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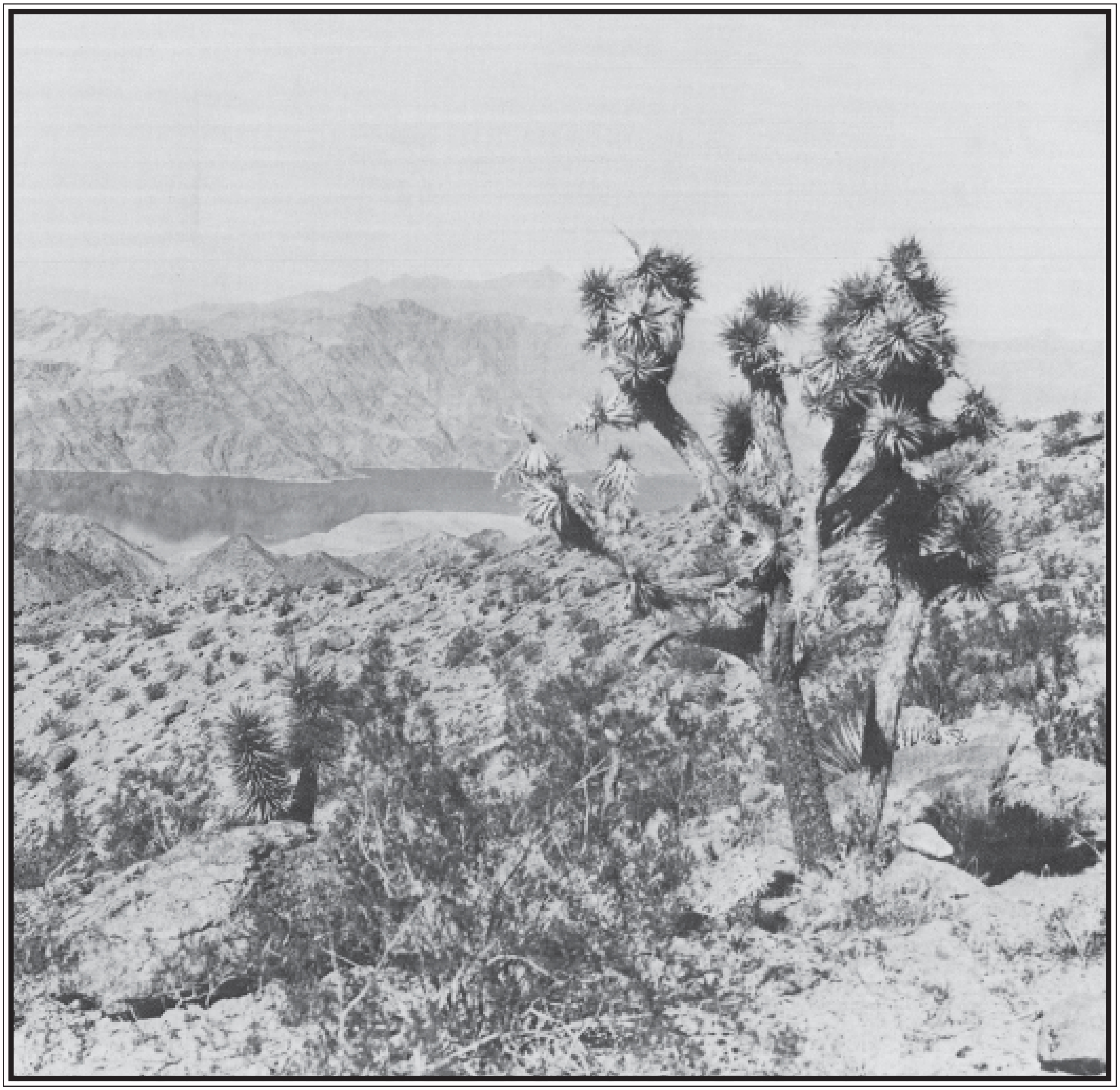

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Proceedings: Wildland Shrub and Arid Land Restoration Symposium

Las Vegas, NV, October 19-21, 1993

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Introduction: Wildland Shrub and Arid Land Restoration

Bruce A. Roundy
E. Durant McArthur

This publication is the eighth in a series of symposia proceedings on the biology and management of wildland shrubs, sponsored by the Shrub Research Consortium (see inside front cover) and published by the Intermountain Research Station. Other cosponsors of the symposium on wildland shrub and arid land restoration included the University of Nevada, Las Vegas, the National Park Service and Fish and Wildlife Service, both in the U.S. Department of the Interior and The Nature Conservancy. Contributions range from broad perspectives on restoration of arid lands to specific studies of arid land plant ecology and improvement. The proceedings emphasizes the use of revegetation to rehabilitate arid to semiarid lands for a variety of objectives. The symposium consisted of oral presentations including a plenary session, posters, and field trips. For convenience, we have divided these entries into six sections: Overview, Restoration and Revegetation, Ecology, Genetic Integrity, Management Options, and Field Trip. This volume includes 62 of the 82 papers and posters presented at the symposium (Shrub Research Consortium 1993) and one of the three field trips. The Nevada Test Site field trip is written up in these proceedings. The Viceroy Gold's Castle Mountain Gold Mine field trip featured a tour of a greenhouse used to propagate Mojave Desert plants from seed and tissue culture and a demonstration of salvaging topsoil and plants for Mojave Desert restoration. The Lower Colorado River and Mojave Desert Spring Restoration field trip featured problems with an alluvial desert river and riparian ecosystems and various attempts to restore health and function to them. The symposium also included workshops on Large-Scale Rangeland Revegetation and on Revegetation Contracting and Practice.

This symposium proceedings reflects the growing interest in and the development of the science and practice of restoration ecology. See for instance, Baldwin and others (1993); Berger (1990); Cairns (1988a,b); Harker and others (1993); Hobbs and Saunders (1993); Jackson (1992); Jordan and others (1987); Morrison (1987); Wali (1992a,b). The variety of disturbances, ecological consequences of disturbances, and site and organism-specific successional responses on wildlands throughout the world prohibit simple, generalized restoration procedures. The science of ecology has provided the framework within which restoration approaches can be developed. However, these approaches must be based on an understanding of the biology of the organisms and the ecology of the specific sites of interest. To be successful, restoration ecologists must leave the generalities and learn specifically the effects of particular disturbances on ecosystem attributes and the biological characteristics of the appropriate restoration organisms (Aronson and others 1993a,b). Such specific scientific knowledge has lagged far behind the demand for restoration efforts. Im- portant contributions of this symposium proceedings include not only information on wildland ecology and biology, but also case examples of applied revegetation practices that work. The mix of science and practice in the symposium proceedings should give readers a picture of the challenge and potential for wildland restoration.

The Ninth Wildland Shrub Symposium, "Shrub Ecosystem Dynamics in a Changing Environment" will be held in Las Cruces, NM, from May 23 to 25, 1995. The previous seven symposia covered a wide range of shrubland biology and management issues (Clary and others 1992; McArthur and others 1990; McArthur and Welch 1986; Provenza and others 1987; Tiedemann and Johnson 1983; Tiedemann and others 1984; Wallace and others 1989).

Acknowledgments

We thank our organizing committee colleagues, Jennifer S. Haley and David K. Mann, for their assistance with all aspects of the planning and conduct of the symposium. We also thank our Shrub Research Consortium, University of Arizona, and Intermountain Research Station colleagues and personnel of the Division of Continuing Education at the University of Nevada, Las Vegas, for their help in planning and staging the symposium, and in preparing the symposium proceedings volume. Symposium sessions were moderated by Bruce Roundy, Jennifer Haley, David Mann, Sherry Barrett, Jayne Belnap, Teri Knight, Jerry Barrow, Mark Holden, Jerry Cox, Mike Anable, and Jim Marble. Field trips were led by Raymond Franson, Von Winkel, David Busch, Stan Smith, and Jennifer Haley.

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Overview

Restoration and Revegetation

Ecology

Genetic Integrity

Management Options

Field Trip


SHRUB RESEARCH CONSORTIUM
WILDLIFE – LIVESTOCK
BEAUTIFICATION
RECREATION
SOIL STABILIZATION

Overview

Restoration Ecology: Limits and Possibilities in Arid and Semiarid Lands

Edith B. Allen

Abstract—Most attempts at repairing the damage caused by anthropogenic disturbance in arid and semiarid lands of the western United States have historically consisted of revegetating with monocultures or simple mixtures of mainly exotic species. Most revegetation was done for utilitarian purposes, typically to increase forage. The realization that biodiversity has been lost in many arid lands because of grazing, agriculture, and mining has prompted an interest in restoration which has conservation goals. Because of the extent of damage, restoration has limitations to simulating the original ecosystem before disturbance. Three major ecological limitations are discussed. The invasion of exotic weeds has reduced the diversity of native species, and they can be controlled with variable success. Where topsoil has eroded or been altered by compaction or other means, the community that develops is often floristically dissimilar from the original, as is its functioning. Restoration of biodiversity may be our greatest challenge, as even the best examples of restoration have been able to reintroduce only a fraction of the plant species richness, and natural recolonization is slow at best. Water for plant establishment in arid lands is discussed as well, but this is a limitation that can be overcome with ingenuity and patience. The costs for restoration can be borne if society decides that restoration is important enough. Even with our best efforts we cannot simulate what was once there, but we can improve the habitat value for many declining species.

Revegetation has been practiced for many decades in arid and semiarid lands of the western United States, but most often the goal has been to improve grazing for domestic animals. In the past few years the emphasis in North America has shifted from a strictly utilitarian purpose, to revegetation for conservation of plants and animals (West 1993). A great deal is known about range improvements for livestock, which typically consists of revegetating depleted rangelands with exotic monocultures or low diversity mixtures (e.g., Johnson 1986; Pendery and Provenza 1987), or of removing unpalatable species, such as shrubs or weeds. Less is known about restoring a diverse, native vegetation. However, there have been recent attempts at restoration for the sake of conservation, with varying degrees of success. The decisions that need to be made before restoration is undertaken are social, economic, and ecological. The social and economic decisions involve the valuation of conservation, which can sometimes include multiple use of lands. Here I will describe the ecological limitations that managers must consider to decide what lands can be restored, and to what degree.

The goals that can be achieved with different revegetation practices are captured in the definitions of restoration, reclamation, and rehabilitation that were put forth by the National Academy of Sciences (NAS 1974). Restoration means to reproduce the ecosystem structure and functioning that existed prior to disturbance, assuming the site was a relatively undisturbed, late successional or otherwise desirable native ecosystem. This was seen by the committee as the most difficult goal to achieve, if not impossible, because the entire diversity of native species would need to be reintroduced, and the late seral soils would need to be preserved or restored. Reclamation could, however, be achieved, because exotic species might be used that establish more readily than native species, and a lower diversity of native species would be acceptable. Reclamation still requires a high level of functioning of ecosystem processes, as the new ecosystem would also need to be self-organizing and stable, capable of existence with a minimum of human input. Reclaimed land would, however, be structurally less complex than restored land.

The third goal is rehabilitation, which implies that the land has been made productive again, but that an alternate ecosystem has been created, with a different structure and functioning from the original system. A rehabilitated system might be low in diversity, include only exotic species, and require continual inputs, such as fertilizer or irrigation, to exist. Improved rangelands that have been converted to monocultures are an example of rehabilitation. These three goals of revegetation were considered a continuum by Bradshaw (1984, Fig. 1), although I have changed the definitions from his model to reflect the NAS (1974) definitions.

The concern for rangeland restoration, rather than rehabilitation, has arisen as a loss in biodiversity and in habitat has occurred. For instance, mammal species diversity was lower in a monoculture of western wheatgrass than in adjacent Great Basin shrub grassland (Smith and Urness 1984) and bird species diversity was greatly reduced in lovegrass pastures in Arizona (Bock and others 1986). Even forty years of natural succession did not increase the plant or animal diversity of these pastures (Bock and others 1986). Biodiversity in rangelands has recently become a management goal (West 1993; Pyke and Borman 1992). As a result of these concerns for biodiversity, we can begin to expect changes in management practices that address the multiple use of arid and semiarid lands for people, livestock, and native organisms.

The values of arid land management vary with the revegetation goals (Table 1). Restoration is the highest

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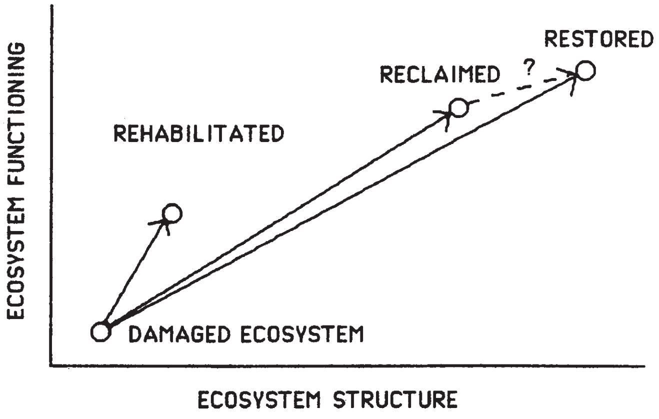

Figure 1—Model of goals to achieve restoration, reclamation, or rehabilitation. Restoration replicates the structure and functioning of the original system, or nearly so. Reclamation still requires a high level of functioning, but is structurally less complex. A reclaimed site may, through natural succession, approximate the original ecosystem, depending on species and treatments used. A rehabilitated ecosystem has little similarity to the original ecosystem in structure or functioning. Revised from Bradshaw (1984), definitions from National Academy of Sciences (1974).

conservation goal that can be attained. Reclaimed land still has some conservation value, but rehabilitated land is used for utilitarian purposes entirely. The economic value of these goals is at odds with the conservation value, as high input, rehabilitated lands yield more income than restored lands. The true economic value of restored lands is determined, of course, by how society views the cost of protecting rare species, and the indirect return of the "ecosystem services" (Westman 1977) restored lands will provide. However, the cultural, scientific and intrinsic values of restored lands are highest, where intrinsic value means value for its own sake, not associated with any other human benefit (Naess 1986). Restoration may be more costly to implement initially, but it results in ecosystems that require less maintenance input in the long term, are more stable, and have higher species diversity.

In some instances restoration may be accomplished economically by allowing natural succession to return the original ecosystem, but this is typically a slow process that is not accomplished within human lifetimes. Where lands have been severely disturbed, as after mining, overgrazing, or severe erosion, or when rare species are at stake, restorationists hasten the rate of succession by introducing late successional propagules of plants, animals, and microorganisms. Thus we may speak of "active" and "passive" restoration, where passive restoration consists of removing the stresses that caused the original degradation, such as heavy grazing, air pollution, and so forth, and then allowing natural succession. Active restoration means applying a number of management techniques, such as introducing propagules of organisms, weeding, burning, alleviating compaction, improving soil moisture, nutrients, or organic matter, and so forth. Typically, restorationists rely on a combination of both active and passive approaches, depending upon the severity of the disturbance. For instance, restoration may only require weeding and reintroduction of a few species if the seed bank is largely intact.

Table 1—Comparison of values of restoration with reclamation and rehabilitation.

