheat production system near Vernon (25 inches/ yr rainfall). Diking followed planting; all other operations were conventional. Slope averaged 0.3 percent in the fine sandy loam soil and runoff measurements were recorded from September through May. Diking reduced runoff by 46 percent over the 3-year period compared to the nondiked treatment. The reduction was 21 percent, 72 percent and 45 percent and rainfall was 23.4, 15.8 and 25.8 inches/crop season, respectively.

Further information on the chain diker is discussed by Wiedemann and Smallacombe (1989). Construction of the chain diker is in collaboration with its inventor, Bruce Smallacombe, Capella Sales and Engineering, Capella, Queensland, Australia.

BASIC UNIT

The disk-chain-diker is a combination of several components, each of which influences its performance. A basicsize unit will be described that has functioned well over a broad range of conditions. Tests with this basic unit will be discussed, and then component variation will be referenced to the performance of the basic unit. The basic diskchain-diker is a 20-disk-blade unit using 2.5-inch diameter anchor chain with 28-inch diameter disk blades welded to alternate links for tilling; a 20-inch diameter flexing roller for a center brace (35 feet wide); and a 3-inch diameter anchor chain with specially shaped blades welded to each link for diking (basin formation), see figure 1.

DRAWBAR PULL

Drawbar pulling requirements are significantly influenced by operating mass (weight) while soil type has little

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Figure 1—Disk-chain-diker implement under development by the Texas Agricultural Experiment Station for enhanced seedbed preparation on debris-littered rangeland. The combination of the disk chain (front portion of implement) and chain diker (rear portion) provides tillage, land smoothing, and basin formation in a single pass.

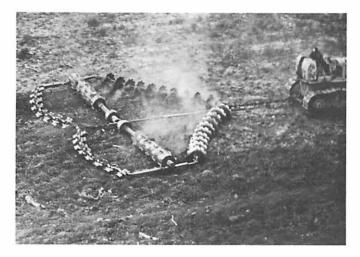


Figure 2—Basins are formed as the anchor chain with specially shaped blades rotates.

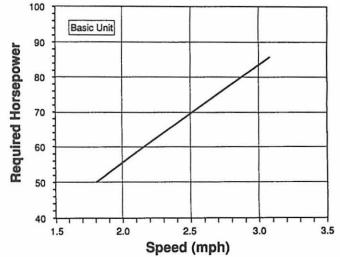


Figure 3—Drawbar horsepower requirements to pull the "basic-unit" disk-chain-diker at various speeds. Horsepower values are based on a 20-blade unit and a regression equation with an $r^2 = 0.94$.

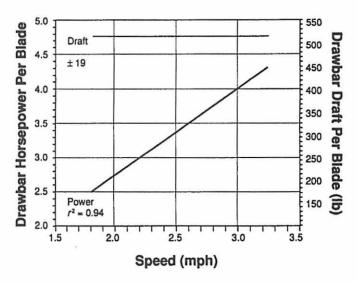


Figure 4—Per-blade drawbar power and draft requirements of the basic disk-chaindiker for various speeds (Wiedemann and Cross 1990).

influence. The heavier the unit the more power is required for pulling, and the deeper the disk blades penetrate the soil. Pulling tests with the basic unit were conducted in a well-tilled, clay loam soil. Average draft force was 515 lb/ blade \pm 19 lb when pulled at 2-, 2.5- or 3-miles/hour (mph). It follows that the 20-blade unit would require 10,300 lb of drawbar pull. Horsepower, which combines pull and speed inputs, is significantly increased as speed is increased (fig. 3). It requires 81.3 drawbar horsepower to operate the basic unit at 3 mph. A 140-engine-horsepower crawler tractor with direct drive can pull a 20-blade unit easily at 2 mph, but it is a full load at 3 mph. A 200engine-horsepower crawler tractor is best for 3 mph operation over a broad range of slopes. Number of blades to be pulled must be matched to the drawbar pulling capacity of the tractor. Additional tractor information is available from Wiedemann and Cross (1990). Power requirements for units other than 20 blades can be determined from data in figure 4.

Table 1-Specifications of disk chains that have been tested

						Roller		Disk o	hain	
Disk chain size ¹	Chain link			Disk blade		length	Blade	Length	Operating ³	
	Diameter	Pitch	Weight	Diameter x thick	weight	weight pin/pin ²	spacing	1-gang	Width	Mass/blade
	Inche	 75	Lb	Inches	Lb	Ft	Inches		-t	Lb
1 ⁷ /e x 24	17/8	7.5	21	24 x ¼	32	27.8	15	13.1	25.8	74
17/a x 28	17/a	7.5	21	28 x 3/8	55	27.8	15	13.1	25.8	97
21/2 x 24	21/2	10	49	24 x 1/4	32	35.4	20	17.5	33.4	130
21/2 x 28	21/2	10	49	28 x 3/8	55	35.4	20	17.5	33.4	154
3 x 24	3	12	86	24 x 1/4	32	41.5	24	21.0	39.6	204
3 x 28	3	12	86	28 x ³/a	55	41.5	24	21.0	39.6	228

'Size is chain diameter x blade diameter (inches).

²Roller, 20-inch OD diameter pipe with ¹/4-inch wall thickness, pin to pin length.

*Triangular system with 30 degrees between roller and line formed by disk-chain. Width equals 87 percent of length of two gangs plus 36 inches of attachment hardware. Mass/blade equals weight of two links plus one disk blade. Each gang has 21 chain links and 10 disk blades.

OPERATING MASS

Operating mass is influenced by both anchor chain and disk blade weight and is expressed in lb/blade. Operating lb/blade is calculated as the weight of two chain links and one disk blade (blades welded to alternate links). Anchor chain size largely determines the operating mass, which influences performance. Sizes and weights of six disk chains that have been tested are listed in table 1. Sizes and weights of other anchor chains suitable for use are listed in table 2. An addition of 1 lb of operating mass per blade will increase the draft requirement by 1.9 lb. This relationship is illustrated in figure 5 for operating masses between 74 and 228 lb/blade. The basic unit weighed 154 lb/blade. A 3-inch chain with 28-inch disk blades would weigh 228 lb/blade.

DISK BLADE SIZE

Disk blades 24, 28, 30, and 32 inches in diameter have been evaluated. Performance of the 30- and 32-inch disk blades was unsatisfactory because blades did not remain in a vertical position all the time. The blades "flopped" as

Table 2-Stud-link anchor chain specifications1

			Link			
Chain diameter		Length Pitch Weight			(90 ft)	
Inches	(mm)	Inch	0 S	Lb	Number	
2	(51)	12.0	8.0	25	133	
2¹/s	(54)	12.75	8.5	30	125	
21/4	(58)	13.5	9.0	36	119	
2³/8	(60)	14.25	9.5	42	113	
21/2	(64)	15.0	10.0	49	107	
25/a	(67)	15.75	10.5	57	103	
2¾	(70)	16.5	11.0	66	97	
27/8	(73)	17.25	11.5	75	93	
3	(76)	18.0	12.0	86	89	

'Actual weights and lengths may vary slightly.

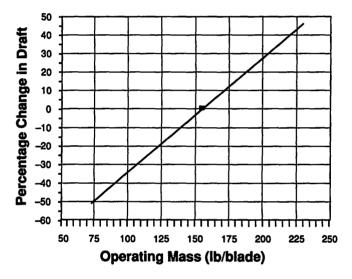


Figure 5—Change in required drawbar draft for various changes in operating mass/blade of the disk chain referenced to the "basic-unit" 154 lb/blade. Regression data adapted from Wiedemann and Cross (1987).

the chain was pulled, and this increased wear in the chain links (Wiedemann and Cross 1982, 1987). The preferred blade diameter is 28 inches because it weighs more, blade thickness is greater, and it traverses debris better than the smaller blade. If the chain diker is not used and a lighter roller is utilized, then the 24-inch blade is a better choice.

CHAIN SIZE

Chain size selection is influenced by soil condition. The harder the soil (resistance to penetration), the more mass per blade is needed to achieve satisfactory disking action (soil cutting). Tests were conducted in three different soil conditions to predict depth of disking. A soil cone penetrometer meeting ASAE Standards was used to characterize the penetration resistance of soils and establish a cone index (CI) rating. Site one was a clay loam soil that had been rootplowed (12 to 14 inches deep) and disked (8 inches deep). The CI was 164 psi. A similar value would be expected in an undisturbed deep sand. A CI of 351 psi was measured in a dry (near wilting point), clay loam soil on a 15-year-old rootplowed site. At a third site, a CI of 1,238 psi was measured in an undisturbed, very dry (below wilting point), fine sandy loam soil. Chain sizes of 2, 2.5, and 3 inches and two disk blade sizes were tested covering an operating mass range of 74 to 228 lb/blade. Further information on this study is covered by Wiedemann and Cross (1987).

The 2-inch chain has given adequate performance in disturbed soil when conditions were favorable (adequate moisture, loamy soils, little turf, and minimal brush debris). The 2.5-inch chain, however, can perform satisfactorily over a much broader range of adverse conditions than the 2-inch chain, and draft is about one-third less than the 3-inch chain. Adequate disking action with minimum draft is desirable. The 2.5-inch chain size has given the best performance in disturbed (rootplowed) and some undisturbed soils (soils with less than 300 psi CI). Disking depth was 3 to 4 inches. This chain size has also functioned well in shinnery-infested deep sand. The relationship of disking depth to operating mass/blade is shown in figure 6. The three soil conditions cover a wide range of soil strength. If both the mass (M in lb/blade) and cone index (CI in psi) are known, the depth of cut $(\pm 0.5 \text{ inches})$ can be predicted by the formula Y = 2.25 + 0.01M - 0.002CI.

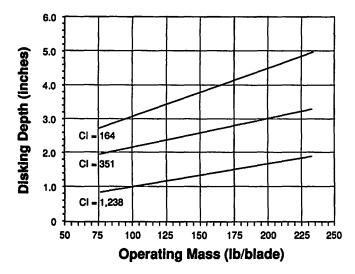


Figure 6—Depth of disking for various operating masses/blade in three different soil conditions described by an ASAE Soil Cone Index. CI 164 psi is a tilled soil; a deep sand would be similar. CI 351 psi is an average, undisturbed, clay loam rangeland. CI 1,238 psi is very-dry, very-hard, fine sandy loam rangeland. Regression data are from Wiedemann and Cross (1987).

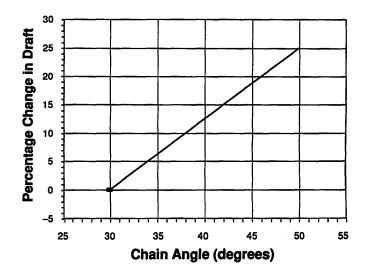


Figure 7—Change in required drawbar draft for various chain angles referenced to the standard 30-degree angle. Regression data adapted from Wiedemann and Cross (1985).

In soil with a CI over 300 psi, the 3-inch chain is necessary for satisfactory performance. At the site with a CI of 1,238 psi, two passes with the 3-inch chain were required for satisfactory tilling. If the disk chain is to be used mostly in undisturbed soil, the 3-inch chain is favored. It must be kept in mind that rangeland needing renovation most probably will be dry and hard.

CHAIN ANGLE

Disking action also can be influenced by changing the chain angle. Chain angle is the angle between the roller and the line formed by the disk chain (fig. 1). An angle of 30 degrees was determined to be the optimum by Wiedemann and Cross (1985). Aggressiveness of disking action can be increased by increasing the chain angle, but pulling requirements will be significantly increased as shown in figure 7. Increasing the disk's aggressiveness destroys more surface vegetation because of increased soil disturbance. The chain angle may be changed by changing the width of the roller or length of the disk chain. Chain angle also influences the effective width between blades as noted in table 3.

ROLLER

The roller serves as a brace to hold the two disk chains at the selected chain angle (fig. 1). It is made from 20-inch outside diameter (O.D.) pipe with a 0.25-inch wall thickness. A flexing center joint is crucial for proper operation on uneven soil surfaces. Design of the flexing joint allows vertical movement only. The ridged bar that must be

Table 3—Disk-chain blade spacing

		Inches between blades ¹			
Chain size	Chain angle	Actual	Operating		
Inches	Degrees				
2.0	30	16	13.9		
2.0	40	16	12.3		
2.0	50	16	10.2		
2.5	30	20	17.4		
2.5	30	20	15.4		
2.5	50	20	12.8		
3.0	30	24	20.9		
3.0	40	24	18.5		
3.0	50	24	15.4		

¹At 30 degrees operating is 87 percent of actual, at 40 degrees operating is 77 percent of actual, at 50 degrees operating is 64 percent of actual.

pin-attached between the flexing joint and the front attachment plate is necessary for proper operation of the disk chain. Cleats on the roller prevent "pipe-skidding," which can stall forward motion and damage the roller. Tests with a 12-inch diameter pipe were unsatisfactory when operating width was over 20 ft. The roller accounts for 11.6 percent of the required draft. A major increase in the roller size and weight would increase the draft requirement.

DIKING CHAIN

A 3-inch chain was selected over smaller chains for the diking unit because of better blade penetration into the soil on rough, uneven, debris-laden surfaces. The diking chain accounted for 2,065 lb of draft. This equates to 103 lb/blade or 20 percent of the required drawbar pull for the basic unit. Action of the disk chain was greatly improved when the chain diker was added to the system. Soil cutting was equal across the entire operating width because blade flopping was virtually eliminated. Increased soil cutting was reflected by the draft force of 7,411 lb for the disk chain without the diker unit attached compared to a force of 8,254 lb for the disk chain when the chain diker was attached.

GENERAL APPLICATION

Prototypes of the basic unit have given satisfactory performance over a broad range of conditions on selected test sites. Soil type, condition, moisture content, percent slope, and surface roughness can all influence performance. However, brush debris can be a limiting factor. The unit was designed to traverse brush debris, but not excessive amounts of timber. In field tests it has traversed 16-inch diameter logs 6 ft in length and 24- by 36-inch stumps on rootplowed land. Problems develop when several logs or irregular-shaped logs lodge in the unit or when excessive debris prevents the blades from penetrating the soil. Standard smooth chaining ahead of disk-chain-diking can be helpful in some situations to break up brush debris. Brush debris (following rootplowing) breaks up better after a short drying period. When excessive amounts of timber are present, the site must first be raked or chained and burned before the disk-chain-diker can be used successfully.

BRUSH DEBRIS CONSIDERATIONS

Determining when brush debris is excessive is, to a large degree, a practical judgment based on experience. The following explanation may help in making that decision. First to be discussed is standing mesquite regrowth that is to be rootplowed. On sites where mesquite regrowth is less than 8 ft tall and stem diameters are less than 3 inches (at the base), tree density makes little difference in the unit's operation. Moderate stands of trees 8 to 12 ft tall with stem diameters averaging 4 inches or less will usually not be difficult to traverse. However, dense stands will need to be chained following rootplowing to break up the limbs so the disk-chain-diker can operate without difficulty. Dense stands are difficult to walk through. Moderate stands of 12 to 18 ft tall trees with 6-inch stem diameters will need to be chained following rootplowing to break up limbs. Dense stands of these size trees may require two-way chaining to break up the limbs sufficiently. Stands with trees over 20 ft tall or stem diameters more than 8 inches will need to be raked or chained and burned before plowing. Rootplowed stumps or stumps partially lodged in the soil have not been a problem.

STANDING BRUSH CONSIDERATIONS

In standing brush, the disk-chain-diker has not had difficulty traversing shrubs less than 8 ft tall that break easily or are shallow rooted. In tests conducted in tarbush (average height 3 ft) and shinnery (height <2 ft) the implement either severed or uprooted the plants. In shinnery mottes, the basic unit (2.5-inch chain) traversed trees 8 to 10 ft tall (trunk diameter 4 inches), but little disking was accomplished. In standing mesquite, the heavier implement (3-inch chain) has traversed trees up to 18 ft tall when top growth had been sprayed; however, when stems were alive trees taller than 10 ft occasionally tangled in the disk chain. Mesquite less than 8 ft tall has not been a problem to traverse. Tall trees in moderate-todense stands may require two passes with the disk-chaindiker for satisfactory tilling.

CONSTRUCTION PLANS

Construction plans were drawn to convey concepts and are offered as a guide for fabrication (see fig. 8). Dimensions were based on the selected components of the basic unit. Dimensions for units having other than 20 disk blades or different chain sizes are listed in tables within the set of engineering drawings.

The complete set of plans is available from the Texas Agricultural Experiment Station, P.O. Box 1658, Vernon, TX 76384. Request Center Technical Report TR-2, "Disk-Chain-Diker Construction Plans." The Experiment Station offers the construction plans as a public service and

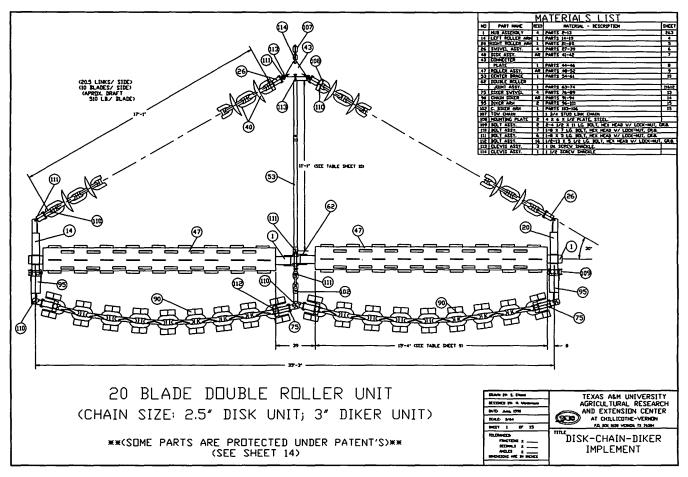


Figure 8-Plan view of disk-chain-diker.

does not assume responsibility for construction, manufacturing, or use of this device. Some components are covered by patents.

ACKNOWLEDGMENTS

I am grateful for the technical assistance provided by B. T. Cross and G. G. Schulz in design, construction, and testing of the disk-chain-diker implement. To Sam Stone I am especially indebted for his skillful drawing of the plans. Appreciation is expressed to Bruce Smallacombe for his advice and trips to the United States to cooperate on this project.

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DECISION SUPPORT SYSTEMS FOR RESTORATION AND MANAGEMENT OF ANNUAL RANGELANDS

J. Ross Wight

ABSTRACT

Natural resource managers are required to deal with an increasing amount of information to maintain proficiency in their management skills. The integration and interpretation of information is beyond the means and time constraints of most resource managers. Computerized decision support systems utilize tools like expert systems and databases that include geographic information systems for organizing, structuring, and delivering information from basic and applied research as well as heuristics. This paper discusses the application of these systems to problems of restoration and management of annual rangelands.

INTRODUCTION

Natural resource managers are required to deal with an increasing amount of information to maintain proficiency in their management skills. The integration and interpretation of information is beyond the means and time constraints of most resource managers. Computerized decision support systems utilize tools like expert systems and databases that include geographical information systems for organizing, structuring, and delivering information from basic and applied research, as well as heuristics. This paper discusses the application of these systems to problems of restoration and management of annual rangelands.

Exotic annuals are becoming the dominant vegetation on vast areas of rangeland in the Western United States. Environmental concerns associated with biodiversity and soil stability, both of which are adversely affected by invasion of annual species, are at an all-time high. Restoration and management of these rangelands have become a critical environmental issue and a challenging assignment. Rangeland ecosystems are complex systems of interacting components where management or manipulation of one component causes corresponding responses throughout the system. Because of extreme spatial variability, changes due to management or treatment effects are difficult to measure. Annual fires fueled by cured stands of cheatgrass (Bromus tectorum) cause additional problems on these annual rangelands. Such fires have reduced vast areas to near monoculture stands of cheatgrass, which increases the incidence and extent of these

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J. Ross Wight, Range Scientist, USDA Agricultural Research Service, Northwest Watershed Research Center, 800 Park Blvd., Plaza IV, Suite 105, Boise, ID 83712. fires. Fire management and subsequent rehabilitation have become major problems associated with the management of these rangelands.

Technical information on ecosystem components, their interaction, and response to management and restoration technology continue to increase. The information and technology are scattered throughout the literature. Considerable knowledge has never been published and is available only through interrogation of living experts. Such fragmentation makes it difficult to organize the information and develop management practices and policies.

Assimilating, integrating, and interpreting information from so many diverse sources is beyond the means of individual rangeland resource managers. Decision support systems (DSS), which include components such as databases, expert systems, natural resource models, and geographical information systems (GIS), provide a means of interpreting and integrating the available knowledge and information into useable formats. Such systems appear to be ideal tools for the management and restoration of annual rangelands.

DECISION SUPPORT SYSTEMS

Expert systems, GIS, and natural resource models are basic components of natural resource DSS. Expert systems can be described as computer programs that simulate the problem solving capabilities of several experts and are able to draw and store inferences from information (Rajotte and Bowser 1991). Such information is supplied by experts in specific disciplines or domains and model simulations. In addition to knowledge bases, expert systems include user interfaces, and inference engines, mechanisms that control the reasoning processes (Stock 1987).

GIS are becoming the common method for storing information associated with specific unit areas of geography. Such unit areas can be of almost any magnitude and include such information as soil slope, aspect, texture by soil horizon, vegetation cover, herbage yields for the past several years, and artificial structures.

Natural resource models such as SPUR (Simulation of Production and Utilization of Rangelands) (Carlson and Thurow 1992; Wight and Skiles 1987), WEPP (Water Erosion Prediction Project) (Lane and Nearing 1989), and SHAW (Simultaneous Heat and Water) (Flerchinger and Saxton 1989a,b) have become increasingly important as management tools. They can be used to predict the impact of proposed management strategies or the probability of occurrence of soil-water and temperature regimes that are favorable for the germination and establishment of specific plant species or the hatch and development of specific insects. In a DSS, models are used interactively with the expert system to evaluate various management strategies and supply information to the knowledge base. The GIS databases are major sources of input information for running the models.

To be an effective management tool, DSS must be easy to use. Input requirements must be within the expertise of the DSS users. Once installed on the computer, the DSS can be put in operation by typing a key word. The user is then asked for information, usually one item at a time. For example, one of the first requests might be for the longitude and latitude. A map might then be displayed on the screen and the user is asked to use the cursor to outline the boundaries of the resource area under consideration. This would allow appropriate information to be transferred from the GIS database. Help screens are available to explain each input request. If the DSS requires the operation of complex models, the expert system component must be able to develop the parameters for these models through user-supplied information such as soil series name and plant species being grown. Much of this information could be supplied by the GIS database.

No single DSS will provide all the information needed by rangeland resource managers. At least initially, such systems will be of limited scope and problem specific. Within the Bureau of Land Management (BLM), rehabilitation of burned rangeland is a major concern and a good example of a management problem that could be well addressed by a DSS. Fire rehabilitation is expensive. For example, in 1992 fires burned on about 98,000 ha of Idaho rangeland managed by BLM. Rehabilitation plans were developed for about 37,000 of these hectares with an average projected rehabilitation cost of about \$92/ha or approximately \$3.4 million (BLM 1992). Currently, rehabilitation is based on official guidelines and the expertise and past experience of the responsible individual(s). The guidelines are general in nature and lack sensitivity to the individuality of each burn and site condition. Different personnel using the same guidelines for the same fire could develop rehabilitation plans that are considerably different. The development of a DSS to assist fire rehabilitation planners would significantly enhance the efficiency of the planning process and effectiveness of the rehabilitation treatments.

PROPOSED REHAB DSS

A proposed prototype DSS for making fire rehabilitation plans is described by Wight and He (1993). In this system, GIS techniques are applied for gathering, processing, storing, analyzing, and displaying information. Global Positioning Systems could be used to accurately locate the burned sites and provide other details of the burned areas. Simulation models are suggested for predicting the dynamic states of the hydrology, climate, and soil microenvironment in postburned areas. For example, the SHAW model may be employed to predict the temperature and water content in the 1-cm soil surface layer. The temperature and water information may then be imported into a grass seed germination model for predicting the optimal seeding plan (Hardegree 1993). The WEPP model may be used to predict soil loss and deposition on the burned site, which is part of the environmental analysis. The SPUR model, which includes climate, hydrology, plant, animal (both domestic and wildlife), and economic components, may be included in the fire rehabilitation DSS as another part of the environmental analysis. Different models may be used to focus on the different perspectives in the decision-making process. Knowledge acquisition through model studies such as sensitivity analysis may be an essential part in the development of the expert system.

In the prototype DSS described by Wight and He (1993), a database management system would provide most of the inputs for the simulation models. A knowledge-based system would be used to simulate the reasoning process of fire rehabilitation planners or resource managers in a normal condition, which means the knowledge involved in this process is based on past fire rehabilitation experiences, established routines of fire rehabilitation planning, or both. Uncertainty knowledge could be used as part of the rule base. However, since unexpected situations do occur as a natural part of ecosystems dynamics, the resource managers would still play a key role in evaluating and adjusting the recommendations made by the DSS.

The development of a DSS, as described by Wight and He (1993), requires the coordination of an interdisciplinary effort and a vast array of site and other information. Potential users of the DSS need to be involved in all phases of system development. A team of domain experts may include disciplines such as hydrology, soil science, geology, range science, forestry, wildlife, fire management, engineering, and personnel management. Required site information includes: soil and vegetation characteristics. climate, erosion hazards, threatened or endangered species' habitats, fences and other structures, fire history, past rehabilitation treatments, and wilderness and critical environmental concerns. This information is often available in various formats and forms such as maps. documents, and electronically stored data. An interdisciplinary team of experts and DSS users gather, process, and analyze all available information for inclusion in the DSS.

Development of DSS is an expensive, time-consuming process. However, once completed, they can be distributed on computer diskettes and provide a common basis among natural resource managers for making management decisions. DSS are so constructed that they can be continually improved and updated based on user experience and availability of new information.

SUMMARY

DSS will be a great asset to the management and restoration of annual rangelands. Storage and retrieval of information, especially expert knowledge, will be greatly enhanced. The time and cost of the decision-making process will be reduced. Fire has become a critical issue on western rangelands. Development of fire rehabilitation plans for burned areas is an example of many applications of DSS in the management of rangeland ecosystems. In addition to organizing information and providing a format or structure for making decisions, the use of DSS will provide a much needed consistency within and among agencies managing rangeland resources.

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DRILLS FOR RANGELAND SOD SEEDING

F. B. Dyck G. G. Bowes J. Waddington

In western Canada, there are about 8.9 million hectares of range and marginal cropland that could be improved by establishing tame grass and legume species (Johnston and Smoliak 1977). It is estimated that tame seeded forage crops will yield three to five times as much as native rangeland. The traditional method of improving pasture productivity is to break up the existing sod, prepare a firm seedbed, and seed tame forage species. This is expensive on marginal land because much of the topography is rocky, rough, and hilly. Further, breaking leaves the soil exposed to wind and water erosion, which is environmentally not desirable. Also, in years of drought, adequate moisture is not available for germination of small forage seeds, which must be placed at a shallow depth in the soil.

Two alternate methods to improve rangeland are: directly sod seed a legume or grass species after suppressing or killing the existing vegetation with herbicides; suppress or kill the existing vegetation by mechanically undercutting a strip of sod (36 cm wide) at about 3 cm depth and removing a ribbon of sod from the center of the strip, and seeding a row of legume or grass in the center of the slot. Two drills were developed to assess these two methods.

ZERO-TILL RANGELAND DRILL

A zero-till rangeland drill facilitating the first concept was developed by Dyck and Bowes (1982) and has been assessed for renovating pasture and haylands in Saskatchewan by Malik and Waddington (1990), Waddington (1992), and Bowes and Zentner (1991) and in Quebec by Belzile (1988, 1991) and Belzile and Rioux (1983). This machine (fig. 1) originally had a sprayer attachment mounted on the seeder; thus the spraying and the seeding operation could be done at the same time. However, it was soon discovered that the optimum time to spray differed from the optimum time to seed and the success rate was enhanced by separating the two operations.

The seed frame was constructed of 100- by 100- by 4.75-mm wall square tubing with a vertical adjustment on the hitch to enable leveling of the frame.

The disc coulters and double-disc openers had 60-cm diameter pans, 4-5 mm thick (fig. 1). The disc coulters were clamped to the tool bar without a trip mechanism or spring cushion, but they can pivot horizontally, which enables the unit to turn when operating in the soil. This simple design has the disadvantage of the whole machine lifting should the coulters encounter an obstruction like a rock or a tree stump. On a commercial zero-till drill, it would be advisable to design a trip mechanism for each disc coulter. This was incorporated on the unit used in Quebec (fig. 2). The double-disc openers pivot at the tool bar to enable them to follow the soil contour. Depth bands were mounted on the pans to limit seed placement to 2 cm below the soil surface. Cast iron weights were mounted at the rear of the opener to ensure penetration. This increased the weight of each opener to 125 kg. The openers were raised and lowered by a rockshaft and chain attached at the rear of the opener.

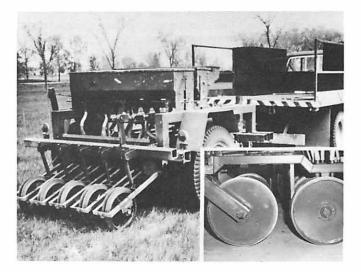


Figure 1-Zero-till rangeland drill, western prototype.

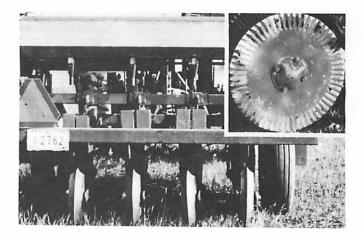


Figure 2-Zero-till rangeland drill, eastern prototype.

Poster paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992.

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Table 1—Seedling alfalfa establishment following zero-till seeding into a bluegrass sod treated with glyphosate at Parkerview, SK

Exp. No.	Herbicide treatment	Seed alfalfa	Alfalfa count	Control	Gly- phosate
		Date		Alfalfa plai	nts m/row
1	22 Sept. 771	25 Oct. 77	28 Aug. 78	12 ± 4 ³	20 ± 5
2	29 May 781	29 May 78	28 Aug. 78	9±2	16±4
3	29 Sept. 78 ²	10 Oct. 78	14 Aug. 79	1±1	9±3
4	22 May 80 ²	22 May 80	12 Aug. 80	14±3	24 ± 5
5	22 Sept. 80 ²	15 Oct. 80	13 Aug. 81	1±1	6±1

'Glyphosate applied at 2.0 kg/ha. 'Glyphosate applied at 2.5 kg/ha.

³Means ± SE.

The seed box for coarse grass seed has a fluted roll seed cup from a John Deere grain drill. In the seed box, 8-mm round steel bars were welded in the form of a "T" and were attached to a shaft that ran the length of the unit. The T-unit oscillates over the fluted rollers to prevent light, hairy grass seeds from bridging. The seed box for alfalfa had a small fluted roll seed cup from a John Deere forage seed attachment. In both seed boxes, rate adjustment was made by sliding the fluted roll in the cup.

The two fertilizer boxes were constructed of galvanized iron and used a C.C.I.L. (Canadian Cooperative Implements Ltd.) fluted roll seed metering cup modified to operate in the overshot mode. This reduced the grinding of the fertilizer. Rate adjustment was done by sliding the fluted roll in the cup. One fertilizer applicator placed the fertilizer with seed and the other one broadcast fertilizer behind the furrow opener.

The seed and fertilizer boxes were driven by chain from the ground wheel and later from one packer wheel. The unit was fitted with tail and signal lights to enable towing by truck to various test plots in the Province. Performance and seedling establishment was greatly improved by the addition of packer wheels on both units. On the western unit two cast, sharply shaped wheels were mounted together to pinch the furrow shut and pack in the seed zone (fig. 1). On the eastern unit wide V-shaped cast packer wheels were used (fig. 2).

Results for the western unit are given in tables 1 and 2 and figure 3. Results from the eastern unit are described by Belzile (1983, 1988, 1991) and Rioux and Belzile (1983, 1989).

SOD SLOT SEEDER

A drill featuring the second approach was also developed by Dyck and Bowes (1991) (fig. 4). The renovation technique is illustrated in figure 5.

The machine consists of a rugged frame constructed of 100- by 100- by 6-mm tubing supported on two 9.5Lx15 wheels. Overall width is just under 2.6 m to meet highway transport specifications. Five opener assemblies are individually attached to the frame in a staggered pattern with a flexible link and two pressure springs, which accommodates surface irregularities while maintaining operating depth. Each opener assembly can move vertically ± 7.5 cm from the normal operating position. Adequate ballast is provided with four 225-liter water tanks, thus 900 newtons of force can be exerted at each end of the opener assembly to ensure penetration and contour following in uneven terrain. This is accomplished by hydraulically adjusting the position of the wheels to put most of the weight of the frame plus ballast onto the opener assemblies, thus compressing the pressure springs to about one-half their original length. The wheels also serve to stabilize the machine laterally.

The opener assembly is made up of two or three disc coulters 45 cm in diameter (fig. 6) with a depth band in between, or on the outside; a fabricated shank equipped with a sweep; an offset disc opener (Dyck and Tessier 1986; Lawrence and Dyck 1990) with a depth band for precise seed placement; and two narrow V-shaped packer wheels to pinch the furrow shut (fig. 7). The packer

			Plant count/m of row				or/m of row
		All	alfa	a Milkve		Alfalfa Milkvet	
Treatment	Rate ²	Rate ² 30/8/84		30/8/84	24/10/85	15/10/86	15/10/86
	kg a.i./ha						
Check		32 b	8 c	15 a	6 b	20 b	4 b
Glyphosate + ammonium sulfate	0.05 + 5%	46 a	14 a	25 ab	8 a	36 a	9 a
Glyphosate + ammonium sulfate	1.1 + 5%	52 c	12 b	21 ab	8 a	29 ab	8 a
Glyphosate	1.1	46 a	11 b	22 ab	9 a	32 ab	7 ab
Glyphosate	2.2	50 a	13 ab	26 a	9 a	32 ab	8 a

'Means followed by the same letter are not significantly different at P = 0.05 according to Duncan's multiple range test. 'a.i. = active ingredient.



(a) Ribbon of Sod Removed Soil Surface 3.8 cm 2 cm 3.8 cm (b) Undercut Dnly 20 - 40 cm Undercut Seed Seed Seed

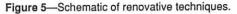


Figure 3—Forage establishment using the zero-till rangeland drill.



Figure 4—Rangeland slot seeder.

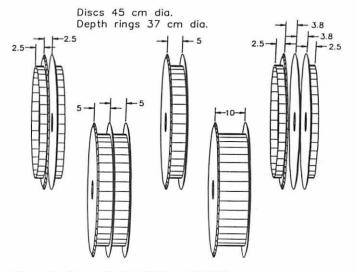


Figure 6—Schematic of coulters used to define depth and width of the slot (all measurements in centimeters).

wheels also act as a gauge wheel for the rear portion of the opener assembly.

The coulters and the sweep shanks are fitted with a hydraulic trip for protection from obstacles such as rocks. This system was previously reported by Dyck and Tessier (1986) and performs very well. The pressure can be adjusted to match the conditions encountered and the size of sweep used.

The opener assembly can be modified (fig. 8) to enable seed placement by the sweep shank with the addition of a seed tube and by adjusting the wear rod of the sweep to cut a furrow approximately 2 cm deep in the center of the trench created by removing the sod. The disc portion of the opener assembly is replaced by a packer wheel 38 cm in diameter and 9 mm thick cut from plate steel. Thus the packer wheel is narrow enough to pack to the bottom of the furrow created by the wear rod, which is 12 mm wide. In this mode the double packing wheel is banded with a hoop of flat iron 5 mm thick providing a gauge wheel function with minimal packing. This assembly can also be used to meet specification (b) (fig. 5) by replacing the double coulter with a single coulter fitted with a depth band, removing the mold boards from the sweep assembly, and adjusting the sweep wear rod to the sweep level. Thus the sod is undercut without removing the center ribbon.

The seed boxes are divided for each row to enable alternate row seeding of a legume and a grass species or seeding of fewer rows at a wider row spacing. The grass seed box is fitted with an agitator to prevent bridging of seed and to maintain flow through the metering cup. John Deere fluted roll cups are used for both the legume box and a grass seed box. The legume cup is small in size to maintain accurate metering of small seed. The larger cup used for grass seed is a standard grain cup. It features the seed roll close to the bottom of the box to achieve good

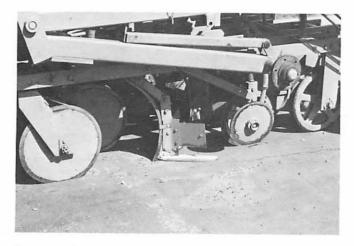


Figure 7—Coulter, sweep, and disc opener assembly.

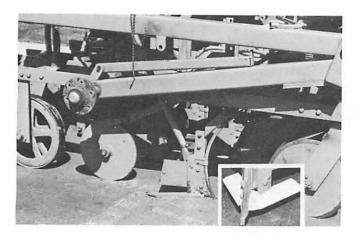


Figure 8—Coulter and sweep assembly with seed placement attachment.

metering roll contact with the seed and to minimize bridging. The seed and fertilizer boxes are ground driven from a separate wheel.

All of the options outlined have not been evaluated to date. Plots using the technique illustrated in figure 5a were seeded with alfalfa at several locations in the Province. For these tests, three opener assemblies were set up using the disc opener to place the seed and two opener assemblies were modified to place the seed by the sweep shank with the hoe point. Seeding was done at Neudorf, SK, on May 28, 1991, with two varieties of alfalfa. Plant counts were taken on June 19, 1991. The results are summarized in table 3.