	Rehabilitation	Reclamation	Restoration
Conservation value	low	medium to high	higher
Economic value	high	medium	low
Intrinsic value	none	medium	high
Cost to implement	low	medium	high
Species diversity	low	medium	high
Maintenance input	high	low	lower
Stability	low	high	higher

A strict reliance on succession will also not be sufficient to achieve restoration after many kinds of disturbances, if succession will no longer restore the original ecosystem. This seems to apply especially to arid and semiarid rangelands, where numerous observations on release from grazing or other disturbance have not shown a return to the original vegetation (Laycock 1991; Allen 1988; Westoby and others 1989). Succession may result in a new vegetation type, either consisting of exotic species or of new combinations of native species that were not formerly part of the landscape. For instance, mechanical disturbance that disrupted the soil and seed bank in southern California shrublands resulted in stands dominated by exotic annual grasses up to 70 years after abandonment (Davis 1994). Burned blackbrush (*Coleogyne ramosissima*) shrublands in southern Utah gave way to different kinds of shrublands, each dominated by different native shrub species in different areas (Callison and others 1985). Rest from grazing in sagebrush (*Artemisia tridentata*) steppe did not result in reduced shrub density with improved grass productivity in the understory, as classic succession theory would predict (West and others 1984). The native plant species that recolonized naturally after mining in Alberta, Canada, formed such an unusual community that no similar native communities existed (Russell and La Roi 1986).

In these and numerous other cases, disturbance resulted in a new trajectory of succession that involved both native and exotic species. Multiple stable states of vegetation types may coexist after disturbance, such that succession will not return to the original vegetation, but may result in one of several types. The concept of global stability has implications for the practice of restoration. The vegetation may return to a native type depending upon the kind of disturbance, but it may change to another vegetation type with another disturbance regime or with exotic introductions (Laycock 1991). Arid lands are especially subject to changes in trajectory of succession when the interval of disturbance becomes too short for recovery, as with increased anthropogenic disturbance (Turner and others 1993). In such cases, restoration may be the only solution to restoring an ecosystem that approximates the original. However, restoration may not always be the solution either, as there are limits to restoration.

I will discuss three primary ecological limits to restoration: invasion of weeds, loss of topsoil, and biodiversity. A fourth limitation that applies especially to arid lands, moisture, will be discussed as well. However, moisture is not a serious limitation, as water or a water harvesting system can be provided for most restoration efforts. The first three are limitations that usually cannot be cured by technological means.

The Limits to Restoration

Moisture for Plant Establishment

Water has frequently been studied as a limitation to arid land restoration and reclamation. Before the Surface Mine Control and Reclamation Act of 1977 was passed, many arid land scientists feared that the western rangelands would become "national sacrifice areas" because we did not have, and possibly could not develop, the technology to reclaim after mining. Western researchers at that time showed that we could, indeed, reclaim using native species, although these studies did not necessarily include all or even mostly native species (McArthur and others 1978; DePuit and Coenenberg 1979; Aldon 1981). These studies often used irrigation, sometimes at a higher level than necessary for establishment. High levels of initial irrigation may improve productivity, but at the cost of species diversity (DePuit 1988). The most drought-adapted species are lost under high irrigation levels, while species that respond to high soil moisture dominate. There were many early anecdotal reports of loss or decline of plant communities after irrigation was removed. While the literature is replete with reports of the effects of moisture on plant productivity, especially on crop plants, there is little information on the minimum critical moisture required for establishment of arid land plants.

Precipitation is more variable in deserts and semiarid lands than any other ecosystem, so plant establishment often occurs in pulses that are related to high precipitation years. Natural plant establishment varies from year to year in hot deserts, because the plants may need a wet year, or a series of wet years, for establishment to occur (Jordan and Nobel 1981; Romney and others 1987). Conversely, West and others (1979) did not detect any evidence for a pulse phenomenon of establishment in the cold desert of Idaho. Restorationists working in the hot deserts might be able to take advantage of the pulse phenomenon of desert plant establishment, either by waiting for the appropriate sequence of high precipitation years or by irrigating.

Based upon infrequent establishment of many species in hot deserts and the fact that precipitation is highly variable, MacMahon (1981) observed that succession is slow in deserts not because desert plants grow slowly, as was previously thought, but because of delayed establishment if an appropriate precipitation year occurs infrequently. There has been relatively little work on growth rates of native desert shrubs. However, several hot desert species exhibited rapid growth rates once they were transplanted as seedlings, even with only a minimum of water once at the time of planting (Bainbridge and others 1993). After only three years, species such as mesquite had achieved a volume as large as that of many shrubs from adjacent undisturbed areas. Thus, irrigation may be necessary to overcome a series of dry years, and the only problem is determining the amount. A rule of thumb is to irrigate no more than the average amount of precipitation, or no more than a wet year if it is known that certain species require higher than average moisture for establishment. However, in recent studies, irrigation to make up the deficit of a dry year did not improve the establishment of Indian rice grass in Utah (Belnap and Sharpe 1993), nor did irrigation improve the establishment of shrubs in the Wyoming Red Desert (Powell and others 1990). Thus, it is necessary to know the individual moisture requirements of species for establishment.

In a study on off-season irrigation, I studied the effects of dry season irrigation on purple needle grass (*Stipa pulchra*). This grass has had poor establishment success in revegetation trials in native California grasslands where it was once abundant, probably because of competition from exotic annual grasses (Nelson and Allen 1993; Bartolome and Gemmill 1981). The Mediterranean climate grasslands where purple needle grass occurs will probably have enough winter/spring precipitation to allow germination in most years, but seedlings must be able to survive a six-month dry summer for establishment. Thus I experimented with a low level of off-season (summer) irrigation. The site was in Santee, southern California, and the experiment was performed during the below normal precipitation spring of 1991. I irrigated at two levels from mid-March through early June, either 1 cm daily or 1 cm weekly, to assure adequate germination in four 0.5-m^2 replicate plots. Species other than purple needle grass were weeded. After June 11 half of each of the high and low level irrigation plots were irrigated with 1 cm water weekly, the other half were not irrigated further. The high spring irrigation level resulted in a higher proportion of large plants with crown diameter greater than 3.0 cm, while the low level had a higher proportion 2.9 cm or smaller (Fig. 2). However, leaving the

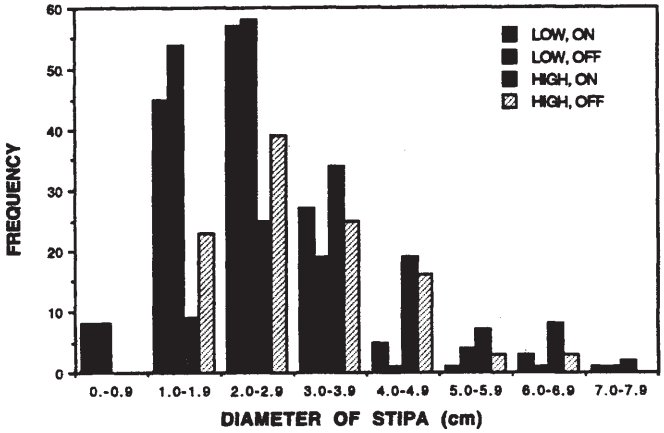

Figure 2—Frequency of diameter classes (crown cover) of purple needle grass subjected to four irrigation treatments. Low and high are spring (March through June) irrigation levels, on and off refer to presence or absence of summer (June through August) irrigation. Data collected in August.

Table 2—Density of purple needle grass in plots with high and low irrigation levels. Irrigation was left on or turned off in one-half of the plots on 11 June.

Treatment	No./m² 5 June	No./m² 7 August	% mortality
high on	82.5	75.5	8.4
high off	97	73	24.7
low on	70.5	52	26.2
low off	67	54.5	18.7

water on during the summer only resulted in reduced mortality of the high spring irrigation plots (Table 2), where most of the plants were already quite large. In the two low spring irrigation treatments, the mortality was equally high whether there was summer irrigation or not. In effect, the many small plants of the low spring irrigation treatment died whether they had summer irrigation or not. The results suggest this grass must have seedlings that are in the range of 2 cm diameter or greater for survival during the dry summer. Spring irrigation was important to assure that the plants were large enough to survive the normal summer drought.

If water is a limitation to arid land restoration in the short term, in the long term moisture will eventually become available for natural establishment via the pulse phenomenon, or moisture can be provided by irrigation or surface treatments such as pitting, furrowing, imprinting, and so forth. More imaginative methods, such as deep pipe irrigation or water catchment systems, have also been used (Bainbridge 1992). These methods have proven capable of increasing establishment even in hot deserts. Thus I will not further consider water as a limitation to restoration, because it is one that can most often be overcome with management, technology and imagination.

Exotic Plant Competition

The arid and semiarid lands of the western U.S. are experiencing an unprecedented invasion by exotic plant species that threatens native ecosystems and reduces the success of restoration. Disturbance is often considered necessary for plant invasion to the extent that natives will be entirely replaced, but invasion is occurring even in lands that are subject to relatively little anthropogenic disturbance. Fox and Fox (1986) list a number of characteristics of ecosystems that make them subject to invasion, and open vegetation structure with large interspaces, such as is typically found in the desert, explains why exotics have dominated to a much greater extent than they have in forested ecosystems, for instance. Even a natural disturbance such as fire has become an agent for opening native vegetation to invasion in the semiarid shrublands of southern California and the Great Basin, especially when the frequency exceeds that occurring naturally (Freudenberger and others 1987; Billings 1990).

These exotics are almost certainly reducing the diversity of native plant communities, as a number of them form persistent near-monocultures. Some of them occur on a large scale, such as the Mediterranean annual grasses that have displaced the native Central Valley grasses in California, or cheatgrass (*Bromus tectorum*) that has invaded Great Basin shrublands (Billings 1990; D'Antonio and Vitousek 1992). These are the better known examples, but more recent invasions cause range managers to long for the days when the dominant invaders were at least palatable forage grasses. For instance, several species of knapweed are replacing large acreages of annual grasslands in California and northwestern North America, as are artichoke thistle and mustards in southern California shrublands. Some of these invasions are occurring so recently that even sites that were dominated by natives in the last few decades are now dominated by exotics. For instance, the exotic annual grass *Schismus barbatus* and the mustard *Brassica tournefortii* have been invading the southwestern deserts since about the 1930's, and are spreading into areas with relatively little recent disturbance such as the Anza Borrego Desert State Park.

Controlling these weeds and the restoration of these sites has become a major problem. Range managers continue to use productive, exotic perennial grasses and shrubs to reclaim the land from annuals because the seedlings of native species typically are not able to compete with the aggressive annuals (Johnson 1986; Nelson and Allen 1993). The "greenstripping" program, which consists of planting strips of less flammable vegetation in a matrix of cheatgrass, has been initiated to begin controlling wildfires in cheatgrass grasslands (Pellant 1990). However, the planted vegetation is typically a mix of exotic plus native species, and does not constitute restoration. A successful effort at perennial grassland restoration has been provided by the Nature Conservancy at the Santa Rosa Plateau Preserve in southern California. This site had past grazing, but the grasslands have persistent native perennial grasses with the colonizing exotic annuals. Burning was timed to destroy the annual seed crop in June when the seeds were mature but before they had shattered. In the next growing season, burned sites were dominated by the native purple needle grass (*Stipa pulchra*) (Gary Bell, The Nature Conservancy, pers. comm.). Since the seeds of these grasses, members of the genera wild oats, wild barley and brome, do not have a long-lived soil seed bank (Marshall and Jain 1967), fire is an effective restoration technique. In the case of cheatgrass, the seed bank is more persistent (Hassan and West 1986), so multiple spring fires would likely be required to deplete the seeds. I am not aware of such an effort, which would likely need to be supplemented by seeding and planting of native species that have been eliminated in cheatgrass monocultures.

The cheatgrass problem is one of the largest and perhaps most difficult to solve for restoration purposes. Others have been solved, if not to result in perfect restoration, at least to recreate communities dominated by native species. Natural succession in disturbed sagebrush grasslands of northeastern Wyoming that were dominated by Russian thistle (*Salsola kali*) resulted in a return to native vegetation, whether Russian thistle was controlled or not (Allen 1988). The difference was that plots dominated by Russian thistle had reduced sagebrush seedling establishment in the early years following discing. Even though Russian thistle disappeared naturally after 3 to 4 years, it had a persistent depressive effect on sagebrush, so Russian thistle plots were grass dominated, while weeded plots were sagebrush-dominated (Allen and Knight 1984; Allen 1988). In another experiment on mined land reclamation, Russian thistle was a nurse plant in upland sites because its litter catches snow and shelters grass seedlings (Allen 1992). More recently we have learned that the soil under Russian thistle is elevated in phosphorus because of the high levels of oxalate in its tissue, so this weed may facilitate establishment of the next stage of seral plants where phosphorus is limiting (Cannon 1993). Thus, not all weed problems of arid lands are insurmountable, and in the case of Russian thistle there may even be some benefits.

In general, restoration has not been practiced on a large enough scale to eliminate large scale weed problems, or has not necessarily had the goal of reducing exotic species. Oak savanna "restoration" in southern California consists of replanting oaks and leaving the exotic grass understory. Even after fire has greatly reduced the exotic grasses, exotic forbs such as storksbill cannot be eliminated because of their deep roots (Gordon and Rice 1992) and possibly persistent seed bank. In spite of our best efforts, we will need to accept that a certain percentage of the plant community will consist of exotics, and some lands may be so weedy that they are beyond our abilities to restore.

Loss or Alteration of Topsoil

Restoration often consists of planting late successional species into early successional soils that have had topsoil removed, eroded or compacted. Even with the best restoration efforts, it takes time for soil genesis, and a return to a soil that will support the previous community may take decades to millennia. Many species of soil microorganisms are slow to recolonize impacted soils, and inoculation is not possible for most of them. The soil surface hydrology may be altered, as after leveling for agriculture or heavy grazing, limiting plant establishment (Anderson and others 1976; Allen and Jackson 1992). The mining laws in this country have assured that, at least for coal mining, the topsoil is replaced. Even here, the resultant "topsoil" is a mix of topsoil, subsoil, and parent material that is lower in nutrients, organic matter, and mycorrhizal fungi than undisturbed soils (Allen and Allen 1980). Another problem exists for degraded rangelands, where topsoil has eroded away leaving the B horizon exposed (Schlesinger 1985). The problem of eroded rangelands is typically solved by planting exotic species that both stabilize the soil and provide forage (Johnson 1986; Vallentine 1989), but restoration is seldom a goal. To assess the effects of soil material on vegetation establishment and succession, it is necessary to compare restoration on topsoiled and untopsoiled sites. Although native species are often included in range improvement mixtures, I am only aware of experiments that compare topsoiled and untopsoiled sites in mined land reclamation and restoration experiments. Therefore, I will restrict the examples to illustrate my points to mined soils. Only those examples will be discussed that studied soils that were not toxic or otherwise different from the original subsoil or parent material, so the conclusions drawn from these studies can be extrapolated to non-mine soil disturbances.

The first bit of evidence that untopsoiled soils are unsuitable for restoration comes from studies on natural succession of mine spoils. For instance, even after 30 years the grasslands that developed in Oklahoma mine spoils did not resemble the species composition of native prairie (Johnson and others 1982), and in Alberta, Canada, the plant community that developed naturally on mine spoils did not resemble any native communities as shown by ordination (Russell and La Roi 1986). These sites were dominated by early and mid-seral species, but also by species that came from different habitats entirely. Restorationists would of course hasten succession by using later seral species, but even here the evidence shows that topsoiled and untopsoiled sites have very different vegetation. For instance, in a simple community dominated by four species of planted wheatgrasses and a few dozen invasive species, western wheatgrass was more abundant on subsoil, thickspike wheatgrass on topsoil, and the invasive community was different on the two soils (Waaland and Allen 1987; Waaland 1985). In a study that compared succession of native sagebrush-steppe, the weed community, including shrubs such as rabbitbrush, was more persistent on subsoil while the native grasses and late seral shrubs were more abundant on topsoil (McLendon and Redente 1990). These studies indicate that, even where the same mix of native species was planted in topsoiled and untopsoiled plots, the effect of soils was key in sorting out the species composition.

The problem of restoring degraded soils is one of soil genesis. It may take centuries to millennia for natural soil building processes to restore the soil naturally. Soil genesis has been studied in mine soils, and where vegetation has been successfully reestablished, the formation of horizons may occur more quickly than many researchers had suspected (Schafer and others 1980). Soil amendments, primarily nutrients and organic mulches, are used to hasten the rate of soil genesis, and can help build a soil that has similar chemical and biological characteristics to undisturbed soils (Whitford 1988). However, there is no substitute for time in rebuilding certain features of the soil, especially soil structure.

Undisturbed desert soils that are already low in organic matter and nutrients may not be very different from disturbed soils from the standpoint of soil chemistry, although microorganisms are still impacted (Allen 1988). The native species are probably already adapted to early successional soils with poor chemical qualities, and in fact, deserts exhibit autosuccession where the late stage seral vegetation is also the colonizing vegetation. The loss of topsoil may not be as much of a problem for desert plants, where there is no true topsoil. The exceptions to this would be where there is no nearby source of natural inoculum of soil microorganisms, and where the topsoil has eroded away leaving a hardpan such as a caliche layer, that would either require millennia of weathering or artificial treatment for any plant to grow on it at all. Where topsoil has been lost and is essential to the reestablishment of native vegetation, restoration is not a realistic goal, but reclamation may certainly be practiced to assure that many of the values of the land are reestablished for protection of some of the wildlife and plants.

Biodiversity

The greatest conservation threat that we face is the loss of biodiversity, but restoration cannot be viewed as the cure. Of the many restoration projects in the western U.S. and elsewhere, none have achieved the goal of bringing back the diversity of species that once existed at a particular site. Most prescriptions for revegetation include only a few dozen species at most. Usually these are the most dominant species, and the goal in choosing species is to include those that represent vegetation life forms and structural layers, such as trees, shrubs, forbs, and grasses, where those life forms are part of the natural vegetation. Once these dominant life forms are reestablished, restorationists hope that rare plant species and animals will recolonize. However, the number of rare species in any natural community is always so much greater than the number of abundant species, that the task seems hopeless. We are slowly learning to propagate many rare species, but we do not yet have knowledge or economic resources to introduce them all.

Learning the rates of natural plant recolonization into disturbed areas is important to predicting whether restoration efforts may someday result in vegetation with its original diversity. Large tracts of abandoned farmland in the Sonoran Desert may require 200 years or more just for the recolonization of the dominant creosote bush (Jackson 1992). Obviously, restorationists can hasten the rate of dispersal by artificial introduction of creosote seeds, but we must still wait long time periods for the rare species, hopefully less than 200 years if creosote bush attracts animal seed dispersers or acts as a nurse plant. The scale of the revegetation and the proximity of adjacent disturbed vegetation is critical to the rate of recolonization, and these abandoned farmlands certainly constitute some of the largest restoration problems.

There are still relatively few restoration efforts that are long-term enough to have measured species recolonization. The restored Curtis Prairie in Wisconsin is over 50 years old and probably has most of the species indigenous to native prairies, but these were largely planted by researchers working over many years (Cottam 1987). In a survey of highway revegetation in southern California with sites up to 18 years old, a maximum of 15 native species colonized in the oldest sites (Fig. 3, Allen and others 1993). These native species colonized only where the roadside was adjacent to native shrubland, while exotic Mediterranean annual grasses and forbs colonized everywhere. Generally no more than a dozen mostly native species were planted at any one site along a 50 mile stretch of Interstate 15, so the maximum richness obtained was some 40 species, including the exotics, in plots of some 200 m^2. The local coastal sage shrubland may have, by contrast, some 70 species in an equal area (Allen, unpublished data).

The most ambitious restoration effort I have seen to reestablish diversity was on a bauxite mine in SW Australia, where some 80 species were seeded that were collected from adjacent jarrah (eucalyptus) forest (Nichols and others 1991). This forest type actually contains some 200 species, and the numbers of species that established, survived and perhaps colonized after 16 years was considerably fewer than those seeded (Gardner pers. comm.).

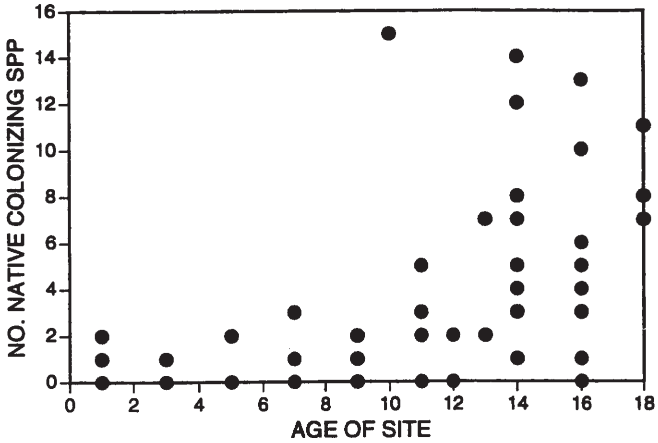

Figure 3—Age of revegetated site vs. number of colonizing native species along Interstate 15. No more than 15 native species colonized any one site, which each had a dozen or fewer planted species. Older sites with few colonizing species were always adjacent to urbanized areas; those with more colonizers were adjacent to native shrublands.

A number of restoration projects have been done with the express purpose of saving a threatened or endangered species, but these usually focus on one or two species and are not done for the purpose of reestablishing biodiversity. For instance, fiddleneck (*Amsinckia grandiflora*) was seeded into areas where it had become locally extinct in California annual grassland (Pavlik and others 1993). This has been done now for a number of other rare plant and animal species in California and elsewhere, although the prospects for long-term survival are still variable (see Pavlik and others 1993 for a brief review). Vegetative restoration was done to attract the endangered least Bell's vireo, which lives in riparian habitat, but the vegetation itself was relatively low in diversity (Baird 1989). Thus, single rare species restoration efforts to date have typically not included a high diversity in the restoration plant mix, but they have rather focused on the needs of the rare species, such as appropriate shrub architecture to attract an endangered bird.

Conclusions

There are other ecological limits to restoration of arid lands in addition to those discussed. Herbivory is known to reduce establishment success in natural and restored communities (McAuliffe 1986), and without protection of seedlings, restoration in some areas may be impossible. This, like lack of moisture, is a limitation that can be overcome with hard work and imagination. An irreversible situation is created by the many dammed rivers and trans-basin water diversions in the western U.S., that have changed surface and groundwater hydrology and assured that restoration cannot take place. This brief paper has dealt with the uplands, but riparian areas in arid lands are also in great need of restoration. The successful restoration of arid landscapes may depend on restoration of both aquatic and terrestrial systems, as these are interrelated by movement of water, nutrients and biota.

Because of these limitations, our restoration efforts will not be as successful as we would like them to be. The limitations show how important it is for us to conserve those remaining lands that do have high biodiversity, as restoration is not a substitute for conservation. Restoration efforts will still play an important role in conservation even if they are not perfect, because so many lands have been impacted by humans and are in need of restoration. Those lands that are hopelessly weed infested or have very poor soil quality should be identified, and might not be important candidate sites for restoration. Aronson and others (1993) have discussed the concept of "thresholds of irreversibility" beyond which restoration is no longer possible, but revegetation efforts will still be fruitful to improve the ecological and economic value of the land. The cost of restoration may vary from a few hundred to tens of thousands of dollars per acre, depending upon the degree of disturbance and the restoration effort needed. It is up to society to decide to what extent these costs are justifiable. But even with the best restoration efforts, the result will not be vegetation precisely like it was prior to human disturbance. Restoration becomes a valuable exercise even with these limitations if we can increase the habitat value for declining species that would otherwise not be able to exist in an ever more impacted western landscape that is dominated by agriculture, livestock, and urbanization.

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Implications of Early Intermountain Range and Watershed Restoration Practices

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Abstract—Ecological restoration of disturbed wildlands continues to gain acceptance as the most desirable approach to site improvement. However, some disturbed sites have been so seriously altered that native communities cannot recover. In addition, weeds are dominant over large areas, and appear more resilient and persistent than many native species. In these and related situations, introduced species and altered plant communities will have to be maintained to protect all resources. Previous site rehabilitation practices provide information to better restore disturbed watersheds, rangelands, and weed-infested sites. Previous research and project plantings have provided information to better identify sites that are suitable for restoration, and to define more appropriate planting practices. Native species and ecotypes have been identified and tested to define their range of adaptation and use in reconstructing native communities. Equipment has been developed to culture plants, prepare seedbeds, control weeds, and seed a variety of species. Considerable information can be gained by examining previous rehabilitation practices, including documentation of secondary succession of seeded as well as protected natural sites. This information is important in developing ecologically sound restoration measures.

Restoration of range and watershed sites within the Intermountain area evolved after early Anglo-American settlement. Settlers converted some native plant communities to agricultural crops and pastures. Disturbances associated with the development of irrigation delivery systems, roads, timber harvesting, and mining required remedial seeding and construction of protective structures such as dams and debris basins. Growing livestock herds and sustained heavy grazing seriously altered plant and soil resources (USDA Forest Service 1936; Williams and Lyon 1993). Although livestock grazing changed species composition and diminished plant cover in many areas, the impacts were not considered serious enough to require remedial action until watersheds began to erode and degrade. As unstable watersheds began to affect downstream resources, remedial treatments and regulation of onsite activities became a major concern (Keck 1972).

Early conservation measures implemented to rectify major disturbances have influenced the current perception of problem areas, the need for remedial actions, and methods used to treat disturbances. Remedial treatments have largely been to stabilize watershed disturbances, improve range conditions, and control weeds (Vallentine 1989). Most improvement practices would be classified as rehabilitation or revegetation treatments, not as restoration (Allen, this proceedings; Jordan and others 1987). Rehabilitation or vegetation involves seeding or planting a group of native or introduced species to rectify existing disturbances. Plantings are usually completed to stabilize watershed, range, or wildlife disturbances. Restoration implies that the native communities will be reestablished; introduced species would not be used. Ecologists and land managers have shifted their emphasis, recognizing that resource values are closely integrated, and function within the context of large ecosystems and landscapes (Allen and Hoekstra 1992).

Rehabilitation measures were initially implemented at high-elevation sites on National Forest lands. The first research program designed to investigate the causes of watershed deterioration and ways to ameliorate the problem began in 1912 in Ephraim Canyon, UT, on what became known as the Great Basin Experimental Range (Keck 1972). Later, similar efforts were established at other locations. By the mid-1940's many scientists were working to rehabilitate rangelands, watersheds, and other lands. Reseeding trials and plant selection efforts started in 1912; they were greatly expanded in the early 1920's when an organized testing program was developed to evaluate a large number of species planted throughout the Intermountain area (Forsling and Dayton 1931; Plummer and Stewart 1944). Since these beginnings, much has been accomplished in land restoration, but much remains to be done (Institute for Land Rehabilitation 1984; Jardine and Anderson 1919; Jordan 1981; Jordan and others 1987; McGinnies and others 1983; Monsen and Shaw 1983a; Monsen and Stevens in preparation; Plummer and others 1968; Renner and others 1938; Sampson 1913; Thames 1977; Wright 1978). This paper reviews past revegetation efforts and evaluates past management principles and practices as land managers moved to more holistic practices emphasizing natural and native ecosystems (Allen, this proceedings; Jordan and others 1987).

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Land Use: Its Effects on Early Restoration and Rehabilitation

Most revegetation or rehabilitation programs on public lands have attempted to rectify disturbances caused by grazing, logging, mining, road construction, and recreation. The extent or degree of plant and soil removal and impacts on associated resources dictate the need for restoration. Although disturbances continue today, the cumulative effects of extensive resource uses following settlement dramatically affected future management and remedial treatments. Measures developed to stabilize watersheds, improve range sites, and contain weeds often were closely related. Problems often existed in quite different sites, requiring different treatments. Research practices and objectives were largely driven by needs to correct problems, and the initial approaches set the stage for efforts that continue today.

It took decades to regulate and stabilize grazing practices in the Intermountain area (Alexander 1987). Rangeland carrying capacity and watershed stability were concepts that developed after soils and plants had been degraded by exploitative grazing (Alexander 1987; Williams and Lyon 1993). The early buildup of livestock numbers in the Intermountain area led to confrontations between public land managers seeking to reduce stocking and livestock managers for most of this century (Alexander 1987; Ellison 1954; Paulsen 1975; Thilenius 1975). The thousands of grazing animal units (five sheep = one cow = one grazing animal unit) in Idaho, Nevada, and Utah grew from:

Year	Grazing animal units (in thousands)	Percent increase (by decade)
1870	95.2	—
1880	670.5	704
1890	959.6	145
1900	2,678.4	279

Over 30 years the grazing pressure increased 28-fold. The pressure peaked on National Forests in Idaho, Nevada, and Utah at nearly a million animal grazing units from World War I through 1920. Permitted use declined by about 45 percent from 1920 to 1946 and an additional 18 percent from 1950 to 1969 (Alexander 1987). Populations of large native ungulates (elk and deer) have increased since settlement, probably as a result of management activities that changed forage bases, controlled predators, and controlled hunting (Alexander 1987; Robinette and others 1977). Grazing by domestic livestock and wildlife stimulated secondary succession, often in directions that led to less productive and more erodible rangelands (Ellison 1960).

Watershed Restoration and Revegetation

The first efforts to restore disturbed lands used artificial plantings to stabilize watersheds and improve range forage. The objectives for treating these sites have significantly influenced revegetation and restoration efforts ever since. Early watershed stabilization studies demonstrated that ground cover was the primary factor affecting soil stability and protecting watersheds. Plantings that provided dense cover quickly stabilized even drastically disturbed, highly erodible sites. The search for ground cover species focused on plants that established themselves quickly, provided dense cover, and were adapted to disturbed areas. This approach resulted in the selection and use of a number of introduced grasses that performed well through a broad range of ecological sites. This policy resulted in the acceptance and use of a limited number of species. Diverse mixtures were not encouraged. Although some plantings were designed for seeding different sites or communities with separate mixtures or species, a few primary introductions were developed for most sites. Plants used in watershed improvement programs evolved through extensive research, including screenings and field trial plantings. Various native species were included in all phases of testing, and some individual species became primary candidates for extensive plantings. Selections of mountain brome (*Bromus carinatus*) and slender wheatgrass (*Agropyron trachycaulum*) were developed from early testing for watershed restoration plantings. Many native shrubs and broadleaf herbs were examined. Initial plant adaptability studies conducted by Sampson (1917) describe the utility of a broad group of introduced and native species.

Watershed restoration plantings were primarily confined to high-elevation communities and riparian areas with substantial erosion and site stability problems. However, plantings were employed over a wide range of plant communities, ranging from subalpine to mountain brush types.

Although a large number of native species were included in the initial selection and testing process, plant communities themselves were not evaluated for artificial seedings or plantings. In many situations, managers attempted to retain the principal ground cover or forage species that persisted amid most disturbances; however, the compatibility of planted mixtures with native plant communities was not strongly emphasized. The use of pioneering species on severely disturbed sites was not a primary consideration, although studies demonstrated that certain species prevalent in late-seral communities may not be well adapted for pioneering. The most widely accepted practice has been to seed or plant the most abundant native grasses with selections of introduced species that have proven successful in screening trials. This practice has established successful stands in most situations, furnishing the desired ground cover. Although this approach does not satisfy all concerns, it restores a broad range of ecosystems and has been widely implemented.