Establishment was considered to be adequate. The data indicate that the sweep hoe point combination has given equal (no significant difference) or slightly better establishment than the disc opener. This may be due in part to the different packer wheels used. The former uses a narrow packer wheel that packs to the bottom of the furrow, while the latter uses a double packer wheel to pinch the furrow shut. This may result in less packing pressure Table 3—Results of sod slot seeder tests, removing a ribbon of sod, with two alfalfa varieties

	Alfalfa v	ariety
Treatment	Rangelander	Beaver
	Plants/m	eter
Sweep + disc opener	5.6	5.5
4c hoe point opener	7.2	8.3

in the seed zone and also push a greater amount of soil over the seed. However, the success of the sweep hoe point combination is encouraging because it indicates that perhaps one can simplify the design and construction of the machine, making it shorter and more economical to construct. Continued evaluation in a greater variety of environments will be carried out before conclusions are drawn.

Producer reaction to the prototype has generally been favorable. One suggestion was to reduce the width of the slot to minimize the roughness left in the field by the ribbon of sod. This has been done and is illustrated in figure 6. Field trials with various slot widths were seeded in spring 1992. The desired reduction in roughness is not evident except for the 2.5-cm slot.

CONCLUSIONS

The zero-till rangeland drill has been very successful in the parkland area of the prairies; however, farmers have been reluctant to adopt this technique because of the application of glyphosate required.

Initial testing of the sod slot seeder has also been very positive and provides a once-over method of renovating range. Further testing will be carried out, and the benefits and costs of the two methods will be compared.

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EFFECT OF SEEDING DATE AND FURROW OPENER ON FORAGE CROP ESTABLISHMENT AT SWIFT CURRENT, SASKATCHEWAN

N. W. Holt F. B. Dyck S. Tessier

In arid and semiarid climates, perennial forage crops are difficult to establish and this is a deterrent to their use for pasture and conservation programs. Soil water content, soil temperature, and seed-soil water contact have major effects on seed germination and seedling establishment. Seeding date can be selected to coincide with adequate soil water content and favorable temperatures. In the dry regions of the northern plains, three dates of seeding have been recommended for the establishment of perennial forages: early fall; late fall (dormant seeding); or early spring seeding.

Seeding equipment that places the seed in firm, moist soil at the correct depth will increase the likelihood of a successful stand.

The objective of this study was to determine the effect of seeding date and furrow opener on forage crop establishment.

METHODS AND MATERIALS

These experiments were conducted near Swift Current, SK, at two sites: the soil at one site was fine sandy loam (fallowed prior to seeding) and loam at the other (always wheat stubble).

Dates of seeding were early September, early October, "dormant" seeding in late October, and one to three dates in April and May. Altai wildrye (*Leymus angustus* [Trin.] Pilg. cv 'Prairieland') (AWR) was selected originally as it is difficult to establish. After the September 13 seeding date in 1988, Russian wildrye (*Psathyrostachys juncea* [Fisch.] Nevskii cv. 'Swift') (RWR) was substituted as it is also difficult to establish in sandy soils and is much more widely grown than AWR. Intermediate wheatgrass (*Elytrigia intermedia* [Host] Nevskii cv. 'Clarke') (IWG) is reported to be easy to establish and more rapidly growing than AWR or RWR.

The seeding was carried out with a one-row plot seeder attached to the tool bar on the three-point hitch of a small tractor. The seeder was equipped with a fluted gear to disperse seed from the seed box. Four furrow openers could be interchanged. The standard for this experiment was a double disc with depth bands at 2 cm, the recommended opener to seed forages in this area. The double disc was interchangeable with a hoe opener, a flat metal bar, 1.2 cm wide and 5 cm long equipped with a seed delivery tube. The hoe opened a furrow about 1 cm wide. Depth control was provided by the support wheels of the tool bar. Flat metal pieces could be attached to the hoe opener to provide for lister (trench) seeding. The lister was adjusted to provide a trench 10 cm wide at soil surface and tapering to a point at 5 cm furrow depth. The lister could be used with the hoe or the double disc.

The study was initiated in September 1988 and continued for 3 years to examine the effect of seeding dates and furrow openers on the establishment and subsequent yield of seeded grasses. Data were collected on days to emergence, stand (plants per m row), and establishment year yield. In September 1988 data were also collected on speed of emergence of the forage crop and effect of opener on soil water, soil bulk density, and water loss after seeding.

Treatments (openers nested in species) within each date were arranged in a split plot design of two replicates. Each date of seeding was adjacent and was replicated only by location. The analysis of variance was carried out on all of the data for each year and then for each date within years if there was a significant location and date interaction. Means were compared by Duncan's multiple range test at P = 0.05.

RESULTS

Weather Data — Long-term average precipitation at Swift Current for the months of September, October, April, and May is 31, 19, 22, and 43 mm, respectively. In 1988, September precipitation was 33 mm. Amounts were 10 mm higher and 28 mm less than average in 1989 and 1990, respectively. October precipitation was less than 10 mm in each year of the test. April and May precipitation was normal in 1989 and 1990 and much above normal in 1991. Mean air temperatures were near the long-term averages of 12, 6, 5, and 11, respectively. Average monthly soil temperatures at 10 cm depth were similar to the air temperatures for the same month.

1988/1989—Altai wildrye was successfully established on each of two dates in the fall of 1988 and on one date in the spring of 1989 (data not shown). Percentage stand

Poster paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992.

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Grass ¹	Date of seeding	Days to emerge	Stand	Yield ²
			No./m row	g/m row
IWG	Sept. 14, 1989	14c	205	31a
	Oct. 24, 1989			5c
	Apr. 17, 1990	27a	24a	12b
	May 4, 1990	21b	23a	10b
	May 29, 1990	11d	24a	3c
RWR	Sept. 14, 1989	15x	34x	8z
	Oct. 24, 1989	_	—	4y
	Apr. 17, 1990	26z	47y	7z
	May 4, 1990	22y	50xz	8z
	May 29, 1990	12w	58z	2y

Table 1—Date of seeding effects on days to emerge, stand count, and establishment year yield of two grasses at Swift Current, SK, 1989-90

¹Grasses were intermediate wheatgrass and Russian wildrye. Data for each grass were analyzed individually.

²Harvest date was September, 1990.

was greatest for plantings in early September (fall established) and April.

1989/1990—Seeding IWG or RWR in September, April, or early May provided satisfactory stands and highest establishment-year yields (table 1). Highest first-harvest forage yields (July 1991) were obtained from the April and early May dates of seeding (data not shown). Stands from all dates were assessed as adequate, that is, 75 percent complete. Seeding IWR or RWR in early October in 1989 did lead to a satisfactory stand in 1990, but dormant seeding in late October was successful. The double disc or double disc with lister provided complete stands most consistently.

1990/1991—At the sandy soil location, which was previously fallowed, the fall plantings in September and October of 1990 did not result in established stands of forage. Rows were eroded by wind in the fall and water in the spring. At the loam soil site (wheat as the previous crop), no germination occurred in the fall due to the dry soil conditions. Three of four seedings in the spring were satisfactory (table 2). In the fall of 1991, seeding year yields for all dates of seeding were similar. **Openers**—While speed of emergence was highly variable among treatments, it was quickest for the double disc and double disc with lister. Plants per meter of row were also generally greater with these openers, and this was reflected in establishment-year yield.

The openers were marginally different for effect on soil bulk density and soil water loss. Soil water was at field capacity and this may have affected the results.

CONCLUSIONS

1. In 3 years of adequate April and May precipitation, there was no clear advantage of dormant-season (late October) over spring-season (April or May) seeding of perennial forages.

2. No one opener was superior. Depth control and stands were generally best with double disc and attached depth band. A lister with double disc or hoe opener cleared surface litter or dry soil for seeding into moist soil below trash cover. Hoe openers passed through straw and chaff, while the double disc tended to lay the seed on top of litter, if present.

3. When the soil water was at field capacity in the fall of 1988, the four openers were not different for effects on soil moisture and were only marginally different for effects on soil bulk density and soil water loss.

Table 2—Date of seeding effects on stand and establishmer	it-year
yield of intermediate wheatgrass and Russian wild	rye at
Swift Current, SK,1990-91	

Grasses	Date ¹	Stand	Yield ²
		No./m row	g/m row
IWG	Sept. 13, 1990	_	68a
	Oct. 19, 1990	6b	84a
	Apr. 18, 1991	15a	84a
	May 17, 1991		44a
RWR	Sept. 13, 1990		17z
	Oct. 19, 1990	7x	28z
	Apr. 18, 1991	18z	27z
	May 17, 1991	_	22z

¹One location only for September, October, and May results. ²Establishment-year yield, September 1991.

DISK-CHAIN-DIKER OPERATION

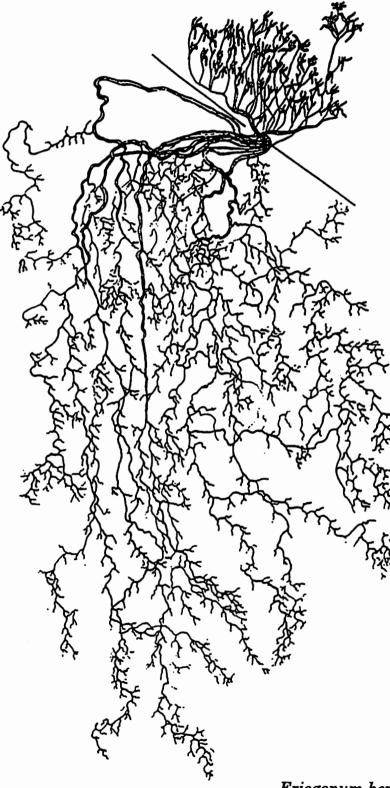
H. T. Wiedemann

The disk-chain-diker implement has shown promise for seedbed preparation on shrub-dominated rangeland. In one pass the unit tills, smoothes the land, and forms small basins. The poster was a video of the implement traversing shrubs 3 to 12 feet tall, and stumps and uneven terrain, and scenes of soil condition following single and double tilling. Detailed information on the implement is covered in the article entitled "Disk-Chain-Diker Considerations for Seedbed Preparation" in the paper section of these proceedings.

Poster paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992.

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Restoration: Species Utility





Eriogonum heracleoides

FRUCTAN METABOLISM AND COOL-TEMPERATURE GROWTH IN CHEATGRASS

N. Jerry Chatterton

ABSTRACT

Cheatgrass (Bromus tectorum) dominates many acres of previously disturbed rangeland, particularly in the Intermountain West where it successfully competes for limited moisture. Its success is due in large part to plant adaptations that facilitate early and rapid growth. An important element of cheatgrass' early growth is a type of carbohydrate metabolism that permits growth to occur at relatively cool temperatures. That adaptation involves the metabolism of a class of carbohydrates called fructan. Fructans are essentially fructose polymers synthesized from sucrose that contain one glucose and from two to several thousand fructose molecules. They are synthesized and metabolized within plant vacuoles thus minimizing the limitations and inefficiencies of starch metabolism that generally occur within chloroplasts. Cheatgrass maintains its dominance on many disturbed areas by, among other adaptations, having a carbohydrate metabolism that permits photosynthesis and other growth processes to occur at very cool temperatures. If moisture is available, cheatgrass seeds germinate soon after fall rains. Plants then remain green over winter and have a head start on many other species when temperatures begin to warm with the end of winter.

INTRODUCTION

Considerable attention has focused on the ecology, management, and opportunities for restoration of annual rangelands in the Intermountain region. If progress is to be made in restoring these rangelands, by enhancing site stability, increasing plant cover and production, and by reducing dominance by weedy annuals, it will be necessary to understand how and why species such as cheatgrass (*Bromus tectorum*) are so successful in maintaining a tenacious hold on so many acres. This paper will discuss one physiological adaptation that provides cheatgrass with a competitive advantage.

Relatively high temperatures and low available soil moisture are common occurrences during the summer months on many cheatgrass-dominated ranges. Most of the dry matter produced by cheatgrass occurs during a few weeks in spring when moisture is available and temperatures are favorable for growth. During a significant portion of the winter when soil moisture is often most plentiful, temperatures are too cold for significant plant growth (Chatterton and others 1988). Although photosynthetic processes remain quite functional at relatively cool temperatures in many species, the rates of carbon metabolism and the utilization of photosynthates are reduced when temperatures fall below about 20 °C.

If temperatures are warm enough for photosynthesis to continue but cold enough to reduce plant growth, significant amounts of carbohydrates are often temporarily stored in leaf tissues. In many plants these carbohydrates are stored as starch. Starch hydrolysis is relatively cool-temperature sensitive (Chatterton and others 1972; Garrard and Carter 1976; Pollock 1986a; West 1969). Thus, ambient temperatures from just above freezing to about 20 °C result in an accumulation of leaf starch. This is the case with species such as bermudagrass, corn, sorghum, and soybeans. If starch accumulation occurs for very long, the internal structures of the chloroplast are physically distorted by the starch grains and photosynthesis is reduced (Chatterton and others 1972; West 1970).

Plants that accumulate predominantly starch and have no alternative mechanism for storing photosynthates as polymers are generally classified as warm-season plants. In contrast, temperate plants have evolved other types of carbohydrate metabolism that are generally less well understood than that of starch (Pollock and Chatterton 1988; Pontis and del Campillo 1985). Alternative synthetic path ways involve oligo- or polysaccharides such as sucrosylsaccharides that contain multiple fructose molecules (Housley and Volenec 1986).

The presence of alternative mechanisms for carbohydrate storage has long been recognized, but only during recent years have they been intensively studied. Within the grass family, C-4 photosynthesis is closely associated with starch-type metabolism; C-3 type photosynthesis is almost exclusively associated with sucrosylsaccharide or fructan-type metabolism (Bender and Smith 1973; Chatterton and others 1989). In any case, these alternate pathways provide mechanisms by which carbohydrates can be stored outside the chloroplast (in the cell vacuole, Wagner and Wiemken 1986), thereby avoiding possible problems caused by starch accumulation and chloroplast disruption.

COOL-TEMPERATURE PLANTS

The significance of a plant's ability to grow under cool temperatures is extremely important in the Intermountain region. Plants capable of growth under cool temperatures are positioned to exploit the use of available soil

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moisture in the fall, winter, and spring when soil moisture is most plentiful.

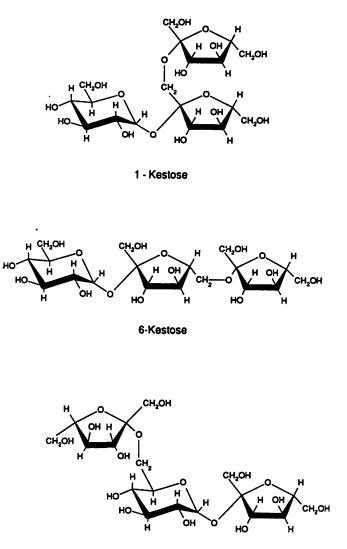
Many range plants, classified as weedy species, have an alternate carbohydrate metabolism that involves fructan. Fructan is a sugar polymer built on sucrose and consists primarily of fructose moieties (Pollock and Chatterton 1988). Dandelion (Taraxacum officinale), a widely dispersed weed, is a cool-temperature adapted plant that reaches maturity early in the spring and is just one example of many Compositeae that metabolize fructan. Other fructan-accumulating weeds include burdock (Arctium minus), ragweed (Ambrosia artemisiaefolia), Canada thistle (Cirsium arvense), knapweed (Centaurea repens), and hawkweed (Hieracium scouleri). Cheatgrass, as well as wild oats (Avena fatua) and quackgrass (Elytrigia repens), is also a fructan accumulator. Obviously fructan metabolism occurs in many of the world's most dreaded temperate weeds.

To understand how fructan metabolism may offer a competitive advantage, it is enlightening to consider some differences between starch and fructan. While starch is comprised of glucose molecules attached to form either linear or branched chains, fructan is comprised primarily of fructose. Fructan can also be in either linear or branched forms (Pontis and del Campillo 1985). Starch and fructan are strikingly different in their solubility. Fructan is much more water soluble and is hydrolyzed into fructose without the energy (ATP) requirement of starch (Edelman and Jefford 1968; Henry and Darbyshire 1980; Pollock 1986b; Shiomi and others 1979a,b). Fructan synthesis may be slightly more efficient than starch synthesis in that the substrate is phosphorylated in starch but not in fructan synthesis (Pollock 1986b).

CHEATGRASS FRUCTANS

Inasmuch as cheatgrass is the current focus of interest, I will discuss relationships of cheatgrass fructans with those of other species. Recent efforts in my laboratory have focused on the purification and identification of fructan structures in representative species including cheatgrass. Fructan metabolism and structures differ widely among species. One-kestose is the most common simple fructan in Gramineae species (Housley and others 1989; Pontis and del Campillo 1985). It is synthesized by the addition of one or more fructose molecules from sucrose onto another sucrose. Thus, one sucrose is split into fructose and glucose (Scott and others 1966). The fructose is attached to a second sucrose to form the fructan molecule and the glucose is used in the synthesis of another sucrose. Each fructan moiety contains one glucose and from two to several thousand fructose moieties (Grotelueschen and Smith 1968; Shiomi and others 1976). Degree of polymerization (DP) is used to describe fructan size. For example, a fructan containing three monosaccharides is DP3. Fructans involve bonds between carbons 2 and 1 and between carbons 6 and 2 (Pontis and del Campillo 1985). There are three possible DP3 fructan structures (fig. 1). They are 1-kestose, 6-kestose, and neokestose (Pollock and Chatterton 1988). Only in the case of neokestose is glucose not in a terminal position (Gross and others 1954).

FRUCTAN TRISACCHARIDES



Neokestose

Figure 1—Chemical structures of 1-kestose, 6-kestose, and neokestose. Although each trisaccharide consists of sucrose (one glucose and one fructose) plus one additional fructose molecule, the manner in which the second fructose is attached onto sucrose varies among the three molecules.

Although there are only three possible ways of attaching a second fructose onto sucrose, there are nine possible DP4 structures if one adds a fructose to a DP3 fructan. Considering the many possible structures with increasing DP, the complications of synthesis are obvious. Much of the early work on fructans was done using Jerusalem artichoke (*Helianthus tuberosus*) (Edelman and Jefford 1968). Figure 2 shows a separation of all the water soluble carbohydrates (fructans) from Jerusalem artichoke tubers. Each peak represents a different size fructan.

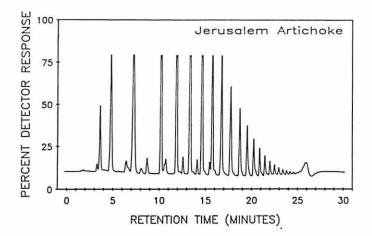


Figure 2—Anion exchange chromatogram of the water-soluble carbohydrates from Jerusalem artichoke (*Helianthus tuberosus*) tubers. Each peak differs from its neighbor by one fructose molecule. Retention times increase with molecular weight.

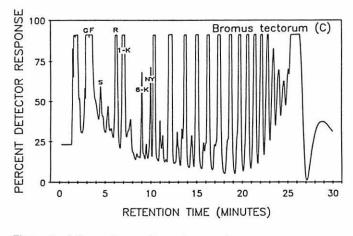


Figure 3—Anion exchange chromatogram of the water-soluble carbohydrates, primarily fructans, from cheatgrass (*Bromus tectorum*) leaves.

Thus, each peak represents a fructan that differs from the peak on either side by a single fructose molecule. Note how relatively simple and symmetrical the pattern is for Jerusalem artichoke. It turns out that Jerusalem artichoke tubers contain only one isomer or structure for each polymer size.

Cheatgrass contains multiple forms or isomers for each DP (fig. 3) and therefore contains a much more complicated family of fructan structures than Jerusalem artichoke. Relatively little is known about either the structures or the enzymology of fructan biosynthesis. Advances have come slowly, not only because of the complexity of the structures, but because procedures have not been available that adequately separate and purify the various kinds of fructan (Pollock and Chatterton 1988).

Figure 4 is a chromatogram of a mixture of the extracts (fructans) from cheatgrass and orchardgrass (*Dactylis glomerata*). The shaded peaks are those from orchardgrass. It remains to be determined how the different families of fructans affect metabolism and plant adaptation.

CHEATGRASS ADVANTAGES

In summary, fructan biosynthesis is a type of carbohydrate metabolism that facilitates carbohydrate storage away from the chloroplast (Wagner and Wiemken 1986) and provides a significant advantage to plants in environments such as the Intermountain region where moisture is generally most available when temperatures are cool. Fructan metabolism, combined with other adaptations, including excellent seedling vigor, allows cheatgrass to become established in the fall when adequate moisture is available. It remains green during the winter months and is then capable of immediate photosynthesis when temperatures are only slightly above freezing.

Because cheatgrass can metabolize carbohydrates at cold temperatures and the photosynthetic potential of its leaves is often maintained over winter, cheatgrass is able to fix significant amounts of CO_2 and to grow under very cool temperatures. Thus, cheatgrass gets a head start on many other Great Basin taxa. Such early growth may allow cheatgrass to more efficiently utilize limited soil moisture, thereby allowing it to out-compete other plants for available resources. The early spring growth and very short life cycle of cheatgrass permit the production of

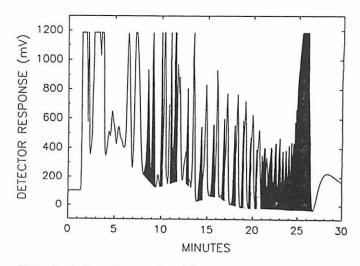


Figure 4—A chromatogram of a mixture of the fructans from cheatgrass (*Bromus tectorum*) and orchard grass (*Dactylis glomerata*). The anion exchange separation clearly shows the presence of different and distinct families of fructans in the two species.

mature seed before soil moisture is either lost to evaporation or used by other species.

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SELECTION FOR ENHANCED SEEDLING ESTABLISHMENT IN COOL-SEASON RANGE GRASSES

Douglas A. Johnson Kay H. Asay

ABSTRACT

Improved stand establishment should be a major objective of most range plant breeding programs. Various seed and seedling characteristics have been evaluated for their ability to predict field establishment in breeding lines of crested wheatgrass (Agropyron cristatum [L.] Gaert. and A. desertorum [Fisch. ex Link] Schult) and Russian wildrye (Psathyrostachys juncea [Fischer] Nevski). Seed weight and ability to emerge from a deep planting depth are the two characteristics that have been most closely associated with field establishment. Selection for these characteristics has been instrumental in the release of 'Nordan' and 'Hycrest' crested wheatgrass and 'Swift,' Mankota,' and 'Bozoisky-Select' Russian wildrye. Results from this work indicate that significant improvement in stand establishment can be made in cool-season range grasses.

INTRODUCTION

The objectives for seeding desirable cool-season range grasses into semiarid rangelands include (Stoddart and others 1975): revegetation of deteriorated rangelands and abandoned croplands, vegetation replacement following fire, expansion of the grazing season, improvement of the quantity and quality of forage, and protection against erosion. Use of seeding mixtures that contain well-adapted species with a high probability of successful establishment will optimize the returns from range seedings.

Johnson (1980, 1986a) and Johnson and others (1981) discussed the five main points that must be addressed for meaningful progress in any plant improvement program: (1) characterization of the environment, (2) identification of the selection criteria, (3) assemblage of a broad genetic base, (4) development of reliable screening techniques, and (5) incorporation of the screening techniques into the breeding program. In this paper, we will discuss range plant improvement in relation to these five points and provide examples of how this process has been used to develop improved cool-season range grasses for the Western United States.

Characterization of the Environment

Many environmental factors affect the growth and production of cool-season range grasses on semiarid rangelands (fig. 1); however, drought is probably the most prominent environmental stress on western U.S. rangelands (Johnson 1986b). Although drought can influence plant growth and development at any phenological stage, drought has particularly deleterious effects at the germination and seedling establishment phases. Drought can interrupt the germination process, arrest seedling development, and cause seedling mortality.

Seedlings are particularly susceptible to drought because they have not accumulated carbohydrates necessary to support maintenance respiration during the drought period or developed extensive root systems for extracting water and nutrients from deep soil depths. Consequently, seedlings have few options available to withstand exposure to drought.

Seedlings of range plants typically are exposed to low temperatures during establishment. Early spring and late fall are periods when water availability is typically most favorable for seed germination and seedling establishment on rangelands of the Intermountain region. However, low and freezing temperatures are common during this period, making it necessary for seedlings to have adaptations that allow them to grow and survive under low temperatures.

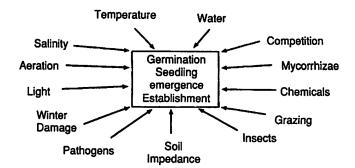


Figure 1—Environmental factors that are known to affect germination, emergence, and establishment of range plants (from Johnson 1986b).

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Identification of Selection Criteria

The ability of seedlings to establish is critical for stand success, and the advantages gained at the seedling stage frequently are retained through the mature plant stage (TeKrony and Egli 1991). Harper (1977) defined establishment as the time "when the seedlings have expanded a photosynthetic surface and are theoretically capable of pursuing an existence independent of their seed reserves." Because of a generally low photosynthetic capacity and very limited carbon and nutrient reserves, seedlings are particularly susceptible to stresses such as drought, low and high temperatures, and defoliation.

The term seedling vigor often is used to described the general aggressiveness of seedlings to germinate, emerge, and become established (Kneebone 1972; McKell 1972). The ability of seeds to rapidly germinate under cold conditions, initiate early root development, and quickly extend their roots into the underlying soil layers enables seedlings to effectively compete with nondesirable range species such as cheatgrass (Bromus tectorum L.). In addition, these characteristics assist seedlings to avoid the effects of drought caused by evaporative water losses of the upper soil layers. Also, growth during the early, cool portion of the growing season, when vapor pressure deficits between the atmosphere and leaf are at a minimum, increases the efficiency of water use. Growth during this period allows a greater proportion of the water to be utilized for transpiration and subsequent growth than is lost by evaporation from the soil. Consequently, the ability of seedlings to rapidly establish under low temperatures and withstand drought are key characteristics that should be selected for and improved in a breeding program for coolseason range grasses. Johnson and Asay (1993) comprehensively reviewed the literature pertaining to selection for improved drought response in cool-season grasses.

Assemblage of a Broad Genetic Base

Genetic advance in a plant improvement program critically depends on assembling a broad genetic base of germplasm from plant introductions, released cultivars, experimental strains, and old plantings. The greater the diversity of the germplasm base, the greater likelihood that the gene pool contains variation for the particular characters that will be selected. Potential progress in a breeding program is directly tied to the diversity of the assembled germplasm and the degree of heritability for the desired characteristic.

Development of Screening Techniques

Even if sufficient heritable variation is present for desirable characteristics within a breeding population, appropriate selection procedures must be developed to evaluate the various breeding lines for their level of expression for the desired combination of characters. Hanson (1972) emphasized that progress in plant breeding and selection has been impeded by the lack of reliable screening procedures. Levitt (1964) and Cooper (1974) underscored the importance of appropriate screening techniques as an integral component of any plant improvement program. These techniques are used to evaluate the phenotypic expression of the desirable characteristic in the base breeding population, and then individuals that best exhibit these traits are selected and used as parents for the next generation (fig. 2). If the measured characteristic is genetically heritable, progeny of these selected parents will exhibit a higher mean expression for the desirable characteristic than the base population. Additional selection cycles could lead to further advances in the expression of the desirable characteristic.

A number of requirements must be met for a technique to be used in a plant breeding program. Johnson (1980) and Johnson and others (1981) indicated that plant screening techniques should (1) assess plant performance at the critical development stage, (2) be completed in a relatively short time, (3) use relatively small quantities of plant material, and (4) be capable of screening large populations. Few techniques are able to meet these stringent requirements.

The ability of seedlings to establish under rangeland conditions is related to seed size in many range species (Asay and Johnson 1980; Berdahl and Barker 1984; Hunt and Miller 1965; Plummer 1943; Rogler 1954b). Generally, large-seeded strains within a species emerge sooner from deeper planting depths and grow more rapidly than do small-seeded strains. As a result, seed weight has been suggested as a reliable characteristic for improving seedling establishment. However, characteristics of long coleoptile length (Berdahl and Barker 1984; Hunt and Miller 1965) and emergence from a deep planting depth

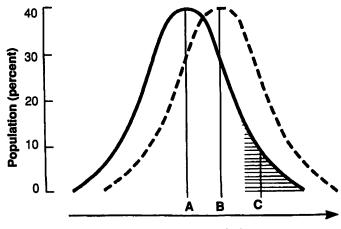




Figure 2—Diagram showing the theoretical effects of selection on the expression of a genetically inherited plant characteristic. The mean expression of the desirable characteristic in the base population is depicted by line A, line C represents the mean expression in the selected individuals, and line B is the level of expression in the progenies of the selected individuals. Amount of advancement in the expression of the desirable characteristic depends on the heritability of the particular characteristic and the amount of selection pressure (from Johnson 1986a).

Breeding Scheme

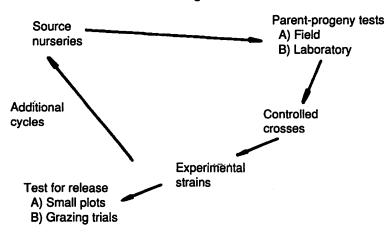


Figure 3—A representative sequence for breeding improved range grasses. Screening procedures play an important role in selecting plants from the source population, evaluating progenies, identifying superior crosses, and comparing performance of experimental strains to released cultivars (from Johnson 1980).

(Asay and Johnson 1980, 1983; Lawrence 1963) are additional criteria that improve the predictability of seedling establishment in some cool-season grasses. Although the relationship between seedling emergence and improved response to drought is somewhat indirect, rapid seedling emergence and development have important implications concerning adaptation to drought in cool-season grasses.

Although ability of range seedlings to grow under low temperatures and withstand freezing would appear to be beneficial characteristics for selection, few breeding programs for cool-season grasses have been selected specifically for these characteristics. Genetic variation for seedling root growth under low temperatures has been documented for bluebunch wheatgrass (Pseudoroegneria spicata [Pursh] Love). Harris and Goebel (1976) evaluated root growth in 45 collections of bluebunch wheatgrass from sites as far south as Nogales, AZ, and as far north as Fairbanks, AK. Seedling root growth at 2 °C ranged from 1.4 to 11.9 mm at 21 days. Although differences in seed size and the seed production environment may have explained some of this variation, significant genetic variation may be present for root growth at low temperature in cool-season range grasses. Additional research concerning seedling growth under low temperatures is required.

Incorporation of Screening Procedures

After appropriate selection techniques have been identified, plant improvement involves screening of the breeding lines to identify plants that have the desired combination of characteristics. These screening procedures can be effectively used to identify superior parent plants from the source population, evaluate the response of the progeny from the source population, isolate superior individuals from controlled crosses, or evaluate the performance of experimental strains in comparison to released cultivars (fig. 3). These screening results can be incorporated into a selection index, which contains results from other field or laboratory evaluations.

CRESTED WHEATGRASS

Since its introduction in the early 1900's, the crested wheatgrasses (Agropyron cristatum [L.] Gaertn., A. desertorum [Fisch. ex Link] Schult., and A. fragile [Roth] Candargy) have been used widely for revegetating depleted rangelands in western North America (Asay 1986). The seed and seedling relations of crested wheatgrass have been reviewed by Johnson (1986b). Although crested wheatgrass is generally known for its good seedling vigor and relative ease of establishment, Rogler (1954b) found a positive relationship between seed size and seedling vigor in A. desertorum. In view of this positive relationship, Rogler (1954b) suggested that selection for larger seeds would be a useful criterion for improving seedling vigor in crested wheatgrass. The cultivar Nordan' of A. desertorum was selected for seed size among other characters and represented a significant improvement in seedling performance (Rogler 1954a). Since its release, Nordan has been used successfully on semiarid rangelands throughout the West (Rogler 1973).

Asay and Johnson (1983) evaluated the genetic variability for characters affecting stand establishment in crested wheatgrass (A. cristatum and A. desertorum). The seedling responses examined included seedling emergence under controlled drought, seedling recovery after exposure to drought, and seed weight. Evaluations involved either 168 or 175 progeny lines of crested wheatgrass, and results from the laboratory and greenhouse tests were compared with results from actual field establishment trials. Seed weight was the characteristic most consistently correlated with field establishment. Based on these results, seed weight, emergence from a deep planting depth, and field agronomic performance were used to develop the crested wheatgrass cultivar 'Hycrest' (Asay and others 1985b). Hycrest has demonstrated excellent vigor and productivity during the early phases of stand establishment and under drought conditions (Asay and others 1986).

RUSSIAN WILDRYE

Russian wildrye (*Psathyrostachys juncea* [Fisch.] Nevski) is a valuable forage grass on western rangelands of North America. Once established, this grass is persistent and productive, and provides an excellent source of high-quality forage during late summer and fall. However, Russian wildrye is noted for its poor seedling vigor and poor stand establishment. Consequently, Russian wildrye has not achieved its full potential as a valuable forage grass. As a result, improved seedling establishment has been a primary objective in most Russian wildrye breeding programs.

Lawrence (1963) evaluated several procedures for screening Russian wildrye breeding populations for improved seedling vigor. He concluded that the most effective screening approach for Russian wildrye would be to select breeding lines with heavy seed weight and subsequently evaluate these selected lines for their ability to emerge from a 5-cm planting depth. These procedures were instrumental in the development of 'Swift,' an improved cultivar of Russian wildrye (Lawrence 1979), which has shown improved establishment vigor in field evaluation trials.

Asay and Johnson (1980) screened 134 progeny lines of Russian wildrye for several seedling responses including seed weight, ability to emerge from a 7.6-cm planting depth, seedling emergence under controlled drought, and seedling recovery after exposure to drought. Besides these greenhouse and laboratory tests, the same breeding lines were seeded at two range sites in northern Utah and southern Idaho and evaluated for their field emergence. Except for seed weight and emergence from a 7.6-cm seeding depth, none of the other greenhouse and laboratory data were significantly correlated to actual field emergence. Field emergence was more closely related to emergence from a deep seeding depth than seed weight, suggesting that improvement in field emergence would be more effective by selecting for emergence from a deep seeding depth. Evaluations of ability to emerge from deep planting together with field agronomic performance resulted in the release of the Russian wildrye cultivar 'Bozoisky-Select' (Asay and others 1985a), which has shown marked improvement in seedling establishment under rangeland conditions.

The genetic variability for seedling vigor and other related characteristics was studied in 30 progeny lines of Russian wildrye by Berdahl and Barker (1984). Seed weight was significantly correlated with emergence and coleoptile length; however, the correlation decreased when seed weight increased beyond 3 mg/seed. Based on estimates of realized heritabilities from parent-progeny relationships, they suggested that genetic progress for improved seedling vigor would most effectively be achieved by first screening for seed size, followed by selection for coleoptile length. Selection for dry matter yield along with coleoptile length and emergence from a 5-cm planting depth led to the development of the cultivar 'Mankota,' which has demonstrated improved stand establishment (Berdahl and others 1992).

SUMMARY

Seedlings of cool-season grasses sown on semiarid rangelands are exposed to various stresses such as competition from aggressive annual weeds, too shallow or excessive planting depth, drought, temperature stress, and poor seedbed. Successful stand establishment on these areas critically hinges on how effectively seedlings respond to these various stresses. Seed weight, ability to emerge from a deep planting depth, and coleoptile length have been used successfully to improve stand establishment in crested wheatgrass and Russian wildrye. Promise exists for further improvements in stand establishment of these and other cool-season grasses.

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PERENNIAL FORB LIFE-HISTORY STRATEGIES ON SEMIARID RANGELANDS: IMPLICATIONS FOR REVEGETATION

Stanley G. Kitchen

ABSTRACT

Establishment and persistence of perennial forbs are priority objectives in revegetation. Species adapted to semiarid regions of the Western United States employ lifehistory strategies suited to unpredictable and often extreme environmental conditions. Long-lived forbs grow rapidly in spring and survive drought through vegetative dormancy. Short-lived species are opportunistic and utilize soil seed reserves to persist through long periods of unfavorable conditions. Seeded forbs must be adapted to site conditions for successful establishment and long-term survival.

INTRODUCTION

The evolution of terrestrial plant morphologies reflects tradeoffs between maximization of growth rates by allocation of photosynthate to production and display of photosynthesizing tissues (principally leaves) and the need to invest in other structures (roots, stems) needed to survive in resource-limited environments (Tilman 1988). The development of roots increases in importance as soil resources (such as water and mineral nutrients) become less available. Conversely, plant height becomes increasingly important as soil-surface light intensity decreases due to increases in plant canopy shade, a change generally associated with increases in soil resource levels. Plant height is greatly increased through the development of perennial (woody) stems. The "cost" of root and stem investment is a decrease in growth rate. Competitive strength of a species is dictated by its ability to adjust photosynthate allocation between plant parts, balancing the tradeoff between growth rate and stress tolerance for the often-changing conditions of its environment.

Perenniality is generally favored in environments experiencing seasonal pulses in resource availability (Tilman 1988). While increases in both frequency and severity of disturbance favor annual growth, herbaceous perennials may be favored when disturbance-caused losses are primarily to aboveground structures.

Herbaceous perennials are characterized by perennating belowground structures and herbaceous, nonwoody, aboveground structures. As a general rule, these plants have relatively rapid potential growth rates; there is no investment in aboveground woody tissues. Because they run the risk of being shaded by taller woody species, some benefit from frequent aboveground disturbance such as herbivory and fire. Herbaceous perennials are divided into two fairly distinct groups: grasses and grasslike species and forbs (dicots and some monocots). Though extremely diverse, perennial forbs are competitively distinct from grasses, differing significantly in anatomical, physiological, and reproductive features.

The seasonal nature of resource pulses in the Intermountain West favors species with perennial life histories. The often short and unpredictable growing season (as dictated by soil moisture and soil and air temperature) typical of valley and foothill landscapes results in numerous combinations of perennial shrub, grass, and forb species (Ream 1963). Perennial forb species are responsible for much of the diversity in these communities even though coolseason grasses often dominate the herbaceous component. Frequent spring cold spells and a continental climate also favor wind-pollinated grasses and shrubs over the predominantly insect-pollinated forbs. Forb diversity is generally greater in communities associated with more mesic sites. On these sites, the canopy cover of tall shrubs and trees may increase, resulting in a shift to conditions that favor shade-tolerant forbs.

PERENNIAL FORB STRATEGIES

Grime (1977) proposed three primary plant strategies in which traits have evolved in response to different levels of competition, stress, and disturbance. He described competitive, stress-tolerant, and ruderal strategies, each adapted to conditions of high levels of one of these environmental forces and lesser levels of the remaining two. He also described conditions that select for secondary or intermediate strategies and suggested that perennial forbs have a range of strategies wider than other plant groups.

Successful forb strategies have evolved to address both norms and extremes of the environment. Physical factors such as dependability of growing season, severity and length of drought, and nature and frequency of disturbance are important in determining the "shape" of each strategy. Abrahamson (1979) documented differences in resource allocation between forb species and ecotypes associated with forest understories and those found in open fields. Field forbs allocated a greater share of resources to

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reproductive organs and a lesser share to leaves and belowground organs than did forest understory species. Specialized animal pollination strategies are favored in wooded understory habitats because of improved efficiency in long-distance pollination among dispersed plants bearing relatively few flowers (Regal 1977).

This paper describes life-history strategies suited to non- or open-forested habitats and gives examples native to the Intermountain West.

Strategy A: Long-Lived/Summer Dormant

Strategy A species are typically slow to reach reproductive maturity and are long lived. They inhabit communities where the favorability of microsites is relatively constant (Gadgil and Solbrig 1972). Resource pulses are generally predictable (seasonal) and at least adequate for maintenance growth. This strategy is intermediate between the competitive and stress-tolerant strategies proposed by Grime (1977), though species are also tolerant of some forms of disturbance.

A distinguishing trait of Strategy A species is the storage of large quantities of mineral resources and photosynthate in belowground perennating structures. These reserves are mobilized rapidly to produce photosynthesizing leaves and stems early in the growing season, making mature plants excellent competitors. Reproductive output intensity is tied to these stored reserves; mast seed production (cycles of bumper crops spaced by years of minimal or no seed production) is common. Summer drought is avoided through vegetative dormancy. The successful establishment of new individuals or cohorts may be either slow and gradual or rare, as these species are typically associated with somewhat closed, late seral communities (Gadgil and Solbrig 1972).

Arrowleaf balsamroot (*Balsamorhiza sagittata*) is a typical Strategy A species. This long-lived species produces a large taproot with deep soil penetration (Shaw and Monsen 1983). Large basal leaves emerge quickly from the taproot as spring conditions permit. Mast seed production is synchronized, at least in part, by the effects of weather (such as precipitation and spring frost) on resource allocation. Plants enter dormancy in early to midsummer.

Seeds are relatively large and are sought out and cached by rodents (Everett and others 1978). Seed dormancy prevents precocious summer or fall germination. Young and Evans (1979) speculated that excessive seed stratification requirements reduce spring germination. In laboratory experiments, I found that seed dormancy is broken with moderate periods of moist chilling (stratification) (Kitchen 1993). Mean germination percentages for 10 collections after 8 and 10 weeks of moist chilling were 59 and 91 percent, respectively. In a parallel field retrieval experiment conducted on an arid Wyoming sagebrush (*Artemisia tridentata* spp. *wyomingensis*) site in southern Idaho, less than 1 percent of seeds planted in midsummer and fall remained dormant in the following spring. Seedling growth and maturation rates are slow; most plants do not flower for several years after seedling establishment (Shaw and Monsen 1983).

Other long-lived forb species used in revegetation with high levels of belowground resource storage include Pacific aster (Aster chilensis), western yarrow (Achillea millefolium), Louisiana sagewort (Artemisia ludoviciana), and scarlet globemallow (Sphaeralcea coccinea) (Menke and Trlica 1981; Shaw and Monsen 1983). As with these species, belowground reserves are often related to vegetative reproduction. Allium, Calochortus, Erigeron, Eriogonum, Lomatium, Senecio, Solidago, and Wyethia are examples of other forb genera represented by Strategy A species.

Strategy B: Short-Lived, Opportunistic

Strategy B is associated with species that experience episodic recruitment and die-off events, often correlated with extreme weather events or harsh disturbance. Though these species usually benefit from seasonal pulses in soil moisture, vegetative and reproductive growth responses can occur any time effective moisture becomes available and temperatures permit. High mortality rates often follow explosive seed production events apparently due to depletion of stored reserves (Fenner 1985). Species are generally classified as short lived. Strategy B is best described as a stress-tolerant ruderal strategy when Grime's (1977) classification is applied.

Strategy B species rapidly reach reproductive maturity and have a proportionately high investment of resources in seed production (Fenner 1985; Gadgil and Solbrig 1972). Individual seeds require relatively small investments in resources and are mobile, allowing the species to explore numerous new sites on both a spatial and temporal scale. Seed dormancy mechanisms, such as hardseededness, that function to ensure that a portion of the seeds produced are committed to a soil seed reserve (remain ungerminated through periods favorable for seedling growth) are essential for species or ecotypes employing this strategy. The successful establishment of new cohorts, though more common than with Strategy A species, is probably tied to disturbance events or sequences of one or more seasonal pulses with higher than normal amplitude or longer than normal duration.

A good example of a Strategy B species is Palmer penstemon (Penstemon palmeri). This short-lived perennial forb flourishes on disturbed sites such as washes and canyon bottoms (Cronquist and others 1984). Populations have been successfully established and have persisted on human-caused disturbances such as roadcuts. When soil moisture is plentiful during the growing season, mature plants produce copious quantities of seeds. Typically, these plants become weakened and many die by the following spring (personal observation). Mortality is likely due, at least in part, to stresses caused by high reproductive output. Cold-induced seed dormancy, a light requirement, and a long imbibition requirement before radical emergence ensure maintenance of a soil seed reserve (Kitchen and Meyer 1992; Meyer and Kitchen 1992). Numerous other penstemon species exhibit strategies for

preserving a soil seed reserve (Kitchen and Meyer 1991; Meyer 1992; Meyer and Kitchen 1993).

Gooseberry-leaf globemallow (Sphaeralcea grossulariifolia) has a strategy similar to that of Palmer penstemon. This short-lived species (West 1979) is well adapted to drought and is widely distributed in desert shrub, pinyon-juniper, and low-elevation mountain brush communities (Welsh and others 1987). Persistent soil seed reserves allow populations to cycle in response to variable weather patterns (Sharp and others 1990). Typically, extended periods of favorable conditions result in populations spending themselves in explosive reproductive events often followed by episodic die-off (personal observation). The strategy of the closely related munro globemallow (S. munroana) is similar.

Intermediate Strategies

Strategies A and B are not mutually exclusive. Species with intermediate strategies combine elements of both. In addition, the relative importance of each strategy, as expressed by key traits, may vary considerably among ecotypes of a single species occupying a wide range of habitats. This variability is not surprising when the differences in moisture regime, disturbance factors, and competition patterns among these habitats are considered. Solbrig and Simpson (1974) observed phenotypic variability in seed production and competitive ability among biotypes of common dandelion (*Taraxacum officinale*). Biotypes with relatively high reproductive output dominate on sites with frequent disturbance (mowing), while more competitive biotypes dominate less frequently disturbed sites.

Ecotypes of Lewis flax (Linum lewisii) are adapted to shadscale, sagebrush, pinyon-juniper, grassland, mountain brush, ponderosa pine, aspen, and spruce-fir communities (Welsh and others 1987). In a common garden study with populations selected from diverse habitats, reproductive output varied by more than two times as measured by flower number and total seed weight per plant (Kitchen and others 1993). After 3 years, mortality among ecotypes ranged from 3 to 100 percent (fig. 1). Differential resistance of ecotypes to rust infection significantly contributed to differences in second-year losses. Short-lived ecotypes subject to frequent density-independent mortality events may gain little or no advantage by investing in rust resistance. In addition, much of the mortality over a 3-year period occurred in plants that were rust-free and prolific during the year before death, suggesting that patterns of reserve depletion during seed production may be important to longevity among ecotypes of this and possibly other species (Gadgil and Solbrig 1972).

In laboratory germination studies with Lewis flax seeds, a significant fraction of seeds developed cold-induced secondary dormancy for five of 21 collections tested (Meyer and Kitchen, in press). Nine of the remaining collections had a portion (13 to 68 percent) of viable seeds that did not become germinable after 24 weeks of stratification. Field retrieval experiments verified the ability of this species to seedbank for multiple years. These results suggest that Lewis flax tactics include provisions for maintaining a soil seed bank, and that the relative importance of a seed bank varies among ecotypes.

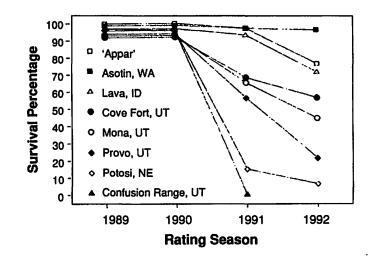


Figure 1—Survival of Lewis flax collections in a common garden near Nephi, UT. Greenhousereared seedlings were transplanted in April 1989. Mortality from 1990 to 1991 was significantly correlated with an index of severity of rust infection $(p < 0.05, r^2 = 0.75)$. All plants were treated for rust in 1991, minimizing infection. Mortality from 1991 to 1992 is presumed unrelated to rust infection. The cultivar 'Appar' belonging to the European species perennial blue flax (*Linum* perenne), remained free of infection though it experienced 26 percent mortality, similar to that experienced by some of the North American Lewis flax collections.

Another forb with an intermediate strategy is northern sweetvetch (Hedysarum boreale). This moderate to long-lived legume is most common in midelevation communities and may have been reduced in distribution and density by past overgrazing (Plummer and others 1968). Its roots penetrate deeply into the soil. Vegetative dormancy occurs as soil moisture is reduced in mid to late summer. First bloom occurs in spring to midsummer. A second minor flowering sometimes results when initial fruit set fails (personal observation). Both weather and carbohydrate reserves probably play an important role in determining the intensity of single-year reproductive allocation. Seeds are generally hard (do not imbibe water) (Kitchen and others 1987; Redente 1982) and are sought out and possibly cached by rodents. The hard-seeded trait allows for a significant portion of uneaten seeds to carry over in the soil. The species responds favorably to removal of competitive shrub species such as big sagebrush (Artemisia tridentata) and Gambel oak (Quercus gambelii). Large increases in vegetative and reproductive output are common following fires (personal observation).

IMPLICATIONS FOR REVEGETATION

Familiarity with perennial forb strategies is essential to avoid costly mistakes in revegetation projects and in formulating appropriate expectations for seeded species in modified environments. Species and ecotype life-history strategy must be matched to planting site environmental conditions. The following questions and discussions should be addressed in determining appropriate species or ecotypes for each revegetation project.

1. Is the species adapted to the climate of the site? For example, when considering precipitation, seasonality and extremes may be as important as annual means in affecting success.

2. Is the expected disturbance regime compatible with the long-term persistence of each planted species? Disturbance effects can be positive or negative depending on the nature and timing of their occurrence. Intensity and frequency of disturbance are also important. For example, occasional fire is beneficial for northern sweetvetch and arrowleaf balsamroot, because of fire's negative effect on competing species, while herbivory is not. Other species such as Palmer penstemon benefit from frequent soil erosion such as is found on steep slopes and in wash bottoms. The severity of damage, if any, to perennial forbs caused by selective herbivory and trampling associated with large ungulates (whether livestock or wildlife) is largely dependent on season of use. There may be times when it is appropriate to plant Strategy B species on sites where they may not persist; their value is as nurse plants for later seral species.

3. Are the forb species to be seeded compatible with other seeded species and remnant perennials on this site? An understanding of the competitive relationships among species in seeded communities is largely lacking, so evaluation of this question is difficult. At the very least, caution should be used to not overplant aggressive long-lived grasses on sites where a good representation of forbs is desired.

4. How weed prone is the site? Competition from annual grasses such as cheatgrass (*Bromus tectorum*), medusahead (*Taeniatherum asperum*), and jointed goatgrass (*Aegilops cylindrica*) inhibits successful establishment of perennial seedlings. Weed control should be a standard consideration for any seeding project. However, if seeded species are short lived, requiring relatively frequent recruitment episodes, long-term persistence may be prevented by weeds.

5. Will a fraction of viable seeds remain ungerminated after the first season of growth? The seeds of most rangeland species are best planted in the fall. This permits moist chilling of dormant seeds and accelerates spring germination and growth of nondormant seeds. A viable portion of the seeds of many forbs, including penstemons, globemallows, Lewis flax, and northern sweetvetch, will remain ungerminated the first spring following planting (Strategy B). A knowledge of the seed-banking tendencies of each species is useful in planning seeding rate and in judging first- and subsequent-year establishment success. Germination percentage can be increased for some species using appropriate seed pretreatments. For example, hardseeded species such as sweetvetch and globemallows can be scarified prior to planting (Redente 1982; Roth and others 1987) while species such as Lewis flax need only time in dry storage to increase first-year germination (Meyer and Kitchen, in press). Such tactics conserve the genetic capacity for seedbanking, a trait important for the longterm persistence of some species and ecotypes.

6. How important is seed size in planning seeding rate and method? The seeds of some forb species are very small (table 1) and are not able to emerge from typical drilling depths. These seeds must be sown at or near the soil surface. Seeding rates of these species can often be quite low, a real plus considering the cost of obtaining the seeds.

Efficacy in the use of a great variety of perennial forb species will improve as research provides a more complete understanding of perennial forb life-history strategies and their interactions within different communities. Many species with potential value are presently poorly understood.

Table 1—Seed size (seeds/ib) for 10 native perennial forb species.	Quantities reported are adapted from
Kitchen and others (1987) and Shaw and Monsen (1983).	. Recommended seeding rates (lb/acre) are
based on the species being a part of a diverse seed mix.	Alfalfa and small burnet are included for
comparison	

Common name	Scientific name	Seed weight	Recommended seeding rate <i>Lb/acre</i>		
		No./Ib			
Western yarrow	Achillea millieolium	4,000,000	0.1 - 1.0		
Louisiana sagewort	Artemisia ludoviciana	3,800,000	0.2 - 1.25		
Pacific aster	Aster chilensis	2,700,000	0.5 – 1.5		
Arrowleaf balsamroot	Balsamorhiza sagittata	55,000	1.0 - 4.0		
Lewis flax	Linum lewisii	280,000	0.25 – 2.0		
Palmer penstemon	Penstemon palmeri	600,000	0.25 – 2.0		
Firecracker penstemon Rocky Mountain	Penstemon eatonii	350,000	0.5 – 2.5		
penstemon Gooseberry-leaf	Penstemon strictus Sphaeralcea	760,000	0.25 – 2.0		
globernallow	grossulariifolia	500,000	0.75 – 3.0		
Northern sweetvetch	Hedysarum boreale	59,000	1.5 – 4.0		
Alfalfa	Medicago sativa	225,000	0.5 - 3.0		
Small burnet	Sanguisorba minor	45,000	2.0 - 4.0		

Our success in managing diverse communities in the semiarid West will depend on carefully planned research and its application.

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ECOLOGY, DISTRIBUTION, AND VALUES OF SAGEBRUSH WITHIN THE INTERMOUNTAIN REGION

E. Durant McArthur

ABSTRACT

Information for 11 sagebrush species, and their subspecies, of the Intermountain West is summarized. Big sagebrush (Artemisia tridentata) with its five subspecies is the most common and widely distributed. Sagebrush taxa are distributed in patterns generally controlled by moistureelevation gradients, seasonal moisture, and soil properties. Individual sagebrush taxa result from reticulate, hybridizing, polyploid evolution facilitated by migrations of ancestral stock in response to changing climatic patterns. Sagebrush is valuable for soil stabilization, wildlife habitat, animal feed, and ecosystem stability. Rehabilitation of sagebrush communities degraded by fire and other disturbances may be accomplished by planting appropriate wildland stock or selected germplasms. Hybrid forms show promise.

INTRODUCTION

The genus Artemisia (wormwood, wormseed, sage, sagebrush, etc.) is comprised of some 250-400 species of shrubs and forbs distributed mainly in the northern temperate zone but extending to the southern hemisphere in some upland situations. The true sagebrushes (subgenus Tridentatae of Artemisia) are one of four subgenera within the genus and are confined to western North America with a center of distribution in the Intermountain area (Airy Shaw 1973; McArthur and others 1981). The sagebrushes are wholly woody with homogamous flowers and are adapted to a semiarid, continental climate. Wide distribution and large populations make them a landscapecharacterizing plant of the North American West. This report is limited to the 11 sagebrush species and their subspecies (table 1). For information about other nonsagebrush Artemisia species of the Intermountain region, for example, sandsage or oldman sage (A. filifolia), fringed sage (A. frigida), longleaf sage (A. longifolia), Louisiana sagewort (A. ludoviciana), fuzzy sage (A. papposa), birdsfoot sage (A. pedatifia), and budsage (A. spinosa), see Hall and Clements 1923, McArthur and others 1979, McArthur and Stevens, in preparation, and Rosentreter 1992.

ECOLOGY AND DISTRIBUTION

Sagebrushes occur from southern British Columbia to southwestern Manitoba, south to northern Baja California and west Texas, and from approximately the 100th meridian west longitude (the Dakotas to west Texas) to the Cascade Mountains of Oregon and Washington and the northern Sierra San Pedro Martir of Baja California (McArthur and Plummer 1978; McArthur and others 1981). Each taxa has an ecological niche preference as described in table 1. Some taxa are broadly adapted and distributed; other taxa are narrow endemics. The most broadly distributed species is big sagebrush (A. tridentata) with its subspecies, especially basin big sagebrush (ssp. tridentata), mountain big sagebrush (ssp. vaseyana), and Wyoming big sagebrush (ssp. wyomingensis). These three taxa occur over most of the general sagebrush distributional range and partition out the environment on an interacting moisture-elevation gradient (fig. 1). Two less common big sagebrush subspecies are confined to dry foothills in south-central Idaho (xeric big sagebrush, ssp. xericensis) and high elevations in northern Utah, eastern Idaho, northwestern Colorado, and western Wyoming (snowbank big sagebrush, ssp. spiciformis) (Goodrich and others 1985; McArthur 1983b; Rosentreter and Kelsey 1991; Winward 1983). In addition to moisture-elevation gradients, seasonal moisture and soil properties are important in the distribution of sagebrush taxa (table 1).

Sagebrush ecosystems in natural condition had various rates of catastrophic disturbance prior to settlement by Europeans. These ecosystems were and are dominated by various sagebrush taxa but varied and vary widely in the diversity and density of their herbaceous components (Blaisdell and others 1982). Big sagebrush communities had fire cycles of greater than 50 years before European settlement (Whisenant 1990); some depauperate communities, such as stiff sagebrush (A. rigida) and black sagebrush (A. nova), may have had very little disturbance. Insect irruptions were no doubt occasionally devastating prior to European settlement as they occasionally are now (McArthur and others 1979).

Fire frequency in sagebrush communities has been greatly increased due to invasion of alien annuals such as cheatgrass (*Bromus tectorum*) in their understory. Fire cycles on some large areas that are dominated by cheatgrass and other alien annuals are down to a 5-year return (Whisenant 1990). Consequently, large areas of non-fire tolerant sagebrush ecosystems, especially Wyoming big sagebrush communities, are converted to annual grasslands lacking a shrub component (McArthur and others

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Species	Subspecies	Distribution and site adaptation
Low sagebrush (A. arbuscula)	Low sagebrush (arbuscula)	W. Wyoming to SC. Washington and N. California on dry, sterile, rocky, shallow, alkaline, clay soils.
	cleftleaf sagebrush (<i>thermopola</i>)	W. Wyoming, N. Utah, and E. Idaho on spring-flooded, summer-dry soils.
	Lahontan sagebrush (not formally named ¹)	NW. Nevada extending into adjacent California and Oregon on soils of low water holding capacity and shallow depth usually around and above the old shoreline of Lake Lahontan.
Coaltown sagebrush (A. argillosa)		Jackson County, Colorado, on alkaline spoil material.
Bigelow sagebrush (A. bigelovii)		Four Corners area extending to NE. Utah, SE. California, and W. Texas on rocky, sandy soils.
Silver sagebrush (<i>A. cana</i>)	Bolander silver sagebrush (<i>bolanderi</i>)	E. Oregon, W. Nevada, and N. California on alkaline basins.
	Plains silver sagebrush (<i>cana</i>)	Generally E. of Continental Divide, Alberta and Manitoba to Colorado on loamy to sandy soils of river bottoms.
	Mountain silver sagebrush (<i>viscidula</i>)	Generally W. of Continental Divide, Montana and Oregon to Arizona and New Mexico on mountain areas along streams and in areas of heavy snowpack.
Alkali sagebrush (<i>A. longiloba</i>)		SW. Montana, NW. Colorado, W. Wyoming, N. Utah, S. Idaho, N. Nevada, and E. Oregon on heavy soils derived from alkaline shales or on lighter, limey soils.
Black sagebrush (<i>A. nova</i>)		SE. Oregon and SC. Montana to S. California and NW. New Mexico on dry, shallow, stony soils with some affinity for calcareous conditions.
Pygmy sagebrush (A. pygmaea)		C. Nevada and NE. Utah to N. Arizona on desert calcareous soils.
Stiff sagebrush (A. <i>rigida</i>)		E. Oregon, E. Washington, and WC. Idaho on rocky scablands.
Rothrock sagebrush (A. rothrockii)		California and Nevada in deep soils along the forest margins of the Sierra Nevada and outliers.
Big sagebrush (A. tridentata)	Snowbank big sagebrush (<i>spiciformis</i>)	Wyoming, Idaho, Colorado and Utah in high mountains.
	Basin big sagebrush (<i>tridentata</i>)	British Columbia and Montana to New Mexico and Baja California in dry, deep, well- drained soils on plains, valleys, and foothills.
	Mountain big sagebrush² (<i>vaseyana</i>)	British Columbia and Montana to S. California and N. New Mexico in deep, well-drained soils on foothills and mountains.
	Wyoming big sagebrush (<i>wyomingensis</i>)	North Dakota and Washington to Arizona and New Mexico in poor shallow soils often underlain by a caliche or silica layer.
	Xeric big sagebrush (<i>xericensis</i>)	WC. Idaho on basaltic and granitic soils.
Threetip sagebrush (A. tripartita)	Wyoming threetip sagebrush (<i>rupicola</i>)	Wyoming on rocky knolls.
	Tall threetip sagebrush (<i>tripartita</i>)	E. Washington and W. Montana to N. Nevada and N. Utah on moderate-to-deep well-drained soils.

 Table 1—Sagebrush (subgenus Tridentatae) taxa (species and subspecies) with their general distributions and site adaptations. After Beetle 1960, Harvey 1981, McArthur 1983b, McArthur and Plummer 1979, Winward and others 1986

¹This taxon is currently in the process of formal description. Winward and others (1986) informally described and characterized it. ²For additional treatment of subspecific taxa (forms) see Goodrich and others (1985).

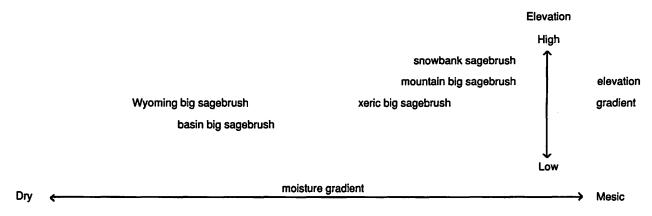


Figure 1-Moisture-elevation gradient for big sagebrush and its subspecies.

1990, these proceedings). Much of the basin big sagebrush ecosystem has been converted to urban development and agriculture. The animal components of sagebrush ecosystems are rich and varied and are also subject to the disturbances of the system (McArthur 1983a).

SYSTEMATICS, GENETICS, AND EVOLUTION

The sagebrushes (subgenus *Tridentatae* of *Artemisia*) are a natural group comprising 11 species and their 13 subspecies (table 1). They differ in stature, vegetative and floral branching patterns, leaf shape and lobation, and leaf and bract pubescence. Bigelow sagebrush (*A. bigelovii*) differs from all other taxa; its flower heads have from 0 to 2 ray or marginal flowers in addition to the homogamous central disc flowers characteristic of the subgenus. Taxonomic keys are available; I recommend Beetle 1960, McArthur 1983b, McArthur and others 1979, Schultz 1986, and Winward 1980.

Sagebrushes have a base chromosome number of x = 9 with polyploidy common in most taxa (McArthur and others 1981; Ward 1953). Polyploidy up to 8x is known. The diversity in the group is enhanced by outcrossing (wind pollination) although self-pollination also occurs (McArthur and others 1979, 1988). Outcrossing is not confined within populations of the same taxa; natural hybridization also occurs between sympatric and parapatric populations under certain temporal conditions (Beetle 1960; McArthur and others 1979, 1988; Ward 1953). The evolutionary history of sagebrush is one of dynamic reticulate connections facilitated by hybridization, polyploidy, and migration as contemporary taxa came into and out of contact as a result of past climatic change (McArthur and others 1981, 1988; Ward 1953). Sagebrush hybrid zones are leading to a better understanding of theoretical underpinnings of hybrid zone stability (Freeman and others 1991).

VALUES

Sagebrushes' principal values are for soil stabilization, wildlife habitat, animal feed, and ecosystem stability.

Other values include being living snowfences and sources of industrial chemicals (McArthur 1983a; Welch 1983). In addition to providing natural soil binding, several species are suitable for stabilizing disturbed soils, by either transplanting or seeding. When using sagebrush for revegetation purposes it is important to match precipitation, soil, elevation, and plant germination characteristics with the plant's original source site and to bear in mind the importance of special care in initial establishment (McArthur 1983a; Meyer and Monsen 1992).

The importance of sagebrush communities as wildlife habitat is illustrated by the fact that at least 87 wildlife species use them as habitat in Intermountain States; several species are obligately tied to sagebrush habitats including sage grouse (Centrocerus urophasianus) and pygmy rabbits (Brachylagus idahoensis) (McArthur 1983a). Sagebrush provides nesting, hiding, and thermal cover for various animal species. The feed value of sagebrush is generally good especially when it is used as mixed winter feed. Big sagebrush in particular is very good in digestibility, winter crude protein, and winter phosphorus and carotene (Welch 1983; Welch and McArthur 1990). Some forms are much more palatable to browsing animals than others (McArthur and others 1979; Wambolt 1993; Welch 1983; Welch and others 1986, 1992). There is a concern that the essential oils of sagebrush make it undesirable forage because the oils may interfere with animal digestion. Welch (1983) concluded that this is a minimal problem because the plant is generally taken as a mixed feed and the oils are benignly lost in eating and digestive processes.

Some natural populations have been shown to be superior for certain traits such as palatability to browsing animals, nutritive quality, growth rates, and wide adaptation. Welch and his colleagues (1986, 1992) have characterized and released the germplasms 'Hobble Creek' mountain big sagebrush and 'Gordon Creek' Wyoming big sagebrush for commercial seed production and reclamation plantings. Other germplasms are currently under evaluation.

Some of our current work is directed to make novel hybrid combinations between sagebrush taxa. This work might allow us to combine desirable nutritive quality (including palatability) and growth characteristics, or drought and fire tolerance (McArthur and others 1988, 1992). The latter potential combination is particularly appropriate in the context of these symposium proceedings. Large areas of the sagebrush ecosystem have been lost to the cheatgrass fire cycle, dramatically reducing wildlife habitat, carrying capacity, ecosystem integrity, and structural diversity on these lands. Our putative artificial hybrids between Wyoming big sagebrush (drought tolerant but not fire tolerant) and silver sagebrush (*Artemisia cana*) and three tip sagebrush (*A. tripartita*) (fire tolerant but not drought tolerant) hold some promise of rebuilding a badly damaged and perhaps partially lost ecosystem (McArthur and others 1992).

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ROLE OF NITROGEN AVAILABILITY IN THE TRANSITION FROM ANNUAL-DOMINATED TO PERENNIAL-DOMINATED SERAL COMMUNITIES

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ABSTRACT

A conceptual model of secondary succession with emphasis on early seral stages is presented. This model is based on experimental data from 7 years of secondary succession on an induced disturbance site within a semiarid shrubland ecosystem in northwestern Colorado. Annuals dominated the first 3 years of this succession, followed by a 2-year transition to dominance by perennials, primarily grasses and early seral shrubs.

Nitrogen (N) availability was found to be a primary mechanism controlling the rate of succession. As N availability increased, the rate of succession decreased. Conversely, as N availability was experimentally decreased, the rate of succession increased. The abundance of annuals and the length of time annuals dominated plots was increased by increased N availability. Conversely, the abundance of perennials and the rate at which perennials became sitedominant was inversely related to N availability.

The conceptual model explains these dynamics on the basis of N availability, relative growth rates, lifeform, and decomposition dynamics. The model can also be applied to related problems of ecosystem dynamics such as possible effects of atmospheric and agricultural N depositions on the stability of established ecosystems.

INTRODUCTION

Annuals are found in virtually all plant communities, and yet they dominate very few. Those communities that are dominated by annuals occur primarily in the earliest stages of succession, especially in secondary succession. Such a widespread seral limitation suggests a basic functional linkage between the ecological characteristics or conditions during early secondary succession and those of the annual lifeform. Consequently, a better understanding of this linkage, and the mechanisms controlling it, should result in an increase in our ability to control the degree to which, and the length of time that, annuals dominate a site. This may be of special importance in reclamation of disturbed lands and management of annual-dominated rangelands. Change in species composition over time is the most obvious characteristic of secondary succession. A disturbance site is first dominated by annuals, which are replaced in time by herbaceous perennials, either perennial grasses or perennial forbs followed by perennial grasses. Eventually, the herbaceous perennials are replaced by woody species, either shrubs or trees, on most sites. Although this pattern is common to most ecosystems and has been recognized since the earliest period of ecology (Clements 1916; Cowles 1899), the mechanisms causing species replacement are still not clearly understood.

The addition of nitrogen (N) has been shown to be a major factor modifying successional dynamics in a number of ecosystems following disturbance (Carson and Barrett 1988; Heil and Diemont 1983; McLendon and Redente 1991, 1992a; Parrish and Bazzaz 1982; Tilman 1984, 1986), and this effect has been attributed to changes in competitive relationships among species induced by changes in N availability (Miller and Werner 1987; Peterson and Bazzaz 1978; Raynal and Bazzaz 1975). Species with higher growth rates are favored over those with slower growth rates under conditions of high N availability (Aerts and Berendse 1988; Berendse and others 1987; Heil and Bruggink 1987), and early seral species characteristically have high growth rates (Bazzaz 1979). Therefore, early seral species, predominantly annuals, may dominate sites by rapidly utilizing the available resource or causing other resources (for example, light) to become limited to slower growing species. These rapidly growing early seral species might continue to dominate a site as long as they can maintain their high production levels. However, high available nutrient levels are required for these species to reach their growth potentials and, if resources become too limited to meet these requirements, species with lower nutrient requirements should begin to have a competitive advantage (Grime 1979; Leps and others 1982; McGraw and Chapin 1989).

Central to this explanation is the concept that secondary succession occurs, at least in part, because of competitive displacement of species (Grace 1987). If true, and if degree of competition increases as a specific resource (for example, soil N) becomes more limited, the rate of replacement of early seral species by mid-seral species should increase as the resource becomes more limited. Resource limitation dynamics may therefore explain, at least in part, the replacement of annuals by perennials or, in some cases, the lack of such replacement.

In this paper, we present a summary of the results of a series of experiments we conducted within a disturbed

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semiarid shrubland ecosystem in northwestern Colorado that investigated the role of N availability as a primary mechanism controlling the rate of secondary succession. We also present a conceptual model, based on our experimental results, that we believe explains how N availability functions as a successional control mechanism. Particular emphasis is given in this paper to the seral replacement of annuals by herbaceous perennials.

METHODS

The discussion and conceptual model presented in this paper are based primarily on the results of three experiments: two field experiments conducted in the Piceance Basin of northwestern Colorado, and one greenhouse experiment utilizing seral species from that site. The first field experiment was begun in 1984 and investigated the effect of added N on secondary succession dynamics of a mechanically disturbed sagebrush community. The vegetation and top 5 cm of soil were removed by a bulldozer and the next 35 cm were mixed. Four 500-m² treatment plots were established in each of four blocks of the disturbed sagebrush community and one 500-m² plot of undisturbed sagebrush community was included within each block. The blocks served as replications, and there were five treatments:

Treatment 1: Control—disturbed but not fertilized. Treatment 2: Phosphorus—disturbed and fertilized with triple super phosphate at 100 kg P/ha/yr.

Treatment 3: Nitrogen—disturbed and fertilized with ammonium nitrate at 100 kg N/ha/yr.

Treatment 4: Nitrogen + phosphorus—disturbed and fertilized with both ammonium nitrate (100 kg N/ha/yr) and triple super phosphate (100 kg P/ha/yr).

Treatment 5: Undisturbed—not disturbed nor fertilized.

Each year, ten 0.5-m² quadrats were randomly located and clipped at each of two sampling dates (early and late summer) beginning in 1985. Current-year aboveground biomass was harvested to ground level by species, ovendried, and weighed. Harvested material from the years 1987-91 was analyzed for N concentration by the micro-Kjeldahl process. The addition of P did not have a significant effect on seral dynamics overall, for any lifeforms, or for any major species. Therefore, control and P data were combined as a single treatment (control), the two N treatments were combined as a second treatment (N), and the undisturbed community served as a third treatment.

The second experiment tested the effect of decreased N availability on secondary succession. An N-availability gradient was established on unfertilized plots that had been disturbed in 1984 but which had been kept free of plants by hand weeding. In November 1987, these plots were seeded with a mixture of early and late seral species to minimize any possible migration effect. The N-availability gradient was established by adding N to one plot per block (high available N, same rate as in experiment 1), sucrose (1,600 kg C/ha/yr) to another plot per block (low available N, achieved by the sucrose increasing microbial biomass and thereby decreasing available N, Lamb 1980), and one plot received neither N nor sucrose (intermediate available N = control). Sampling began in 1988 and was conducted at the same two dates as in the first experiment. At each sampling date, 20

quadrats (0.25 m² each) were randomly located within each plot and canopy cover was estimated by species within each quadrat. At the end of the third growing season (September 1990), samples of five major seral species were collected from each plot and analyzed for tissue N concentration, and soil samples (1-20 cm composite) were collected and analyzed for total N. The five species included two annual forbs (Kochia scoparia, Salsola iberica), one perennial forb (Aster canescens), one perennial grass (Agropyron smithii), and one shrub (Chrysothamnus nauseosus), and formed the seral gradient

Salsola —> Kochia —> Aster —> Agropyron —> Chrysothamnus

based on temporal position of dominance or subdominance of each species.

The greenhouse experiment measured the effects of an N-availability gradient on above- and belowground production and tissue N concentration of seedlings of five seral species: one annual (Salsola iberica), two perennial grasses (Sitanion hystrix = early seral, Koeleria pyramidata = late seral), and two shrubs (Chrysothamnus nauseosus = midseral, Artemisia tridentata = the late seral dominant). Details of this experiment may be found in Redente and others (1992), and more complete descriptions of the methods and results of the two field experiments may be found in McLendon and Redente (1991, 1992a, b).

RESULTS AND DISCUSSION

Annuals dominated control plots for 4 years following disturbance (fig. 1). Migration and establishment were primary factors the first year. Aboveground production was relatively low and composition variation among plots was relatively high (table 1). However, annual forbs were the dominant lifeform on all plots. In contrast, aboveground production was high the second year and most of the production (57 percent) was by Salsola iberica (table 1). Salsola decreased dramatically the third year and was replaced as site dominant by Bromus tectorum. Total aboveground production decreased to approximately half the level of the previous year and decreased at the same rate the fourth year (table 1). Transition from site dominance by annuals to dominance by perennials began the fourth year, with perennials becoming almost as abundant as annuals (29 percent and 44 percent relative biomass, respectively). Bromus tectorum and the biennial legume Melilotus officinalis were the most productive species the fourth year, producing 58 percent of the aboveground production of the seral community. Five years after disturbance, perennials became dominant (64 percent relative biomass), with shrubs and perennial grasses approximately equal.

The addition of N significantly altered this seral pattern. Plots receiving additional N remained dominated by annuals through the seventh year (table 2). Aboveground production of shrubs was lower on N plots than on control plots each year of the study, species richness and production of perennial grasses were lower after the second seral year, and production of annual forbs was greater after the first year (fig. 2). The first-year seral community on N plots was similar to that on control plots. Species composition of the second-year community on N plots was similar to that of

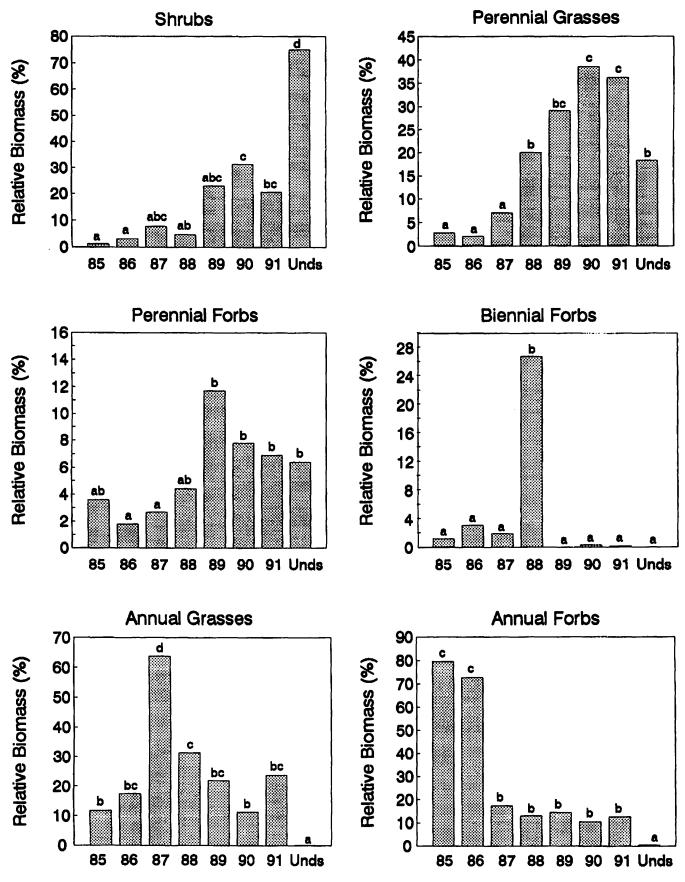


Figure 1—Relative aboveground annual production by lifeform during 7 years of secondary succession on control plots within a disturbed sagebrush ecosystem and within an adjacent undisturbed (Unds) portion of the same ecosystem. Means (16 replications for undisturbed, eight replications for all others) with the same letters are not significantly different (P < 0.05).