The ecological effects of seeding introduced species and the simultaneous natural recovery of native communities were major concerns of early investigators. They established studies to evaluate long-term trends and the response of individual species. Exclosures and weather stations were established within representative community types to document climatic conditions, adaptation of seeded or transplanted species, and plant succession. Although some sites have been abandoned, reassessment of these areas is providing excellent information (Monsen and Anderson 1993). Areas of current research include the relationship of introduced species to native species and the recovery of native communities. Some papers in this proceedings report data of this nature (Biedenbender and others, Downs and others, Livingston and others, McArthur and others, Roundy, Walker and others).

Range Improvement and Revegetation

The rapid, widespread loss of herbage and vegetative cover caused by grazing in the late 19th century and extending into the second decade of the 20th century led to programs to stabilize the livestock industry and prevent further site deterioration. The primary objectives addressed in early range improvement programs were to:

- Stabilize and retain livestock grazing
- Prevent further loss of herbage and vegetative cover
- Control the invasion of weeds
- Improve forage production and herbage quality.

These combined factors determined the selection of plants for revegetation or rehabilitation. Forage species, principally introduced grasses, were selectively developed for nearly all planting sites. Those species, developed for rangeland plantings, continue to be used for most rangeland and watershed disturbances.

The largest acreages of artificial plantings have been on rangelands. Practices and methods accepted for rangeland plantings have dominated restoration measures proposed for other lands.

Weed Ecology

Invasion and expansion of weeds continues to be a major problem in protecting and rehabilitating plant communities throughout the Intermountain area (Monsen and Kitchen 1994). Previous range and watershed rehabilitation efforts have been plagued with weed-related problems. Although considerable research has been directed to weed control, new species continue to appear; many early invaders are rapidly expanding their area of occupation. Troublesome weeds initially invaded disturbed areas where native species had been removed or lost by mismanagement (Platt and Jackman 1946). The most successful weeds include cheatgrass (*Bromus tectorum*), medusahead (*Taeniatherum caput-medusa*), bur buttercup (*Ranunculus testiculatus*), and halogeton (*Halogeton glomeratus*). These species have generally populated open, disturbed areas (Young and others 1972). They spread rapidly after first gaining a foothold in openings in stable communities.

Managers quickly recognized the need to reduce weedy competition to facilitate almost any seeding. Once desired species were reestablished, weeds diminished. Studies demonstrated that controlling weeds usually required eliminating existing weedy plants and regulating seed germination and establishment (Evans and others 1970). Many weeds that occupy wildland sites are extremely productive seed producers. Eliminating 90 percent of their seed crop has little effect on plant cover or weeds ability to outcompete native species. Although many different species of weeds occupy wildland sites, the most troublesome species are those that produce an abundant annual seed crop and that can become established quickly during favorable seasonal moisture or climatic conditions (Young and Evans 1973). The continued spread of many perennial noxious weeds is extremely difficult to reduce or eliminate. Effective control measures have been developed for many species, but the measures are often difficult to implement.

Significant changes have occurred with many weeds, creating new problems. Changes have generally occurred in three principal areas of weed biology and ecology:

(1) New individuals have evolved that are adapted to additional environments and plant communities (Beckstead and others, this proceedings). Cheatgrass, medusahead, and goatsbeard (*Aegilops cylindrica*) ecotypes were initially adapted to specific plant communities. Through natural selection accentuated by short (usually annual) life cycles, populations have evolved that are adapted to a wider set of circumstances. Significant expansion of cheatgrass, medusahead, and goatsbeard have been documented within the past two decades (Billings 1990). Cheatgrass has spread and continues to occupy more extensive areas in the ponderosa pine and in the salt and cold desert communities. Harper (1959) reported that cheatgrass was a minor, infrequent constituent of plant communities on the Intermountain Research Station's Desert Experimental Range in southwestern Utah; Now some 35 years later cheatgrass occupies nearly all open spaces within the range's salt desert shrub and black sagebrush communities. Medusahead has made dramatic expansions into sites once dominated by cheatgrass. Goatsbeard, once an obscure novelty, has invaded and dominates bunchgrass sites in north-central Utah and is expanding its range to occupy mountain brush communities, where it becomes established under tall shrubs.

(2) Recently, several aggressive weedy species have invaded apparently stable communities. Rush skeletonweed (*Chrondrilla juncea*) and yellow starthistle (*Centaurea solstitialis*) are two examples (Piper 1983). Control of these and other weeds that can invade stable communities requires reconsideration of rehabilitation practices. It may be practical to control these weeds by shifting the density and composition of native communities. In some situations, planting more acceptable introductions may be an initial measure to prevent the uncontrolled spread of these weeds. This problem is a major concern in land management and requires immediate attention.

(3) Species composition of native stands in some communities has shifted due to habitat deterioration or changes in site conditions (Johnson 1964). Throughout the Intermountain area, past grazing practices have diminished plant cover, resulting in soil losses (Fullmer 1983). Some changes are less apparent than others. Tall forb communities occupying sites at mid- and high elevations were seriously impacted by early grazing. Many sites were converted to tarweed (*Madia glomerata*), mulesear wyethia (*Wyethia amplexicaulis*) and California false-hellebore (*Veratrum californicum*), all native species. Many disturbed areas were seeded with introduced species and were managed to restore more desirable natives. Practices and procedures were developed to restore these sites, and extensive areas were treated. The weedy plants were effectively controlled for extended periods and many seeded introductions and native herbs appeared well established. However, many treated sites have deteriorated to pretreatment conditions. Apparently, changes in site or soil conditions now favor less desirable species and the late-seral, more diverse communities are difficult to maintain. Restoration measures have not been effective in maintaining these seeded communities.

Progress in Rehabilitation

Site Identification and Potential for Remedial Treatments

Disturbances occur within most plant communities, requiring different methods to rectify the problems. Although many different factors must be considered to successfully restore any site, some general principles apply to most restoration projects. Plummer and others (1968) described "ten major commandments" or principles that should be addressed in planning restoration programs. Various other scientists have recognized the need to follow similar principles. In general, problem sites should be carefully inventoried to assure that artificial restoration measures are needed and that natural recovery will not occur within an acceptable period. Adapted species must be selected and planted using procedures that remove competition and create suitable seedbeds. In addition, plantings should be conducted at the appropriate season using high quality seed or planting stock. Other factors, including proper management of the modified sites, may be necessary. These general, but effective, guidelines have been developed through numerous plantings and serve to direct rehabilitation and restoration.

Appropriate planting practices are generally not too difficult to develop, and various guidelines provide needed direction. The most difficult decisions are determining whether a disturbed area can be restored and determining the overall approach to accomplish the task. Sites without desirable species normally have few options for restoration. In most instances, weeds must be removed and suitable seeds or plants reintroduced by artificial plantings. Various measures may be required to prepare a seedbed and complete planting, but the approach is well understood.

The most complicated situations are those where weeds partially occupy a site and only a small number of natives remain. Developing measures to remove or lessen weed competition and interplant additional species is very difficult. In many situations a lack of suitable seed hinders reestablishment of native plants. In addition, many sites are inaccessible to normal site preparation and seeding practices. Failure to implement all proven measures (such as site preparation) significantly lessens the chance of a success. Developing alterative measures that can better assure success often comes from experience; these measures may not be well documented in the literature.

In many arid or semiarid regions, adhering to well-defined practices and procedures may not always assure successful plantings. Adverse and unpredictable climatic conditions often dictate establishment and plant survival (Bleak and others 1965). Failure to recognize the limitations of planting these and other disturbed areas frequently leads to failures and the loss of considerable funds and other resources. No matter how much money is spent, some disturbed areas cannot be effectively treated; alternative measures must be considered.

Planting success has often been judged by seedling density and the composition of developing communities. Although these are important criteria, ultimate development and community stability cannot be assured by early evaluations. Some seedings that were considered successful have not persisted, deteriorating to preplanting conditions. These situations are not unique or infrequent. Problems have been identified in the treatment of high summer ranges occupied with tarweed and, to a lesser extent, mules-ear wyethia. Long-term ecological studies are needed to determine causes associated with the unexpected changes in successional development of planted communities. Site deterioration often occurs when unadapted species and mixtures are planted; however, unexpected changes have occurred when adapted ecotypes and species were planted in combinations that reflect late-seral communities. Planting species prevalent in late-seral communities may not be advisable in rectifying all disturbances. This factor presents additional concern in matching remedial treatments with different disturbances.

Some key species have demonstrated broad applicability in planting different disturbances. These species may dominate late-seral communities, yet are equally adapted as pioneering species, establishing well from artificial plantings (Monsen and McArthur 1985; Monsen and Plummer 1978). Many of these plants are used to treat a broad range of disturbances. Species included in this group are antelope bitterbrush (*Purshia tridentata*), Lewis flax (*Linum lewisii*), ponderosa pine (*Pinus ponderosa*), and winterfat (*Ceratoides lanata*). When seeded within their area of occurrence, these species become established and persist with regularity. Planting combinations are often based on including these species in seed mixtures. The successful development of these plants has often influenced the acceptability of planting programs. Although these species may be important and adaptable, in many situations the desired composition of the entire community has not been attained. The composition of the entire community, not just the success of a few species, must be considered when choosing adapted species to plant on disturbed sites. This situation potentially is a major concern, as many sites are planted with a limited number of native species that may not persist or allow natural development of other species. Specific guidelines matching disturbances with adapted species have been prepared for large, common disturbances, but this information is often based on preliminary data; modifications may be needed for specific cases (Monsen and Stevens, in preparation).

Species Selection and Development

The primary goal of early revegetation efforts was to recover site productivity and stability with the best adapted and most productive plant materials available, regardless of the materials' origin or source (Plummer and others 1968). Native and introduced species were screened, tested, and used. Testing and development of plant materials has two distinct phases (McArthur 1988). The first is to discover and characterize (evaluate) plant germplasms that are useful for particular management objectives. This phase depends on discovering natural plant populations and their uses in land management practices. The second phase is the manipulation of plant materials by selection and other genetic procedures. Currently, land managers, ecologists, and researchers seem to be moving toward a consensus that whenever possible, native plant materials indigenous to the site should be used and that native, natural ecosystems should be restored whenever possible. In counterpoint, Asay and others (1992) advocate using the most productive and best-adapted plant materials, whether those materials are native or introduced. Our own view is that site rehabilitation work should be divided into two broad categories:

Type 1—Sites that are badly degraded or otherwise changed by loss or change of topsoil or by radical change of topography, hydrology, or fire cycles, or that have a high-priority use such as watershed protection.

Type 2—Sites that have a good potential for restoration to natural condition.

Type 1 sites can be treated with the traditional revegetation technique of using all desirable plant materials, including introduced plants, to stabilize the site and fulfill important land management objectives such as forage production, weed control, water harvesting, and so forth. For Type 2 sites the management objective should be to maintain and restore the sites to a natural state. In order to meet this objective, these sites should have their natural topsoil, topographic, and hydrologic regimes in place.

Utility of Introductions—Traditionally, introduced plant materials have been used as the preponderant material in most wildland rehabilitation projects (Hafenrichter and others 1968; McArthur 1988). By preponderant we mean that a greater volume of seed was used, we suspect that if other measures were used, such as the number of accessions or taxa, native plant materials would predominate. In McArthur's (1988) summary of plant materials available for rangeland seedings, about two-thirds of the herbaceous (grasses, forbs) accessions were native and about 90 percent of the woody materials were native. Much of the commercially available herbaceous material is introduced, for instance, crested and other wheatgrasses (*Agropyron* spp.), smooth brome (*Bromus inermis*), orchardgrass (*Dactylis glomerata*), Russian wildrye (*Psathyrostachys juncus*), alfalfa (*Medicago* spp.), clover (*Trifolium* spp.), and small burnet (*Sanguisorba minor*).

The introductions that have been commonly used share a suite of characteristics including ease of establishment from seed, seedling vigor, broad adaptability, competitive ability, forage value, the ability to withstand grazing, and the ability to serve as a good ground cover. Cultural practices for ample seed production have been developed, and good supplies of reasonably priced seed are available.

Development of Natives—Sampson (1917) pioneered the use of native plant materials for revegetation and soil stabilization at the Great Basin Experimental Range in central Utah. However, because of the competitiveness, adaptability, and availability of introduced plant materials, native plant materials were used relatively infrequently for several decades. Big-game habitat programs and soil stabilization programs (such as windbreaks and roadside beautification) began in the late 1940's and early 1950's. Several State and Federal agencies as exemplified by the State/Federal cooperative effort in Utah led by A. P. Plummer promoted this work (McArthur 1992; Plummer and others 1968). In these programs use of native plants was emphasized, including adaptation, cultural care, seed production and processing, and plant establishment. Native plant communities were recognized as important for seasonal forage and soil stabilization. Other important uses of native plants were for horticultural and aesthetic purposes and for multiple-use management. These uses resulted in a growth of native plant programs, including the development of research testing programs, studies of plant biology, agronomic rearing and planting of seed and transplant stock, the development of appropriate planting equipment and seed processing facilities, and the establishment of a viable commercial native plant seed industry (Blaisdell 1972; McArthur 1988).

Equipment Development, Site Preparation, and Seeding Methods

The first range and watershed seeding projects used farm implements including horse drawn plows, grain drills, single row seeders, brush drags, and harrows (Platt and Jackman 1946). Many items were not adapted to irregular and rough terrain; consequently, equipment was modified to improve its features and its durability (Pellant 1988). However, it was obvious that specialized equipment was lacking, and considerable research was directed to seedbed ecology, site preparation, and weed control (Stark and others 1946). This work aided in designing and developing needed equipment. Plows, disks, seeders, and harvesters are constantly being developed for conventional agriculture, but commercial equipment companies have largely been unwilling to develop range and watershed equipment (Larson 1980). The small potential market for such equipment cannot sustain expensive investment in research and development.

Early researchers recognized the need to work collectively to develop needed equipment. In 1942, a group of range scientists organized the "Equipment Development Committee" that initially addressed the development of a disk and drill seeder for rangeland conditions. This committee later became the Vegetative Rehabilitation and Equipment Workshop (until 1989) and the Rangeland Technology Equipment Council (since 1990). It has successfully advanced other useful implements; it continues to function as an independent organization with membership from diverse organizations, agencies, companies, and services (Larson 1982; USDA Forest Service 1970, 1991).

Various types of equipment are needed for wildland rehabilitation projects. Researchers initially recognized the need for equipment to prepare seedbeds and eliminate weeds, including live plants and their seeds. Although restoration efforts were needed on steep slopes, most early equipment was designed using farm-type prime movers—wheel tractors. Consequently, most equipment was developed to treat level sites with deep, rock-free soils.

Early range scientists were strongly influenced by their agronomy training and farming experiences (Bridges 1942; Hull and Johnson 1955; Short and Woolfolk 1943; Stewart and others 1939). Their approach to range seedings has significantly influenced the methods and equipment used today. An important development was the adoption of seedbed preparation practices adapted from conventional farming. Under this system, plowing or disking is used to eliminate existing competition, loosen, and overturn the seedbed. This practice normally removes all existing vegetation; it may even destroy the seedbank. Drill seeding using row-type seeders that deposit the seed at a uniform depth usually follows (Forsling and Dayton 1931; Robertson and Pearse 1945). The use of these practices has conveyed the impression that all sites need to be plowed and seeded, using standard drill spacing and seed placement practices. In addition, the practices have usually combined mixing and planting seeds of all species together in the same rows and at similar planting depths (Cornelius and Talbot 1955; Rummell and Holscher 1955). All seeded species were assumed to be equally competitive and able to establish and persist in uniform rows. Conventional drills have been modified to adjust row spacings, seeding rates, and planting depths, and to allow seeds of different species to be separated so the requirements of native species can be accommodated (Pellant 1988; Plummer and others 1968). Although plowing and drilling are appropriate treatments in many situations, many land managers mistakenly use conventional tillage practices without regard to site conditions.