Table 1—Aboveground annual production (g/m ²) by major species during the first 7 years of succession on control plots within a sagebrush
ecosystem in northwestern Colorado disturbed in 1984 and for an adjacent undisturbed portion (Unds) of the same ecosystem

				Year			_	
Species	1985	1986	1987	1988	1989	1990	1991	Unds
Shrubs								
Artemisia tridentata	0	± 1	2	•	٠	2	2	86
Chrysothamnus nauseosus	1	11	11	5	21	20	21	2
Gutierrezia sarothrae	•	1	٠	•	2	10	13	1
Perennial grasses	•							
Agropyron dasystachyum	0	2	2	2	4	4	•	6
Agropyron smithii	1	1	4	9	12	16	18	2
Koeleria pyramidata	•	•	•	õ	•	1	2	8
Oryzopsis hymenoides	•	2	4	6	8	12	20	2
Sitanion hystrix	*	ō	•	•	•	2		1
Stipa comata	1	2	3	6	5	6	18	7
Perennial forbs								
Aster canescens	1	*	3	•	5	3	4	•
Erigeron engelmannii	ò	0	•	•	•		÷	1
Phlox bryoides	õ	õ	0	0	0	*	. *	6
Sphaeralcea coccinea	1	4	1	1	1	2	3	1
Biennial forbs								
Melilotus officinalis	1	13	5	32	•	•	*	•
Annual grasses								
Bromus tectorum	11	71	142	38	23	12	42	2
Annual forbs								
Chenopodium berlandieri	37	•	•	•	•	•	•	0
Descurainia sophia	1	5	2	0	1	•	1	+
Kochia scoparia	3	10	8	3	6	5	13	•
Lactuca scariola		2	4	9	š	÷	0	•
Salsola iberica	26	229	17	ĭ	3 3	5	7	•
Sisymbrium altissimum	5	25	9	i	•	ŏ	Ó	+

1*indicates a trace amount (>0.5 g).

 Table 2—Aboveground annual production (g/m²) by major species on nitrogen plots during the first 7 years of succession within a sagebrush ecosystem in northwestern Colorado disturbed in 1984

				Year			
Species	1985	1986	1987	1988	1989	1990	1991
Shrubs							
Artemisia tridentata	+1	0	+	+	+	1	1
Chrysothamnus nauseosus	•	1	3	1	*	11	5
Gutierrezia sarothrae	0	•	1	0	0	•	1
Perennial grasses							
Agropyron dasystachyum	•	•	0	0	0	1	0
Agropyron smithii	•	•	3	4	4	1	7
Koeleria pyramidata	•	0	•	Ó	Ó	0	0
Oryzopsis hymenoides	•	2	1	•	3	2	2
Sitanion hystrix	0	1	2	+	1	+	•
Stipa comata	1	1	2	1	•	2	1
Perennial forbs							
Aster canescens	•	1	•	•	•	•	•
Erigeron engelmannii	•	•	0	0	0	*	0
Sphaeralcea coccinea	٠	3	1	•	1	1	1
Biennial forbs							
Melilotus officinalis	3	24	3	8	٠	*	0
Annual grasses							
Bromus tectorum	11	83	197	26	21	9	64
Annual forbs							
Chenopodium berlandieri	8	1	•	*	•	•	0
Descurainia sophia	Õ	15	12	1	13	5	6
Kochia scoparia	17	134	275	51	94	51	165
Lactuca scariola	1	7	7	7	1	0	0
Salsola iberica	90	385	36	9	20	2	3
Sisymbrium altissimum	12	29	10	5	0	Ō	0

1*indicates a trace amount (>0.5 g).

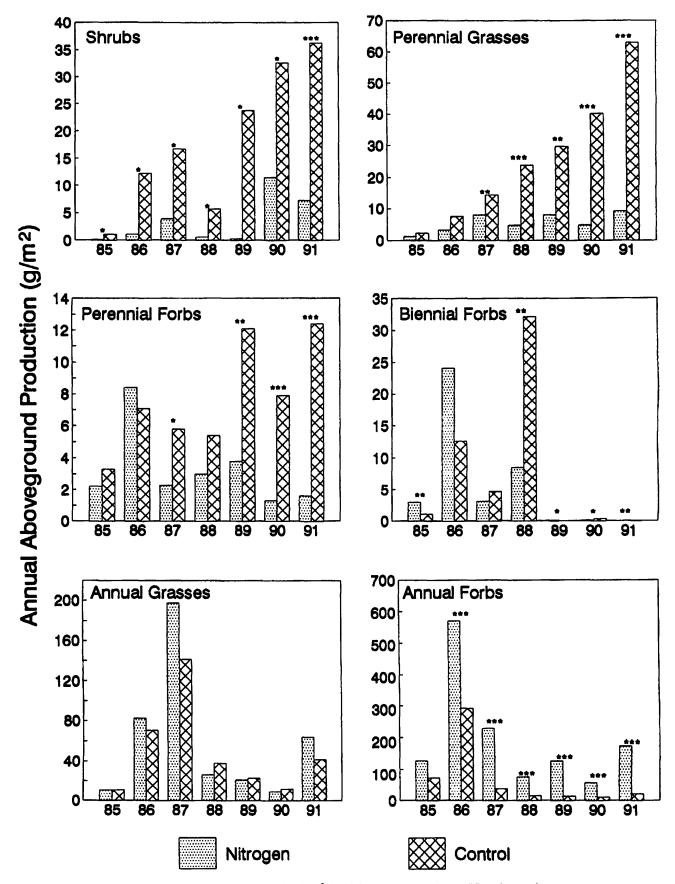


Figure 2—Comparison of aboveground annual production (g/m^2) by lifeform between nitrogen (N) and control (C) plots during the first 7 years of secondary succession within a disturbed sagebrush community. Means are of eight replications per treatment per year. Significant differences between treatment means within the same year, based on paired-*t* tests, are indicated by asterisks (* = P < 0.10, ** = P < 0.05, *** = P < 0.01).

the control plots and was also dominated by Salsola iberica, but total aboveground production was 70 percent greater. Seral communities on N and on control plots became increasingly dissimilar after the second year. Whereas shrubs and perennial grasses became increasingly important on control plots from the third year, annuals continued to dominate N plots. The third seral year, Bromus tectorum dominated control plots but was the second most important species on N plots. The annual forb Kochia scoparia was the single most important species on N plots from the third year and increasingly dominated N plots from the fourth year (43 percent, 58 percent, 61 percent, and 61 percent relative biomass, 1988-91 respectively).

Therefore, the net effect of N addition was to arrest secondary succession, at least for 5 years (third-seventh seral year). Secondary succession patterns on control and N plots in experiment 2 were similar to those of experiment 1. Third-year control plots had less annual forbs and more annual grasses and perennials and greater species richness than N plots (fig. 3). In addition, plots receiving sucrose had more advanced seral communities than either control or N plots, indicating that a decrease in soil N availability, caused by the increase in C to the decomposer subsystem, increased the rate of secondary succession.

The results of these two experiments indicate that the rate of secondary succession within the disturbed semiarid shrubland that we studied can be manipulated by controlling N availability. An increase in N availability slows the rate of secondary succession and a decrease in N availability increases the rate. Annuals are favored by increased N availability and perennials are favored by decreased N availability. Similar results have been reported in other studies (Muller and Garnier 1990; Seastedt and others 1991). However, two remaining questions must be answered before a conceptual model of the process can be developed: (1) How do such changes in N availability occur in natural systems? and (2) What is the plant response mechanism that is affected by these changes in N availability?

Nitrogen availability should have been relatively high the first seral year and it should have remained so until the beginning of the second year of our studies. Most of the belowground biomass at the time of disturbance remained within the soil following the disturbance and should have been decomposed and most of the incorporated N mineralized by the beginning of the second year. This, plus the atmospheric N deposited within the soil from 1984 to mid-1986, would have increased the available soil N pool. Since incorporation of this N into plant tissue was relatively low the first seral year because of low primary production (table 1), N availability should have remained high until the beginning of the second year.

Although available soil N levels were not measured in 1985 or 1986, they can be estimated. Available soil N $(NO_3-N + NH_4-N)$ levels within the 5-35 cm soil profile of the undisturbed community are approximately 4.94 g/m² (9.89 ppm, Stark 1983; 10.64 mg/kg, McLendon and Redente 1992b). Root biomass within this soil zone may have been approximately 400 g/m² (*Artemisia tridentata* community in southeastern Washington, Rickard 1985), with a tissue N concentration of 1.4 percent (McLendon and Redente 1992b). Assuming a decomposition rate of 50 percent (Berg and Ekbohm 1983; Birk and Simpson 1980; Buyanovsky

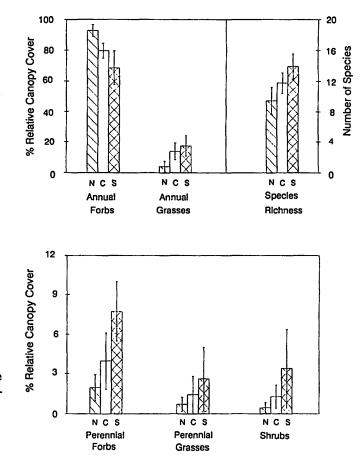


Figure 3—Relative canopy cover (percent) of lifeform groups and species richness on nitrogen (N), control (C), and sucrose (S) plots. Values are means of 12 observations (four replications x 3 years). Confidence intervals (P < 0.05) of the means are given by the vertical lines.

and others 1987) between July 1984 and June 1986, this would have released approximately 2.8 g N/m² into the upper 30 cm of the soil profile. The site received approximately 53.7 cm of precipitation from July 1984 through May 1986, which would have added an additional 0.1 g N/m² to the soil, assuming an input of 1.7 mg N/cm of precipitation (Schlesinger and Hasey 1980). These sum to 7.8 g N/m². From this sum, N incorporated in tissue production during 1985 must be subtracted. Aboveground tissue incorporation on control plots in 1985 was approximately 1.45 g N/m² (McLendon and Redente 1992b). An additional 0.19 g N/m² may have been incorporated into belowground biomass (0.13 root:shoot ratio for desert annuals, Forseth and others 1984). This would have left a balance of 6.2 g N/m^2 at the beginning of the second growing season (assuming no N losses to the atmosphere or to lower profiles, no net symbiotic or nonsymbiotic N fixation by microorganisms, and no net N release from decomposition of litter between September 1985 and May 1986).

Aboveground primary production on control plots in 1986 was 404 g/m², which incorporated 5.7 g N/m² in aboveground plant tissue (McLendon and Redente 1992b) with perhaps an additional 0.9 g N/m² in belowground biomass (0.15

root:shoot ratio for Salsola iberica, Redente and others 1992). These two values sum to 6.6 g/m², which exceeds the estimated available soil N pool in the upper 30 cm of the soil profile. If these estimates are reasonable, the second-year seral community would have depleted the available N pool to a depth of 30-35 cm.

Vitousek (1983) reported that only 13 percent of N within ragweed (Ambrosia artemisiifolia) litter in a mesic oldfield community was returned to the soil within 5 months. Pastor and others (1987) found that after the first month, N in little bluestem (Schizachvrium scoparium) litter in Minnesota was immobilized for at least 18 months. Decomposition of, and N release from, Salsola litter is probably slower because of the semiarid climate at our site and because most Salsola litter is not deposited at the soil surface but remains well above the surface for 1-3 years. Decomposition rate increases as contact with the soil is increased (Holland and Coleman 1987). Therefore, little of the N incorporated within the Salsola litter the second seral year probably was returned to the soil by the beginning of the third growing season. The result would have been a significant N deficiency in the upper 30-35 cm of the soil profile, the zone most

annuals depend on (at least as seedlings) for their N supply. This could explain why annual forbs, with their high N requirement, did not dominate control plots the third year. In support of this hypothesis, annual forbs did dominate those plots the third year that received additional N.

An annual did dominate the control plots the third year, but it was the grass Bromus tectorum. This species has a very low tissue N requirement. We measured the tissue N concentrations of 39 species at our study site over a period of 5 years (McLendon and Redente 1992b), and Bromus tectorum had the lowest values (overall mean of 1.11 percent) of all species except one (Opuntia polyacantha). The ability of Bromus tectorum to begin growth early in the growing season gives it a competitive advantage over most associated species (Eckert and Evans 1963; Harris 1967) and at our site would have allowed it to preemptively utilize whatever small amounts of N may have become available through decomposition or from precipitation. The high N-use efficiency of this annual grass (table 3) would have given it a strong competitive advantage over the associated annual forbs, and its rapid growth rate would have given it at least temporary advantage over associated young perennials in

Table 3—Aboveground tissue N concentration (percent) and N-use efficiencies (g aboveground production/g N content of aboveground tissue) of major seral species during the first 7 years of succession within a disturbed sagebrush ecosystem. Values are means of eight plots per year for 5 years for control (C) and for nitrogen (N) treatments and four plots per year for 2 years on the undisturbed (U) treatment

		N concentration			N-use efficiency	
Species	U	С	N	U	С	N
Shrubs						
Artemisia tridentata	1.39	1.82	2.39	72	55	42
Chrysothamnus nauseosus	1.51	1.77	2.11	66	57	48
Gutierrezia sarothrae	1.53	1.75	2.14	66	57	47
Opuntia polyacantha	.46	.84	na	218	119	na
Perennial grasses						
Agropyron dasystachyum	1.03	1.29	na	97	78	na
Agropyron smithii	1.02	1.19	1.83	98	84	55
Koeleria pyramidata	1.04	1.31	2.09	96	77	48
Oryzopsis hymenoides	1.08	1.23	1.67	93	81	60
Sitanion hystrix	.88	1.31	1.95	114	77	51
Stipa comata	.99	1.21	1.90	101	83	53
Legumes						
Astragalus diversifolius	1.59	2.20	2.41	63	46	41
Melilotus officinalis	na	2.38	2.60	na	42	38
Trifolium gymnocarpon	2.38	1.94	2.06	42	52	49
Perennial forbs						
Aster canescens	1.50	1.80	2.56	67	56	39
Erigeron engelmannii	1.47	1.61	na	68	62	na
Phlox bryoides	.85	1.35	na	118	74	na
Senecio multilobatus	1.31	1.38	na	76	72	na
Sphaeralcea coccinea	1.55	2.19	2.67	65	46	37
Annual grasses						
Bromus tectorum	1.09	1.11	1.51	92	90	66
Annual forbs						
Chenopodium berlandieri	na	2.16	3.19	na	46	31
Descurainia sophia	na	1.87	2.54	na	53	39
Kochia scoparia	1.01	1.67	2.57	99	60	39
Lactuca scariola	na	2.05	2.43	na	49	41
Salsola iberica	na	1.81	2.81	na	55	36
Sisymbrium altissimum	na	1.84	2.48	na	54	40

preemptive utilization of N and soil moisture (Link and others 1990).

Total aboveground annual production decreased by approximately 50 percent again the fourth seral year and then stabilized at approximately the annual production level of the undisturbed community (table 4). The fourth year was the first year that annuals produced less than 50 percent of the total annual aboveground production on control plots. and perennials produced over 60 percent of total annual aboveground production on control plots from the fifth year (table 1). Perennial grasses have low tissue-N concentrations, which should give them competitive advantage over annual forbs under conditions of low N availability. Once established, perennial grasses have advantage over Bromus tectorum, in part, because their perennial and more extensive root systems give them a competitive advantage belowground (Bookman and Mack 1982). We believe that by the time decomposition and mineralization return significant amounts of the N incorporated in the second-year (Salsola) and third-year (Bromus) litter (perhaps by the fifth seral year) perennials have become sufficiently established to effectively exploit these N resources, as well as moisture and other soil resources, as they became available.

Therefore, we suggest that incorporation of large amounts of available N in the biomass produced by annuals and a subsequent slow rate of decomposition and mineralization cause a decrease in available soil N early in secondary succession. Differences in growth rate, tissue-N concentration, and growth habit then result in changes in competitive advantage among species as N availability decreases. We believe these dynamics are the primary causes of the replacement of annuals by perennials during early secondary succession.

CONCEPTUAL MODEL

We have developed a conceptual model of the role of N availability as a mechanism controlling the rate of secondary succession and in particular the replacement of annuals by perennials (fig. 4). This model is compatible with experimental results obtained from 15 years of research on the dynamics of a disturbed semiarid shrubland in northwestern Colorado and is currently being tested in experiments in shrubland communities in other areas.

The available soil-N pool is initially high following most disturbances in most ecosystems. This allows annual forbs

Table 4—Summary of aboveground seral dynamics on control and nitrogen plots within a sagebrush ecosystem in northwestern Colorado that was disturbed in 1984 compared to an adjacent undisturbed community

				Year			
	1985	1986	1987	1988	1989	1990	1991
Undisturbed							
Major lifeform: ¹	Shrub	Shrub	Shrub	Shrub	Shrub	Shrub	Shrub
Major species: ²	Artr	Artr	Artr	Artr	Artr	Artr	Artr
Number of species:	21	15	19	na	na	na	17
Abvgrnd production: ³	203	75	149	na	na	na	129
Tissue N (percent):	1.32	1.34	1.37	na	na	na	1.34
N incorporated (g):	2,669	1,025	1,881	na	na	na	1,714
N-use efficiency:4	76	74	73	na	na	na	75
Precip-use efficacy:5	76	24	49	na	na	na	52
Control							
Major lifeform:	AForb	AForb	AGrss	Mixed	PGrss	PGrss	PGrss
Major species:	Chbe	Saib	Brte	Brte	Brte	Chna	Brte
Number of species:	12	14	19	18	19	18	17
Abvgrnd production:	92	404	222	121	103	104	175
Tissue N (percent):	1.60	1.44	1.46	1.54	1.47	1.43	1.24
N incorporated (g):	1,449	5,724	3,247	1,884	1,461	1,469	2,193
N-use efficiency:	63	69	69	65	68	70	81
Precip-use efficacy:	3.4	13.0	7.3	5.2	3.4	6.5	7.1
Nitrogen							
Major lifeform:	AForb	AForb	AForb	AForb	AForb	AForb	AForb
Major species:	Saib	Saib	Kosc	Kosc	Kosc	Kosc	Kosc
Number of species:	9	12	13	12	10	9	9
Abvgrnd production:	146	692	445	120	161	84	256
Tissue N (percent):	2.60	2.62	2.19	2.17	2.43	2.32	2.28
N incorporated (g):	3,793	18,129	9,741	2,607	3,928	1,944	5,834
N-use efficiency:	39	38	46	47	41	43	44
Precip-use efficacy:	5.5	22.2	14.7	5.1	5.9	5.3	10.4

¹Lifeforms: AForb = annual forbs, AGrss = annual grasses, PGrss = perennial grasses.

²Major species: Artr = Artemisia tridentata, Brte = Bromus tectorum, Chbe = Chenopodium berlandieri, Chna = Chrysothamnus nauseosus, Kosc = Kochia scoparla, Salb = Salsola iberica.

³Abvgrnd production = aboveground annual production (g/m²).

4N-use efficiency = g aboveground annual production/g N content of aboveground tissue.

⁵Precip-use efficincy = g aboveground annual production/cm precipitation received.

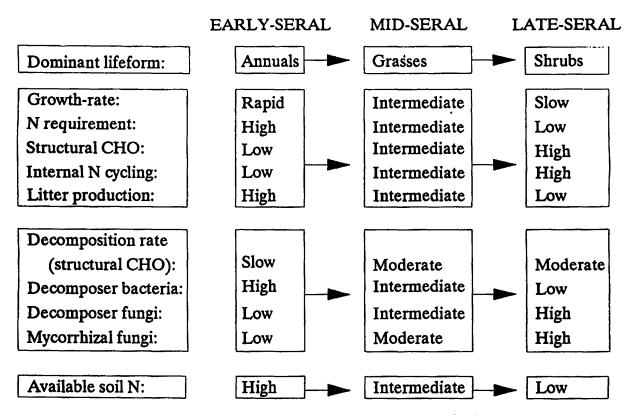


Figure 4—Conceptual model of available nitrogen dynamics and decomposer subsystem redevelopment during secondary succession in a disturbed sagebrush ecosystem in northwestern Colorado.

to dominate early seral stages because of their rapid growth rates, which allow them to accumulate large quantities of resources. Although perennial seedlings may also be present in these early seral communities, the accumulation of soil resources by rapidly growing annuals effectively denies these resources to the perennials, thereby limiting their growth early in succession. However, annuals cannot deny all resources to perennials. Therefore, perennials do increase in biomass and relative importance over time. As they do, they eventually dominate the site, but the rate is slow as long as available N remains high.

Relatively high levels of available N are required to support the high biomass production that allows annuals to dominate the site. Annuals are effective accumulators under conditions of high available N (table 3), in part because of rapid growth rates; thus annuals possess a significant competitive advantage over slower growing perennials. As available N decreases, annuals do not have sufficient N available to sustain the rapid and abundant production of biomass required for them to dominate the site. Since perennials have lower N requirements per unit biomass than annuals (table 3), conditions of lower available soil N affect them less. As a result, growth rates of perennials are nearer their optimum, resulting in increased competitive advantage to perennials. Similar relationships involving growth rate, lifeform, N availability, and seral position also exist within perennial species characteristic of mid- and late seral stages (fig. 4).

However, for N limitation to be a possible control mechanism in secondary succession, there must be a naturally occurring process that could cause such limitations. We believe that there are at least five:

1. Incorporation of N Within Biomass Produced by Annuals—Annuals produce large amounts of biomass in relatively short periods even in semiarid zones. Annualdominated early seral communities on control plots within our system produced as much as 300 g/m^2 aboveground biomass within 60 days. Annual N incorporation within this tissue exceeded 6 g/m² on some plots.

2. Slow Rate of Decomposition Early in Secondary Succession—At least two factors slow decomposition. First, annuals typically have high shoot:root ratios; therefore, most of their production becomes aboveground litter, which has a slower decomposition rate than belowground litter. Second, as available soil N levels decrease because of incorporation into the biomass of annuals, less N is available for decomposers and immobilization exceeds mineralization (Pastor and others 1987). Because of these two factors, mineralization of N during early secondary succession may lag 2-3 years behind incorporation.

3. Incorporation of N into Perennial Structures— As perennials increase in abundance, a smaller proportion of the N incorporated by the seral community returns to the decomposer subsystem via litter in a given year.

4. Decrease in Litter Quality—As succession proceeds, litter produced by the seral community decreases in quality because mid- and late-seral species have higher C:N ratios and are higher in structural materials such as lignin, cellulose, and hemicellulose than early seral species. This decrease in litter quality slows decomposition and delays mineralization of N contained in the litter (Buyanovsky and others 1987).

5. Competitive Advantage of Perennials as Soil N Becomes Limited—Perennials become increasingly more competitive for limited soil N because of four characteristics: (a) greater structural development (for example, more extensive root systems), (b) lower N requirements per unit biomass (table 3), (c) greater ability to supply a portion of their N requirements from internal sources, and (d) increased directing of soil N to perennials because of increased mutualistic coupling relationships between perennials and the decomposer subsystem.

CONCLUSIONS

Our results indicate that the transition from annualdominated to perennial-dominated communities during early secondary succession is controlled, at least in the semiarid system we have studied, by N availability. An increase in N availability slows the rate of seral change, allowing annuals to dominate longer, and a decrease in N availability increases the rate of change, allowing perennials to dominate sooner. Annuals dominate primarily because they have more rapid growth rates than perennials and are therefore able to more quickly accumulate available soil nutrients and moisture and perhaps also reduce perennial growth through shading. Such a high level of production requires high levels of available N, but it also reduces the available soil-N pool by incorporation in aboveground tissue. Decomposition of this aboveground litter is much slower than production, and, therefore, mineralization is slow and immobilization increases for several years. During this time, perennials increase in importance and dominate the site since they are better able to tolerate these low N-availability levels because of their lower N requirements and their greater structural development (for example, greater root:shoot ratios, rooting depth, and mycorrhizal fungi infection). Perennials have lower N requirements than most annual forbs because of lower tissue-N concentrations (especially grasses) and perennial storage between vears.

Bromus tectorum has the potential for extending the dominance of annuals on semiarid disturbed sites longer than would be otherwise possible because of its low N requirement and its early growth characteristic. This appears to be most significant as a factor in seral dynamics on those sites where resource availability, especially soil moisture, has a single maximum early in the growing season. On sites where availability of soil resources is not characterized by a single maxima, or where that maxima is later in the growing season, the effect of Bromus tectorum on seral dynamics should be relatively minor after the third or fourth year following disturbance.

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SELECTION OF PLANTS FOR FIRE SUPPRESSION ON SEMIARID SITES

Stephen B. Monsen

ABSTRACT

Within the Intermountain region, extensive wildfires frequently occur on disturbed range and wildlands occupied by annual weeds. Subdividing large areas occupied with cheatgrass (Bromus tectorum) by planting less flammable species in borders or greenstrips around each subunit could be a means of containing large fires and could also aid in fire suppression. Species used as greenstrips or fuelbreaks must possess a number of attributes, including: (1) adaptability to semiarid sites, (2) competitiveness with annual weeds, (3) ease of establishment, (4) low flammability, (5) open canopy and plant interspacing, (6) palatability, (7) resilience and regrowth capabilities, (8) management considerations. Various species currently under study exhibit many of these traits, and could be used to reduce the incidence of wildfires

THE PROBLEM

Many native plant communities occurring within the western United States have been disrupted by poor management practices resulting in the loss of herbs and woody species (Stewart and Hull 1949). Disturbances have occurred throughout the salt desert and cold desert shrublands (Blaisdell and Holmgren 1984), big sagebrush and mountain brush communities (Blaisdell and others 1982; Britton and Clark 1985), and juniper-pinyon woodlands (Everett and Clary 1985). Annual weeds have invaded many disturbed areas, increasing the spread and frequency of wildfires; this has resulted in the demise of many native species and the perpetuation of weedy annuals (Holmgren 1976; Tisdale and others 1969; Wright and Klemmedson 1965; Young and others 1979). Cheatgrass (Bromus tectorum) is the principal annual grass that has invaded and spread to occupy a broad range of sites (Mack 1981; Sparks and others 1990). This species is particularly adapted to arid and semiarid environments, and is able to persist under frequent fire regimes (Hunter 1990). Whisenant (1990) reported that sites occupied by cheatgrass may burn every 2-4 years without a reduction in cheatgrass density although other species may suffer significantly.

Sites dominated by cheatgrass include some rather large and contiguous acreage occupying both foothill and valley bottoms (Morrow and Stahlman 1984; Yensen 1981). Stewart and Hull (1949) reported cheatgrass dominated nearly 4 million acres in Idaho, occupying a major percent of the land in the Snake River Plain. It is particularly abundant in big sagebrush (*Artemisia tridentata*) communities where wildfires are naturally quite common (Yensen 1981).

Fire containment and suppression costs are now a major expense for land management agencies. Pellant (1990) reported the number of fires and acres burned on Bureau of Land Management, U.S. Department of the Interior, lands in southern Idaho had increased dramatically since 1979. Over 3 million acres have burned in the last 15 years (table 1), but most sites have not been revegetated due to high costs associated with seeding. If disturbed areas are not seeded to perennial vegetation, cheatgrass normally reoccupies most burns; increasing the frequency of reburning (Whisenant 1990).

In addition to the monetary costs associated with fire suppression and restoration are the losses in resource values, including further degradation of the disrupted communities (Buckhouse 1985; Klebenow 1985). The incidence of fires could be significantly diminished if native plant communities were restored and properly managed (USDI, BLM 1987; Pellant 1990; Whisenant 1990). Restoring the complex of native communities is, undoubtedly, the primary objective and desire of management personnel. However, restoration practices have not been fully developed to accomplish this task, and native plant materials are not currently available for extensive

Table 1—Acres of rangelands burned in Southern Idaho, 1979-1993

Year	Acres burned			
1979	105,000			
1980	120,000			
1981	650,000			
1982	98,000			
1983	260,000			
1984	200,000			
1985	290,000			
1986	430,000			
1987	260,000			
1988	70,000			
1989	70,400			
1990	120,000			
1991	82,000			
1992	479,000			
1993	5,600			
Total	3,240,000			

¹Data on file at U.S. Department of the Interior, Bureau of Land Management, Idaho State Office, Boise, ID.

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plantings. Seeding substitute species such as crested wheatgrass (Agropyron cristatum) is not advisable in many situations, although the incidence of wildfires and weed invasion is reduced with establishment of a perennial grass cover. Although introduced species, particularly perennial grasses, can be highly useful in reduction of fires, conversion of large disturbed sites to these perennials does not always result in the recovery of wildlife values, esthetics, and other resources. In some situations seeding introduced perennial grasses has prevented the recovery of native species.

Protection of undisturbed sites and control of wildfires on annual rangelands are major problems. If these sites could be insulated from burning, more funding and resources could be directed to restoration of existing disturbances.

Fire or fuel barriers have been used to reduce the spread of fires in various wildland situations (Green and others 1963). Fire barriers are normally created by replacing highly flammable vegetation with species that are less likely to burn. Barriers are designed to reduce the amount of fuel present and decrease contiguous fuel patterns that favor the rapid spread of fire. Fire barriers have been successfully used to control wildfires in the chaparral communities of southern California (Green 1977; Nord and Green 1977), and perennial grass fires in upland plant communities (Green 1977; Wilson 1988). Firebreaks and fuel modification plantings have also been used to protect structures and dwellings where commercial developments interface with flammable plant communities.

Fuelbreaks or fuel modification plantings have not been extensively tested, particularly on semiarid sites, yet Platt and Jackman (1942) recognized that cheatgrass fires could be significantly diminished by planting perennial grasses around sites infested with annual weeds. They provided an early set of proposals for fire prevention on cheatgrass ranges in Oregon. Of seven proposals considered by these investigators, seeding crested wheatgrass as a firebreak was the most practical measure listed. They also recognized that the majority of acres that were burned resulted from only a few large fires. If fire barriers were adequately used to hold any one fire to a relatively small area, a significant reduction in total acres burned would be accomplished. This same situation still occurs throughout the Intermountain region. Individual fires frequently burn large acreages, and containment of a single fire could significantly reduce resource damages in any given year. Fuel modification plantings have been established in Idaho and Utah within the past 10 years, but the effectiveness of these plantings has not been adequately evaluated.

Various species used for range or watershed plantings in the Intermountain region have been developed for their succulence and summer greenness (Plummer and others 1968). Some species with these attributes are adapted to semiarid sites and appear capable of controlling fires (Monsen and Kitchen 1992). It is possible these species could be planted in strips or borders around sites occupied by annual grasses where wildfires are likely to occur. Plantings could be designed to contain or reduce the spread of fires. Although greenstrip or fuelbreak plantings may require extensive seedings, most areas that are highly prone to burning are well identified. Fire history data can be used to define sites that are most frequently reburned, as well as areas that have not burned in the past 20-40 years. With careful planning the major problem areas could be selectively treated, which would greatly reduce the number of acres now burned each year.

ATTRIBUTES OF GREENSTRIP OR FUELBREAK SPECIES

Plants used to contain or control fires must possess a number of attributes including: adaptability to semiarid sites, ability to compete with annual weeds, ease of establishment, low flammability, open canopy and plant interspacing, palatability, resilience and regrowth capabilities, and management considerations (table 2).

Various plant materials have been evaluated during the past 7 years to identify species and plant features that would be useful in greenstrip plantings within big sagebrush communities of the Intermountain region. Results of preliminary work are presented in this paper. Specific attributes that are important in providing a fuel barrier are discussed.

			Attrit	outes		
Selected species ¹	Areas of adaptation	Competitiveness (seedlings)	Ease of establishment	Piant flammability	Litter and flammability	Resprouting
Agropyron cristatum	Extensive	Excellent	Excellent	Moderate	Moderate	Good
Leymus multicaulis	Undetermined	Fair	Poor	Low	Low	Excellent
Stipa thurberiana	General	Moderate	Good	Low	Low	Good
Achillea millefolium	General	Good	Excellent	Moderate	Moderate	Excellent
Linum lewisii	General	Moderate	Excellent	Low	Low	Good
Sanguisorba minor	Limited	Moderate	Excellent	Low	Low	Good
Artemisia cana	Undetermined	Fair	Good	Moderate	High	Excellent
Atriplex canescens	Limited	Fair	Good	Moderate	High	Fair/good
Kochia prostrata	General	Excellent	Excellent	Low	High	Excellent

Table 2—Attributes of select species currently being evaluated as fuel modification plantings for Intermountain rangelands

'Information based on select ecotypes or collections.

Adaptability to Semiarid Sites

Plants used to control fires must be adapted to the planting sites. Although this feature is a primary consideration for any planting, it is important that a greenstrip species be widely adapted and able to occupy and dominate almost all microsites. Species planted in a long, narrow fuelbreak must be able to establish and maintain continuous and dominant cover over a wide range of edaphic and climatic conditions. The seeded species must also be able to resist reinvasion of weeds that would decrease effectiveness of the fuel barrier. Few species demonstrate the ability to completely dominate a wide range of sites. Most native grasses, although widely distributed and abundant, normally coexist with a number of other species.

Whisenant (1990) reported that fire frequency within the sagebrush-steppe region increases as the diversity of annual plants increases and other life forms decrease. The presence of a continuous fine fuel cover provided by cheatgrass is more important in increasing fire frequency than the amount of fuel present. This is an important consideration in designing fuelbreaks or greenstrip plantings. Species that provide an open, discontinuous. but competitive cover reduce the spread of ground fires even though the plantings may increase the amount of fuel present. Open stands must be sufficiently competitive to eliminate and control cheatgrass. Generally, open and discontinuous stands can be attained by planting a single bunchgrass species or plants that form individual, distinct clumps. Plantings of crested wheatgrass provide fewer and smaller interspaces than fields of desert wheatgrass (Agropyron desertorum), although competition provided to annual weeds is quite similar.

Although single-species plantings may reduce the continuity of fine fuel, it is sometimes hazardous to plant only one species in semiarid environments (Stark and others 1946). Full or complete stands may not always establish or persist when planting diverse sites. Consequently, seeding more than one species is often recommended to improve planting success and provide more competition to annual weeds. The planted species must be compatible during periods of establishment and subsequent community development.

It is important that planted species establish easily and develop a closed stand that can persist for extended periods without dieoff. Plantings must be successful using conventional seeding techniques. Plants that require special seedbed preparation or unique planting practices usually cannot be uniformly established over a wide range of sites. Weak or erratic stands do not provide competitive ground cover. Plant adaptability and ease of establishment are critical features when attempting to establish one or only a few species as a dominant closed stand. If seeded species establish in only portions of a planted site, the effectiveness of the entire project in reducing spread of wildfires is significantly diminished.

Few species are widely adapted to semiarid sagebrush rangelands and can serve as greenstrip plantings. Two widely adapted and uniformly establishing possibilities are crested wheatgrass (Hull and Holmgren 1964; Stark and others 1946) and forage kochia (Kochia prostrata) (McArthur

and others 1990). Few native species demonstrate the broad adaptability, establishment, or competitive attributes of these two species (Monsen and Turnipseed 1990; Stevens and McArthur 1990). Collections of western yarrow (Achillea millefolium ssp. lanulosa), a native broadleaf forb, are widely distributed throughout this shrub type but are not universally adapted to all sites. and establishment is quite erratic. Sandberg bluegrass (Poa secunda) is perhaps the most widespread native grass to occur in this community type. It has vegetative features useful for fire containment, including a low fuel load and competitiveness with annual weeds. During years of above-average moisture this plant can produce sufficient fine fuel to carry fire. Pure stands can be established by direct seedings, but sufficient testing has not been completed to universally recommend this species for extensive fuelbreak plantings.

The number of species that are adapted to a wide range of arid communities is quite limited. Combinations of several species will likely be required to provide fuelbreaks for different sites. Although mixed seedings have been widely planted to improve and stabilize herbage production, plantings have not been carefully evaluated as fuel barriers or greenstrips. However, mixed seedings certainly demonstrate the ability to fully establish and maintain closed stands.

Competitivness with Annual Weeds

Species that are planted to control fires will normally be sown in areas occupied by annual weeds, consequently the seeded species must be capable of establishing and persisting under different amounts of competition. Species used as fuel or greenstrip barriers not only must be able to establish with some degree of weedy competition, but ultimately they must be able to suppress the weeds.

Plants used as fuel barriers or greenstrips must be competitive as mature stands (Edmunson and Cornelius 1961). Established plantings must be capable of restricting entry and growth of annual weeds that create increased fire hazards. Plants must be able to establish in a dense pattern or arrangement that allows for natural growth of the seeded species, yet prevents establishment of annual weeds. Seedings of Lewis flax (Linum lewisii) establish well within sites where it is adapted. A large number of seedlings may establish providing competition to annual weeds. Most broadleaf herbs do not grow in pure, dense stands, and although many species are seeded alone, few plantings persist as monocultures. Individual seedings of small burnet (Sanguisorba minor), alfalfa (Medicago sativa) and many native forbs do not maintain pure stands for many years after initial establishment. The breakup in ground cover often allows weeds to re-enter.

Most recent revegetation plantings have been designed to allow establishment of a diverse mixture of seeded species. In addition, plantings are often designed to allow natural recovery of native species. In these situations low seeding rates are often used, selected sites are purposely left open to allow for natural plant invasion, and less aggressive species are planted that do not interfere with seedling recruitment of other species.

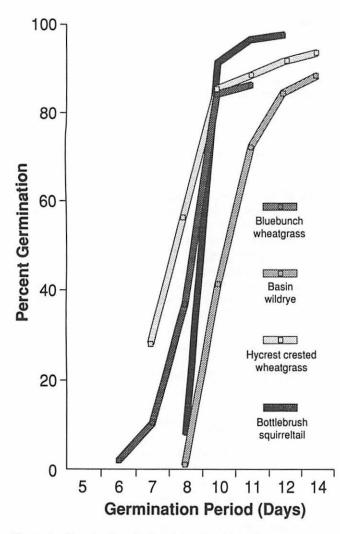


Figure 1—Germination rate from laboratory trials of four grass species germinated at 12-hour alternating temperatures of 5 and 15 °C.

Greenstrip plantings are not designed to allow establishment of a broad composition of species. Plantings are designed to assure establishment of only the seeded species, which become a stable community. As seeded stands mature, plant spacings and density should not change appreciably; change would allow more flammable species a chance to establish. Seeded communities must also be capable of persisting during periods of fluctuating climatic events or attacks by biotic agents.

Ease of Establishment

Most species currently seeded in range and wildlife habitat improvement projects have been selected for their establishment characteristics (Meyer and Monsen 1990; Monsen and Turnipseed 1990; Stevens and McArthur 1990). Species that are able to establish despite annual competition usually germinate quite uniformly and predictably (Plummer 1943; Young and Evans 1977). These species do not require special pretreatment to germinate and are able to establish with minimal seedbed preparation.

Seeds that germinate uniformly under various seedbed conditions can normally be planted at periods or seasons that favor their establishment. The germination rate of some seeded species is quite rapid (fig. 1), and germination is confined to relatively short periods in the spring and fall when conditions may be favorable. Seeds of 'Hycrest' crested wheatgrass (Agropyron cristatum X Agropyron desertorum) and bottlebrush squirreltail (Elymus elymoides) may germinate in fall or early spring and become well established before midsummer drought occurs (Plummer 1943). A somewhat similar pattern of germination appears with bluebunch wheatgrass (Pseudoroegneria spicata), although germination is normally extended over a longer period in the spring. Early establishment may not be entirely necessary for all species, yet seeded plants must be able to establish with intense competition.

Seed dormancy and rate of germination are unquestionably factors influencing establishment and seedling survival of some species (Baskin and Baskin 1973). Studies with Asian beardless wildrye (*Leymus multicaulis*) demonstrate the importance of seed dormancy and rate of germination to seedling establishment and utility of this species for greenstrip seedings. A high percentage of seeds of

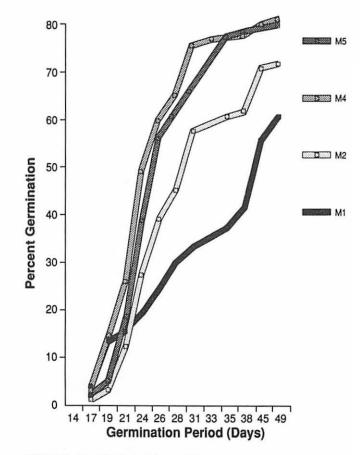


Figure 2—Germination patterns of four accessions of (*Leymus multicaulis*) from laboratory trials. Seeds germinated at 12-hour alternating temperatures of 5 and 15 °C.

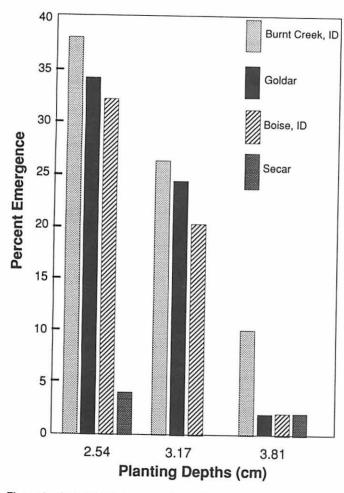


Figure 3—Seedling emergence of four different accessions of bluebunch wheatgrass from different planting depths.

this grass are dormant and germination is often delayed beyond that of other species (fig. 2). The poor germination features of this species reduce its utility for greenstrip seedings, although it maintains midsummer succulence better than any other grass currently under study. Differences in seed germination among ecotypes of various species illustrate that germinability is, in part, genetically controlled (Meyer and Monsen 1992; Meyer and others 1990; Shaw and others 1994). Seeds of some ecotypes of winterfat (Ceratoides lanata) germinate at much later dates than others (Moyer and Lang 1976). Slower rates of germination are reported by Meyer and Monsen (1992) for different selections of big sagebrush (Artemisia tridentata). Although these features may better assure natural establishment of individual ecotypes, the regulatory attributes may contribute to erratic stands from artificial plantings.

In arid or semiarid environments, a high percentage of developing seedlings are often lost to adverse conditions (Plummer and others 1955). Selecting and developing species with improved seedling vigor would significantly enhance establishment success in many arid environments. Measurements to determine seedling vigor or persistence have not been adequately developed, although planting seeds at different depths and recording emergence and growth have been used to evaluate seedling vigor (Asay and Johnson 1980; Kitchen and Monsen 1994). The technique has been used to identify difference among species and between ecotypes (fig. 3). Large seeds have demonstrated better emergence and survival from deeper planting depths than smaller seeds of the same species (Rogler 1954).

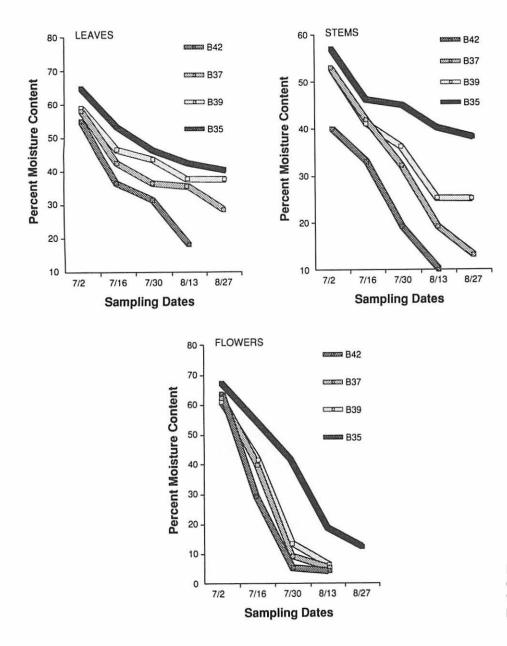
Although seedling vigor and establishment are important features of any advanced cultivar, these attributes are critical in selecting species for greenstrip plantings and weed control. Selecting species with aggressive seedlings, such as 'Hycrest' crested wheatgrass, to plant in areas occupied by annual weeds is advisable (Horton and others 1985). In addition, selecting ecotypes of native species from wildland collections that demonstrate aggressive seedling attributes is possible (fig. 3). Differences in seedling emergence from different planting depths of various collections of bluebunch wheatgrass indicate improvement of this trait may be possible through selection processes (Kitchen and Monsen 1994).

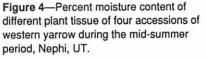
Low Flammability

Plant flammability is a primary feature of any species used in greenstrip plantings (Ching and Stewart 1962; Green 1977). Plant flammability is influenced by moisture (Rothermel 1972) and mineral content (Clark and others 1985) of live plant tissue and litter. Other features include the surface area/volume ratio of the fuel (Brown 1970, 1982; Rothermel 1972), the accumulation and packing ratio of fuel (Rothermel 1972), the ratio of live and dead material, and the continuity of down dead material (Christensen 1985). Clark and others (1985) described 18 variables that affect fire spread in three perennial grassland fuels. Fuel load, green fuel load, and characteristics of the litter are the primary features that affect the rate and spread of fire.

Wildfires occur with increasing frequency as the vegetation dries and plants senesce (Clark and others 1985). During periods of growth the moisture content of most species is sufficiently high to limit burning. Most lowelevation ranges within the Intermountain region that are occupied by big sagebrush receive adequate spring moisture to sustain plant growth. Most sites receive little summer moisture and plants normally are dry and highly flammable by early June. Most wildfires occur during June to August (Pellant 1990). Reducing this period by 1-3 weeks would significantly lessen the fire problem. Plants that are capable of sustaining a high percent of moisture in their tissue during the midsummer period are obviously potential species for greenstrip plantings.

Certain range and wildlife forage plants have been developed for their ability to retain green succulent herbage during midsummer. Alfalfa, small burnet, and various species of penstemon (*Penstemon*) have been selected for this attribute. All are useful candidates for upland sites receiving 30-35 cm of annual precipitation. Under more arid conditions, selections of western yarrow, Thurber needlegrass (*Stipa thurberiana*), and western wheatgrass (*Pascopyrum smithii*) are better adapted.





The moisture content from different collections of western yarrow has been found to vary throughout the growing season (fig. 4). Moisture retained in the leaf, stem, and floral tissues varied among collections, although collections that retained higher amounts of moisture in the leaves also retained higher amounts in the stem and floral parts. In addition to western yarrow, selections of Thurber needlegrass, western wheatgrass, and various species of penstemon all appear to differ in moisture retention. Other features may restrict their usefulness, but these plants demonstrate the potential to reduce the period of burning.

Improving moisture content in the vegetative tissue is important in reducing burning, but other factors also influence flammability. Although plants of western yarrow do contain considerable moisture in the leaf tissue, the floral stems and flower bracts dry soon after seed maturation. Some ecotypes produce an abundance of stocks that form a dense canopy over the plant. This material is highly flammable and, once ignited, generates enough fire to engulf the entire plant.

The accumulation of litter around a plant also influences flammability (Clark 1983). Plants that produce an abundance of fine stems, leaves, or floral tissue that accumulates around the plant are highly susceptible to burning. Some shrubs, particularly forage kochia, winterfat, and low rabbitbrush (*Chrysothamnus viscidiflorus*) produce a number of seed stocks and small stems each year that die but may not detach from the plant. This material may persist for a year or more. Periods of drought increase the rate of dead fuel accumulation and reduce the moisture content of live fuels (Buck 1951). During this period the dry matter enhances the chance and spread of fires.

Flammability is also influenced by the presence and composition of plant chemicals and mineral content (Broido

and Nelson 1964). Plants containing tannins and oils that ignite at low temperatures but generate high temperatures when burned, should be avoided as fuelbreak species. Differences in flammability have been correlated to the ash or mineral content of different herbs and shrubs (Philpot 1970). Lindenmuth and Davis (1973) reporting on studies in California, found that chaparral plants having a mineral content at or above 0.235 burned much slower than plants with a lower ash content. Other studies reveal that various woody species of saltbush (*Atriplex*) and creeping sage (*Salvia sonomensis*) contain sufficiently high levels of minerals to utilize these species as fuelbreak plantings in the chaparral communities of California (Nord 1972; Nord and Goodin 1970; Nord and Green 1977; Nord and others 1969).

Species that produce a low volume of fuel that dries and disintegrates quickly can also reduce fire problems. Plants of Sandberg bluegrass characteristically grow very early in the spring, producing very fine leaf blades. Leaves dry rapidly and uniformly leaving little material exposed to be burned. Although fires can and do burn Sandberg bluegrass communities, fuel loads can be maintained at a low level by grazing or clipping, and this species effectively controls the presence of annual weeds.

Open Canopy and Spacing

Accumulation of litter along with plant density, spacing, and foliage production influence burning in semiarid shrublands. These features affect the spread of fire and burning characteristics. An important feature of fire spread in semiarid shrublands is the presence or absence of a contiguous fuel supply (Clark and others 1985). Plant communities that support a closed canopy of interconnecting plants with a contiguous layer of surface litter enhance the spread of fires. Plant spacing and patterns of distribution regulate deposition and accumulation of litter. Plantings can be designed to provide interspaces with minimal litter and flammable fuel. Under arid conditions desert wheatgrass produce large, robust, widely spaced plants. The interspaces are occupied by roots of the wheatgrass, which prevents establishment and growth of annual weeds. Consequently, large openings that are free of litter lessen the spread of fire. In comparison, crested wheatgrass forms a greater number of smaller stature plants that form almost an interconnected canopy with much smaller interspaces and a more continuous layer of surface litter. Fuel characteristics are markedly different between pure stands of these two species. Early spring grazing of both species removes much of the vegetative tissue that otherwise would remain on the plant for a short period as dry stubble, but eventually would be deposited on the soil as litter. Light or moderate grazing causes some stooling or vegetative spread of crested wheatgrass that can diminish the size of openings, resulting in a more continuous live ground cover. Grazing desert wheatgrass may reduce plant stature but does not result in enlargement of plant crowns and reduction of interspaces. Controlled grazing of desert wheatgrass is likely to improve the usefulness of this species in controlling fires than would be achieved with crested wheatgrass.

Plantings of desert wheatgrass could be spaced at distances approaching 60 cm to lessen fire spread and fuel loading and yet provide sufficient competition to control invasion of cheatgrass.

Palatability

Palatability is an important feature of greenstrip plantings. Plants that can be grazed provide a means to easily remove or control the buildup of litter and fine fuel that contributes to burning. Grazing can also be used to stimulate regrowth, extend the period of summer succulence, and decrease plant cover while increasing bare ground.

Resilience and Regrowth Capabilities

A major consideration in selecting species for greenstrip plantings is the ability of the plant to recover following burning. In most situations, greenstrip plantings will be subjected to burning. Fires may occur on a frequent basis, and plantings must be able to recover without extensive reseeding. Although plant survival is dependent on the severity of a burn, some species can survive highly intensive fires. Most native and introduced grasses are capable of survival if the crowns are not severely damaged (Wright 1985). Rhizomatous species are obviously more resilient. Various broadleaf herbs and shrubs have resprouting capabilities and may also be used in fuelbreak plantings.

Forage kochia has demonstrated excellent utility as a greenstrip species for semiarid shrublands. Ten accessions of this species were burned to determine percent resprouting of mature plants for 2 years after treatment (fig. 5). Burning trials were conducted employing temperatures that were much higher than would occur in natural fires. Some plants of all accessions were capable of resprouting although considerable differences were recorded among sources tested. Studies demonstrate that differences among accessions are in part genetically controlled, and root sprouting sources can be utilized in fire related plantings. The cultivar 'Immigrant' is sufficiently fire tolerant and can be used in greenstrip seedings in semiarid shrub communities. Forage kochia is a relatively recent introduction (Stevens and others 1985) and exhibits excellent seedling establishment characteristics. The plant is viewed with some concern as a potential weed of semiarid communities, but studies conducted in the big sagebrush and salt desert communities do not indicate the plant is highly invasive or uncontrollable (McArthur and others 1990; Stevens 1992).

MANAGEMENT CONSIDERATIONS

Greenstrip or fuelbreak plantings will likely be established and managed with adjacent rangelands. The plantings will not be fenced or managed separately from associated sites. However, the planted sites will require some level of management to assure perpetuation of the stand. Planting sites will likely be grazed in a similar manner or at even greater intensities or longer duration

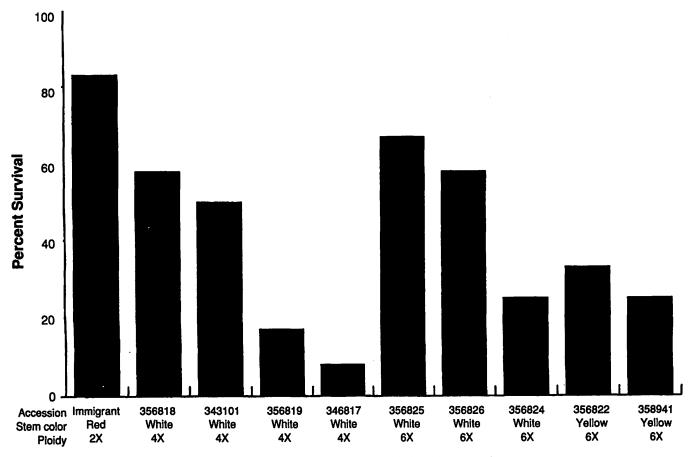


Figure 5—Percent survival following burning for select accessions of forage kochia (*Kochia prostrata*) growing in central Utah. Ploidy (chromosome number) provided by McArthur and Sanderson (1993).

than adjacent ranges. It is imperative that the seeded species are capable of persisting under different periods of use. Species that are seeded should not be items that attract or concentrate animal use. In addition, species sown should be plants that can be managed to retain their effectiveness. It is unlikely that any plant can be seeded and left unattended. Plantings may require clipping or grazing to reduce the buildup of flammable litter, control insects and rodent damage, or maintain proper age structure and plant density.

Greenstrip plantings will undoubtedly be proposed for areas of high visibility. Planting long, continuous strips may not be acceptable in some situations. Planting design and areas treated must be compatible with associated resources objectives. Single strip plantings will be difficult to manage, although they may be highly effective. It is important that associated disturbances are restored as quickly as possible. As this occurs the necessity of the greenstrip will diminish. Hopefully, greenstrips can be removed as adjacent native communities recover. Species planted in the greenstrip should be items that can be removed as needed. Plants with weedy attributes should not be used, particularly species that may spread into desirable communities. It is important that consideration is given to the life span and long-term utility of the planted species. Items that can be carefully managed or removed as warranted should be planted.

CONCLUSIONS

Numerous species exhibit useful attributes for greenstrip plantings throughout the Intermountain region. Although plant selection studies have received limited attention, a number of species with specific features can be recommended for fire preventative plantings (table 2). Few species are adapted to the more arid regions where cheatgrass occurs and wildfires are a major problem. However, plantings of desert wheatgrass and forage kochia perform adequately in these sites. Additional species are adapted to more mesic sites, although further studies are required to provide an adequate number of species for all major plant types. A number of individual plants possess certain desirable features for fire preventative plantings but may also have noticeable weaknesses. To be most effective, greenstrip plants must be adapted to sites and produce low flammable fuels. Certain species may establish and persist well under semiarid conditions. In addition, these same plants may produce green, succulent foliage that is not easily burned, but high amounts of litter may accumulate that is guite flammable. A number of

species have been identified as potential plants for greenstrip plantings, and research has been designed to correct specific weaknesses.

A number of species are available to seed fire prone areas if plantings are planned far enough in advance to obtain seeds of the desired species.

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WOODY CHENOPODS USEFUL FOR RANGELAND RECLAMATION IN WESTERN NORTH AMERICA

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ABSTRACT

A number of woody and semiwoody chenopods are potententially useful in annual grassland reclamation. Ceratoides lanata, Grayia spinosa, Atriplex canescens, and other species of Atriplex, especially those showing the potential of fire tolerance through an ability to rootsprout or crownsprout, may be valuable in regulating cheatgrass.

INTRODUCTION

Members of the chenopod family tend to tolerate high soil salinity and drought, permitting them to grow in places where competition from other plants is limited. Many woody chenopod species are equipped with C⁴ photosynthesis, which is advantageous for growth in deserts and summer heat.

Some chenopods defend themselves from mammalian and insect herbivores with spines or thorns. Members of the family also may protect themselves by accumulating unpalatable or toxic substances such as oxalates, salts, or triterpene saponins. However, these are harmful only under particular conditions and in particular species (Ihnat 1989; Oakenfull and Sidhu 1989; Young and James 1988). They do not detract from the forage value of the family as a whole.

Chenopods, due to their overall benign defensive syndrome and high protein content, tend to be very desirable browse plants. This is fortunate because in the salt deserts of western North America they constitute almost the only vegetation on millions of acres of rangeland. This paper outlines a number of the more valuable chenopod species. Tables 1 and 2 list species' characteristics.

ATRIPLEX SPECIES

Atriplex aptera (aptera fourwing) (4x) is more appropriately classified as a variety of A. canescens, where it becomes the type variety, var. canescens, as explained elsewhere (Sanderson and Stutz, in review). It is a highly variable hybrid of tetraploid fourwing saltbush and A. gardneri. From these parents it obtains a tendency to produce four-winged fruits and also an ability to rootsprout. All of the genetic variability from the parents is combined in this variable species. It occurs in the northwestern Great Plains, often in badlands, but where effective precipitation may be somewhat greater than in valleys of the Intermountain area.

Atriplex canescens (fourwing saltbush) (2x-20x; 2x-6x in the Intermountain area) is usually a medium to large shrub. It has numerous chromosome races, mostly found in the warm deserts of the southwestern United States and northern Mexico (Sanderson and Stutz, in review; Stutz and Sanderson 1993). Because of the chromosomal diversity, care should be taken to select seed sources of like chromosome numbers to avoid the development of chromosomal sterility in later generations. Many of the chromosomal races of fourwing saltbush are described as species or varieties. Some of these are limited in nature to sand dunes; others are found both on sand and heavy soils. Leaf length of fourwing saltbush races tends to decrease while leaf width may increase somewhat with ploidy.

Fourwing saltbush is able to resprout when browsed or burned (Tirmenstein 1986a). Rare, highly rootsprouting individual plants have been found that are also able to spread extensively by vegetative means (Barrow, in review). Such plants, if frost hardy, seem to have promise in annual grass remediation. In the Intermountain area diploid, tetraploid, hexaploid, and possibly a few octoploid fourwing saltbush populations are found. The most abundant are tetraploids, which grow in all of the western States and on a variety of soil types.

There are three diploid fourwings in the Intermountain area. Atriplex canescens var. gigantea is a large bush with unusually long leaves, growing only on the Little Sahara Dunes in western Utah. Var. angustifolia, identified by its very narrow leaves, is another large bush growing on dunes. It grows chiefly in Mexico, but is also found in southern Arizona and New Mexico. In New Mexico there are some roadside plants as far north as Farmington. The third diploid is A. garrettii, or A. canescens var. garrettii, a small yellowish-green bush with round or oval leaves, found only along the Colorado River in southeastern Utah.

Tetraploid fourwing saltbush occupies a variety of habitats. Leaves of the tetraploid are shorter than those of vars. *gigantea* and *angustifolia*. 'Rincon,' from northern New Mexico, and 'Marana,' from southern Arizona, are released cultivars of tetraploid fourwing saltbush.

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Table 1-Characteristics of selected species of North American perennial Atriplex

Taxon	Ploidy	Forage use	Soil salinity	Rootsprouting	Remediation potential
A. canescens	2x-20x	palatable	medium	crown sprouts	good
A. confertifolia	2x-10x	spiny	medium to higher	no	usually poor
A. aptera	4 x	palatable	medium to higher	Yes	moderately good
A. gardneri	2x, 4x	palatable	medium to higher	yes	moderately good
A. falcata	2x	palatable	low to higher	yes	good
<i>A. tridentata</i> Hybrids with	4x, 6x	palatable	high	yes	specialized sites only
A. canescens	4x, 6x	palatable	low medium	yes	good

Populations of tetraploids contain occasional plants that are hexaploid; occasionally entire populations of hexaploids are found. As shown in Stutz and Sanderson (1979), hexaploids are quite common in Arizona, New Mexico, and Nevada. In addition there is a small hexaploid population growing at Grantsville, UT, which we called "tooelensis." It lacks saponins, has furfuraceous foliage, and flowers very late (mostly in September). The hexaploid race in western Nevada has a distinctive flavonoid pattern compared to other tetraploids or hexaploids, and because it is shorter in stature, is referred to as "nana." It seems that polyploids have an advantage in being able to grow in saltier soils (Sanderson and others 1987). "Nana" grows in transitional areas between the warm desert and cold desert.

Fourwing saltbush races and their ecotypes provide a rich variety of useful genotypes that may prove helpful in revegetation. In addition to those mentioned, there are numerous others existing in the southwestern United States and Mexico that would be useful in warmer climates.

Atriplex confertifolia (shadscale) (2x-10x) occurs from Oregon and California to North Dakota and Texas, and marginally into Mexico. It consists of numerous chemical and chromosomal races (Sanderson and others 1990; Stutz and Sanderson 1983). For this reason, as with A. canescens, care must be taken in selecting seed sources of shadscale so that incompatible chromosome races are not interplanted. Shadscale is usually a small- to mediumsized shrub. Although spring growth is palatable and nutritious and the plants are saponin free, young branches rapidly develop into spines, reducing the accessibility of forage. Shadscale palatability is lower at other times of year (Dayton 1937). Shadscale is the Atriplex dominant most often replaced by cheatgrass because, except for occasional restablishment from seed, the species does not recover from fire. Unless cultivars with much more favorable characteristics can be developed, it seems unlikely that shadscale will be of value in recovering cheatgrassinfested sites. It will remain important on sites where annuals are not a problem.

Atriplex falcata (falcate saltbush) (2x) is a low-growing subshrub that can grow on badland outcrops or on welldrained valley slopes. It is mainly found in the States of Utah, Nevada, Idaho, and Oregon. The spring leaves are linear, somewhat like those of fourwing saltbush, but these are replaced by very small, persistent leaves in the fall and winter. Falcate saltbush tends to exclude other vegetation, forming monotypic stands. Even cheatgrass may be excluded on more saline soils. Although predominantly caespitose, it sprouts readily from the crown and roots when damaged, and most populations also occasionally vegetatively reproduce by rootsprouts.

Because it forms small, isolated populations (suggesting that larger, more continuous populations are unstable), and has been observed to die out suddenly, disease problems may exist. Nevertheless, because of its resprouting ability, *A. falcata* is a species that should be useful in fireaffected areas. Falcate saltbush can be distinguished from *A. tridentata*, which is vegetatively similar but occupies a different ecological setting, by the presence of bitter saponins in the foliage and by the distinctive falcate (curved) fruit beak (fig. 1).

Atriplex gardneri (A. gardneri var. gardneri) (Gardner saltbush) (2x, 4x) is a prostrate to upright, low shrub found on saline and often barren clays, frequently growing in large pure stands, mainly in Wyoming and Montana. With age, plants spread into circular patches. It differs from A. falcata and A. tridentata in having roundish, oval to cuneate or obcuneate leaves. Gardner saltbush resists fire through low flammability and also through resprouting (Tirmenstein 1986b). Often found with grasses or sagebrush, it has at least a degree of competitive ability. Atriplex gardneri is a species that merits experimentation on cheatgrass sites.

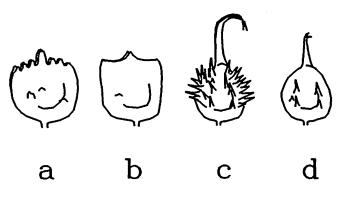


Figure 1—Fruits of *Atriplex tridentata* (a, b) and *A. falcata* (c, d). The seed is covered by two clamshell-like bracts that have teeth along their margins or a long beak. Both species can have bumps or soft spines on the sides of the fruiting bracts, but they are more common in *A. falcata*. Atriplex tridentata (trident saltbush) (mostly 6x) is a strongly rootsprouting subshrub similar in appearance to falcate saltbush. However, in contrast to that species, it is free of bitter saponins and is found in highly saline bottomlands, often with Sarcobatus vermiculatus. Because of abundant rootsprouting, it may spread into large clonal patches. The plants have narrow, linear leaves like those of falcate saltbush, but the fruits have three to seven marginal teeth rather than a long beak (fig. 1). As discussed later, trident saltbush has a tendency to form hybrids and hybrid derivative populations by crossing with fourwing saltbush.

ATRIPLEX HYBRIDS

Atriplex canescens x A. gardneri: Individual first generation plants having this evident parentage are common where fourwing saltbush plants have established themselves along roadsides near Gardner saltbush populations. Hybrids are also found occasionally at considerable distances from plants of fourwing saltbush, apparently due to wind transport of the pollen. The hybrids are easy to find because they tower above Gardner saltbush plants. Although Gardner saltbush has both diploid and tetraploid populations, most of the hybridization occurs at the tetraploid level. Because of genetic segregation among the progeny of hybrids, hybrids can form a large source of variation for natural or artificial selection. There are also vast areas where populations of both parents have come together in the past and formed populations of aptera saltbush, a new and still developing species, as already mentioned.

Atriplex cansecens $\times A$. falcata: These hybrids have been formed synthetically in the garden, and a number of distinct native hybrid populations in the Great Basin are suggested to have this parentage (Hanson 1962). Evidence has been presented (Stutz and others 1979), however, that some of the populations in question are derived from the hybridization of A. canescens and A. tridentata, as discussed later. Even if there are no hybrids in nature having A. falcata as a parent, interesting selections could be produced using synthetic hybrids as a source of variation.

Atriplex canescens x A. tridentata: An odd-ploid seedling with a chromosome count of 2n = 45 (pentaploid) (Pope 1976) was grown from seed collected from a lone female A. canescens plant near Grantsville, UT, pollinated by distant male bushes. Other seedlings from the same plant had counts of 2n = 36 (tetraploid), which was inferred to be the chromosome number of the A. canescens plant. A search of the site revealed numerous plants of A. tridentata close at hand; these proved to have a higher chromosome number of 2n = 54, which could have produced the pentaploid seed by hybridization. Several adult hybrids were found. Many other such areas of hybridization were eventually encountered—huge populations that appeared to have resulted from hybridization of these parents (Stutz and others 1979).

Although odd-ploidy is unstable in sexually reproducing organisms because most of the gametes are unbalanced, it was found in this case to rapidly resolve itself, apparently because euploid (balanced) gametes, which are occasionally produced, have a viability advantage. Through backcrossing to one of the parental species, these gametes might have given rise to either tetraploid or hexaploid hybrid derivatives. However, those in nature that clearly belong to this parental combination are, so far, all 2n = 54(hexaploid). The numerous distinctive populations of these hybrid derivatives provide a rich source of genetic variation for use in reclamation.

SHRUBBY NON-ATRIPLEX CHENOPODS

Allenrolfea occidentalis (iodine bush) is a succulent shrub or subshrub with jointed green stems that grows at the margins of salt marshes and on salt flats, from Oregon and California to Texas and Mexico (Welsh and others 1987). Great Basin plants are small shrubs to subshrubs, but plants from other places may be larger. Those in California's Central Valley are strong, woody shrubs several feet high, and perhaps deserve to be classified as a separate species or variety. The consumption of its foliage by herbivores is limited by a high salt content. Because it is very halophilic and dependent on high water tables, it does not grow to any extent in cheatgrass habitats, and is therefore not likely to be useful in remediation of such areas.

Ceratoides lanata (winterfat) is a densely pubescent shrub or subshrub occurring from southern Canada to California and Texas. Winterfat often forms huge, pure stands excluding other shrubs. It also grows with Atriplex or Artemisia. Although its hairiness would be a deterrent to insect attack (Smith 1989), the plant is eaten readily by mammals and is an important source of browse. There are two widespread forms of winterfat, a short-statured one more northern in distribution, and a large one (for example, Hatch winterfat) mostly found in warm deserts. Winterfat resprouts after fire (Holifield 1987a); however, a solid stand of winterfat often partly excludes cheatgrass, reducing the frequency of fire. It is readily established from seed (McArthur and Monsen, in review).

Grayia brandegii (spineless hopsage) is palatable but uncommon (Holifield 1987b), found only on steep, welldrained outcrops of highly saline and seleniferous shales on the Colorado Plateau, mostly in eastern Utah but including portions of neighboring Wyoming, Colorado, New Mexico, and Arizona. These shales are often brightly colored red, or white and purple, such as the Morrison Shale formation. Usually, little cheatgrass is present, and it is expected that the competitive ability of spineless hopsage is low except on unusually saline soils.

Grayia spinosa (spiny hopsage), which occurs from Washington to Montana and California to New Mexico, is common in the upper elevations of the Mojave Desert. It grows in valleys and hills of the Great Basin well into the pinyon-juniper community, on soils of low to moderate salinity. It is very palatable when bearing leaves but its usefulness as a range plant is limited; it sheds leaves and fruits in early summer (McArthur and Monsen, in review). Spiny hopsage resprouts readily after light burning (Holifield 1987c), but can sometimes be killed by fire.

Kochia americana (gray molly) occurs from Oregon to Montana and from California to New Mexico. It is a small subshrub that forms stands of rather widely spaced plants Table 2---Characteristics of shrubby North American chenopod species

Taxon	Ploidy	Forage use	Habitats	Halophylicity	Apparent cheatgrass remediation potential
Allenrolfea occidentalis	2x	low	salt flats, marshes	very strong	none
Ceratiodes lanata	2x	palatable	valleys, hills	weak to moderate	very useful
Grayia brandegii	2x, 4x	palatable	saline shale outcrops	strong	low
Grayia spinosa	4x	early decid	valleys, hills	weak	probably good
Kochia americana	2x	palatable	saline barrens & hills	strong	low
Sarcobatus baileyi	12x	spiny	arid slopes	moderate	moderate? should be tested
Sarcobatus vermiculatus	4x, 8x	low	saline bottomlands	moderate to strong	good for specialized sites
Suaeda torreyana	2x	low	saline bottoms & flats	strong	low
Zuckia arizonica	2x	palatable	saline clay, shale	strong	low

in barren, highly saline areas such as valley bottoms. Because it spreads vegetatively by occasional root- sprouting, it should withstand fire well. However, its habitat suggests that most ecotypes of gray molly would have relatively little competitive ability against communities of introduced annuals.

Sarcobatus baileyi (Bailey greasewood) is a densely spiny, deciduous shrub, up to about one-half meter in height, that forms solid stands on arid hillsides in western Nevada and adjacent California. It often grows with Atriplex confertifolia. Bailey greasewood's leaves are fleshy and narrow, like those of Sarcobatus vermiculatus. It can presumably resprout after fire like that species. It occurs slightly below and to the south of major cheatgrass zones, but because it is not dependent on water tables like its congener, Bailey greasewood may be worth a trial with cheatgrass.

Sarcobatus vermiculatus (black greasewood) is a larger deciduous shrub with much variability, found from Sonora to Alberta and California to Texas. It has tetraploid and octaploid races, but plants in the Intermountain region are all octaploid. It grows mainly in saline bottomlands having high water tables. There are some populations occurring in soils where cheatgrass is able to grow abundantly, and in such cases greasewood resprouts vigorously from its roots after the grass has been burned (Tirmenstein 1987).

Suaeda torreyana (inkbush) occurs from California and Wyoming to Mexico. It is a plant of more saline soils, often growing in the presence of high water tables. The leaves are narrow and fleshy, similar in form to those of Sarcobatus. They turn inky black upon dying in the fall. Inkbush seldom grows where annual grasses are abundant.

Zuckia arizonica (zuckia) is an uncommon plant of barren clay or shale in the Colorado Plateau, in eastern Utah and northern Arizona. It hybridizes with *Grayia brandegii* and is therefore related to it, though the fruits are dissimilar. Like that species, it is not found in dense stands of grass.

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'APPAR' LEWIS FLAX: BEAUTY AND WILDLIFE FOOD IN ONE PLANT

J. Chris Hoag Gary L. Young

'Appar' Lewis Flax (*Linum lewisii* Pursh) is a shortlived (5-7 years) native perennial forb growing from a woody crown and taproot. Multiple-stemmed, 'Appar' has a deep-blue flower and tiny, alternate, linear, deep-green leaves. It reaches a height of 30 cm (12 inches) on dry sites to 91 cm (36 inches) when irrigated. 'Appar' is widely adapted to western North America, from Alaska to Mexico. It is suitable for sites with an average annual precipitation that ranges from 25.4 cm (10 inches) to 58.4 cm (23 inches).

'Appar' is recommended for seeding on well-drained soils. It should not be used as an understory plant because it does not tolerate shade. 'Appar' is used extensively to diversify range seedings and to provide cover for minespoils and highway rights-of-way, and generally adds color to sites that are too dry for ornamental flower varieties. It is sought out by big-game animals, livestock, and birds for early green forage and, later in the season, for seeds.

'Appar' establishes slowly and can survive heavy grazing after it is established. It will maintain itself naturally if allowed to set seed. 'Appar' is excellent for low-precipitation areas where color, diversity, and forage are the objectives.

'DELAR' SMALL BURNET: AN OUTSTANDING RANGE FORB

J. Chris Hoag Gary L. Young

Delar' small burnet (Sanquisorba minor Scop.) is a hardy long-lived perennial evergreen forb that is multiple stemmed, growing from a taproot. It has a nonshowy flower that is greenish to rose tinged. The leaves are alternate, pinnately compound, and coarsely serrate. Delar' reaches a height of 15 cm (6 inches) on droughty sites and 60 cm (23.6 inches) when irrigated. When planting 'Delar,' poorly drained soils with high water tables should be avoided. 'Delar' is widely adapted throughout the Intermountain region on sites with a pH as high as 8.0 and harsh winter conditions. It grows well in areas that receive more than 30.5 cm (12 inches) of average annual precipitation. 'Delar' can be planted as late winter or early spring forage for big game, livestock, and game or nongame birds. It is also used as part of a mix for seedings on range, minespoils, and disturbed areas. It does not tolerate shade and does not work well seeded alone or as the predominant plant in a mix.

Delar' is one of the best forbs for moderate-precipitation range diversity seedings that have an objective of late winter and early spring forage for a wide variety of animals.

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CYPERACEAE AND JUNCACEAE— SELECTED LOW-ELEVATION SPECIES

Emerenciana G. Hurd Nancy L. Shaw Lynda C. Smithman

Sedge (Cyperaceae) and rush (Juncaceae) species of lowland riparian communities in the Intermountain area are widespread geographically, but distributed locally in response to water availability, soil conditions, and microclimate. Many species are highly rhizomatous, producing dense stands valuable for stabilizing streambanks, controlling soil erosion, enhancing fisheries, and filtering agricultural waste water. Sedges and rushes provide food and cover for many wildlife species. Their palatability to wildlife and livestock varies, as does their response to grazing and trampling.

Many low-elevation riparian and wetland communities have been physically and biologically degraded by livestock grazing practices and the vegetation replaced by more mesic species, including introduced weeds. Agriculture, urbanization, recreation, and other human activities have also heavily impacted these communities. Proper identification and an understanding of the distribution and ecology of major sedge and rush species of Intermountain lowlands are essential for estimating site potential, evaluating management practices, and planning revegetation projects.