The advancement of site preparation and planting equipment has progressed slowly. Some highly useful and functional machinery has emerged, including the anchor chain, Hansen Seed Dribbler, interseeders, and aerial seeding devices (Bouse and others 1982; Dewald and Wiedemann 1985; USDA Forest Service 1991; Wiedemann 1983; Wiedemann and others 1980; Wiedemann and Smallacombe 1989). Recently a number of highly useful drills have been developed by commercial equipment companies (Pellant and Boltz 1992; Wiedemann 1983, 1991; Wiedemann and Cross 1981). These drills can plant into unprepared seedbeds, plant different seeds simultaneously at different planting depths, and dispense trashy seeds through separate planting boxes.

The adaptation and use of the anchor chain, coupled with aerial seeding, has been the most significant practice developed to seed steep, irregular, and rocky sites (Plummer and others 1968). The combined techniques unfortunately, are not well understood or accepted by some land managers. Chaining can effectively create the desired soil disturbance required to cover seeds, yet retain existing plants. Trained operators can regulate the degree of soil disturbance by using chains of different weights, varying the speed, direction, and positioning of the tractors pulling the chain, or by using swivels at different positions in the chain.

Seeds of all species cannot be seeded with all drills or with all planting devices; this includes aerial broadcasting. In addition, all species are not able to establish in combination with other species. The seedbed requirements of many species have been determined and planting equipment has been developed to accommodate most seeds.

Perhaps the most important contribution that has facilitated seeding or planting wildlands has been the development of site preparation and planting equipment. Although a number of highly specialized plows, disks, seeders, and harvesters have been developed for conventional agriculture, relatively few machines have been designed especially for irregular topography. Many existing items function extremely well, but with the exception of the rangeland drill, most are not widely known to land managers. A serious concern is the lack of commitment and research to produce needed implements. Research dealing with artificial rehabilitation requires considerable investment; including study of seedbed ecology and development of planting equipment. Unless the sale of a new machine can recover research costs, progress is stymied.

Problems Associated with Conventional Rehabilitation Practices

So far, conventional rehabilitation has relied on several introduced grass species or species complexes: crested wheatgrass (*Agropyron cristatum*) complex, intermediate wheatgrass (*Agropyron intermedium*) complex, smooth brome, orchard grass, Kentucky bluegrass (*Poa pratensis*), hard fescue (*Festuca ovina*) complex, timothy (*Phleum pratense*), tall oatgrass (*Arrhenatherum elatius*), and meadow foxtail (*Alopecurus pratensis*). These grasses have proven well suited to stabilize disturbed sites, diminish soil erosion, provide high forage yields, enhance seasonal livestock grazing, control the spread of weeds, and minimize management input (Plummer and others 1968). These are desirable traits but pose a dilemma because their longevity, adaptation, and competitive ability have made it difficult for native plants to recover or reestablish.

A particular problem is recruitment of native plants such as mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) and antelope bitterbrush (*Purshia tridentata*) in closed stands of these introduced grasses (Monsen and Shaw 1983b). All these grasses are sward-forming or competitive bunchgrasses. Populations of some native plant species decline after introduced grasses become established (Walker and others, this proceedings).

Site preparation required to establish new grass stands by seeding often eradicates existing native plant populations and prevents native plants from recruiting. This reduces biodiversity. Native animal populations are also disrupted; their interactions and numbers are skewed. Management of these sites with introduced plants and adjacent natural plant communities sometimes causes problems because animal concentrations, fire regimes, and other natural phenomena may be disrupted.

Applying Knowledge of Rehabilitation Practices and Plant Ecology to Restoration

The techniques developed for rehabilitation of rangeland sites provide a basis for restoration techniques. Site analysis indices developed for remedial treatments are well suited for other rehabilitation measures. Planting techniques for uneven terrain and for mixed species have been developed. Many restoration planting sites will require using techniques developed for rehabilitation.

Weed Problems

Most areas that need rehabilitation, including restoration, are those that are occupied by weeds. Sites occupied by weeds do not respond to secondary successional processes as do sites free of weeds. Weeds must be removed for many of these areas to heal. Some weeds are highly competitive. However, if existing weed problems are not treated, conditions can deteriorate further. For example, cheatgrass has displaced native plant communities over immense areas, but is now being replaced by medusahead rye in some areas (Hironaka 1961). Sites occupied by medusahead rye are much more difficult to rehabilitate than areas dominated by cheatgrass. Likewise, rush skeletonweed is invading sites dominated by cheatgrass (Piper 1983) and does not respond to control by conventional tillage as does cheatgrass. New or additional means of control are needed.

Native Species Ecology

The existing knowledge of native species synecology (ecology of communities) and autecology (ecology of individual species) needs to be better used in developing restoration projects. A wealth of published information exists on the distribution, adaptation, reproduction, seedbed ecology, agronomic culture, and field planting of many native species, although much work remains to be done (Blauer and others 1975, 1976; Fraiser and Evans 1987; McArthur and others 1979; Monsen and Shaw 1983a; Monsen and Stevens, in preparation; Plummer and others 1968; Wasser 1982).

Species composition and density is not static in native communities. Restoration procedures ideally should stimulate secondary succession toward a late-seral community. All the components for the desired community should be identified at the beginning of the restoration effort, including the residual plants and the seed bank or propagules. The restoration plan should allow for natural population and community fluctuations. The plan should also recognize that environmental and climatic conditions may drive community development in several possible directions.

Evaluation of results is important. Restoration science is new and needs validation on as many sites and under as many conditions as possible. We recommend that managers evaluate conditions before and after treatment, publishing the results.

Indigenous Species

Depending on how "pure" the particular restoration effort is to be, plant materials may come from native "cultivar" or germplasm stock or from populations indigenous to the region or site (Young, this proceedings). For restoration to be implemented on a broad scale, we believe that the native seed industry needs to be involved in the projects.

To date, industries have evolved to furnish the seed and planting stock required to support rehabilitation programs. Regional seed companies and nursery centers are developing native plants of local ecotypes for restoration. Commercial seed companies and nursery centers also are developing the cultural practices to propagate seeds and planting stock of a number of native species. Federal, State, and private seed companies and research and development groups have been established to develop plant materials for rehabilitation and restoration plantings. They are developing and testing many native and introduced species. Restoration programs will benefit from existing seed and plant centers that can supply native species for a wide range of conditions.

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Landscape Dynamics and Arid Land Restoration

Steven G. Whisenant

Abstract—Restoration strategies that initiate autogenic succession—by using rather than by combating natural processes—have great potential for arid ecosystems. Damaged ecological processes must be restored to restoration sites. Landscape dynamics can be directed toward restoration objectives with strategies that: (1) reduce or eliminate the causes of degradation; (2) address soil degradation and initiate soil improving processes; (3) establish vegetation that addresses microsite availability, soil improvement, and nutrient cycling problems; and (4) arrange landscape components to reduce detrimental landscape interactions while increasing synergies among landscape components. Landscape configuration can be designed to: (1) encourage synergies among landscape components; (2) reduce nutrient losses to adjacent landscape components; (3) facilitate natural seed dispersal mechanisms; (4) attract beneficial animals; and (5) reduce detrimental animal activities.

Artificial revegetation of arid ecosystems is expensive, risky, and the benefits are often short-lived. Current approaches to ecosystem rehabilitation are extensions of traditional agronomic technologies developed under more hospitable climates. These agronomic approaches produce linear rows of uniformly spaced plants rather than naturally occurring vegetative patterns. Ecological restoration is an alternative approach that attempts to minimize management intervention (and expense) by stimulating natural successional processes to develop stable structural and functional dynamics.

Restoration efforts have traditionally been designed and implemented for specific sites—with the boundaries determined by fences or ownership patterns. These restoration efforts focused on site specific attributes and objectives without considering interactions with the surrounding landscape. Since all parts of a landscape are functionally linked, this site specific focus contributed to several problems. The failure to view restoration sites as integral components of a larger, highly interconnected landscape has often produced inherently unstable "restored" landscapes. The processes and products of unstable landscape components can disrupt the stability of the other parts, resulting in widespread failure throughout the landscape. We have the potential to improve restoration success by incorporating landscape processes essential in the establishment and maintenance of ecological systems.

Most rangeland improvement recommendations begin with the premise that activities (investments) should focus on sites with the greatest potential for a positive economic return. That is sound advice from a financial investment viewpoint. However, the failure to consider landscape interactions may create unanticipated problems. For example, in arid regions, depositional areas at the base of hills are commonly selected for restoration efforts because of their inherently better soil, nutrient and water relations. The best restoration effort on those sites may fail due to problems on other parts of the landscape. Accelerated sheet erosion on hill slopes can lead to channel deposition that steepens the slope gradient. This initiates channel entrenchment that creates steep channel banks susceptible to mass failure or slumping. This leads to lateral erosion of the stream channel against an adjacent hill slope and further steepens the hill slope gradient and removes the concave portion of the valley bottom. This increases surface erosion rates while reducing the opportunity for sediment storage at the bottom of the hill slope. Other landscape scale problems (such as those involving nutrient cycling, geomorphology, hydrology, herbivory, granivory, propagule transport) are less obvious, but can be just as disruptive.

Landscapes are an assemblage of different vegetative elements that may have patches or corridors of other vegetation types embedded in a matrix of a distinct vegetation type. Unique landscape combinations are formed from interactions of geomorphology, hydrology, colonization patterns, and local disturbances (Forman and Godron 1986). The landscape matrix is the primary vegetation type surrounding patches of other vegetation types. The distribution—not the movement—of energy, materials, and species in relation to the sizes, shapes, numbers, kinds, and configurations of landscape elements makes up the 'structure' of that landscape (Forman and Godron 1986). Landscape function—or dynamics—is the interaction among the landscape elements that involves the flow of energy, materials, water, and species among the elements.

The concepts of landscape restoration ecology can be applied to all ecosystems, but this discussion is focused on large arid ecosystems that cannot be completely restored by artificial methods. Western North America is an excellent example, since it contains millions of hectares that require restoration or rehabilitation, but the need far exceeds our ability to provide it. This situation is common, perhaps the rule rather than the exception in arid and semi-arid ecosystems. Our success in rehabilitating these systems has not been good, but even if we had the capability to restore them, we would never have the money to apply that technology to all the areas that need it. Restoration strategies that initiate autogenic succession—by using rather than by combating natural processes—are most appropriate for extensively

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managed arid ecosystems. The objectives of this paper are not to outline a comprehensive restoration program—but to introduce concepts that contribute toward landscape-level planning of restoration efforts on arid lands.

Directing Landscape Dynamics

The restoration of degraded arid lands has several limitations: (1) resource (water, nutrients, soil organic matter, propagules) levels are uniformly low; (2) harsh microenvironmental conditions limit seedling recruitment; and (3) animals have a greater potential to disrupt restoration efforts in arid systems. Since plant establishment and growth in arid lands is limited by available water, successful restoration strategies increase water availability and/or reduce evaporation and transpiration. Water availability is increased with strategies that harvest water, increase infiltration and increase water retention. Evapo-transpiration can be reduced with strategies that lower soil and leaf temperatures (shade) and increase litter accumulations on the soil surface. Herbivores and granivores may have large impacts on the vegetation of arid landscapes. They affect the vegetation directly by consuming the vegetation and seeds and indirectly by altering the fire regime. Animals and the arrangement of landscape components also influence the movement of seed across landscapes.

The application of landscape considerations to arid land restoration problems might focus on capturing flows of scarce resources across the landscape or on reducing fragmentation and reintegrating fragmented landscapes. Tongway (1991) suggested a landscape approach that identifies processes controlling the flows of limiting resources into and through landscapes. Hobbs (1993) argued that fragmentation of ecosystem processes leads to significant changes in the water and nutrient cycles, radiation balance and wind regimes. This is particularly important since degraded ecosystems have leaky nutrient cycles compared to undamaged landscape elements (Allen and Hoekstra 1992). Aronson and others (1993a) presented a general model for the restoration and rehabilitation of degraded arid and semi-arid ecosystems that included "vital ecosystem attributes," of which several are landscape scale attributes.

There are several examples of landscape level planning of restoration or rehabilitation activities. Aronson and others (1993b) described an ecologic and economic rehabilitation program for landscape scale problems of a degraded Espinales landscape in central Chile. Thurow and Juo (1991) described an integrated management program for an agropastoral watershed in Niger and argued that watersheds are the most appropriate level for manipulating hydrological and geochemical processes. Our understanding of the functional interactions controlling landscape dynamics is far from complete and our ability to direct those processes is less well developed. However, existing theoretical, empirical, and practical information provides insight that suggests the elements of a new paradigm for arid land restoration.

Processes to Increase Resource Availability

Landscape considerations are incorporated into arid land restoration efforts with strategies that: (1) reduce or eliminate the causes of degradation; (2) address soil degradation and initiate soil improving processes; (3) establish vegetation that addresses microsite availability, soil improvement, and nutrient cycling problems; and (4) arrange landscape components to reduce detrimental landscape interactions while increasing synergies among landscape components.

Remove Causes of Degradation—Deforestation and abusive grazing practices reduce soil organic matter, litter, vegetation and infiltration. The reduced perennial plant cover associated with degradation results in less organic matter being produced and added to the soil. As soil organic matter is reduced, aggregate stability is reduced and the soil is more easily crusted by raindrop impact. Raindrops falling on exposed soil surfaces with low aggregate stability detach fine soil particles from the soil surface. These fine particles fill soil pores and create soil surface crusts with a continuous surface sealing. Soil surface crusts (soil sealing) are "thin layers of compacted soil with greatly reduced hydraulic conductivity, capable of decreasing the infiltration of soil surfaces subjected to rainfall" (Bohl and Roth 1993). After drying, surface crusts seal the soil surface, reducing infiltration and aeration. Deforestation, overgrazing and cultivation degrade the vegetation and initiate the process of desertification.

Desertification is a common result of degradation. Desertification is the spread of desert-like conditions (Lal and others 1989), or the "…impoverishment of arid, semiarid and sub-humid ecosystems by the impact of man's activities. This process leads to reduced productivity of desirable plants, alterations in the biomass and in the diversity of life forms, accelerated soil degradation and hazards for human occupancy" (UNEP 1977). About 6 million hectares is irretrievably lost or degraded by desertification each year and about 135 million people are severely affected by desertification (UNEP 1984). In 1975 it was estimated that in the Sudan the desert land had expanded south 90 to 100 km in about 17 years (Tivy 1990). Desertification is a dynamic self-accelerating process resulting from positive feedback mechanisms driving a downward spiral of land degradation (Tivy 1990). Desertification has two main physical characteristics—vegetative degradation and soil degradation. Restoration of these degraded sites is restricted by several site-specific obstacles that must be addressed on each site (Table 1). There are also several indicators that may suggest destructive landscape-level interactions with the potential to disrupt restoration efforts (Table 2).