CYPERACEAE

Carex athrostachya Olney (Slender-beaked sedge)-Habit: Caespitose plants with short rhizomes. Culms aphyllopodic, 1.5-10 dm tall. Habitat: Moist or wet places to dry areas from lowlands to the spruce-fir zone. Slender-beaked sedge tolerates seasonal flooding and grows on soils varying from organic to mineral (Hansen and others 1988). Community dominance: Hansen and others (1988) described a Carex athrostachya dominance type occurring at low- to mid-elevations in western Montana. Ecology and management: Palatability is fair to good for cattle and horses (Hermann 1970). Use on submerged or wet sites should be delayed until soils dry (Hansen and others 1988). Culture: Seeds ripen from July to August. Germination is improved by a 7-day stratification at 34-38 °C and exposure to light during incubation (Johnson and others 1965).

Carex douglasii F. Boott (Douglas's sedge)—Habit: Low-growing plants 6-30 cm tall. Stems are produced singly or few together from slender rhizomes. The species is distinctive due to its large heads and dioecious habit. Habitat: Valleys to the spruce-fir zone, but more common at lower elevations, particularly in the sagebrush zone. Frequent in dry meadows on soils that dry out early in the season, but also occurs in wet meadows, along roadways, and near seeps and springs where livestock have compacted the soil. Grows on fine-textured, loamy to clayloam soils with some organic material (Manning and Padgett 1992) and tolerates alkali. Community dominance: Manning (1988) and Manning and Padgett (1992) described Carex douglasii community types for northwestern, west-central, and central Nevada. These communities were considered to be grazing induced with high species richness reflecting the presence of disturbance species. Ecology and management: Erosion control provided by Douglas's sedge is moderate. Palatability is low due to the tough, fibrous leaves, but the species is used by horses and cattle in spring (Manning and Padgett 1992). Douglas's sedge is considered a valuable forage plant due to its abundance and the heavy use it receives when more palatable species are depleted (Cronquist and others 1977). Culture: Seeds ripen from July to August. There are about 2.5 million perigynia/kg (Hurd and Shaw 1992).

Carex lanuginosa Michx. (Woolly sedge)-Habit: Plants of variable heights, often 3-8 dm tall. Nonclumping culms arise from thick, creeping rhizomes. Habitat: Low to moderate elevations in the mountains in wet to dry meadows, headwater basins, floodplains, and along stream, lake, and pond margins. Often found on welldeveloped mineral soils with large amounts of organic matter, but also grows on clayey to sandy sediments. Tolerates spring flooding. The water table usually remains within the rooting zone in summer (Hansen and others 1988). Community dominance: C. lanuginosa and Salix/C. lanuginosa community types, dominance types, and associations have been described for Nevada (Manning and Padgett 1992), central Oregon (Kovalchik 1987), Utah and southeastern Idaho (Padgett and others 1989), and western and central Montana (Hansen and others 1988). Ecology and management: Densely rhizomatous. Useful for improving degraded riparian sites and stabilizing streambanks (Hansen and others 1988). Plants are productive and highly palatable to livestock, often receiving heavy use (Cronquist and others 1977). Hermann (1970) found that deer and elk made extensive use of woolly sedge in the Rocky Mountains and Colorado Basin, while Kovalchik (1987) reported little deer use of the species in central Oregon. Woolly sedge provides

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nesting and feeding areas for waterfowl (Hansen and others 1988) and is sometimes harvested for wild hay.

Woolly sedge is sensitive to trampling, particularly when growing on fine soils subject to compaction. Severe disturbance may lead to its replacement by *Juncus balticus, Carex nebrascensis,* or *Poa pratensis* (Manning and Padgett 1992). Moderate late-season use is recommended to maintain stands and reduce compaction (Kovalchik 1987). **Culture:** Seeds ripen from July to September. There are about 1.2 million perigynia/kg (Hurd and Shaw 1992). Seed fill is often low and seeds are sometimes infested with smut. Comes and others (1976) reported germination was improved by storage in water and exposure to light during incubation.

Carex nebrascensis Dewey (Nebraska sedge)-Habit: Robust plants, 2-12+ dm. Culms are strongly triangular and coarse, single or 2-3 together from stout, scaly, creeping rhizomes. Habitat: Valleys to midelevations. Occurs in pure stands or mixed communities in wet to moist meadows. broad alluvial terraces, and along the margins of marshes, swamps, ditches, seeps, stockponds, lakes, and reservoirs. Common on well-developed mineral soils derived from alluvium. Surface layers are usually fine-textured with accumulations of organic matter (Hansen and others 1988). The water table usually remains near the soil surface, rarely dropping below the rooting zone. Tolerates alkaline conditions. Community dominance: Carex nebrascensis community types, dominance types, and associations have been described for central Oregon (Kovalchik 1987), Nevada (Manning 1988; Manning and Padgett 1992), Utah and southeastern Idaho (Padgett and others 1989), eastern Idaho and western Wyoming (Youngblood and others 1985), and Montana (Hansen and others 1988). Ecology and management: Nebraska sedge is an excellent soil stabilizer, forming a dense mat of roots and rhizomes valuable for holding overhanging streambanks and enhancing fish habitat (Padgett and others 1989). It is highly productive and provides considerable forage due to its abundance (Manning and others 1989). Palatability is moderate to good. Nebraska sedge is sometimes heavily used by cattle, horses, and elk, particularly in spring; use by sheep and mule deer is moderate (Manning and Padgett 1992). It is somewhat resistant to grazing and trampling (Kovalchik and others 1988), but moderate late-season use is recommended (Hermann 1970; Kovalchik 1987). Nebraska sedge communities provide feeding and nesting areas for waterfowl and many other small animals (Hansen and others 1988) and are sometimes harvested as wild hay (Kovalchik and others 1988).

Nebraska sedge is strongly competitive and may persist and increase with heavy grazing, replacing other dominant species (Manning and Padgett 1992). Recovery of these species is unlikely due to the aggressive spreading habit of Nebraska sedge (Hansen and others 1988). Extremely heavy grazing and lowered water tables, however, may result in replacement of Nebraska sedge by such species as *Juncus balticus* or *Poa pratensis* (Manning and Padgett 1992). Such sites become compacted, hummocky, and erosive (Manning and Padgett 1992). **Culture:** Seeds ripen from August to September. Seed fill is highly variable and should be checked before harvest. There are about 2.7 million perigynia/kg (Hurd and Shaw 1992). Stratification for 1 week (Johnson and others 1965) or 4 weeks (E. G. Hurd and N. L. Shaw, data on file, 1990-92) improves germination. Seeds should be exposed to light during incubation (Johnson and others 1965).

Carex praegracilis W. Boott (Clustered field sedge)-Habit: Slender culms, 3-7 dm tall, arise singly or few together from thick, dark, brownish-purple, long-creeping rhizomes. Habitat: Moist, open sites on plains and lowlands to moderate elevations. Borders streams, ditches, lakes, ponds, springs, and seeps. Also occurs in wet meadows, dry meadows, sagebrush/grass communities, and wet, sometimes alkaline, bottomlands. Typically grows on welldeveloped mineral soils, often with large amounts of organic matter (Youngblood and others 1985). The water table is usually near the surface in spring, but may drop 1 m or more in summer. The species tolerates alkaline and saline conditions. Community dominance: Carex praegracilis is a minor dominance type occurring throughout much of Montana (Hansen and others 1988). Ecology and management: Useful for stabilizing degraded wet meadows (Hansen and others 1988). Palatability is variable, but often low. It provides moderate to high amounts of forage in early spring (Hermann 1970) and considerable winter grazing for cattle and horses. It is sometimes harvested for wild hay (Hansen and others 1988). Culture: Seeds ripen from June to September. There are about 1.9 million perigynia/kg (Hurd and Shaw 1992). Germination is benefited by a 4-week stratification (E. G. Hurd and N. L. Shaw, data on file, 1990-92).

Carex rostrata Stokes (Beaked sedge)-Habit: Culms mostly 4-14 dm tall, sharply triangular, arising singly or few together from stout, scaly, deep-seated, creeping rhizomes. Sometimes forms a dense sod. Habitat: Most common at midelevations, but extends to near timberline. Occurs on wet soil or in shallow, usually stagnant to slowmoving water to 45 cm deep along the margins of lowgradient meandering streams, lakes and ponds, active floodplains, swamps, wet meadows, and marshes. Often grows in nearly pure stands, covering broad valley bottoms. Common in silted-in beaver ponds (Padgett and others 1989). Soils are mineral or organic. Mature stands develop thick organic horizons. Water tables are often above the surface year-long and rarely drop below the rooting zone (Hansen and others 1988). Youngblood and others (1985) reported distribution may be controlled more by the presence of high water tables than by the nature of the substrate. Community dominance: Carex rostrata and Salix/Carex rostrata community types, dominance types, and associations have been described for central Oregon (Kovalchik 1987), Nevada (Manning and Padgett 1992), Utah and southeastern Idaho (Padgett and others 1989), eastern Idaho and western Wyoming (Youngblood and others 1985), central Idaho (Tuhy and Jensen 1982), and western Montana (Hansen and others 1988). Ecology and management: The dense sod formed by the extensive rhizome and root systems forms overhanging banks and provides excellent soil stabilization and cover for fish (Hansen and others 1988). These communities are rather stable, but willows and other sedge species begin to invade if the water table drops (Youngblood and others 1985). Productivity is high, but palatability is low to moderate. Livestock and wild ungulates use beaked sedge to some extent

in early spring, but rarely in summer due to the coarseness of mature leaves (Kovalchik and others 1988). Elk and deer use it moderately in late summer and fall (Youngblood and others 1985). Beaked sedge communities provide foraging areas for birds. The fine-texturedsoils of beaked sedge communities are sensitive to compaction (Manning and Padgett 1992). Heavy trampling and recreational use along streambanks can result in sloughing (Hansen and others 1988). **Culture:** Seeds ripen from August to September. Seed fill is often low and smut infections are not uncommon. Stand composition should be checked carefully before harvesting as beaked sedge sometimes grows mixed with inflated sedge (*Carex vesicaria*), a similar-appearing species. Perigynia weight is about 1.3 million/kg (Hurd and Shaw 1992).

Eleocharis palustris (L.) R. & S. (Creeping spikerush)-Habit: Culms slender to stout, 1-10 dm tall, scattered or in small clusters from rhizomes. Habitat: Sea level to midelevations on seasonally to permanently flooded sites, often in moderate to wide valley bottoms with low gradients. Grows in wet meadows and along ponds, sloughs, small permanent lakes, streams, reservoir drawdown areas, and stockponds. Often occurs on alkaline sites. Soils vary from organic to mineral. Sites are either permanently flooded or seasonally flooded with the water table dropping to 30 cm below the surface late in the season (Manning and Padgett 1992). Community dominance: Eleocharis palustris community types, dominance types, and associations have been described for central Oregon (Kovalchik 1987), Nevada (Manning and Padgett 1992), Utah (Padgett and others 1989), and western Montana (Hansen and others 1988). Manning and Padgett (1992) reported species richness is usually low due to anaerobic conditions. Ecology and management: The species provides high erosion control potential (Manning and Padgett 1992). Palatability is low for livestock and wild ungulates (Kovalchik 1987). Kovalchik and others (1988) reported use is limited, even in drought years, while Hansen and others (1988) found use in western Montana increased in dry years due to the reduced availability and palatability of upland forage. Heavy grazing may allow this species to increase and spread (Hansen and others 1988). Broad zones of creeping spikerush along lakes and reservoirs provide valuable feeding and nesting areas for waterfowl (Kovalchik 1987). Culture: Seeds ripen from July to August, disarticulating rapidly when mature. Seeds are collected from the small plants with difficulty.

Scirpus acutus Muhl. ex Bigel. (Hardstem bulrush)— Habit: Large colonies of stout, terete, nearly bladeless culms, 1-3(5) m tall develop from robust rhizomes. Culms are firm and not easily crushed between the fingers. Habitat: Forms tall, dense colonies in marshes, sloughs, seeps, washes, flood plains, and muddy shores of ponds, lakes, and reservoirs. Grows in clear to moderately turbid water to 1 m deep. Tolerant of highly alkaline conditions. Occurs in mineral soils with thick organic surface horizons and textures varying from fine clay to silt loam (Hansen and others 1988). The water table is usually high in spring and stands may remain inundated throughout the year. Water tables in drier stands may drop to 1 m below the soil surface in summer. Community dominance: Hansen and others (1988) described a *Scirpus acutus* dominant type common at low to mid elevations in Montana. **Ecology and management:** Colonies buffer wind and wave action, enhancing vegetation establishment along shores (Hansen and others 1988). Productive, but use by livestock and wild ungulates is generally low unless other forage is limited. Provides an important source of food and cover for waterfowl, muskrats, and other small animals (Hansen and others 1988). Management objectives may emphasize expansion of *Scirpus* communities to improve wildlife habitat. Used in artificial wetlands constructed to filter agricultural waste water. **Culture:** Seeds ripen from July to August and disarticulate rapidly when mature. They are easily harvested as the inflorescences are large and usually readily accessible.

JUNCACEAE

Juncus articulatus L. (Jointed rush)—Habit: Loosely tufted perennial developing from short to elongate rootstocks, often roots from lower nodes. Culms terete, 15-50 cm tall. Habitat: Lowlands to midelevations, wet lowland meadows, sandbars, ponds, streams, seeps, and ditches. Sandy to clay-loam soils. Culture: Seeds ripen from August to September. There are about 64 million seeds/kg (Hurd and Shaw 1992). Seeds are nondormant when incubated at 25/15 °C (8/16 h) with exposure to light during the high temperature phase (N. L. Shaw and E. G. Hurd, data on file, 1990-92).

Juncus balticus Willd. (Baltic rush, wiregrass)-Habit: Small tufts or single, bladeless, terete, dark-green wiry culms, 3-9 dm tall, are produced from coarse, black, creeping rhizomes. An extremely polymorphic species with several varieties. Habitat: Wet, often saline to alkaline sites from valleys to midelevations, alluvial terraces, wide valley bottoms, margins of streams, rivers, ponds, lakes, springs, seeps, and saline to nonsaline meadows. Common on sites where soils are saturated for short periods in spring, but with the water table dropping to 1 m or more below the surface later in the growing season (Hansen and others 1988). The species often grows in fine-textured mineral soils with dark surface horizons containing large amounts of decomposed organic matter (Tuhy and Jensen 1982). Community dominance: Juncus balticus community types and dominance types have been described for northwestern Nevada (Manning 1988; Manning and Padgett 1992), Utah (Padgett and others 1989), Idaho (Tuhy and Jensen 1982; Youngblood and others 1985), and western Montana (Hansen and others 1988). Ecology and management: Valuable species for binding soils and trapping sediment due to its deep, spreading root system (Manning and Padgett 1992). Provides dense cover for birds. It is productive and provides important forage for livestock and wild ungulates early in the season (Hermann 1975). Use declines as leaves mature and toughen. The species is moderately resistant to trampling, spreading aggressively and persisting with grazing. Culture: Seeds ripen in August to September. Seed fill is often low on dry sites. There are about 32 million seeds/kg (Hurd and Shaw 1992).

Juncus effusus L. (Soft rush, common rush)—Habit: Densely tufted perennial arising from stout rhizomes. Culms terete, 4-12 dm tall. An extremely polymorphic complex. Habitat: Moist places, swamps, lake shores, ditchbanks, ponds, and bogs. Sandy to loamy soils. Ecology and management: The extensive root system makes soft rush a valuable soil stabilizer. Plants are grazed by livestock where accessible. Culture: Seeds ripen from August to September and dehisce quickly when mature. There are about 96 million seeds/kg (Hurd and Shaw 1992). Exposure to light is required for germination (Thompson and Grime 1983). Seeds must be surface planted. Young seedlings are sensitive to drying, competition, and mechanical disturbance (Lazenby 1955).

Juncus ensifolius Wikst. (Swordleaf rush)—Habit: Perennial. Culms compressed, 2-7 dm tall, arising singly or in tufts from creeping rhizomes. Habitat: Wet meadows, marshy areas, roadsides, seeps, and streambanks from valley bottoms to subalpine communities. Loamy to sandy soils. Ecology and management: Forage value varies from poor to excellent; palatability is greatest early in the season. Used for wild hay (Hermann 1975). Culture: Seeds ripen in August to September and dehisce rapidly. There are about 152 million seeds/kg (Hurd and Shaw 1992).

Juncus torreyi Cov. (Torrey rush)-Habit: Perennial arising from slender, creeping rhizomes with tuberous nodes. Culms are stout, terete, and solitary or few together. Habitat: Valleys and lowlands on banks of streams, marshes, swamps, ditches, washes, and rivers. Occurs on mineral, often loamy soils. Tolerates alkalinity. The water table usually remains at or near the soil surface year-long (Hansen and others 1988). Community dominance: Hansen and others (1988) described a rare to minor Juncus torrevi dominance type in western Montana. Ecology and management: Used by all classes of livestock where accessible (Hermann 1975). Palatability is generally considered fair. Culture: Seeds ripen from August to September. Seeds may remain within the partially dehiscent capsules throughout the winter. There are about 81 million seeds/kg (Hurd and Shaw 1992).

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'GOLDAR' BLUEBUNCH WHEATGRASS: RELEASE OF A NEW RANGE PLANT

Gary L. Young J. Chris Hoag

'Goldar' bluebunch wheatgrass (*Pseudoroegneria spicata* ssp. *spicata* [Pursh] Scribn. & J.G.Smith) is a native perennial grass collected from a ponderosa pine/bluebunch wheatgrass community at about 1,219 m (4,000 ft) in Asotin County, WA. Bluebunch can be found from Alaska to northern California, New Mexico, and east to Wyoming.

S.

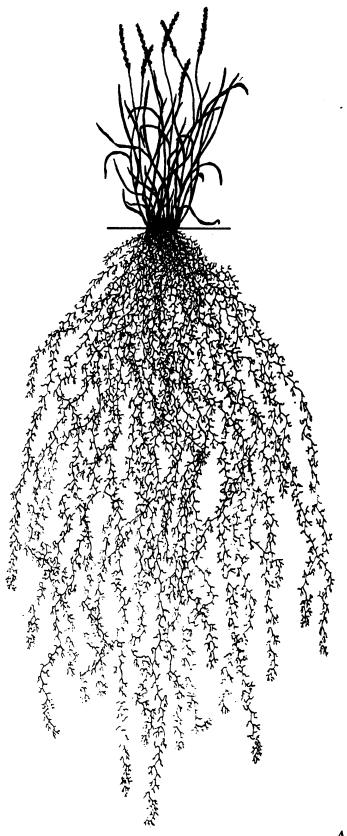
'Goldar' is a densely tufted cool-season bunchgrass with abundant leaves. In comparison to 'Whitmar' beardless wheatgrass (*P. spicata* ssp. *inerme*) and 'Secar' Snake River wheatgrass (*Elymus lanceolatus* ssp. *wawawai*), it had higher forage production and greater basal area, generally superior vigor, and better seed production. It is more cold tolerant than 'Whitmar,' but 'Secar' is better for lower elevations and lower rainfall sites.

'Goldar' was developed for range seedings, critical area stabilization, weed control, and mine spoil reclamation. It is adapted to elevations above 914 m (3,000 ft) and areas with a mean annual precipitation that exceeds 25 cm (10 inches). It prefers medium-textured, loamy soils at least 25 cm (10 inches) deep. 'Goldar' was released in 1989 by the Aberdeen Plant Materials Center.

Poster paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992.

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Management



Agropyron inerme

FORAGE YIELD AND QUALITY TRENDS OF ANNUAL GRASSES IN THE GREAT BASIN

H. F. Mayland R. B. Murray G. E. Shewmaker

ABSTRACT

Grazing animals readily eat medusahead (Taeniatherum asperum [Sim.] Nevski) and cheatgrass (Bromus tectorum L.) during the short time when plants are green and succulent. Cheatgrass, the more important of the two, is a primary source of spring forage in the Great Basin. It is characterized by a short green-feed period, large yearly variations in yield, and declining forage quality as plants dry. However, cattle eat mature cheatgrass and gain as well as cattle grazing on matured perennial grasses growing in the same area.

INTRODUCTION

Fall-germinating winter annual grasses occur throughout the rangelands of the Great Basin and adjacent Snake River Plains. Most are introduced weedy species that complete their life cycle in late spring or early summer. When mature, some species develop hardened and sharpawned florets and become potentially injurious to grazing animals. These plants are generally considered to have little forage value beyond the short green-feed period (fig. 1). Little is known about their nutritive value. However, the forage value of two species has been studied. These are medusahead (*Taeniatherum asperum* [Sim.] Nevski) and cheatgrass (*Bromus tectorum* L.).

Medusahead was first identified in southwestern Oregon in 1884 (Turner and others 1963). It quickly spread across the Pacific Northwest and inland to southcentral Idaho. Its invasion is confined to clay-type soils in the lower desert where it tends to replace cheatgrass. On the edge of the Great Basin near Adin, CA, medusahead often invaded low sagebrush (*Artemisia arbuscula* Nutt.) communities that were at a low seral stage (Young and Evans 1970). In eastern Oregon and western Idaho where medusahead was found, we estimated (unpublished) dry matter yields ranging from traces to 400 lb/acre. Annual yields undoubtedly vary because of composition, edaphic, and climatic differences.

Medusahead is sometimes perceived as having no forage value. But the nutritive value of the immature plants

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H. F. Mayland, Research Soil Scientist; R. B. Murray, Range Scientist (retired); G. E. Shewmaker, Biological Technician, Agricultural Research Service, U.S. Department of Agriculture, Kimberly, ID 83341. is similar to cheatgrass. Sheep, if given free choice, eat the green, but not the dry, plants. However, they eat the dry and headed-out plants if that is the only forage available (Lusk and others 1961).

Medusahead plants accumulate high silica concentrations (11.3 percent compared with 4.4 percent for cheatgrass), probably accounting for the rapid loss in palatability of maturing plants (Van Dyne and Heady 1965). The high silica concentration seems also to slow decomposition of old plant material (Lusk and others 1961), promoting dense fiber mats that are sometimes observed on medusahead-colonized areas.

CHEATGRASS DISTRIBUTION

Cheatgrass is widely distributed throughout Canada, Mexico, and the United States except for five southeastern States. It was introduced to the eastern U.S. prior to 1861 and by 1900 had spread to the West (Klemmedson and Smith 1964; Mack 1981). It is especially abundant in

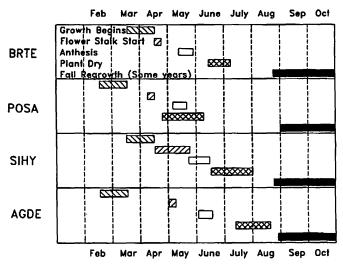


Figure 1—Plant development of cheatgrass (*Bromus tectorum*, BRTE) and three perennials; Sandberg's bluegrass (*Poa sandbergii*, POSA), bottlebrush squirreltail (*Sitanion hystrix* [Nutt.] Smith, SIHY), and crested wheatgrass (*Agropyron desertorum* Fisch., AGDE). Data are from the Saylor Creek Experimental Range in southcentral Idaho for the period 1960 to 1969 (Murray and others 1978).

the upper Great Basin and Columbia Basin. Stewart and Hull (1949) estimated that cheatgrass was the dominant species on approximately 4 million acres in southern Idaho and constituted from 75 to 95 percent of the herbage production. Furthermore, they reported that it was the principal herbaceous species on another 2 million acres and made up part of the cover on another 10 to 15 million acres in Idaho alone. Cheatgrass has also been regarded as a dominant species on about 10 million acres in Oregon (Klemmedson and Smith 1964). Overall, it was found on 60 million acres of rangeland in the 11 western States. Hull and Pechanec (1947) considered cheatgrass an important forage plant in the Great Basin, particularly in southern Idaho.

Like other winter annuals, cheatgrass is an opportunistic plant, a prolific seeder that germinates and grows at cool temperatures. It grows mostly in the 6- to 22-inch precipitation zones, but has been found on more xeric sites in the Columbia Basin (Klemmedson and Smith 1964). It completes its life cycle over a range of soil water conditions. Plant height can range between 2 and 24 inches, although it is ordinarily 10 to 12 inches.

FORAGE YIELDS

Considerable variation occurs in the annual forage yield, ranging from near zero to more than 3,000 lb/acre. At Arrowrock, ID, Klemmedson and Smith (1964) measured 360 pounds of cheatgrass per acre one year and 3,460 the next year. Yields of *Agropyron desertorum* for those same years were 1,290 and 2,470 pounds, respectively. They also reported that the average dry matter yield on four sites in southern Idaho over 4 years was 1,230 lb/acre for cheatgrass and 1,540 for *Agropyron cristatum*.

Native range in eastern Washington yielded 760 lb/acre, of which 13 percent was cheatgrass. Application

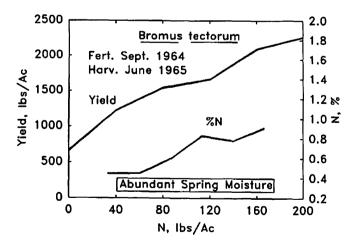


Figure 2—Dry matter yield and nitrogen (N) concentration of cheatgrass (*Bromus tectorum*) during a year of abundant spring moisture after fall fertilization with different nitrogen (NH_4NO_3) rates. Data were taken in June 1965 at the Saylor Creek Experimental Range in south-central Idaho (Murray and others 1978).

of 80 pounds nitrogen per acre increased total grass yield to 3,900 lb/acre, of which 82 percent was cheatgrass (Patterson and Youngman 1960). Murray and others (1978) applied different levels of nitrogen fertilizer to cheatgrass range in southern Idaho and measured a nearlinear yield response to rates as high as 200 pounds nitrogen per acre (fig. 2). Their yield responses to nitrogen illustrated the remarkable ability of the species to respond to favorable edaphic and climatic conditions.

UTILIZATION

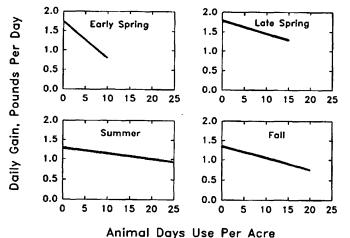
Fleming and others (1942) reported that both cattle and horses utilized cheatgrass. Animal preference was largely determined by herbage water content. Cheatgrass may be fully dried by mid-July, whereas perennials can still contain 65 percent moisture (Murray and others 1978). Cattle and horses continue to use cheatgrass when it is mature and dry if ample water is present or the herbage has been softened by rain (Hull and Pechanec 1947).

Early studies reported that cattle on cheatgrass gained weight through July, but then began to lose weight (Fleming and others 1942). A later study showed that yearling cattle grazing in southern Idaho on cheatgrass continued to gain weight from April to October (Murray and Klemmedson 1968). The yearlings gained 1.70, 2.06, 1.38, and 0.82 lb/animal-day corresponding to (1) slow vegetative growth, (2) rapid growth and maturation, (3) matured and dry, and (4) fall germination and emergence of new seedlings. These weight gains compared favorably with the 2.72, 1.87, 1.00, and 0.22 lb/animal-day gain for yearlings grazing crested wheatgrass (during similar time periods) on the Benmore Experimental Range in Utah (Harris and others 1968).

Murray and Klemmedson (1968) found that there was no advantage to rotational grazing. Animals gained 1.39, 1.45, and 1.45 lb/animal-day when grazing was rotated or continuous at moderate (40 percent utilization) or heavy stocking (60 percent utilization) rates, respectively. In a related study, daily gains were sharply depressed in early spring and least affected in summer by increased stocking rates (fig. 3). Overall, yearling cattle gained 1.43 lb/ animal-day during the 7-month grazing period on cheatgrass at the Saylor Creek Experimental Range in southcentral Idaho and 1.25 lb/animal-day when grazing crested wheatgrass for a similar time period on the Benmore Experimental Range in north-central Utah.

Weight gain data for yearling cattle were pooled across different grazing systems (fig. 4). Results from the 7-year study substantiate the ability of cattle to utilize cheatgrass. Weight gain performance by other classes of cattle, like calves, first-calf heifers, and mature cows, was also determined (fig. 5). The cheatgrass forage provided sufficient energy to first-calf heifers to produce milk for their calves, but not enough energy for their own growth. Other classes of cattle gained at acceptable levels.

Sheep utilized cheatgrass during the green-feed period, but not after it dried (Cook and Harris 1952). Studies quantifying sheep performance when grazing cheatgrass in April and May were conducted at the Saylor Creek Experimental Range (Murray 1971). Sheep carrying capacity was similar on perennial and cheatgrass sites during wet



Animul Duys Use Per Acre

Figure 3—Daily weight gains by yearling cattle grazing cheatgrass (*Bromus tectorum*) at several stocking intensities on the Saylor Creek Experimental Range during early spring (April 1-May 5), late spring (May 6-June 9), summer (June 10-September 1), and fall (September 2-October 27). Data are means of 5 years (Murray and others 1978).

years, but during dry years the perennial pastures produced 60 percent more forage. Sheep (ewes) gained an average 0.34 and 0.29 lb/head-day when grazing cheatgrass and native bunchgrass, respectively. Perennial bunchgrass provided 15 percent more forage.

Cook and Harris (1952) showed that sheep grazed cheatgrass in Utah earlier than perennial grasses, but that the forage quality (protein, Ca, P, and gross energy) of cheatgrass decreased rapidly with increasing plant ma-

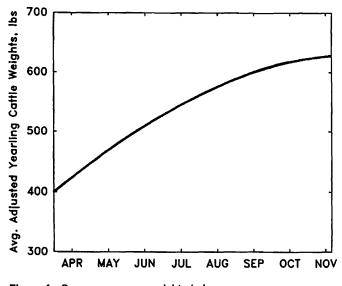


Figure 4—Seven-year mean weights (adjusted to 400 pounds) of yearling cattle grazing cheatgrass (*Bromus tectorum*) on the Saylor Creek Experimental Range in southcentral Idaho (Murray and others 1978).

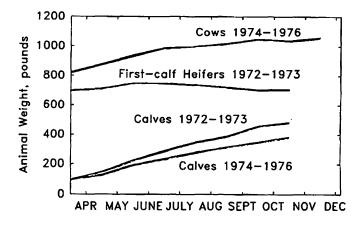


Figure 5—Mean animal weights when grazing cheatgrass (*Bromus tectorum*). Data are from the Saylor Creek Experimental Range in south-central Idaho (Mayland and others 1980; Murray and others 1978).

turity. Lignin and ash increased with plant maturity, and cellulose and other carbohydrates changed little. Similar changes in forage quality have been noted for perennial grasses (Murray and others 1978), but the decline was delayed considerably by the longer green-feed period.

Murray and others (1978) evaluated forage quality changes in cheatgrass and perennial grasses at the Saylor Creek Experimental Range. Nitrogen, phosphorus, and zinc concentrations declined in the maturing cheatgrass

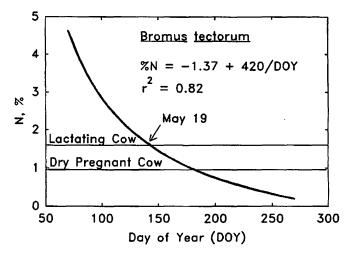


Figure 6—Forage nitrogen (percent N x 6.24 = percent crude protein) requirements of cows and the mean 7-year nitrogen concentration in cheatgrass (*Bromus tectorum*) related to day of year (DOY). Data are from the Saylor Creek Experimental Range in south-central Idaho (Murray and others 1978).

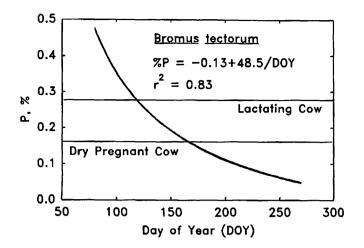


Figure 7–Forage phosphorus (P) requirements of cows and the mean 7-year phosphorus concentration in cheatgrass (*Bromus tectorum*) related to day of year (DOY). Data are from the Saylor Creek Experimental Range in southcentral Idaho (Murray and others 1978).

(figs. 6, 7, 8). Neutral detergent fiber concentrations increased as plants matured (fig. 9), and these increases were accompanied by decreased dry matter intake by the grazing animal. Another measure of forage quality was total digestible dry matter, which also decreased with time (fig. 10). On June 12 and October 14, respectively, cheatgrass forage contained 1.11 and 0.79 percent N, 0.219 and 0.086 percent P, 13.7 and 12.6 ppm Zn, and 49 and 56 ppb Se (unpublished). These forage data were regarded as deficient in N, P, and Zn for growing cattle. However, these

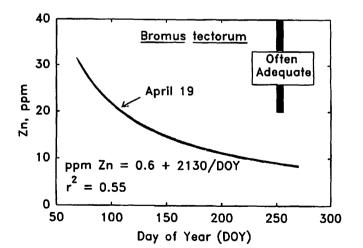


Figure 8—Approximate range in forage-zinc (Zn) levels required by cows and the mean 7year zinc concentration in cheatgrass (*Bromus tectorum*) related to day of year (DOY). Data are from the Saylor Creek Experimental Range in south-central Idaho (Murray and others 1978).

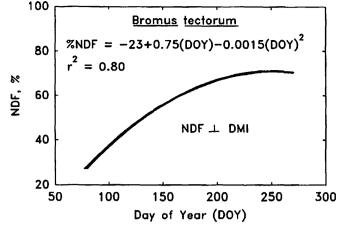


Figure 9—Mean 7-year neutral detergent fiber (NDF) concentration in cheatgrass (*Bromus tectorum*) related to day of year (DOY). NDF is inversely proportional to dry matter intake (DMI). Data are from the Saylor Creek Experimental Range in south-central Idaho (Murray and others 1978).

values were obtained for hand-clipped forage samples. Animals usually select plants and plant parts that provide a higher level of nutrition than that represented by the clipped samples.

Olsen (1971) examined yearling beef cattle response to various supplements while they grazed cheatgrass. He found that supplemental protein increased dry matter digestibility and total dry matter intake (TDDM). Supplemental energy increased energy digestibility during early spring, but depressed dry matter intake. Supplemental P

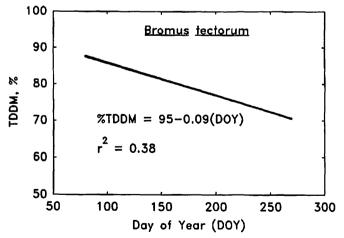


Figure 10—Mean 7-year total digestible dry matter (TDDM) concentration in cheatgrass (*Bromus tectorum*) related to day of year (DOY). Data are from the Saylor Creek Experimental Range in south-central Idaho (Murray and others 1978).

did not significantly increase daily weight gains compared to control animals (1.42 vs. 1.39 lb/animal-day).

Zinc concentrations in the cheatgrass, and other grasses, were generally below levels recommended for cattle. Mayland and others (1980) later reported that supplementing the zinc intake with 900 mg zinc per cow-calf pair significantly increased calf-weight gains by 6 percent.

SUMMARY

Two winter annual grasses, medusahead and cheatgrass, are important to grazing animals in the Great Basin. Horses, cattle, and sheep eat both species while the plants are green and succulent. Of the two grasses, more attention is given to cheatgrass because of its more extensive distribution and availability as spring forage. Yearly variations in dry matter yield and the short green-feed period, however, reduce the reliability of cheatgrass as a dependable forage base. The dry herbage is less desirable, but most cattle having easy access to water will continue gaining weight while grazing matured cheatgrass.

Nitrogen (crude protein), energy, phosphorous, zinc, and other nutrient concentrations decline with the maturation process, and herbage may become deficient in these nutrients for some livestock classes. Benefits have only been shown for zinc supplementation. Forage value of cheatgrass may be regarded as equivalent to other perennial species found in the area. However, perennial species would likely provide a more stable yield, have a longer green-feed period, and produce more usable forage per acre.

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ANNUAL RANGELAND MANAGEMENT PRINCIPLES AND PRACTICES: THE CALIFORNIA EXPERIENCE

Melvin R. George

ABSTRACT

Prevailing weather has a greater influence on annual rangeland forage production than grazing management and agronomic practices. However, these practices can be used to manipulate species composition, forage productivity, and forage quality. Annual rangeland vegetation dynamics on a site can be described using state and transition models. Transitions between states may be controlled by natural events or managerial inputs.

RANGE IMPROVEMENT

The development of annual rangeland management principles and practices can be traced back to early integrated research beginning in the 1930's in the College of Agriculture and at the USDA Forest Service San Joaquin Experimental Range (SJER) in the central Sierra Nevada foothills. Throughout the past 60 years management principles have emphasized resource values associated with forage and livestock production. While basic research focused on ecological and physiological principles of forage production, applied research focused on managing livestock and manipulating forage production, forage quality, and species composition.

Menke (1989) described vegetation management activities used to manipulate forage productivity, forage quality, and species composition. Prescribed fire has been used alone or with mechanical and chemical controls to convert woody plant-dominated communities to open grasslands (Kay and Leonard 1979; Nichols and others 1984). Seeding of native or introduced perennial grasses, annual legumes, or both, was part of the type conversion process from shrubland or oak woodland to open grassland. Less frequently, fire has been used to reduce annual grasse competition with native or introduced perennial grasses (Ahmed 1983; Fossom 1990; Heady 1973; Hervey 1949; Zavon 1982).

Annual rangelands are nitrogen deficient as well as phosphorus or sulfur deficient. Consequently, a great deal of basic and applied research has focused on fertilizer responses (Jones 1974) and nutrient cycling (Jones and Woodmansee 1979). Response to nitrogen fertilization is dependable between 15 and 30 inches of annual rainfall, but economic feasibility varies with site productivity and ranch forage alternatives.

Dr. Merton Love joined the College of Agriculture in the 1940's to develop native or exotic perennial grasses for seeding on annual rangelands. Several perennial grasses were shown to be adapted to California's mediterranean rangelands, but competition from resident annual species limited the success and dependability of perennial grass seedings.

Dr. Love found greater success when he imported and tested rose clover (*Trifolium hirtum*) in the 1940's and 1950's (Love 1985). Rose clover has been so successful that it has spread naturally throughout many areas of the northern Sierra foothills. Annual legume seeding success improved with the development of Rhizobium inoculation technology (Holland and others 1969). Seeding of subterranean clover (*Trifolium subterraneum*), rose clover, and lana vetch (*Vicia dasyacarpa*) continues to be a common practice for improving forage production and quality (Murphy 1973).

GRAZING MANAGEMENT

Year-long or seasonal continuous grazing has been the traditional practice on annual rangeland. Annual variation in forage productivity due to prevailing weather usually has a greater impact on livestock performance than grazing systems. Livestock performance may be reduced or unchanged by seasonal compared to continuous grazing systems. Moderate grazing that allowed about 80 to 90 pounds of dry matter per animal unit per day from February through July at SJER produced the optimum combination of animal performance and per-acre productivity (Bentley and Talbot 1951; Wagnon and others 1959).

The need to control intensity of forage utilization on annual rangelands has resulted in the development of residual dry matter standards and assessment procedures (Clawson and others 1981). Recommended minimum residual dry matter (RDM) levels depend on average precipitation and slope. Adequate RDM moderates the seed germination and seedling establishment microenvironment. Too much RDM or a dense mulch results in a thatch that inhibits early response of new forage growth. Low RDM tends to maintain forbs such as filaree (*Erodium* spp.) and annual legumes. High residue tends to increase the grass composition (Bartolome and others 1980). Hooper and Heady (1970) found that high RDM was followed by higher forage production the following spring.

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992.

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DESIRED PLANT COMMUNITIES

We have accumulated a great deal of information in the past 60 years that is useful in managing annual rangelands. Unfortunately, few natural resource managers working in annual rangelands are conversant with this knowledge base. New and recurring resource management objectives including biodiversity, rare and endangered species, and ecological restoration can benefit from this knowledge base developed primarily for livestock and range forage management purposes.

To more adequately extend this information we propose to use state and transition models (Westoby and others 1989) to describe desired plant communities (states) and the natural and managerial events (transitions) required to reach them. Site protection, biodiversity, habitat, forage, and other resource values will be described for each plant community.

STATE AND TRANSITION MODEL

While annual grasslands are generally considered to be stable (Heady 1977), communities are made up of several transient states that are often described by species dominance. Transition between these states may be triggered by natural events (weather, fire, etc.) or management (brush control, seeding, change in stocking rate, etc.), or combinations of the two. Transitions may occur very quickly (fire) or over an extended period (biological invasions, climate change) (Svejcar and Brown 1991).

Figure 1 and associated descriptions (next page) describe a state and transition example for a shallow gravelly loam site in the Sierra foothills of Yuba County, CA. This approach provides a map for ecosystem management for use by land managers and a means for more quantifiably testing hypotheses about ecosystem response to disturbance and management.

The state and transition model can be applied in the field and used for planning managerial inputs. The transitions describe managerial actions (inputs) required to progress from one state to another. Resource value ratings can be assigned to stable states and potential products (outputs) can be projected. Probabilities of natural phenomena (disturbances) and managerial success can be assigned to transitions.

For example, if a grassland is in State I (fig. 1) and the objective was to convert to the grassland in State III, managerial inputs described in Transitions 1 and 2 would be prescribed. Early rains and favorable growing seasons would accelerate progress toward State III while drought and fire would tend to delay progress for 1 to 3 years. Removal of livestock earlier to leave more residual dry matter would facilitate progress from State II to State III. Application of nitrogen fertilizer may accelerate progress from State II to State III. At State III, management inputs can be designed to maintain State III or to set course for a new objective.

The resource value for cattle grazing would increase with progress from State I to State III, while State II would be of greater value for sheep grazing than cattle. Maintaining adequate cover while increasing forb populations (State II) would enhance upland bird habitat. Increasing cover (State III) would reduce habitat value for ground squirrels (*Spermophilus beecheyi*). As the grassland progresses from State I to State III, increasing cover and residual dry matter may improve the grassland's value as watershed. The landowner's goals, enterprises, and markets would determine the most advantageous mix of patch states on the landscape.

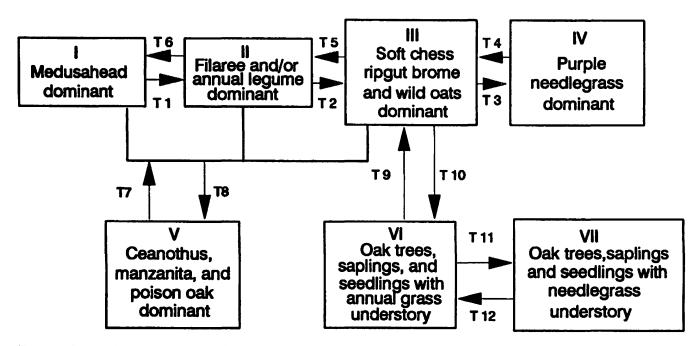


Figure 1—State-and-transition description for a shallow gravelly loam foothill range site in Yuba County, CA, with 675-875 mm of annual rainfall.

Catalog of States

State I—Medusahead (*Taeniatherum asperum*) forms nearly pure stands with heavy litter that effectively excludes most other annual grasses and forbs. High silica content is believed to slow decomposition, resulting in litter accumulation that effectively suppresses establishment of associated species. Late maturity allows medusahead to most effectively exploit soils containing clay (Young and Evans 1970).

State II—Filaree (*Erodium cicutarium*) dominates the seedbank and the aboveground standing crop. Medusahead density is substantially reduced. Soft chess brome (*Bromus mollis*) is present in the seedbank and standing crop but in small amounts. Seeded annual legumes may partially replace filaree.

State III—Wild oats (*Avena fatua*), ripgut brome (*Bromus diandrus*), and soft chess dominate patches. Filaree and other species are present in small amounts. Medusahead is infrequent or not present. Perennial grasses such as purple needlegrass (*Stipa pulchra*) may be present in small amounts.

State IV—Purple needlegrass (*Stipa pulchra*) dominates the grassland. While it is the most common native grass present in today's California annual grassland, it may not have been the dominant perennial grass in the original California grassland (Bartolome and Gemmill 1981). Nodding needlegrass (*S. cernua*), blue wildrye (*Elymus glaucus*), pine bluegrass (*Poa scabrella*), junegrass (*Koeleria cristata*), or California oatgrass (*Danthonia californica*) may have been present in the original grassland.

State V—Wedgeleaf ceanothus (*Ceanothus cuneatus*), whiteleaf manzanita (*Arctostaphylos viscida*), and poisonoak (*Rhus diversiloba*) dominate the community.

State VI—Blue oak (*Quercus douglasii*) and interior live oak (*Q. wislizeni*) savanna with an annual grass understory dominated by wild oats, soft chess brome, and ripgut brome.

State VII—Blue oak and interior live oak savanna with a perennial grass (purple needlegrass) understory.

Catalog of Transitions

Transition 1-Medusahead seedbank reduced by 50 to 90 percent. This can be effected by several forms of disturbance (Hilken and Miller 1980; Major and others 1960), including herbicide applications, cultivation, late May fire, or short-duration, high-intensity grazing throughout the growing season for 2 consecutive years. These disturbances reduce litter and open the site for establishment of other species. Filaree will invade from surrounding patches or become established from residual hardseed. Low levels of litter in summer and fall lead to filaree dominance within patches. Litter abundance is primarily a function of the intensity of herbivory during spring and early summer. Low litter cover increases soil temperature and seed germination with the first fall rains (Rice 1989). Timing of fall precipitation can also influence filaree composition. Early germinating rains followed by several weeks of drought favor filaree. Filaree is more tolerant of drought than annual grass and forb competitors because of the ability to rapidly elongate a tap root. Subterranean (Trifolium subterraneum) and rose clover

(*T. hirtum*) may partially replace filaree if medusahead control is followed by seeding these legumes. Application of phosphorus or sulfur increases the vigor and productivity of these annual legumes. Close grazing maintains legumes by reducing grass shading.

Transition 2—Filaree dominance is reduced as other species, especially annual grasses, successfully invade and colonize the patch from adjacent patches. Increased aboveground production and light to moderate herbivory increase litter during summer and fall resulting in decreased summer soil temperatures and reduced fall filaree germination. Increased litter also improves grass seedling survival by reducing desiccation. Regular or above-average rainfall through the fall and winter increases grass seedling survival. Application of nitrogen fertilizer may accelerate herbage production and litter accumulation if annual rainfall is between 15 and 30 inches. Shading by annual grasses reduces annual legumes, especially subterranean clover. Rose clover remains in the sward due to hardseed in the seed bank.

Transition 3—Annual plant dominance is seemingly irreversible. Purple needlegrass recruitment and survival is suppressed by intense competition with annual species and season-long herbivory. Germination of purple needlegrass is suppressed by moisture stress and high levels of litter (Bartolome and Gemmill 1981). Reversal may be possible with a high level of managerial control of season and intensity of grazing and periodic prescribed burning. Fire reduces litter and annual plant density (Zavon 1982). Heavy early spring grazing followed by late-summer burning increases the frequency of needlegrass seedling emergence and survival (Fossom 1990). Adequate rest between grazing periods improves needlegrass vigor.

Transition 4—Year-long continuous grazing, drought, and competition from annual species reduce needlegrass vigor and survival.

Transition 5—Filaree increases in response to low litter levels or early fall rains followed by several weeks without precipitation. Poor growing season production or heavy herbivory reduces litter levels. Long periods of inadequate rainfall within the normal growing season reduce grass as a component of the herbaceous composition.

Transition 6—Medusahead gradually increases in the patch. Plants produced from the postfire seedbank produce seed, increasing medusahead in the seedbank. Medusahead increases and dominates the patch and gradually invades adjacent patches if clay content of the soil is adequate.

Transition 7—Summer wildfire or controlled burning removes shrubs. Grazing and recurring fire maintain grassland.

Transition 8—Protection from grazing and fire facilitates shrub invasion. Shrubs become dominant in 10 to 20 years. Herbaceous understory declines as shrub canopy increases (Johnson and Fitzhugh 1990).

Transition 9—Drought, wildfire, controlled burning, or herbicides remove blue and interior live oaks leaving an open grassland dominated by annual species.

Transition 10—High density of annual plants suppresses oak seedling emergence and root growth. Competition for soil water with annual species contributes to the increased rate of blue oak seedling mortality (Gordon and others 1989). Blue oak savannas are believed to be more xeric today than during presettlement conditions due to high annual-plant densities and reduced litter associated with domestic livestock grazing (Welker and Menke 1990).

Transition 11—Same as Transition 3. Like purple needlegrass, oak recruitment and seedling survival is suppressed by competition with annual species.

Transition 12—Year-long continuous grazing and drought reduce needlegrass vigor and survival.

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JAPANESE BROME IN THE NORTHERN GREAT PLAINS

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ABSTRACT

Japanese brome (Bromus japonicus) is an alien annual grass that has become an important component of plant communities in the Northern Great Plains. This paper reports preliminary results of studies begun in 1990 examining the environmental effects on Japanese brome seed germination, effects of Japanese brome on western wheatgrass production, comparative herbage quality profiles for Japanese brome and western wheatgrass (Pascopyrum smithii), and effects of simulated grazing on herbage and root production of Japanese brome.

INTRODUCTION

Japanese brome (Bromus japonicus) is an alien annual grass that has become a dominant species of some mixed prairie plant communities in the Northern Great Plains (Haferkamp and others 1993; Whisenant 1990). Its life cycle is somewhat shorter in duration than coexisting perennial grass species such as western wheatgrass (Pascopyrum smithii). Further, as with all annual grasses, annual herbage production is erratic (Hull and Pechanec 1947). Moreover, when present on rangelands, Japanese brome plants may shift the period of peak forage production, causing an earlier decline in overall forage quality (Cook and Harris 1952). Thus, the presence of Japanese brome may negatively impact livestock production.

Perpetuation of Japanese brome on rangelands requires completion of the plant's life cycle beginning with seed germination, continuing through seedling emergence and establishment, and terminating with plant maturation and seed dissemination. Determining how environmental conditions affect the life cycle of Japanese brome plants and their interactions with other plant species is critical for development of grazing management strategies to both reduce the prevalence and efficiently use brome-infested rangelands. To develop a better understanding of these relationships, we began a series of studies in 1990. In separate experiments we examined (1) environmental effects on Japanese brome seed germination, (2) effects of Japanese brome on western wheatgrass production, (3) comparative herbage quality profiles of Japanese brome and western wheatgrass, and (4) effects of simulated grazing on herbage and root production of Japanese brome plants.

METHODS

Research was conducted on the Fort Keogh Livestock and Range Research Laboratory near Miles City, MT. Regional topography ranges from rolling hills to broken badlands with small intersecting ephemeral streams flowing into large rivers located in broad, nearly level valleys. Indigenous vegetation on the 55,000-acre research station is a grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*) mix (Kuchler 1964). Long-term annual precipitation averages 13.3 inches with about 60 percent received during the April through August period. Temperatures often exceed 100 °F during summer and decrease to -40 °F or less during winter. The average frost-free period is 150 days.

Germination

Incubation temperatures, collection dates, and postharvest storage and light conditions were varied so as to span a range of environmental conditions that might be encountered in the field. Seeds were collected in summer in Oklahoma and in summer, fall, and winter in eastern Montana. Summer collections were stored in a laboratory at room temperature. Fall and winter collections were divided into thirds and stored in either an unheated warehouse or a freezer, or ovendried at 115 °F for 6 to 35 days and then stored in a desiccator at room temperature.

Summer collections from 1990 and 1991 were initially incubated in a series of 55 constant and alternating temperatures ranging from 32 to 104 °F, which were divided into combinations related to selected seedbed environments (Young and others 1973). Tests were initiated about 6 months following seed collection, and four replications of 25 seeds of each collection were incubated for 4 weeks in closed dishes arranged in a randomized-block design. Seeds were considered germinated when the radicle was at least 0.2 inch long.

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Summer collections from Oklahoma and Montana and fall and winter collections from Montana were incubated in two temperature regimes beginning in January 1992. A warm regime consisted of 28 days with alternating 12-hour periods of 46 and 73 °F, and a cool+warm regime consisted of 10 days at 32 and 50 °F followed by 18 days at 46 and 73 °F. Light was provided by cool-white fluorescent bulbs during the 12-hour 50 and 73 °F temperature periods. The summer, fall, and winter seeds were also incubated at 46 and 73 °F in total darkness or alternating 12-hour periods of light and dark. Seed treatments were arranged in a randomized-block design with four to eight replications consisting of 100 seeds incubated in each dish. Seeds were considered germinated when the coleoptile and radicle were each at least 0.2 inch long.

Competition

Three treatments were applied in a randomized-block design with 10 replications at two locations. Japanese brome plants were left intact inside a 10.6-square-foot circle, a portion (about 50 percent) were removed, or all were removed. Weeding of plants occurred during late spring and early summer. In early July, biomass of western wheatgrass, Japanese brome, and all other vegetation was clipped at ground level inside a 2.4-square-foot circle located in the center of each plot.

Forage Quality

Replicated samples of Japanese brome inflorescences and herbage and western wheatgrass herbage were collected during June, July, and August 1990 and 1991 from pastures at Fort Keogh (Haferkamp and others 1993). Collected samples were ovendried, ground, and analyzed for nitrogen content and *in vitro* digestible organic matter.

Simulated Grazing

Japanese brome seedlings grown from seed were planted in greenhouse boxes in late winter. Clipping treatments were begun in late June 1991 and early May 1992 and continued for about 60 days. Plants were either not clipped (control) until the end of the study or clipped to a 3-inch or 6-inch stubble height every week or every 2 weeks. Treatments were arranged in a randomized-block design with five replications. All clipped herbage and remaining shoots were dried and weighed. At the termination of the study, roots were washed free of soil, dried, and weighed.

RESULTS

Germination

Mean germination for the 55 temperature regimes for Japanese brome was 71 percent (table 1). Over 95 percent of all temperature regimes supported some germination, and the mean germination for regimes where some germination occurred was 74 percent. Optimum germination, defined as germination not lower than maximum observed minus onehalf confidence interval at 0.01 level of probability, occurred

Table 1—Germination characteristics of Japanese brome seed
collected in eastern Montana in the summers of 1990-91

Characteristic	Percent and standard deviation ¹		
Mean of all regimes	71 (4.2)		
Mean of regimes with			
some germination	74 (4.3)		
Regimes with some germination	96 (1.4)		
Regimes with optimum germination	32 (8.0)		
Mean of optima	99 (1.1)		
Maximum germination	100 (1.1)		

¹Means and standard deviations are based on eight values.

in 32 percent of the regimes and mean of optima was 99 percent. The maximum germination was 100 percent.

Maximum germination of Japanese brome seed occurred in regimes representing moderate and cold seedbed conditions, with germination being somewhat depressed in very cold and warmer-than-moderate temperatures (fig. 1). Responses were similar between years and similar to those reported by Young and others (1984) for downy brome (*Bromus tectorum*). In those studies, seeds germinated best at coldfluctuating, fluctuating, and moderate seedbed conditions, and germination was depressed at very cold temperatures.

When summer, fall, and winter collections were compared, summer collections germinated rapidly to greater than 90 percent regardless of temperature (table 2). Fall and winter collections stored in the warehouse germinated greater than 70 percent in the warm regime, but germination was reduced to less than 20 percent in the cool+warm regime,

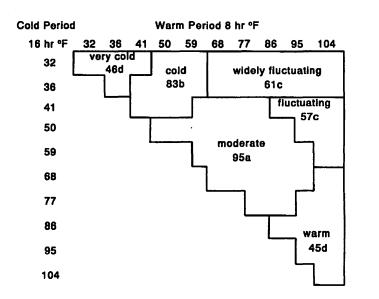


Figure 1—Seedbed requirements of Japanese brome seed collected in eastern Montana during the summers of 1990 and 1991. Means are based on eight values. Mean germinations followed by the same letter are not significantly different at the 0.01 level of probability as determined by Duncan's Multiple Range Test.

Table 2—Maximum germination in two temperature regimes for Japanese brome seed collected in Oklahoma and Montana in summer 1991 and in Montana in fall and winter 1991. Summer collections were stored in a laboratory at room temperature and fall and winter collections were stored in an unheated warehouse. Germination studies were begun in January 1992

	Oklahoma		Montana	
Temperature	July 7	July 12	Nov. 21	Dec. 30
	Percent			
32 and 50 °F + 46 and 73 °F	199	92	18	5
46 and 73 °F	100	100	88	71
		LSD _{0.}	₀₅ = 4.3	

¹Means are based on eight replications of 100 seeds.

suggesting these seeds may have entered a dormant state when incubated at 32 °F. Similar results were reported for downy brome seeds collected in Montana (Warg 1938) and Japanese brome seeds collected in Kentucky (Baskin and Baskin 1981).

When the presence of light was studied, we found darkness, as might be encountered under a dense litter cover, enhanced 7-day germination up to 35 percent, but light improved 28-day germination up to 31 percent, and wintercollected seeds were more sensitive to light than fall collections (figs. 2 and 3). If ovendried seeds are excluded, over 40 percent of the seeds collected in fall and winter and over 90 percent of summer collections germinated in darkness. Thus, it is apparent that seeds may germinate readily under a dense litter cover that restricts essentially all light and reduces moisture evaporation, as was suggested by Whisenant (1990). Care must be taken, however, when forming hypotheses relative to field germination and emergence, since the spectral composition of radiation incident on the seed can be affected by many factors such as time of day, seasonal meteorological conditions, snow cover, shallow burial in soil, and transmission characteristics of the overstory vegetation (McDonough 1977).

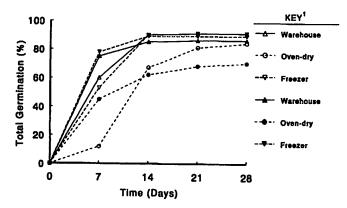


Figure 2—Germination of Japanese brome seed collected in November, stored in an unheated warehouse, ovendried, or frozen; and incubated in February 1992 for 28 days in a 46/73 °F temperature regime in darkness or with light for 12 hours at the high temperature. Means are based on eight values. Filled symbols represent the dark regime.

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Competition

In competition studies, trends suggest western wheatgrass production was reduced with the presence of Japanese brome, but the reduction was not statistically significant in 1991 (fig. 4). In 1992, standing crop of western wheatgrass was increased by total removal of Japanese brome, but not by partial removal. Total standing crop was significantly reduced during both years by an average of 284 pounds per acre at one location and 643 pounds per acre at the other by the total removal of brome.

Precipitation was probably the most important factor affecting the variation in western wheatgrass response in 1991 and 1992. Total precipitation measured on these sites during April, May, and June 1991 (13.2 inches or 203 percent of normal) was three times the amount received on either site in 1992 (4 inches or 62 percent of normal).

Forage Quality

Forage quality of Japanese brome varies with time and plant part. In early May, when inflorescences are emerged, crude protein concentrations in whole plants range from 12

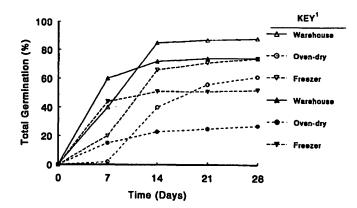
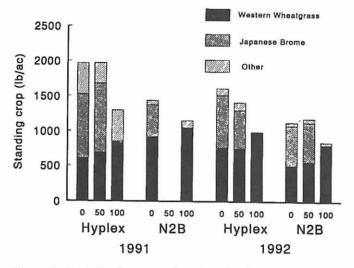
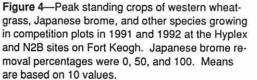


Figure 3—Germination of Japanese brome seed collected in December, stored in an unheated warehouse, ovendried, or frozen; and incubated in February 1992 for 28 days in a 46/73 °F temperature regime in darkness or with light for 12 hours at the high temperature. Means are based on eight values. Filled symbols represent the dark regime.





to 15 percent; concentrations in western wheatgrass plants range from 15 to 22 percent. Later in the growing season, intact inflorescences or seed heads are relatively high in quality, and may be higher or similar in quality to herbage of western wheatgrass (figs. 5 and 6). Herbage quality of Japanese brome, however, decreases from relatively high when plants are in the seedling stage to low when plants are mature.

The profiles of quality varied between the 2 years presented in figures 5 and 6. This phenomenon is generally related to the pattern of precipitation (fig. 7), with quality declining most rapidly as the soil dries and plants begin maturing. In contrast, during a cool-wet growing season, forage quality may remain high for longer periods as it did in 1991. For comparison, 9 percent crude protein is the suggested level for a 1,100-pound beef cow consuming 4.4 pounds forage per 220 pounds body weight with average milking ability during the first 90 to 120 days postpartum (National Research Council 1984).

Simulated Grazing

When plants in the clipping study remained vegetative, all clipping regimes or intensities reduced production of roots, herbage, and total biomass (fig. 8). Increasing the intensity of clipping significantly reduced herbage and total biomass, and although similar trends occurred with root biomass, differences were not significant. Increasing the frequency of clipping from every 2 weeks to weekly did not significantly reduce biomass production.

When plants produced reproductive shoots, increasing intensity of clipping significantly reduced total herbage weight, and reduced total biomass for all but the plants clipped to 6 inches every week (fig. 8). Root weights were similar for unclipped controls and both clipping frequencies at 6 inches, but weights were significantly less for plants clipped at 3 inches. Weight of inflorescences was

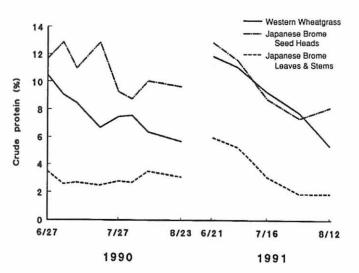


Figure 5—Percentage crude protein of Japanese brome and western wheatgrass plants growing at the N2B site on Fort Keogh. Means are based on 12 values.

greatest for unclipped controls. Frequency of clipping did not generally affect any component as much as intensity of clipping.

More than twice as much biomass was produced in the herbage and root components when plants remained vegetative rather than reproductive. When clipping was begun on vegetative plants, tillers averaged 23 per plant and increased to only 26 per plant by the end of the study. Tillers increased from 7 to 8 per control plant becoming reproductive during the study; they increased from 9 to 26 per clipped plant during the same period. Thus, plants remaining in the vegetative state continued to produce new

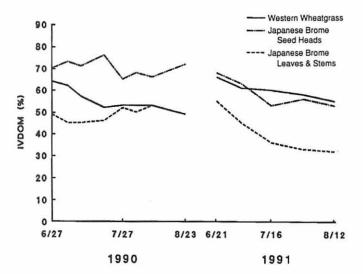


Figure 6—Percentage *in vitro* digestible organic matter of Japanese brome and western wheatgrass plants growing at the N2B site on Fort Keogh. Means are based on 12 values.

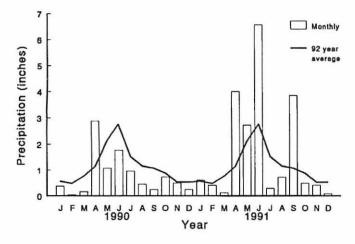


Figure 7—Precipitation recorded during 1990 and 1991 at Frank Wiley Airfield, Miles City, MT.

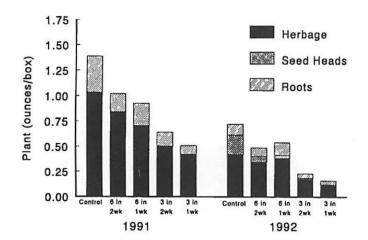


Figure 8—Weights of herbage, seedheads, and roots produced by nonclipped control Japanese brome plants grown in the greenhouse and plants clipped at 3 or 6 inches on a weekly or biweekly schedule. Means are based on five values.

leaves; plants that became reproductive responded to clipping by producing new tillers. Tiller production takes longer than leaf production, and would therefore result in lower yields.

CONCLUSIONS

The results of this series of studies are important because the characteristics of Japanese brome they describe indicate it may be a component of Northern Great Plains rangelands for years to come. Germination studies showed temperature is likely not a limiting factor for fall germination of Japanese brome seed disseminated in summer or fall. If soil moisture is adequate, high levels of germination will often occur during the initial fall period. This results in the emergence of a large population of Japanese brome seedlings that can overwinter and renew growth early the following spring. As with downy brome, complete germination of all seeds in one season is rare. Seeds that are not disseminated, or do not germinate in fall, overwinter and potentially enter a state of secondary dormancy, induced by imbibition of water at cold temperatures. Only a small proportion may germinate before the next fall when secondary dormancy is removed with the warm temperatures of summer.

The germination process appears to shift in response to moisture and temperature from one in which most seeds germinate at once to one in which seed germination is delayed with only a few seeds germinating at any one time. These processes result in a carry-over of a large number of viable seeds from year to year, complicating control of Japanese brome through conventional means. Japanese brome seed germination characteristics also aid its future invasion and perpetuation on rangelands in the Northern Great Plains.

Total standing crop was reduced consistently and significantly both years by removal of Japanese brome at both competition study sites. However, Japanese brome appears to have reduced production of western wheatgrass only when the supply of moisture was insufficient to meet the demands of both species. Thus, Japanese brome appears to be adding to the total forage base, and we can expect a short-term decline in forage production when it is absent. Quality of forage is relatively high when plants are immature or if we only consider inflorescences. Once plants mature and inflorescences are grazed, however, the remaining herbaceous component is of much poorer quality than western wheatgrass herbage. As the data show, the profile of forage quality varies with species and maturation, with the latter being controlled to some degree by the pattern of precipitation.

Although not examined in this study, Japanese brome competition may have a cumulative effect on western wheatgrass plants when encountered during a period of several years. In addition, western wheatgrass plants may respond to competition differently with or without clipping or grazing. Answering these questions will require additional research.

The clipping data suggest biomass production of vigorously growing Japanese brome plants can be reduced by frequent, intensive clipping. Thus, management of this annual growing on Northern Great Plains rangelands can impact the amount of forage produced. Effective control of Japanese brome will be more difficult, however, because some seed was produced even with severe treatments.

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LESSONS FROM 5 YEARS OF VEGETATION MONITORING ON THE NEVADA TEST SITE

Richard Hunter

ABSTRACT

In 1987 the U.S. Department of Energy began continuous monitoring on the Nevada Test Site to understand temporal changes in the distribution and abundance of plants and animals. The need to detect changes, as opposed to mere characterization, required careful parameter selection and permanent plots to distinguish spatial from temporal variation. Repeated measurements revealed errors and imprecision in relocating plants, which required changes in data collection and verification techniques. After several years it is obviously important to monitor not only changes, but causes of change. A requirement for records to be available over long time periods also poses problems of archiving and publication.

INTRODUCTION

In 1987 the U.S. Department of Energy (DOE) set up a long-term monitoring program for the Nevada Test Site (NTS) to monitor the flora and fauna. The stated goal was to maintain and update an understanding of the spatial distribution and changes over time of the flora and fauna on the NTS. That goal persisted until 1991 when "understanding" was changed to "record" in a belief that future monitoring efforts should have an exact record of procedures and results, in preference to interpretations of results.

The basic usefulness of monitoring is to warn of any changes that might have deleterious consequences. On the NTS, the program follows influences relating to human health, NTS land management practices and decisions, and legal proceedings relating to nuclear weapons testing and activities associated with testing. Flora and fauna monitoring focuses primarily on land clearing, because radioactive contamination on the NTS is too lowintensity to significantly affect plants and animals.

Legal Requirement

Monitoring by government agencies is required by the National Environmental Policy Act and the executive order implementing it: "...heads of Federal agencies shall: (a) Monitor, evaluate, and control on a continuing basis their agencies' activities so as to protect and enhance the quality of the environment." DOE order 5400.1 references many government orders, laws, and policies, and requires environmental surveillance of "air, water, soil, foodstuffs, biota and other media...." The objectives of environmental surveillance under 5400.1 are listed in table 1.

The NTS currently consists of about 3,500 km² (1,350 mi²), ranging in altitude from about 884 m (2,900 ft) in Frenchman Flat to about 2,556 m (7,400 ft) on Rainier Mesa. Vegetation at lower altitudes is Mojave Desert shrubland dominated by creosote bush (*Larrea triden-tata*), which gradually changes with altitude and latitude to a transition desert dominated by blackbrush (*Coleogyne ramosissima*), then to Great Basin Desert vegetation dominated by big sagebrush (*Artemisia tridentata*) and black sagebrush (*A. nova*), and above about 1,800 m (6,000 ft) to pinyon-juniper forest dominated by singleleaf pinyon pine (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) (fig. 1, Beatley 1976).

Historical Vegetation Monitoring

Botanists have studied the NTS since the late 1950's, when atmospheric nuclear weapons testing ceased. Goals varied, though most interest was focused on effects of testing (for example, Shields and others 1963). Beatley set up permanent plots where she measured densities and cover of annual and perennial plants from 1963 through 1975. In the 1970's the U.S. International Biological

Table 1—Objectives of environmental surveillance on DOE sites (DOE Order 5400.1)

Verify compliance with applicable environmental laws and regulations;

- Verify compliance with environmental commitments made in Environmental Impact Statements, Environmental Assessments, Safety Analysis Reports, or other official DOE documents;
- c. Characterize and define trends in the physical, chemical, and biological condition of environmental media;
- d. Establish guidelines of environmental quality;
- Provide a continuing assessment of pollution abatement programs;
- f. Identify and quantify new or existing environmental quality problems.

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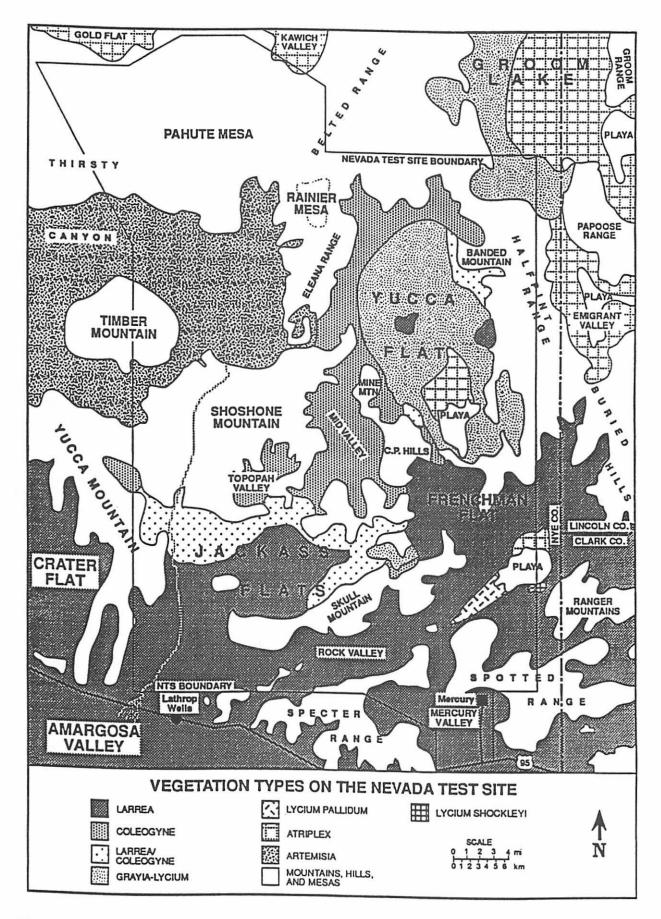


Figure 1-Vegetation types on the Nevada Test Site.

Program's Desert Biome collected data on Mojave Desert annual and perennial plants in Rock Valley. Many scientific papers have been published on the NTS biota by biologists working on these and several smaller projects (O'Farrell and Emery 1976).

The work that most closely approached a monitoring effort was the work by Janice Beatley on 68 plots. Her raw data are stored at the Desert Laboratory, University of Arizona, and can be used to determine annual plant population parameters for periods of more than 10 years at seven plots, and for 5 years at others. She published 1963-75 summary data for perennial population changes on plots grouped by vegetation "type" (Beatley 1979).

My goal for this paper was to provide information on potential problems in setting up programs for monitoring plant and animal populations. It is based on experience over the first 5 years (1987-92) of the NTS monitoring program.

METHODS

The Basic Environmental Compliance and Monitoring Program (BECAMP), set up by DOE in 1987, uses historical data and current measurements of plants and animals at specific sites to assess effects of DOE operations. Historical data include published reports (see O'Farrell and Emery 1976) and a considerable amount of raw data present when BECAMP monitoring began. Raw data were collected, microfilmed, and stored, and reprints were collected from libraries. Attempts were made to compare results from the first years of BECAMP data with historical measurements to detect significant changes in small mammal and plant populations.

Examination of local high-resolution maps enabled us to choose study sites where changes due to DOE activities were likely. These maps included fences surrounding radiation exclusion zones (areas of potential significant

Table 2—Extent of various disturbances on the Nevada Test Site, estimated from high-resolution maps

Disturbance	Percent of total area	Percent o disturbed area	
Burned, 1978-87	4.33	55.0	
Blast zones, 1950's	1.59	20.2	
Radiation exclusion	.57	7.2	
Drill pads	.36	4.6	
Paved roads	.27	3.4	
Subsidence craters	.25	3.2	
Pu contamination	<.18	<2.3	
Dirt roads	>.11	>1.4	
Facilities	.09	1.1	
Waste burial	.08	1.0	
Waste radex	.03	.4	
Tunnel radex	.02	.2	
Total	7.88	100.0	

human exposure), locations of drill holes for test emplacement, outlines of subsidence craters (resulting from underground weapons tests), and roads. The extent of range fires from 1978 to 1988 was estimated by the NTS fire department. Widths of paved and dirt roads were measured, and lengths estimated from maps. The extent of blast zones denuded by shock waves from aboveground tests was estimated from a published map (Allred and others 1963a). The extent of waste burial areas was reported by NTS' Low-Level-Waste-Management personnel. Hunter and others (1992) reported surface areas for these various disturbances (table 2).

The primary reasons for monitoring permanent plots were that they could be located at points of previous studies, they remove spatial variability, they allow efficiencies in work effort, and densities could be determined on plots, whereas techniques based on lines or points only provide relative values. Five permanent baseline plots (300 by 300 m) were set up in 1987 and 1988, and smaller plots were set up in particular disturbances to monitor recovery or changes associated with the disturbance. If possible, plots were set up at sites studied by earlier researchers, to provide historical continuity and to extend the time span monitored. Plots were marked with metal stakes covered by PVC pipe, with brass markers attached to the PVC. Their locations were surveyed by global positioning system equipment (GPS).

An attempt was made to monitor parameters that were not technique dependent. Largely nondestructive measurements were attempted for species composition and mean density, size, sex, or weight, but not for cover, frequency, diversity, or relative abundance. Confidence limits were calculated for each measurement. Estimates for cover and biomass of plants and such parameters as survivorship of animals were derived from primary data. We harvested 0.025-m² randomly placed quadrats for annual plants, made dimensional measurements of perennial plants in permanent belt transects, and made mark-recapture density estimates for lizards and small mammals on permanent plots. Cover and biomass were estimated assuming an ovate cylindrical shape for all shrubs and an experimentally determined regression of weight verses volume (Hunter and Medica 1989).

Certain species are too rare to sample on small plots, and too important to be ignored. Examples include desert tortoises (a threatened species since 1990), deer, and horses, as well as certain larger plants, in particular Joshua tree (*Yucca brevifolia*), Mojave yucca (*Yucca schidigera*), Utah juniper, and singleleaf pinyon pine. To monitor the status of those species we marked individuals and monitored growth, death, and health status at intervals of one to several years. We did not attempt to measure their densities, but did monitor their health status and threats to their health. Convenient, rather than random, populations were selected (generally on or adjacent to permanent baseline plots), and no specific attempt was made to study those species in relation to particular disturbances.

Common names for plant species follow Scott and Wasser (1980) and DeDecker (1984).