Management approaches to the restoration of degraded ecosystems have emphasized artificial revegetation or improved grazing management. Although improved grazing management must be part of any long-term management plan, current ecological understanding suggests it is unlikely to significantly improve severely degraded ecosystems. Even complete removal of livestock does not insure

Table 1—Site-specific obstacles to aridland restoration. Although these obstacles have local origins, they may cause problems on other parts of the landscape or may also occur elsewhere in the landscape.

Deterioration of soil structure (surface crusting, compaction, reduced macroporosity, low aggregate stability, reduced infiltration)
Wind or water erosion
Reduced soil organic matter
Reduced water holding capacity
Soil salinity levels elevated beyond natural conditions
Nutrient depletion
Reduced capacity to retain nutrients
Reduced vegetative and litter cover
Low functional and species diversity
Depleted seed bank diversity
Reduced activity and diversity of soil organisms

secondary succession leading toward recovery (Walker and others 1981; Whisenant and Wagstaff 1991; Friedel 1991; Laycock 1991). The traditional successional concept of vegetation returning to a predictable, relatively stable-state following disturbance is not valid in many arid ecosystems (Westoby and others 1989; Friedel 1991; Laycock 1991). Most arid ecosystems seem to have multiple, alternative stable-states (Friedel 1991; Laycock 1991). Movement between these steady-states (i.e. ecosystem recovery) requires significant management inputs (Friedel 1991). Thus, despite the economic problems of rehabilitating degraded arid ecosystems, some management intervention is required for improvement.

Soil Improvement—Soil erosion is the most common and damaging form of soil degradation since it degrades the physical, chemical and biological components of the soil. Excessive erosion depletes nutrients, decreases rooting volume, reduces plant-available water reserves—and most tragically—is irreversible. Wind erosion is a serious problem in arid and semi-arid regions. The United Nations Environment Program (UNEP 1977) estimated that 80% of the 3,700 million ha of rangeland around the world are affected by wind erosion. Wind erosion has greater impacts on the fine, nutrient-rich components of soil, such as silt, clay and organic matter, leaving less fertile sand, gravel and other coarser materials. The rate of wind erosion generally depends on soil erodibility, surface roughness, climate, the unsheltered travel distance of wind across a field, and vegetative cover. Soil surface crusts reduce permeability and accelerate runoff and erosion. On bare soil surfaces, running water is not slowed or absorbed by organic matter, and the water gains velocity and energy, producing rills, channels and eventually gullies. Several problems occur as soil structure deteriorates, but the more common problems on arid lands are surface crusting, accelerated erosion, salinization, reduced macroporosity, reduced aggregate stability, and reductions in the diversity and activity of soil organisms. These processes reduce infiltration and increase water loss from runoff and evaporation. As soil water reserves are depleted, less vegetation is produced and the degradation of soil condition accelerates.

Soil improvement strategies should be directed toward the eventual goal of retaining and using water where it falls (Sanders 1990). The only sustainable method of accomplishing these objectives is to reduce the amount of bare ground by establishing a vegetative cover. Unfortunately, the potential vegetative cover is typically low in arid ecosystems. Sanders (1990) suggested a strategy to improve degraded soils that has both immediate and long-term objectives. The immediate objectives are to: (1) prevent soil crusts; (2) reduce soil erosion; and (3) retain the precipitation on site. These immediate objectives are strongly correlated but can be considered separately. They are critical steps toward longer-term objectives that require more time for development: (1) increase soil organic matter content; (2) increase water holding capacity; (3) improve soil structure; and (4) restore sustainable nutrient dynamics to the soil system. The immediate objectives are met by increasing the vegetative cover or increasing mulch and litter cover on the soil surface. This reduces the detrimental effect of raindrop impact on the bare soil surface, which is the primary cause of crusting. Providing soil cover reduces

Table 2—Indicators suggesting problematic landscape-level interactions with the potential to disrupt arid land restoration efforts.

Gully cutting (upslope or downslope from restoration site)
Excessive soil deposition
Altered water table (might be higher, lower, or of reduced quality)
Low volume and diversity of seed immigrants
Accelerated nutrient losses to adjacent landscape element (fluvial, aeolian, or subsurface processes)
Low natural recruitment of plants
Increased salinity resulting from accelerated run-on of low quality water
Inadequate pollination
Excessive animal damage (herbivory or seed predation)
Reduced landscape diversity

the extremes of soil temperature, reduces evaporation, reduces erosion, increases infiltration of water into the soil, and increases soil water content. Although arid environments may not have the potential to produce enough vegetation to cover much of the soil surface, the cover and resulting benefits should be maximized.

Soil surface treatments such as pitting, terracing, or microcatchments reduce runoff and increase infiltration. Microcatchments, pits, and contour furrows retain water and increase infiltration and storage of water. Soil modification procedures have a finite design life determined by erosion rate, depth and precipitation events. Previous pitting and contour furrow uses on arid rangelands concentrated on the establishment of herbaceous species. In general, those practices greatly improved establishment success and productivity for several years. However, they were temporary and seldom lasted much beyond the design life of the soil modification and did not expand benefits beyond the soil depression.

Reducing crusting and erosion while increasing the infiltration and retention of water in the soil improves plant establishment and growth. This begins the accumulation of soil organic matter which improves physical, chemical and biological characteristics of the soil. As this process continues, water and nutrient retention are improved and soil structure is increased. Plants contribute to soil organic carbon reserves through decomposition of leaves and stems falling on the soil surface and through exudates from roots and decomposition of dead root material. These processes of soil development increase vegetation production and accelerate the rate of soil development. The processes of vegetation and soil development are mutually dependent. Ultimately, the nutrient dynamics of the system is stabilized.

Soil biological properties are degraded through the effects of reduced organic matter, reduced biological activity, reduced diversity of soil flora and fauna, and unfavorable changes in biological processes (Lal and others 1989). This reduced biotic activity adversely affects nutrient cycling, soil physical properties and makes soils less hospitable for plant growth. Organic matter quality may be another important factor in the recovery, persistence and stability of the soil biota. The reduced soil biotic diversity and activity typical of degraded soils (Fresquez and others 1987; Mott and Zuberer 1991), reduce enzymatic capability of the soil microflora and thus hinders nutrient cycling and organic decomposition. Although bacterial numbers tend to recover rapidly following disturbance, the species balance is altered in favor of ruderal species capable of rapid growth on readily available substrates. These ruderal species correspond to r-selected organisms (Andrews and Harris 1986) and often dominate following disturbance, but are less abundant under stable, climax conditions. In contrast, autochthonous microbes metabolize difficult-to-degrade organic matter (OM), have slow growth rates, high affinities for growth limiting substrates and high starvation survival abilities (Andrews and Harris 1986).

Recalcitrant organic materials produce low, but continuous OM sources that persist until perennial root systems begin to supply organic matter (Santos and others 1981; Santos and Whitford 1981; Whitford 1988). In arid ecosystems bark and wood chip amendments can contribute to a stable below-ground biota that facilitates a more sustainable above-ground flora (Whitford and others 1989). Severely depleted soils treated with readily decomposed organic materials developed soil biota and processes similar to less damaged soils, but the beneficial effects lasted only two years (Whitford 1988). Unlike cultivated soils where nitrogen immobilization by high Carbon/Nitrogen ratio materials is undesirable, recalcitrant organic materials may be desirable in arid environments (Whitford and others 1989).

Decomposition is an essential nutrient cycling process (Whitford and others 1989) regulated by water and organic matter availability in arid ecosystems (Steinberger and others 1984). Stable soil decomposition processes require a diverse soil biota (Santos and others 1981; Santos and Whitford 1981). Decomposition potentials of severely disturbed soils may not recover for many years (Harris and others 1991). Respiration-to-biomass ratios (soil metabolic quotient) in German mined soils were not stabilized 50 years after mining (Insam and Domsch 1988), although soil metabolic quotients were found to decrease with each increasing successional stage (Insam and Haselwandter 1989). This decrease is probably a reflection of K-selected soil organisms beginning to dominate. However, these studies of soil metabolic quotient relative to rehabilitation progress were conducted in mesic environments and have not been examined in arid ecosystems. This possible relationship between the metabolic quotient and succession suggests the potential to influence the speed, direction, and stability of arid land restoration by manipulating the microbial community.

Vegetation Strategies—Vegetation can be used to mediate harsh microenvironmental conditions; capture wind- and water-borne soil, nutrients, and organic matter; improve soil conditions; increase soil nitrogen; and create structural diversity to attract birds that transport seed. Woody plants capture wind-blown organic materials, soil particles, nutrients (Virginia 1986) and microorganisms (Allen 1988). Shrubs also improve microenvironmental conditions by moderating wind and temperature patterns (Allen and MacMahon 1985; Vetaas 1992). Not only do shrubs improve soil and microenvironmental conditions, they may reduce nutrient and water losses from disturbed landscapes. Perennial, nitrogen-fixing legumes are believed to be essential components of many arid and semi-arid ecosystems (Jenkins and others 1987; Jarrell and Virginia 1990) as well as in alternative steady-state systems (Knoop and Walker 1985). Woody legumes can benefit disturbed arid landscapes with low water, nitrogen, and phosphorus levels (Bethlenfalvay and Dakessian 1984) because of their ability to develop symbiotic associations with both rhizobial bacteria and mycorrhizal fungi (Herrera and others 1993). Keystone species are species believed essential to ecosystem structure and function (Westman 1990) and their inclusion may facilitate the restoration of disturbed ecosystems (Aronson and others 1993a). Woody legumes are often considered keystone species in disturbed arid and semi-arid ecosystems and should be among the first species returned (Aronson and others 1993b) during restoration efforts.

Recent studies also suggest the benefits of restoration strategies using species producing low-quality litter in degraded arid ecosystems. Plants with slow growth and plants producing low-quality litter are uniquely adapted to low-nutrient ecosystems (Aerts and van der Peijl 1993). Nutrient-poor ecosystems are dominated by species with a low potential growth rate and nutrient-rich ecosystems are dominated by species with a high potential growth rate (Grime and Hunt 1975; Poorter and Remkes 1990; Poorter and others 1990). In nutrient-poor environments, nutrient conserving species develop a higher equilibrium biomass than species with higher nutrient loss rates, although it may take 3 to 5 years to reach that higher equilibrium (Aerts and van der Peijl 1993). Nutrient conserving species produce slowly decomposing litter. Thus, in degraded arid ecosystems, it is likely that species producing recalcitrant litter have greater potential to produce a sustainable system. These restoration sites are also less attractive to large herbivores from other parts of the landscape.

Landscape Design—There are significant benefits that can result from specific landscape arrangements. We can arrange landscapes to: (1) encourage synergies among landscape components; (2) reduce nutrient losses to other landscape components; (3) assist natural seed dispersal mechanisms; (4) attract beneficial animals such as pollinators and seed vectors; and (5) reduce detrimental activities of large herbivores and seed predators.

Restoration efforts have the largely unrealized potential to work with underlying landscape processes rather than against them by developing strategies that incorporate and direct natural processes. Disturbances, such as cultivation or abusive grazing practices, homogenize arid landscapes by uniformly reducing water availability, soil nutrients and organic matter. This spatial resource leveling produces landscapes where limiting resources are uniformly below the establishment threshold for desirable plants. Under these circumstances, physical or biological features that concentrate resources may initiate recovery by enabling plants to establish and grow on that part of the landscape. This initiates a series of soil and microenvironmental improvements that begin to positively influence an increasingly larger percentage of the landscape. As an example, total productivity in arid and semi-arid ecosystems is believed to be higher if water is distributed in patches rather than uniformly (Noy-Meir 1973).

Recognition that arid ecosystems often have clustered distributions of plants, nutrients, organic matter, and water lead to the term 'fertile islands' (Charley and West 1977; West and Klemmedson 1978; Garner and Steinberger 1989; Schlesinger and others 1990). The sparse resources typical of many degraded arid ecosystems often occur in a clustered spatial arrangement. Soil depths, soil texture, organic matter, nutrient concentrations, irradiance patterns, wind speed, wind direction, and water storage differ greatly on a scale of a few meters. Microenvironmental parameters and soil characteristics vary around individual shrubs, resulting in microbial and plant organizational patterns interacting on a scale of a few centimeters (Allen and MacMahon 1985). This spatial variability affects seedling establishment and plant growth patterns that continue to modify microenvironmental and soil characteristics of the landscape. These spatial patterns suggest functional characteristics useful in restoring degraded arid ecosystems.

Fertile islands are variously viewed as natural triumphs of concentrating biological mechanisms over dispersing physical forces (Garner and Steinberger 1989), a symptom of degradation (Schlesinger and others 1990), or a tool for rehabilitation (Allen 1988). These alternative interpretations are—at least partially—a difference of perspective. Compared to a pristine desert grassland, with a relatively high and uniform distribution of resources (water, N, OM, and other soil resources), the conversion to a *Prosopis* sand-dune landscape, with its clustered resource distribution involves degradation (Schlesinger and others 1990). In contrast, clustered resource distribution on rehabilitated arid mine sites are an improvement over the homogeneous, but uniformly low resource levels on mined sites with little vegetation. Severely degraded ecosystems typically have uniformly low resource levels and high soil erosion rates. Reducing resource loss from severely degraded landscapes is a positive development, even if it partially redistributes resources within the landscape. However, there is much evidence that landscapes capture additional resources during fertile island development (Garcia-Moya and McKell 1970; Allen 1988; West 1989) and that long-term stability and productivity of disturbed arid landscapes may require the development of fertile islands (Allen 1988). Reducing resource loss and capturing or producing additional resources is an essential component of arid landscape restoration that contributes to long-term sustainability.

Garner and Steinberger (1989) hypothesized that biological transport mechanisms concentrate nitrogen (and probably other resources) while physical mechanisms primarily disperse nitrogen. However, physical mechanisms also concentrate resources in certain situations. Depressions in the soil accumulate water, soil, nutrients, organic matter and propagules. Thus, on barren sites, the concentrating effects of physical mechanisms (captured flows of water, nutrients, organic materials and propagules) may contribute to the initiation of autogenic landscape restoration. Thereafter, biological mechanisms (alteration of soil, microenvironmental, and nutrient relations by the vegetation—particularly shrubs) may dominate.

Flows of resources through the landscape are important because no landscape component is completely isolated. The dynamics of processes in individual parts of the landscape are strongly influenced by factors acting in other parts of the landscape. Tongway (1991) studied two Australian sites—one dominated by fluvial processes and the other by aeolian processes. At each location he identified source and sink areas and measured nutrient pool sizes and rate processes (microbial respiration rates). Sink areas were found to contain significantly higher nutrient pools and higher rate processes than the source areas. This led to the recommendation that restoration strategies link soil-vegetation-landscape associations to the dynamic processes controlling the flow of limiting resources. Tongway (1991) suggested a restoration strategy based on understanding how limiting resources ought to be distributed in the landscape and then promoting processes leading in that direction.

Human-dominated landscapes leak materials such as nutrients (Allen and Hoekstra 1992). Cultivated fields and severely disturbed natural ecosystems retain little of their annual nutrient input. Nutrient losses from disturbed landscape elements occur through aeolian, fluvial, and subsurface hydrologic processes. As an example, watershed fragments in Poland were identified where the groundwater flow from agricultural fields passed under a shelterbelt or small forest (Bartoszewicz and Ryszkowski 1989). Although aeolian and fluvial processes are more obvious and probably more widespread in arid ecosystems, nutrient losses through subsurface water flows also occur. Shelterbelts and remnants of natural vegetation within a cultivated landscape control the nutrient fluxes and increase the nutrient holding capacity of the entire landscape. Disturbed landscape elements with depleted nutrient pools may become a sink that accelerates nutrient losses from adjacent, undisturbed landscape elements. Careful landscape design contributes to the retention of nutrients, water, and other materials. The flows of water, energy, nutrients, propagules, soil and organic matter that flow into, within, and out of landscape elements can be manipulated to help achieve restoration objectives, since landscapes rich in ecotones are believed to lose fewer nutrients (Ryszkowski 1992).