RESULTS

Differences in technique of the various NTS researchers were a significant hindrance to use of historical data. Only Beatley's annual data for Rock Valley have been used (Hunter 1990, 1991), and that was possible only for density. Sampling by Brigham Young University (BYU) at the Sedan event site provided data that could be used to calculate small mammal densities, although the authors refrained from doing so (Allred and others 1963b). Other researchers measured parameters like radionuclide content, trap success, or species composition. There were no density estimates of lizards in the historical record.

A comparison of Beatley's line intercept technique and BECAMP's belt transect shows how technique dependence can influence comparisons, and illustrates why technique continuity is so important for monitoring. To make this comparison, in 1989 we used both techniques to examine plant populations within Beatley's plot 3. A total of 335 m (1.100 ft) of line intercept (Beatley 1979) are compared to 100 m² of belt transect (following Hunter and Medica 1989). Summary statistics reveal sizable differences for mean height, percentage of the population, and percent cover (table 3). Mean heights (by species) were estimated to be larger by line intercept than by belt transect (paired t = 4.52, 10 d.f., p = 0.001). This occurs because plants are intersected by a line only when their bases are within one canopy radius of the line. Therefore, larger plants have a greater probability of being selected. Belt transects select all plants with bases within the area sampled, and are not biased toward large plants. Cover by belt transect was inflated because of the inability to correct for overlap in plant canopies. The "mean cover" for the line intercept technique is easily calculated by ignoring species, while "total cover" (table 3) includes overlap. One cannot calculate density for line intercept data (Beatley reported plants per 335 m of

line), and Beatley did not measure widths of sampled plants, so cover could not be derived from her size data as it is with belt transect data. Only carefully worded and vague comparisons, and no firm conclusions as to change in vegetation cover, density, or biomass could be drawn from use of the two techniques.

Determining the extent of disturbance by human activities and natural forces from maps proved very useful in siting study plots. Fires were a very significant disturbance (table 2), and were therefore given some priority in sampling effort. Plots were set up to sample each of the top six disturbances (table 2). Since the program started we ceased sampling the one radioactive plot, primarily because spatial variation in vegetative parameters surrounding the site prevented selection of a suitable comparison plot. We were, however, also unable to postulate any measurable effects of the contamination on that site, considering dose rates effects determined in previous NTS studies (French and others 1974; Kaaz and others 1971; Vollmer and Bamberg 1975). Sampling is still being carried out on burned areas, blast zones, drill pads, subsidence craters, and paved roads.

The value of separating spatial from temporal variability can be demonstrated with an analysis of variability of population densities on five transects within two 9-ha plots sampled in 1987. Not one of 10 common species' mean densities could be determined to within 25 percent by five transects (table 4). Numbers of randomly placed transects needed to detect density differences of 25 percent varied from nine to 964. Transects take two to four person-days each to measure, and considerably longer to analyze, and it was therefore impractical to try to reach even that level of precision by sampling random nearby points. This means there was no effective way to measure multiple random transects to monitor changes in plant density.

Species	Line intercept			Belt transect			
	%n	%с	ht	%n	%с	ht	
desert needlegrass	0	0	<u></u>	0.6	0.0	1	
Indian ricegrass	0	0	—	.6	.0	3	
desert globemallow	0.4	0.0	6	.6	.0	4	
Shockley goldenhead	1.3	.1	32	0	0	0	
bursage	39.3	11.4	39	48.3	10.9	30	
littleleaf krameria	1.7	1.7	44	1.2	1.3	32	
Mojave aster	1.7	.2	49	5.2	.3	27	
winterfat	.9	.1	50	3.5	.3	40	
spiny hopsage	7.4	2.0	56	5.8	1.5	51	
Nevada ephedra	13.5	4.6	58	15.7	6.4	43	
Anderson wolfberry	7.0	3.0	60	7.6	4.5	55	
Fremont dalea	.9	0.5	61	0	0		
common blackbrush	2.6	.6	66	1.7	3.2	64	
pale wolfberry	6.1	2.4	70	2.6	1.5	48	
creosote bush	10.0	6.8	109	5.8	12.8	81	
Total population	229				172		
Total cover	36.2%			42.7%			
Cover, no overlap	29.9%			29.9% —			

Table 3—Comparison of Beatley's line intercept and BECAMP's belt transect techniques. Line intercept overestimated percent of population (%n) and height (ht, cm) for large plants, and belt transects overestimated cover (%c)

Table 4—Average plant numbers per transect from five-replicate,
randomly placed $100 - m^2$ belt transects, and estimated
numbers of transects needed to detect a change in a
species' density of 25 percent at p = 0.05 (Bonham 1989)

	French	man Flat	Yucca Flat		
Species	Number	Transects	Number	Transects	
Shockley					
goldenhead	20.4	19	54.1	9	
bursage	35.2	36		-	
winterfat	7.8	335	63.8	20	
Nevada ephedra	.2	964	24.8	102	
spiny hopsage	2.8	79	34.8	22	
white burrobrush	41.6	29	23.6	123	
creosotebush	8.0	17	_	_	
Anderson wolfberry	1.8	250	7.8	185	
Indian ricegrass	5.1	45	14.1	77	

Temporal variability in plant numbers on a single transect was much lower than the spatial variability in density. For example, on one belt transect in 1990, 412 shrubs were found. In 1991, 395 (91 percent), or their remains, were identified. Only 17 (4 percent) could not be found. In addition, 35 more (8 percent) were found in 1991. Intrayear changes were largely due to difficulties distinguishing separate plants in clumps of similar individuals (ambiguous numbers), to inexact locations (tape placement), and ambiguous locations (inexact measurement). Of the 35 "new" plants, only three were considered seedlings in 1991 (table 5). Thus, we can define a species' density on one permanent transect to within a few percent, but with five transects density on randomly sampled areas could be defined to within a factor of 2 only for the most common species (Bonham 1989: 67-69).

The better precision with permanent transects therefore allows us to follow temporal trends that could only be guessed at with random sampling. Lacking random samples, however, inferences about the broader community cannot be made from permanent transect data, although differences between measured points can be tested with several statistical techniques.

When ambiguous locations were found to be a problem, several changes were made. In 1988 and 1989 plant locations were recorded to ± 25 cm from a steel tape, and within 1 m along the tape. After 1989, distances from the tape were recorded to ± 1 cm, and distances along the tape to the nearest decimeter. The center of the 50-m tape (25 m) was pinned by permanent lath stakes to prevent wind displacement. Plants just outside the edge of the belt were marked, and students measuring the plants were given data sheets generated from the previous year's data, forcing them to try to find each plant. Finally, data from each transect were checked in the field by senior personnel before the data were analyzed. The increased precision is evident in table 5 for the 1990-91 period.

Beatley divided NTS vegetation into "plant associations" defined by the dominant species (for example, pinyon-juniper, *Larrea-Ambrosia*, *Grayia-Lycium*, fig. 1). I examined the distribution of species abundances within five transects located within 300 m of Beatley plot 46 and found they differed significantly by chi-square analysis $(\chi^2 = 253, d.f. = 28, p << 0.001)$. For practical purposes, therefore, measuring the status of an "association" was not considered a goal when setting up the BECAMP monitoring program. Our intent was to measure the status of individual species. We do, however, measure community components (densities, sizes by species), which we presume will allow significant changes to be detected.

DISCUSSION

Hard lessons are embodied in some of the foregoing experiences. The inability to make significant use of the relatively extensive history of biological research on the NTS was not expected, nor were the problems with precision in the perennial plant measurements. Spatial variability in plant species distributions was only guessed at prior to the first analysis of replicate transects. The tentative solution of use of permanent plots or transects is unsatisfying because by aiming at good temporal trends we have eliminated the possibility of measuring spatial distribution, except on a superficial level.

There are some obvious but nevertheless important conclusions to be drawn for others who might be in the initial stages of long-term monitoring programs. It is important to carefully pick parameters to be measured. Some good recommendations have already been made, such as monitoring all trophic levels in an ecosystem (Bruns and others 1991; Wiersma 1990), but such recommendations are divorced from fiscal concerns. I believe it is important to measure absolute rather than relative parameters, because techniques continually change, hopefully improving. We are currently considering changes in trap design, and wider use of GPS for locations. Hopefully, changing traps will not change mark-recapture density estimates, and GPS locations will be accurate enough to compensate for future loss of some plot boundary markers.

"Disturbances" (table 2) that were used to set priorities for plot selection do not include general ones such as air pollution, climate change, grazing, and introduced

Table 5—Reasons for inability to match plants from one transect with the same plants in the previous year's data

Symptoms	1989-90	1990-91	
Plants matched (live and dead)	177	396	
Matched but ambiguously alive	39	13	
Plants that disappeared	8	5	
Tape placement-edge plants			
not measured	26	0	
Ambiguous number of individuals	66	2	
Ambiguous locations	18	0	
Plants missed year 1, present year 2	55	20	
Plants missed year 2, present year 1	15	0	
Mismeasured or misrecorded	10	0	
Misidentified species, year 1	19	3	
New small plants, probable seedlings	15	3	
Totals	446	441	
Percent successfully matched	48	93	

species. Although baseline plots are being affected by these influences, the absence of "controls" is another source of discomfort. How can we isolate the effects of, for example, a 2-degree temperature rise, from concurrent fluctuations in precipitation or increased competition for water due to new species introductions?

Over the first 5 years of monitoring there were changes in all of the populations measured. Drought appeared to cause most changes, but grass and shrub populations on denuded areas were slowly recovering, north- and southfacing slopes of subsidence craters were changing, the species mix of annual plants was changing, and small mammals located near roadsides appeared to be reproducing better than controls. Monitoring was thus detecting change, but one is then led to ask, what was causing these changes? More important, are we collecting evidence that can allow us to choose between, for example, predatorprey interactions and disturbance effects on lizard populations? Answers to those questions posed by the results of monitoring will probably have to be based on shorter term research projects. Thus, a monitoring program should plan to include some mechanism for funding and performing research on ecosystem processes and responses to disturbance.

Finally, the preservation of data and results is an unsolved problem. We produce an annual summary report, which is published as a government document (for example, Hunter and Medica 1989). Data from the NTS will also be archived. Nevertheless, knowledge of the data's existence is liable to depend on publication of selected results in refereed journals.

ACKNOWLEDGMENTS

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ECONOMIC FACTORS FOR CONSIDERATION IN CONVERTING ANNUAL GRASSLANDS TO IMPROVED RANGELANDS

Neil R. Rimbey

ABSTRACT

Economic feasibility analysis has become a critical element in most land treatment projects. This paper details and compares three methods of economic efficiency analysis applicable to annual grasslands situations. In addition, comparisons of results of the analyses are made with recommendations on uses of the techniques. Factors besides livestock forage and wildlife habitat influence improvement decisions. Several of these are detailed, with suggestions made for integrating these into economic efficiency analysis.

INTRODUCTION

The purposes of this paper are to provide range management professionals with a discussion of the theory of economic analysis of range improvement, detail why economic analysis is necessary, and provide an explanation of three methods of analysis. The paper also presents some of the other factors (amenities, nonmarket goods, and risk) that must be considered in any analysis of range improvements.

WHY ECONOMIC ANALYSIS?

Several factors have resulted in range professionals becoming involved in the mundane task of economic analysis of rangeland improvements. The mounting Federal deficit and resulting concerns about government spending have raised the issue of deficit spending throughout most units of government. Concerns about the costs and returns of the Federal grazing programs have emerged as part of this national debate. In fact, the recent update of the 1986 Grazing Fee Review and Evaluation (USDA and USDI 1992) reports that 1990 range management costs amount to \$3.21 per animal unit month (AUM) for grazing administered by the Bureau of Land Management (BLM), U.S. Department of the Interior, and \$3.24 per AUM for areas operated under Forest Service (FS), U.S. Department of Agriculture, jurisdiction. From these figures, one can infer that BLM is spending \$2.41 per AUM for each \$1 received from grazing, while the FS is spending \$3.38 per AUM for each \$1 received. Within this

Paper presented at the Symposium on Ecology, Management, and Restoration of Intermountain Annual Rangelands, Boise, ID, May 18-22, 1992. Neil R. Rimbey is Professor and Extension Range Economist, Depart-

ment of Agricultural Economics and Rural Sociology, University of Idaho, Moscow, ID 83843. Stationed at Caldwell Research and Extension Center. same context, range improvement costs amounted to \$1.13 and \$0.79 per AUM for BLM and FS, respectively.

An issue related to deficit spending that also bears mentioning is the inflation of improvement costs and the impact on improvement projects. We have seen substantial increases in improvement material and machinery costs over the past 20 years. The shortages of petroleum products, which first became apparent in the crises of the mid-1970's, dramatically increased petroleum and petrochemical costs. This created a "double-whammy" for traditional rangeland improvement practices. First, input costs for herbicides, fertilizers, and other direct inputs for projects such as brush control were extremely high. Second, "support" inputs such as labor and tractor and airplane fuel increased the operation costs of equipment used in these types of projects.

Over the same period of time, appropriations for range improvements within the Federal agencies' budgets have shown some increases. However, actual declines in these appropriations have taken place since the early 1980's (fig. 1).

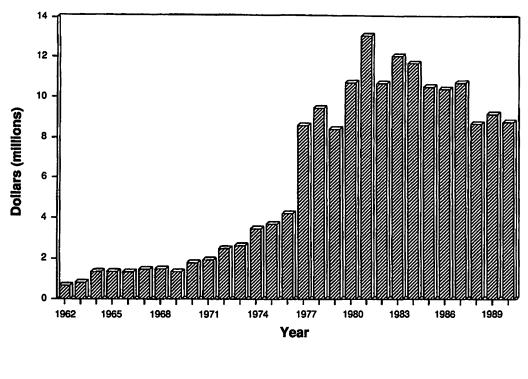
The ultimate impact of these factors has been a dramatic decline in rangeland improvement practices. Figure 2 depicts acres of rangeland seeding projects undertaken by Idaho BLM, by year, since 1960. Recognizing that these projects fluctuate with funding and need, it is still readily apparent from this graph that the general trend is downward.

With limited budgets and concerns about spending and subsidization, the role of economics has become more important in the analysis of range improvements. The issue has thus become, "How can we get the biggest bang for our limited range improvement dollars?" Economics can provide range managers with answers to these types of questions, should they decide to use the tools.

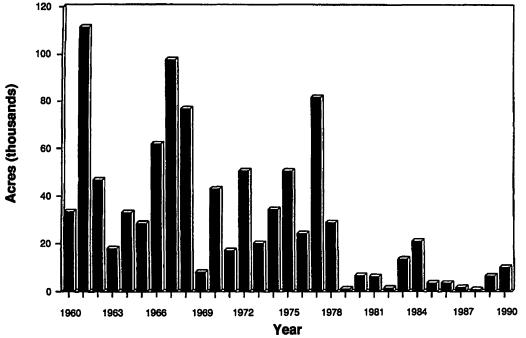
HOW TO DO ECONOMIC ANALYSIS?

Most rangeland improvement projects involve some upfront investments of labor and capital with benefits accruing over a period of years. The usual question posed by range managers is: "Will this pay?"

To answer this critical question, it is necessary to quantify the benefits and costs associated with specific practices and bring all dollar costs and returns into the same timeframe for analysis. It is imperative that the analyst discount future benefits and costs back into today's dollars. Dollars received or spent 20 years from now are not equal to today's dollars. If one wants to have \$5 for a party that will occur 6 years down the road, he or she only









needs to put \$3.52 in the bank today at 6 percent annual interest. In other words, the present value of \$5 that we will receive 6 years from now is only \$3.52 in today's dollars. This concept is known as the time value of money (Nielsen 1984; Workman 1986). Time is a critical component in analysis of range improvements. Benefits coming back from range improvements 20 years from now are heavily discounted. A dollar's worth of benefits received in the year 2012 are only worth about 31 cents in today's terms (again, discounted at 6 percent).

All of the economic efficiency measures covered in the following section are derived using the concept of present value. In other words, the streams of benefits and costs are all discounted back to today's dollars. This is done using the following equation:

$$PV = \frac{Vn}{(1+i)^n}$$

where: $PV = \text{present value}$
 $Vn = \text{dollar value in year } n$
 $i = \text{interest or discount rate}$
 $n = \text{year.}$

The present value of \$3.52 was calculated for the \$5 that one receives six years from now at a 6 percent discount rate using the formula.

MEASURES OF ECONOMIC EFFICIENCY

The following discussion of measures of economic efficiency is all seated in the discounting process and formula just discussed. Each measure relies on the concept of discounting, with variations in the final calculation of efficiency measures.

The range improvement analyst must first develop estimates of the annual benefits and costs over the life of the project. The annual values are then discounted to derive present value. The streams of discounted benefits and costs are summed. Efficiency measures are then calculated using the following methods.

Benefit/Cost Ratio

A common investment analysis tool is the Benefit/Cost Ratio (B/C). This efficiency measure is calculated by taking the ratio of the sum of discounted benefits to the sum of the discounted costs. In other words, discounted benefits are divided by discounted costs. The investment opportunity is deemed efficient if the ratio is greater than 1.

Net Present Value

Net Present Value (NPV) is the difference between discounted benefits and discounted costs, or discounted benefits minus discounted costs. The investment is efficient if the difference is greater than zero.

Internal Rate of Return

Internal Rate of Return (IRR) is the discount rate that equates the sum of discounted benefits to the sum of the discounted costs. IRR indicates the annual rate of return on an investment in rangeland improvement. In efficiency terms, the higher the calculated IRR, the better the investment opportunity. Uses of this efficiency measure may be most applicable in private investment decisions. For example, comparisons can be made between IRR and the interest rate on borrowed capital. An IRR of 15 percent may look quite favorable in relation to current interest rates of 7 percent.

Workman (1984) provides a discussion of the uses and misuses of these efficiency measures and some of the inconsistencies of the different measures. He concludes that NPV should be used as the "exclusive criterion" when choosing between two alternatives. B/C should be used to rank alternatives in attempting to select the optimum combination of projects, with NPV "side calculations" performed to verify the accuracy of the combinations. Workman also suggests that IRR has more application in private land range improvement analysis, where comparisons between the IRR and interest rates on borrowed capital are critical factors.

OTHER FACTORS

Traditionally, rangeland improvement projects have included the value of increased livestock forage as the only quantifiable benefit in the analysis. Recent concern for some of the other factors impacted by rangeland improvements has created some analysis problems for the range professional. There has also been an apparent shift in agency priorities away from the traditional "commodity" programs to factors such as recreation, amenity values, biodiversity, and others.

Options for valuing benefits from market commodities such as livestock forage are fairly straightforward (Wagstaff and Pope 1987; Workman 1986) and should pose very few problems for the analyst. However, attempting to value some of the other factors raises some new issues and problems.

Wildlife numbers have increased dramatically in Idaho and other Intermountain States (Nielsen and McBride 1989; Rimbey and others 1991). With this we are also seeing increased recreational opportunities and associated consumer spending. Opportunities to include wildlife benefits in economic analysis of range improvements are present in most range improvement projects. Research in Idaho (Donnelly and Nelson 1986; Donnelly and others 1985; Sorg and Nelson 1986; Sorg and others 1985) has derived willingness to pay and contingent value estimates of wildlife-based economic values for inclusion in range improvement analysis. These estimates were derived on a species basis and provide an estimate of hunters' and other recreational users' willingness to pay for access to increased numbers of these species. However, one should realize some of the issues and problems in including these in range improvement analysis. There is no direct tie to a market system for use in validating these values of wildlife resources. Questions to ponder include: "What's an additional antelope worth?" "What's an inch of topsoil on this site worth?" "What's this view worth?" They must be answered before including amenity values in the economic analysis of rangeland improvement. In terms of competition for limited forage or habitat (for example, livestock versus wildlife), there are some issues of "apples and oranges" of livestock and wildlife values that need resolution before informed policy decisions can be made.

Similar issues are present in attempting to value other resource values such as erosion control, water quality enhancement, biodiversity, and others. Some peoples' perspective of biodiversity is to add forbs to a seeding mix. From one economist's perspective, the value of biodiversity must more than cover the increased costs of short-lived forbs included in the seeding mix. How do you place an economic value on biodiversity?

Opportunities do exist for valuing some of these other factors in the annual grassland areas of the Intermountain region. Fire danger is an excellent example of one of these. BLM records for Idaho (USDI/BLM) reveal some interesting facts relative to fire rehabilitation costs. Over the last 6 years, there have been 149 fire rehabilitation projects in Idaho. Funding for these projects has amounted to \$9.4 million since 1985. Average annual expenditures amounted to \$1.5 million, or \$63,000 per project. It would appear that there is an excellent opportunity to use these types of figures in conjunction with some fire frequency and probability work to derive estimates of the "cost of doing nothing" to slow the invasion of annual grasses.

Risk is inherent in most activities of our lives. Risk also impacts range improvement decisions through factors such as weather, seeding or improvement technology, and market changes. Bernardo and Engle (1990) provide an assessment of the impacts of private land manager attitudes toward risk on range improvement decisions. In other work, Bernardo and others (1988) concluded that a range improvement practice (prescribed fire) was a risk-reducing practice. From the range practitioner's perspective, consistency in the analysis should be the goal. If risk considerations are included as a cost in the analysis, do not also reduce the benefit side of the analysis by the same risk factor.

SUMMARY AND CONCLUSIONS

This presentation has detailed some of the basis for economic analysis for range improvements, some of the methods available to range managers, and some of the other factors to consider in the analysis. In addition, there are several suggestions that will help with these analyses on annual grasslands. Conflicts in goals of the actors in the management process were fairly obvious during the course of the conference. Are annual grasslands a problem or a solution? Presentations relating to the positive value of cheatgrass as livestock forage conflicted with presentations relating the danger associated with annual grass invasions.

These conflicts must be resolved before consideration of rangeland improvements is undertaken. Seedings may be a benefit in some peoples' eyes and a cost to others. The era of throwing money at problems in hopes that they will fix themselves appears to be over. Limited funding should be spent only on projects where a broad spectrum of support and commitment is present. This implies some type of cooperative management process to determine group goals and objectives for an allotment, to which economic analysis of range improvements is one piece of the puzzle.

Economic analysis of range improvements must be done BEFORE the projects are undertaken. Use the analysis as a tool in making management decisions, not as justification for what was done. Allocation of scarce range improvement funding can only be done efficiently with the use of economic analysis. The goal of range managers should be to achieve the biggest bang for the limited funds available.

Economic analysis must be consistent. Do not reduce benefits to account for nonuse or risk of failure and also include these factors as a cost.

Finally, in terms of conversions of native vegetation to annual grasslands, there appears to be an opportunity for estimating a site-specific "cost of doing nothing" factor for inclusion in economic analysis. Probability theory and fire frequency and danger may form the basis for some future work in this area that will hopefully provide range managers with another tool for use in improvement analysis.

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CAN ANNUAL RANGELANDS BE CONVERTED AND MAINTAINED AS PERENNIAL GRASSLANDS THROUGH GRAZING MANAGEMENT?

Kenneth D. Sanders

ABSTRACT

Essentially three options are available for the management of annual rangelands: (a) management as an annual rangeland; (b) conversion to a perennial rangeland through grazing management; and (c) conversion to a perennial rangeland by reseeding. The second option is most desirable—if it is feasible. Evidence suggests that annual rangelands in higher precipitation zones can be converted through grazing management, providing there are sufficient perennial plants present as a seed source. However, in the drier annual rangelands, the preponderant evidence indicates little chance of conversion through grazing management.

INTRODUCTION

Cheatgrass (*Bromus tectorum*) and medusahead (*Taenia-therum asperum*) dominate several million acres of rangelands in southern Idaho and adjacent States. There are also millions of acres of annual grasslands in California. Much of this area has been dominated by annuals most of this century. Many rangeland management plans in effect in Idaho have the objective of improving low-seral range (cheatgrass) to high-seral bluebunch wheatgrass (*Elytrigia spicata*) or *Stipa* sp., etc., in a few cycles of a grazing system, with, of course, a 30, 50, or 70 percent reduction in livestock numbers. Is this a realistic objective?

SEVERAL VIEWS

In describing the valley grasslands of California, Heady (1977) stated that ecologists should recognize that species labeled as "introduced" and "alien" cannot be removed and perhaps not even reduced from their present state under any known rangeland management practice. Laycock (1991) discussed the concepts of stable states and thresholds of range condition on North American rangelands. Although not new concepts, they have only recently received much attention in U.S. range literature and discussions. Laycock points out that it is important for range managers to recognize that multiple steady states exist for many vegetation types, such as cheatgrass rangelands in southern Idaho. Under our current range condition model, many assume that a reduction in grazing pressure and improved grazing management will result in range improvement. However, in a stable lower successional state, range condition normally will **not** respond to change in grazing or even to no grazing. Friedel (1991) suggested that once a threshold is crossed to a more degraded state, improvement cannot be obtained on a practical time scale without a much greater intervention or management effort than simple grazing control.

Using the California annual grasslands as one example, Johnson and Mayeux (1992) offer the viewpoint that no special significance should be attributed to the label "native" when looking at ecological plant performance. They suggest the evidence they present is "contrary to a common assumption that the dominance of undesirable plants on rangelands always serves as evidence of overgrazing by livestock and that an elimination or reduction in grazing pressure will result in the reduction of undesirable species and a return to 'climax' species composition."

In the higher precipitation zones (14 inches plus) in the Intermountain Region, there is some evidence that cheatgrass rangelands can be reclaimed by native perennial grasses, providing there is a seed source. Even in this precipitation zone, my personal observation has been that the conversion seldom occurs without some means of reducing the annual grass competition (herbicides, fire, heavy spring grazing). There is little evidence that annual rangelands below 12 inches precipitation can be successfully converted to perennial grasslands through grazing management alone. Laycock (1991) and Heady (1977) both point out that there is no known grazing system that will accomplish this feat alone. In fact, failure is more the rule than success in converting cheatgrass rangelands in southern Idaho to perennial grasses, even when burned and seeded to competitive grasses such as crested wheatgrass (Agropyron desertorum, A. cristatum).

Why is it so difficult to convert annual grasslands to perennial grasslands? Laycock (1991) gave the following reasons for "suspended stages" such as cheatgrass rangeland: dominance by a highly competitive species or lifeform; long generation times of the dominant species; lack of seed or seed source; specific physiological requirements that limit seedling establishment except at infrequent intervals; climatic changes; restriction of natural fires or increase in frequency of fires; and others.

In his presentation on medusahead, Dr. Min Hironaka stated that squirreltail grass (*Sitanion hystrix*) is the only native perennial grass he knows of that can compete with medusahead (see Hironaka, these proceedings). Hironaka and Tisdale (1963) studied the Piemeisel exclosures in

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southern Idaho. While they found squirreltail possessed the ability to convert cheatgrass ranges to a perennial cover, conversion requires (1) an ample and mobile seed supply of the perennial species; (2) that the perennial species have an inherent ability to withstand cheatgrass competition as a seedling; and (3) that the perennial seedlings be protected from damage by rabbits as well as livestock. I would add to that list protection from insects such as grasshoppers.

THE OPTIONS

Essentially three options are available for managers of annual rangelands: (a) management as an annual rangeland; (b) conversion to a perennial rangeland through manipulation of grazing management; and (c) conversion to a perennial rangeland by reseeding. The first option is ecologically unacceptable to some and provides a less reliable forage base. The third option may not be economically feasible and is sociologically unacceptable to some if introduced species are used. Most users and managers of annual rangelands would opt for conversion to perennial rangelands if ecologically and economically feasible.

The question is—under what condition is it reasonable to expect to convert an annual grassland to a perennial grassland in southern Idaho? There is no magic formula to answer the question, but I will make the following suggestions. First, get as many knowledgeable people together as you can, including the livestock permittee(s), get out on the site to be discussed and make a group decision.

In the 14-inch and above precipitation zones, you might consider trying to convert to a perennial grassland through grazing management alone, such as a rest-rotation grazing system, if the following conditions are met: (1) an adequate seed source of the desired perennial(s); (2) no large populations of rabbits, grasshoppers, or Mormon crickets; and (3) no extended drought. Do not expect the conversion to occur in just a few years.

Below the 12-inch precipitation zone, either (1) manage as an annual rangeland and quit worrying about using only 50 percent of the current year's growth; or (2) burn, spray, or disk in the fall, reseed with Hycrest crested wheatgrass (don't waste money on anything else) and hope for a wet spring.

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CHEATGRASS, LIVESTOCK, AND RANGELAND

F. H. Tipton

ABSTRACT

The T Quarter Circle Ranch, located at Winnemucca, NV, is an extensive cattle ranching operation where innovative approaches to management have been developed and applied. The ranch operation features winter grazing on desert ranges where cheatgrass (Bromus tectorum) is an important component of the forage base. Ranch management is based on optimizing direct livestock harvesting of forage, with minimum labor and capital requirements for hay production. The basic concept is to manage with cheatgrass, but not for cheatgrass.

INTRODUCTION

The T Quarter Circle Ranch is located near Winnemucca, NV, and utilizes open range that includes both public and private land. The elevation at the ranch headquarters, located on the Humboldt River, is 4,200 feet with some ranges extending up to 8,500 feet.

The ranch is a cow/calf operation. The annual grazing cycle consists of cows being wintered on the desert ranges of valley floors and lower foothills from October to early May. The cattle are moved into higher elevation ranges where they graze until midsummer. Summer gathering of the stock results in the last of the cows reaching the meadows along the Humboldt River in late August.

Cattle graze the meadows in a rotational grazing system until after Labor Day. They are then moved to meadows that have been windrowed. The windrowed hay allows the cattle high-quality forage into the early fall. Hay for winter feeding of bulls and replacement heifers is produced in improved fields rather than native hay meadows.

Marketing begins with the calves in early September and finishes with the final weaning and culling of the cow herd in late September. At this time the cow herd is ready for the winter range.

WINTER GRAZING

As with all winter outfits it is very important that the cattle are in condition to head back out on the range. Our system does not allow us to control our bulls in the spring breeding season as well as some operations, so we take our bulls out of the cow herd for the months of September through November. This ensures that we will not get very many calves in the months of June through August. This system prevents cows with calves being turned out on the winter range in October. Dry cows in good condition and pregnant winter well on the desert. Pregnant cows with suckling calves do not do well on these winter ranges. Fall-calving cows winter well as long as they are in good condition at the time of calving.

DISTRIBUTION CONTROL

We have few fences on our allotments; even allotment boundaries are not fenced. The presence or absence of stock water is utilized to control cattle distribution.

Cattle distribution is additionally enhanced by behavioral training of replacement heifers that are raised on the range. They learn to utilize the available forage and browse sources of various range communities on a seasonal basis. This includes the utilization of saltbush (Atriplex) fruits for a digestible protein source during the winter and Indian ricegrass (Oryzopsis hymenoides) seeds retained in inflorescence as energy sources. Replacement heifers have to learn to use cheatgrass as a forage source on the winter ranges. Cheatgrass is extremely important to the well being of the wintering cow herd. Cows and subsequent replacement heifers that have been behaviorally conditioned to these arid ranges become very adept at utilizing appropriate forage sources. In these relatively low-elevation arid environments the caryopses do not entirely disperse from the cheatgrass inflorescence. When the cows are turned onto the desert winter ranges in October they readily utilize cheatgrass heads. The total digestible nutrients of these seed heads is higher than the herbage of Indian ricegrass or needle-and-thread (Stipa comata).

Cows move through cheatgrass stands and utilize the seed heads first. In early November they began to utilize the top portion of the dry herbage. As cool temperatures of early winter settle in the desert, the cows begin to utilize browse and mature fruits from fourwing saltbush (*Atriplex canescens*), shadscale (*A. confertifolia*), black and Bailey greasewood (*Sarcobatus vermiculatus* and *S. baileyi*), and the browse of white sage or winter fat (*Ceratoides lanata*). During the winter the cows appear to be utilizing the cheatgrass herbage as bulk in their diet.

In early spring the cattle switch their diet to the first species that become green and initiate growth. The first grasses to be utilized are the ephemerals, squirreltail (Sitanion hystrix) and Sandberg bluegrass (Poa sandbergii). These native perennials initiate growth before the winter rosettes of cheatgrass initiate growth and become grazable. Once cheatgrass grows enough, so cattle can utilize the herbage, grazing preference switches to

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this species. On desert ranges the cattle follow the growth of cheatgrass up slope into the foothills.

The nutritional status of cows on the range can be judged by watching the moisture content of their manure. On these desert ranges, as moisture content of manure noticeably drops, the cows will be moving to a new forage source.

WILDLIFE ASPECTS

Cheatgrass on the ranges of the T Quarter Circle Ranch is important to wildlife. Chukar partridges (*Alectoris chukar*) utilize cheatgrass seeds throughout the winter, and also utilize the green coleoptiles of emerging cheatgrass plants when they are available. Mule deer (*Odocoileus hemionus*) use seed heads of cheatgrass in the same manner as cattle. Deer utilization of seed heads appears to start about 2 weeks before utilization by cattle.

WILDFIRES

Portions of the T Quarter Circle's range have burned several times in wildfires in the last 2 decades. About 40 percent of the entire range has burned. Initially, most of the secondary succession after the fires was dominated by cheatgrass. Perennial grasses have increased on many of these burned areas, as shown by precise condition and trend studies sponsored by the T Quarter Circle Ranch and conducted by a private consulting firm.

I feel this increase is a result of careful management of the grazing resource that made cheatgrass the bulk of the forage, while favoring perennial plants for seed production and subsequent seedling establishment. The key to this management is to have enough flexibility to permit winter grazing. Over the time span of a decade there will be more years that favor perennial seedlings than there will be years that favor cheatgrass.

INSECT PREDATIONS

Wildfires are not the only natural disturbance that influences T Quarter Circle rangelands. The western army cutworm (*Euxoa auxiliaris*) has occurred in large numbers for the past several years and has been very destructive to herbaceous seedlings. Mature perennial herbaceous species recover from cutworm damage. Large-scale Mormon cricket (*Anabrus simplex*) outbreaks have occurred, and several different species of grasshoppers (families Tetrigidae, Acrididae, or Tettigoniidae) can become sufficiently abundant to damage forage production.

All of these types of disturbance affect the operations of the ranch and the successional status of the range resources. They have to be accounted for in management plans.

RANGE SITES

Basin big sagebrush (Artemisia tridentata ssp. tridentata)-dominated plant communities occur on soils associated with the lake plains of pluvial Lake Lahontan on the T Quarter Circle ranges. These range sites have many unique characteristics compared to normal upland big sagebrush environments. There is often little herbaceous fuel in these lake plain sagebrush range sites and wildfires occur infrequently in comparison to upland sites. Cheatgrass may be largely excluded from these sites by the soluble salt content of the soils.

A band of moving sand dunes some 80 miles long and 10 miles wide is moving across T Quarter Circle rangelands. The dunes are high enough to cover windmills, and are moving fast enough from the southwest to the northeast that line cabins buried early in the 20th century are just emerging. The dunes apparently were an ancient delta of an antecedent Humboldt River. Where these sand fields move into the foothills, range sites are rich in species diversity and productive in forage. Indian ricegrass, needle-and-thread, and fourwing saltbush are the major forage and browse species. Cheatgrass is not adapted to these productive sand field sites and does not become a factor in their management. The unique seedbed requires species adapted to the continual moving sand and may preclude cheatgrass.

Even more subtle in upland situations are site-specific differences that control the distribution and production of cheatgrass. Sites with the greatest potential seem to recover from disturbances more quickly than shallow-soiled, more erodible sites. Cheatgrass cover on the poorer sites may be protection from accelerated erosion.

MARGIN OF SALT DESERTS

Perhaps the area of greatest ecological significance for cheatgrass on the T Quarter Circle Ranch is on the margin of salt-desert environments. This is a type of environment that Dwight Billings (see these proceedings and Billings 1945) described as too dry for the growth of big sagebrush, but with soils not influenced by appreciable amounts of soluble salts. This is an area where only recently cheatgrass has become an abundant species (Young and Tipton 1990).

The potential plant communities appear to be dominated by shadscale and Bailey greasewood with a sparse understory of squirreltail and occasional perennial forbs. At infrequent intervals, native herbaceous annuals grow and flower in these communities in response to aboveaverage winter and spring precipitation. Cheatgrass invasion has brought two things to this environment: (a) greater forage production than existed under pristine conditions, and (b) the potential for stand renewal by burning in wildfires.

MANAGEMENT OF CHEATGRASS RANGES

It requires more effort and skill to correctly manage cheatgrass than perennial bunchgrass ranges. Cheatgrass management requires fuel management because of the higher incidence of wildfires. Stocking rates and the season of use are very important on these ranges whether they are grazed in the spring, fall, or winter. It is hard for modern range managers to understand that heavy use of cheatgrass may be the correct management. Conversely, rotational grazing systems with rest periods designed in the system favor cheatgrass at the expense of perennial seedlings, as well as violating basic sense in fuel management. When shrub ranges with cheatgrass understories are burned in wildfires an ecological window opens that permits seeding of desirable perennial species. While these seeded areas are being given a chance to establish, alternative forage can be obtained by heavily grazing cheatgrass-dominated areas. With uniform pastures, and adequate fencing and water distribution, flash grazing or intensive short-term rotational grazing may reduce cheatgrass and favor perennial vegetation.

It has long been known that cheatgrass forage production varies from season to season depending on precipitation. I have found on the T Quarter Circle that elevational differences and geographic differences on a ranch of this size usually result in sufficient cheatgrass production and that it is a significant part of the forage base.

I like to characterize our management system on the T Quarter Circle Ranch as managing with cheatgrass, not **for** cheatgrass. We manage the livestock so that we do not do anything for the cow that she can do better.

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Annual weeds continue to expand throughout the West eliminating many desirable species and plant communities. Wildfires are now common on lands infested with annual weeds, causing a loss of wildlife habitat and other natural resources. Measures can be used to reduce burning and restore native plant communities, but restoration is difficult and costly.

Keywords: cheatgrass, weed control, fire ecology, restoration, species utility, seed germination, seedbed ecology

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