Deep-rooted shrubs or trees on parts of a landscape may regulate the hydrology and nutrient retention capacity for the larger landscape (Ryszkowski 1989; 1992; Burel and others 1993; Hobbs 1993). Disruption of that function by removing the trees or shrubs can have catastrophic consequences for other parts of the landscape. Agronomic and degraded landscapes lose nutrients through subsurface flows of water and nutrients. Shelterbelts or patches of woody vegetation can effectively limit subsurface water migrations of nutrients (Ryszkowski 1989).

Vegetation—particularly woody plants—can improve microenvironmental conditions, capture flows of scarce resources, initiate soil development, and capture propagules. Soil nitrogen and OM content are often greater under shrubs than in adjacent interspaces. These increases have been attributed to nutrient mining by the roots and shrub litterfall (Charley and West 1975; West and Klemmedson 1978; West 1989; Garner and Steinberger 1989). Higher soil OM increases infiltration and water availability (Sprecht 1981) which contribute to greater mycorrhizal fungi and phosphorus availability (Allen and MacMahon 1985). These positive interactions increase herbaceous productivity under shrubs (Barth and Klemmedson 1978; Garcia-Moya and McKell 1970) and can be used to promote autogenic landscape restoration.

Fragmentation of natural systems can cause significant changes in the water and nutrient cycles, radiation balance, and wind regimes of the landscape (Hobbs 1993). For example, in a semi-arid portion of western Australia, removal of perennial vegetation reduced evaporation and altered soil water flows, such that peak runoffs increased and water tables rose, bringing stored salts to the surface. This fragmentation of the native landscape into remnant native patches and cultivated fields severely disrupted landscape and ecosystem processes. This not only degraded the agricultural potential but it reduced the restoration potential (Hobbs 1993). External influences on potential restoration sites are believed more important than internal processes and remnant vegetation management must be carried out in the context of the overall landscape (Hobbs 1993).

The shape and boundary form between two different landscape elements can affect rates of vegetation recruitment (Hardt and Forman 1989). Invasion rates of trees and shrubs from woodland patches into grassland patches was greater where grassland patches projected into woodlands (concave border) compared to where the woodland border was straight or convex (Hardt and Forman 1989). This suggests the possibility of directing natural succession by manipulating the boundary form on the scale of tens of meters. The size of an area and distance from seed sources are important considerations that we typically do not consider.

Landscape Configuration—Landscape configuration is a key factor in succession (Risser 1992). Successional changes are driven—in part—by differential species availability. The arrangement of landscape components partially defines their role as propagule donors or receptors. With artificial seeding activities we can manipulate the spatial configuration of propagule donor sites. By concentrating resources on many donor sites distributed over the entire landscape, we provide a continuing source of propagules. In arid ecosystems—where seedling establishment is episodic—this increases the odds of having seeds in the right place at the right time. The size of the problem and the shortage of available resources for arid land restoration suggest the value of a strategy that constructs landscapes with propagule donor patches. These donor sites will continue to release propagules into the adjacent “untreated” areas. The spread of a species is believed to be regulated by the dynamics of small scattered stands rather than by expansion of larger stands (Moody and Mack 1988). Landscape-scale restoration designs based on this principle might initiate long-term successional sequences. The stands containing species with wind-dispersed propagules might be designed with consideration of the prevailing wind direction during the season of dispersal. Ultimately, the success of this strategy in establishing plants on untreated areas also depends on land management practices and site specific factors.

Restoration efforts might be enhanced by strategies that favor certain groups of animals and discourage others (Archer and Pyke 1991). Where animals are important dispersal agents restoration plans should include provisions for suitable cover and food (Archer and Pyke 1991). The seed dispersal of bird-dispersed species into open fields was increased by an order of magnitude when natural or artificial perching structures were available (McDonnell and Stiles 1983). This suggests the potential to insure a continuing seed rain of those species by establishing woody plants as perching structures in certain landscape components.

The development of a comprehensive restoration plan that incorporates landscape-level dynamics requires several considerations (Fig. 1). Immediate and long-term soil improvement objectives are only achieved with vegetation restoration strategies that address soil problems. Sustainable vegetation strategies rely on landscape-level dynamics that contribute to ecosystem maintenance and development. Soil, vegetation, and landscape-level strategies must be fully integrated and developed to maximize beneficial interactions.

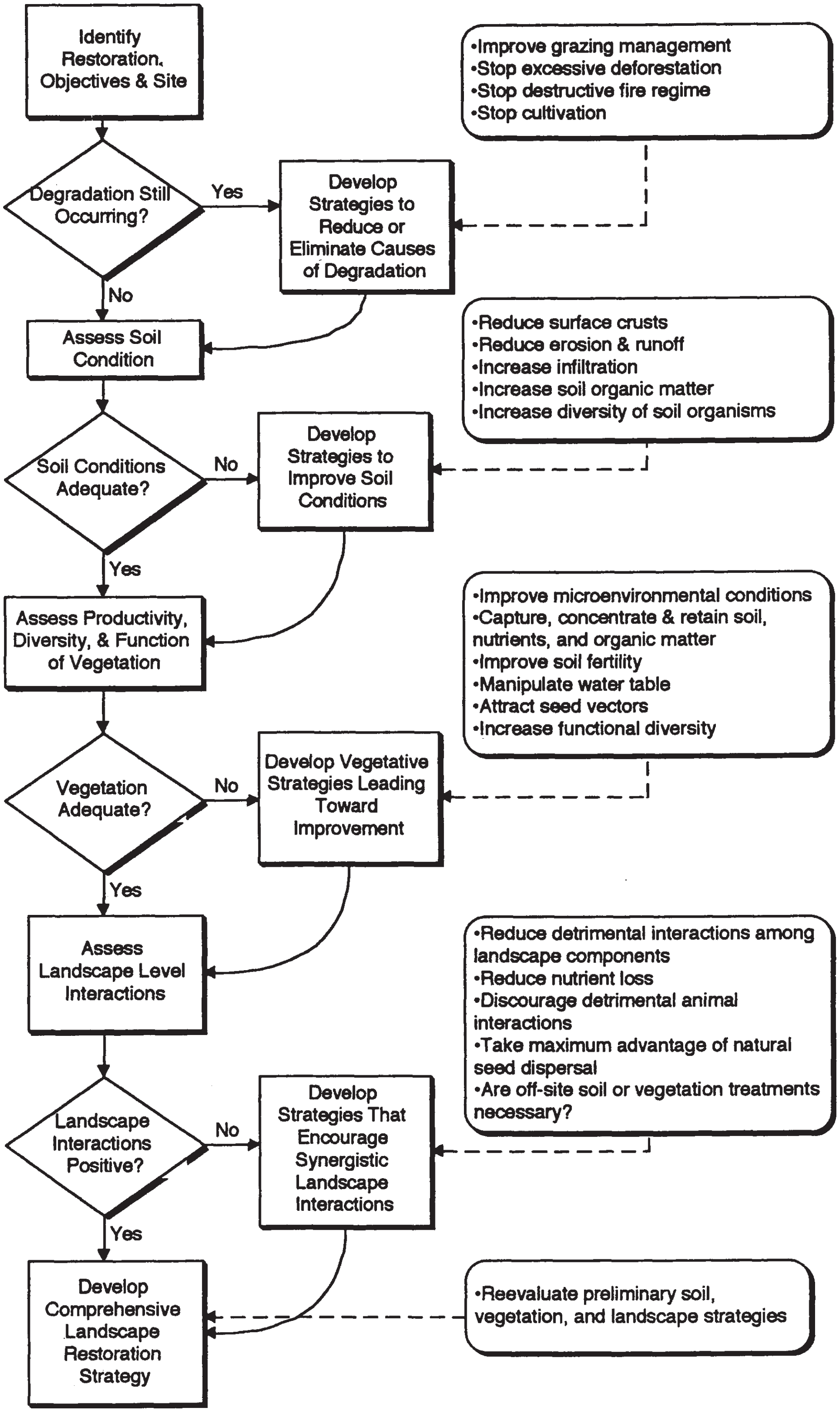

Figure 1—Planning process for incorporating landscape-level considerations into arid land restoration efforts. Planning is presented as a linear process, but implementing restoration efforts requires the simultaneous consideration of several factors. Potential restoration strategies are initially considered and subsequently reevaluated, revised, and incorporated into the overall landscape restoration plan. For example, although initial soil treatments may not involve vegetation (such as pitting or mulching), long-term soil improvement is determined by vegetation at the local and/or landscape level.

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Restoration and Revegetation

Seed Fate of Warm-Season Perennial Grasses

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Abstract—Vulnerability to moisture stress during germination, emergence, and seedling growth stages may be a factor in differential survival of seeded grasses in revegetation projects. The fate of eight warm-season perennial grasses under field rainfall and soil moisture conditions was studied for two summers in southern Arizona. Seeds were retrieved from the field periodically after rainstorms to determine species-specific responses to wetting and drying events. Native grasses germinated a significantly greater portion of their seeds in response to initial rains than the introduced Lehmann lovegrass (*Eragrostis lehmanniana*). Initial rains followed by long dry periods resulted in high native grass mortality. In contrast, ungerminated Lehmann lovegrass seeds remain germinable throughout dry periods following an initial rainfall event.

The use of native plants has become a common goal for revegetation projects in recent years. However, in semidesert grasslands, seedings of native warm-season perennial grasses often fail while plantings of introduced species are successful (Cox and others, 1982; Roundy and Biedenbender, 1994). For example, in southern Arizona, the introduced Lehmann lovegrass (*Eragrostis lehmanniana*) has been commonly used in rangeland revegetation because of its reliable establishment (Roundy, this proceedings). Natural populations of native grasses may exhibit an episodic recruitment pattern. A better understanding of the germination and establishment requirements of these species could be useful for planning revegetation strategies in this region.

Precipitation in the Sonoran Desert region is bimodally distributed, falling primarily in the summer and winter months. Summer rainfall is episodic, such that both the distribution of rain and total precipitation are variable. The amount of soil moisture that is available to a germinating seed follows the same pattern as precipitation and is episodic and highly variable.

The relationship between episodic rainfall and episodic natural recruitment suggests that native and introduced grass species may respond differently to soil moisture availability patterns (Roundy, 1994). This led us to ask the following research questions. First, how does seed fate response of a species vary with different patterns of rainfall and soil moisture availability? Second, does seed fate response to soil moisture vary for different species?

Seed fate is the ultimate destiny of a planted germinable seed. The fate of a seed depends on a combination of environmental cues and genetic characteristics of the species. Depending on the environmental stimulus, a planted seed could follow several different trajectories (Fig. 1). If germination requirements are met, a seed could initiate and complete germination. If conditions continue to be favorable, that germinated seed could then emerge, grow, and establish. If the germination requirements are not met, that same seed would not germinate, but could remain germinable in the seed bank. The seed could remain viable and become dormant under conditions that induce dormancy. Alternatively, environmental conditions or predation could result in seed or seedling mortality at any of these stages. In this paper we report studies that focused on seed fate response at the initial germination stage.

Methods

Field experiments were conducted in the summer months of 1992 and 1993. The research site was the Santa Rita Experimental Range, located approximately 65 km south

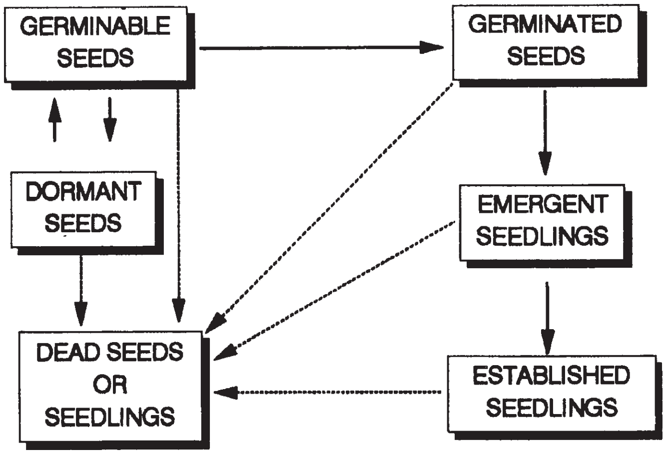

Figure 1—Possible fate of a planted germinable seed.

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of Tucson, AZ. The research plots were located on a 2 to 5% sloped alluvial fan at 1,100 m elevation. Approximately 60% of the 300 to 400 mm annual precipitation falls during the summer rainy season. The soil is a Comoro sandy loam (thermic Typic Torrifluvent) that varies in depth from 0.2 to 2.5 m (Hendricks, 1985). The plots are located in grassland dominated by Lehmann lovegrass with a few mesquite (*Prosopis juliflora* var. *velutina*) and burroweed (*Isocoma tenuisecta*). Trees and shrubs were cleared from the plots prior to beginning the experiments.

Soil moisture content was measured at depth intervals of 1 to 3, 4 to 6, 12 to 14, and 18 to 20 cm using buried fiberglass soil moisture sensors and measurement methods described by Roundy and others (1992). Five sensors were buried at each depth interval in each of three blocks. Ambient climatic data (precipitation, air temperature, relative humidity, wind speed, and incident solar radiation) were measured at the plots. Measurements were recorded every minute using Campbell Scientific Inc., CR-10 data loggers, and stored as an hourly sum for precipitation and as hourly averages for all other variables.

Seeds were planted twice each summer to examine how changes in rainfall patterns affected seed fate response. Seeds were planted on 16 June and 30 July in 1992, and on 15 June and 2 August in 1993.

The experimental design was a split-plot randomized block design; the main plot factor was grass species and the sub-plot factor was retrieval date. A total of eight species were studied. The six native and two introduced species planted are listed in Table 1. Nylon cloth mesh bags containing 10 pure live seeds of each species were buried under 3 to 5 mm of soil. Each bag contained seeds from only one species. For each species, six bags were buried in each of three blocks (N=18).

The design included two separate retrievals of the bags. In each retrieval three of the buried bags were removed and examined to determine the effect of different patterns of wetting and drying on seed fate response. The first retrieval was performed towards the end of the first wet-dry cycle. We defined the initial wetting event when the top 3 cm of soil was wet for at least 24 hr after that rain event. The first retrieval was performed after the top 1 cm of soil began to dry. The second retrieval followed after a series of wetting and drying events to see the effect of subsequent wet-dry cycles on germination and germinability.

Retrieval bags were removed from the soil and brought to the lab, where they were gently rinsed of soil and carefully opened. The seeds were inspected for germination. Field-germinated seeds were counted and listed as 'germinated.' Ungerminated seeds were placed on blotter paper in petri dishes, wetted up and placed in a 25 °C constant temperature incubator. The petri dishes were checked daily for germinated seeds. Seeds that germinated in the petri dishes were counted and listed as 'germinable.' Seeds that failed to germinate were listed as 'dead or dormant.' Analysis of the relative percentages of germinated, germinable, and dead or dormant seeds allowed us to determine the seed fate response of each species as a function of rainfall pattern and soil moisture availability.

Table 1—Warm-season grasses seeded in a seed fate experiment in southern Arizona.

Native	
cane beardgrass	*Bothriochloa barbinodis*
Arizona cottontop	*Digitaria californica*
plains lovegrass	*Eragrostis intermedia*
sideoats grama	*Bouteloua curtipendula*
green sprangletop	*Leptochloa dubia*
bush muhly	*Muhlenbergia porteri*
Introduced from South Africa	
Lehmann lovegrass	*Eragrostis lehmanniana*
Cochise lovegrass	*E. lehmanniana* x *E. tricophora*

Results

Rainfall and Soil Moisture Patterns

The 1992 rainfall patterns and resulting soil moisture availability were strikingly different than the patterns in 1993. The plots received 96 mm of rainfall in July 1992 (Fig. 2). The rainfall was fairly well distributed, resulting in relatively high soil moisture for at least seven days following the first rain. In August 1992 the plots received 115 mm of rain following the 30 July planting (Fig. 3). Rainfall during this period was extremely episodic; nearly 90 mm fell in one 24-hr period. The resulting soil moisture availability was also sporadic and inconsistent over time. Therefore, in 1992 soil moisture availability was more consistent in July than in August.

The seasonal distribution of summer rainfall in 1993 was very different from 1992 (Figs. 4 and 5). The plots received 33 mm of rain during July. The first rainfall was an isolated 11-mm event that resulted in a rapid increase and

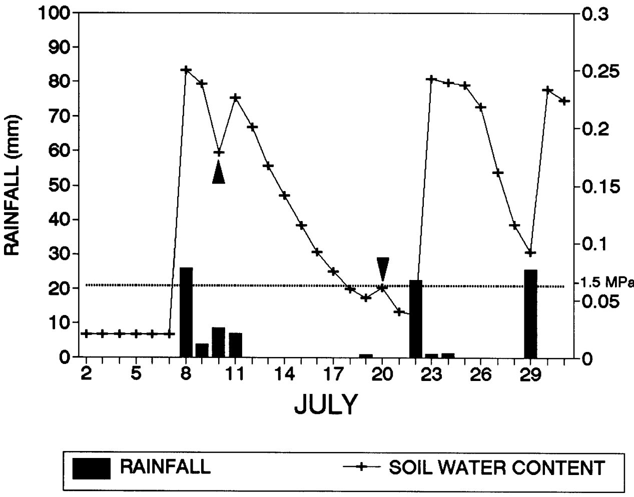

Figure 2—Rainfall and volumetric soil moisture content following the 16 June 1992 planting of warm-season grasses in southern Arizona. Triangles indicate first and second retrievals of seed bags. Dashed black line indicates soil water content at –1.5 MPa soil matric potential.

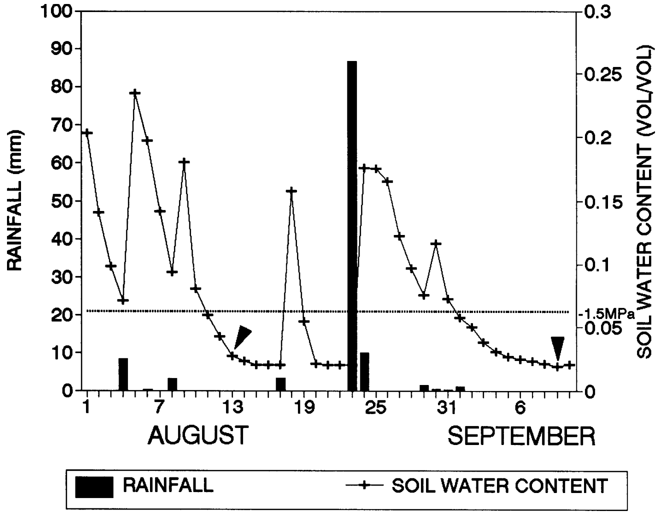

Figure 3—Rainfall and volumetric soil moisture content following the 30 July 1992 planting of warm-season grasses in southern Arizona. Triangles indicate first and second retrievals of seed bags. Dashed black line indicates soil water content at –1.5 MPa soil matric potential.

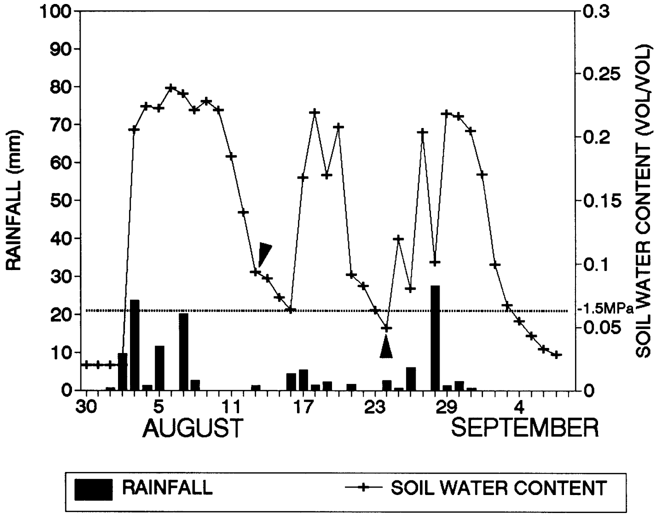

Figure 5—Rainfall and volumetric soil moisture content following the 2 August 1993 planting of warm-season grasses in southern Arizona. Triangles indicate first and second retrievals of seed bags. Dashed black line indicates soil water content at –1.5 MPa soil matric potential.

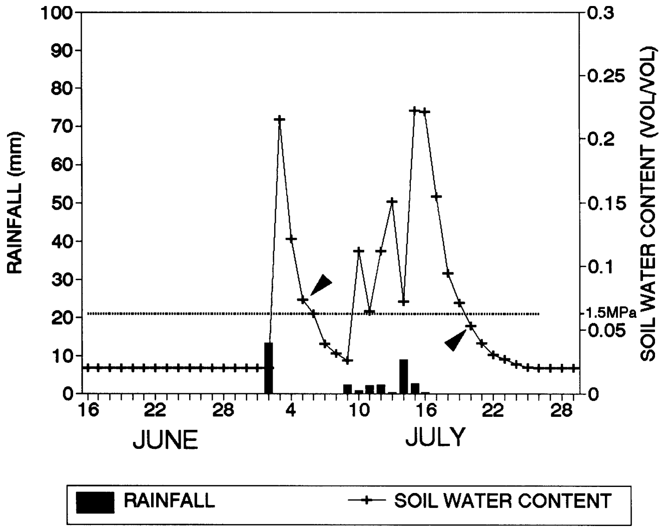

Figure 4—Rainfall and volumetric soil moisture content following the 15 June 1993 planting. Triangles indicate first and second retrievals of seed bags. Dashed black line indicates soil water content at –1.5 MPa soil matric potential.

decrease in soil moisture. The remainder of the rainfall was distributed over 8 consecutive days. However, daily totals during that period were of such small magnitude that the resulting soil moisture availability was punctuated by short dry periods. In August 1993 the plots received 125 mm of rain (Fig. 5). The 2 August planting was followed by 7 consecutive days of rain, resulting in 10 days of high soil moisture.

Seed Fate Response

Within species comparisons of the seed fate response between the first and second retrieval of each planting shows the effect of rainfall and soil moisture availability patterns on seed fate (Table 2). For example, following the 16 June 1992 planting, the percentage of dead or dormant cane beardgrass seeds increased from 1% to 15% between the first and second retrievals. In the June 1992, June 1993, and August 1993 plantings the percentage of field-germinated Lehmann lovegrass seeds was significantly lower ($P<0.05$) in the first retrieval than in the second retrieval.

Between species comparisons following each planting can help to show differences in seed fate response relative to the rainfall and soil moisture patterns. The results for three native species (cane beardgrass, Arizona cottontop, and plains lovegrass) and one introduced species (Lehmann lovegrass) are presented in histogram form to aid in the comparison (Figs. 6 and 7).

Comparison between species sown 16 June 1992 shows an overall trend for the native species to germinate a large portion of their seeds by the first retrieval (Fig. 6). This germination response was triggered by the initial rainfall (Fig. 2). This pattern contrasts with Lehmann lovegrass, which had only 13% of its seeds germinated by the first retrieval. In this case, 59% of the Lehmann lovegrass seeds were germinable but ungerminated. Soil moisture availability was relatively consistent during July 1992, and by the second retrieval 35% of the Lehmann lovegrass had germinated.

Each of the species sown 30 July 1992 shows a trend toward greater seed mortality by the second retrieval (Fig. 7). The rainfall was very sporadic and soil moisture availability during this period generally fluctuated from wet to very dry

Table 2—Seed fate response of warm-season grasses seeded in 1992 and 1993 on a loamy upland range site in southern Arizona. Values are percentage of total planted seeds. The first retrieval was toward the end of the first wet-dry cycle; the second was after a series of wet-dry events.

	1992											
Planting Date	**16 JUNE**						**30 JULY**					
Retrieval	**FIRST**			**SECOND**			**FIRST**			**SECOND**		
Response (%)	**F**	**G**	**D**	**F**	**G**	**D**	**F**	**G**	**D**	**F**	**G**	**D**
Species												
cane beardgrass	96	3	1*	85	0	15*	75	3	22	64	0	36
Arizona cottontop	48	20*	32	54	3*	42	24	19	56	35	2	63
plains lovegrass	42	28	30	69	2	29	37	40	23	18	42	39
sideoats grama	73	6	21	70	0	30	57	3	40	48	1	51
green sprangletop	64	9	27	68	0	32	52	19	29	29	0	71
bush muhly	54	11	36	56	0	44	34	6	60	38	1	60
Lehmann lovegrass	13*	59	27	35*	39	27	4	59	37	13	37	49
Cochise lovegrass	64	16	20	67	3	29	29*	24*	48*	17*	3*	81*

	1993											
Planting Date	**15 JUNE**						**2 AUGUST**					
Retrieval	**FIRST**			**SECOND**			**FIRST**			**SECOND**		
Response (%)	**F**	**G**	**D**	**F**	**G**	**D**	**F**	**G**	**D**	**F**	**G**	**D**
Species												
cane beardgrass	7*	78*	15	80*	3*	17	83	0	17	85	0	15
Arizona cottontop	7	47*	46	28	0*	72	56	0	44	62	0	38
plains lovegrass	0*	91*	9*	42*	9*	49*	66*	11	23	48*	15	37
sideoats grama	48	51*	1*	55	0*	45*	93	0	7	97	0	3
green sprangletop	7*	70*	23	46*	0*	54	79	0	21	88	0	12
bush muhly	6	61*	33*	30	0*	70*	61*	0	39*	78*	0	22*
Lehmann lovegrass	1*	78	21	21*	62	17	11*	68	21	38*	39	23
Cochise lovegrass	0	80*	20	50	8*	42	48	13*	39	61	01*	38

[1] F- field germinated; G- germinable (growth chamber germinated); D- dead or dormant.

* indicates significant difference ($P < .05$) in a response category between the first and second retrievals within a planting.

in most 24 hr periods (Fig. 3). Seeds of both cane beardgrass and Arizona cottontop had high germination in response to the initial rain, and subsequent mortality was probably due to low soil moisture levels that were insufficient to sustain seedling growth and establishment.

Although 11 mm of rain fell during the initial rainfall of the 15 June 1993 planting, each of the species showed a low germination response (Fig. 8). Soil moisture following the initial rainfall was available for only 1 day (Fig. 4) and was not sufficient to initiate germination. However, by the second retrieval, the percentage of germinable seeds retained by the native grasses had decreased significantly. Field germination of cane beardgrass, plains lovegrass and Lehmann lovegrass all increased significantly.

The seed fate responses following the 2 August 1993 planting are typical of a rainfall pattern resulting in consistently high soil moisture. The native grasses had high germination in response to the initial rain, while only 11% of Lehmann lovegrass seeds germinated in the field (Fig. 9). By the second retrieval, Lehmann lovegrass field germination had increased to 38%.

An overall trend emerges in which field germination of the native species is high in response to an initial rainfall event that results in moist soil for approximately 48 hr. In a study on the effect of six different wet-dry periods on seedling emergence and survival, Frasier and others (1985) showed that the length of the initial wet period influenced survival during the following dry period. If the initial wet period was too short to initiate germination, or if that wet period was long enough to promote vigorous seedling growth, then the plant had an increased chance of surviving the ensuing dry period. Thus, a species that germinates quickly has a decreased ability to survive if moisture availability becomes limited. Therefore, moisture availability patterns interacting with germination rates of the native grasses and Lehmann lovegrass may play a major role in their differential establishment.

Conclusions

The native grass species studied tend to require shorter periods of soil moisture availability to initiate germination when compared to Lehmann lovegrass. Once germination has begun, native grass seedling survival is dependent on the pattern of soil moisture availability after the initial rain. These species are subject to early seedling mortality if soil moisture becomes limited. Therefore, the distribution and extent of rainfall is an important factor when seeding native grasses.

In contrast, Lehmann lovegrass retains a comparatively large portion of ungerminated, germinable seeds after the initial rain event. The tendency for a portion of Lehmann lovegrass seeds to remain viable and germinable after the

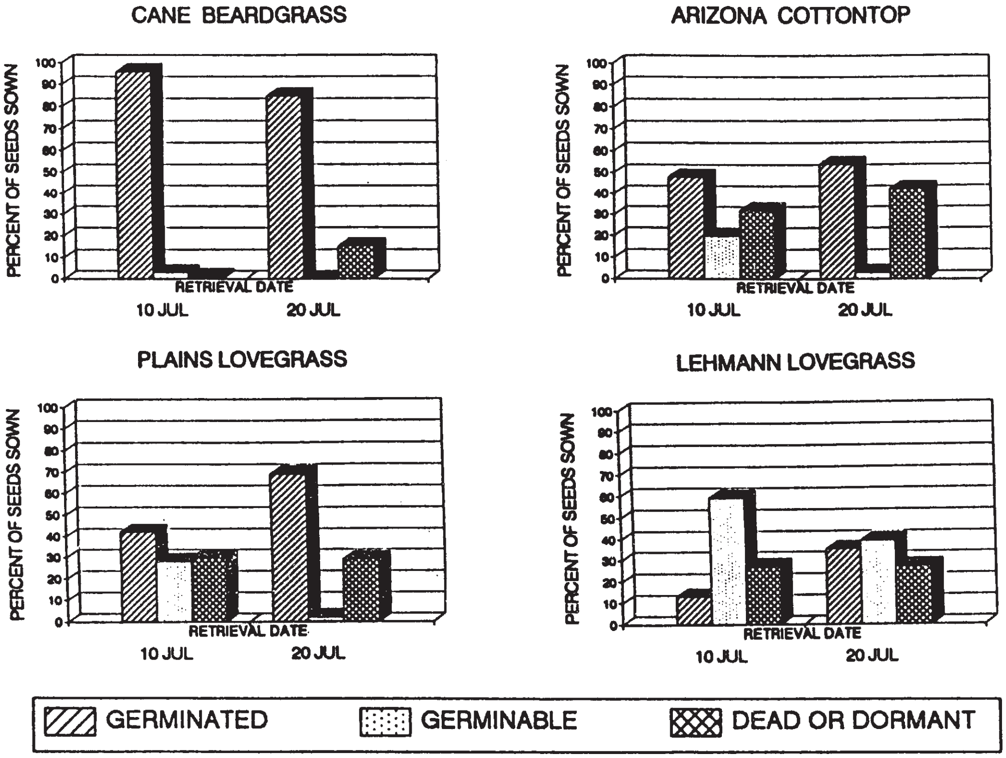

Figure 6—Seed fate responses of cane beardgrass, Arizona cottontop, plains lovegrass and Lehmann lovegrass following the 16 June 1992 planting on a loamy upland range site in southern Arizona.

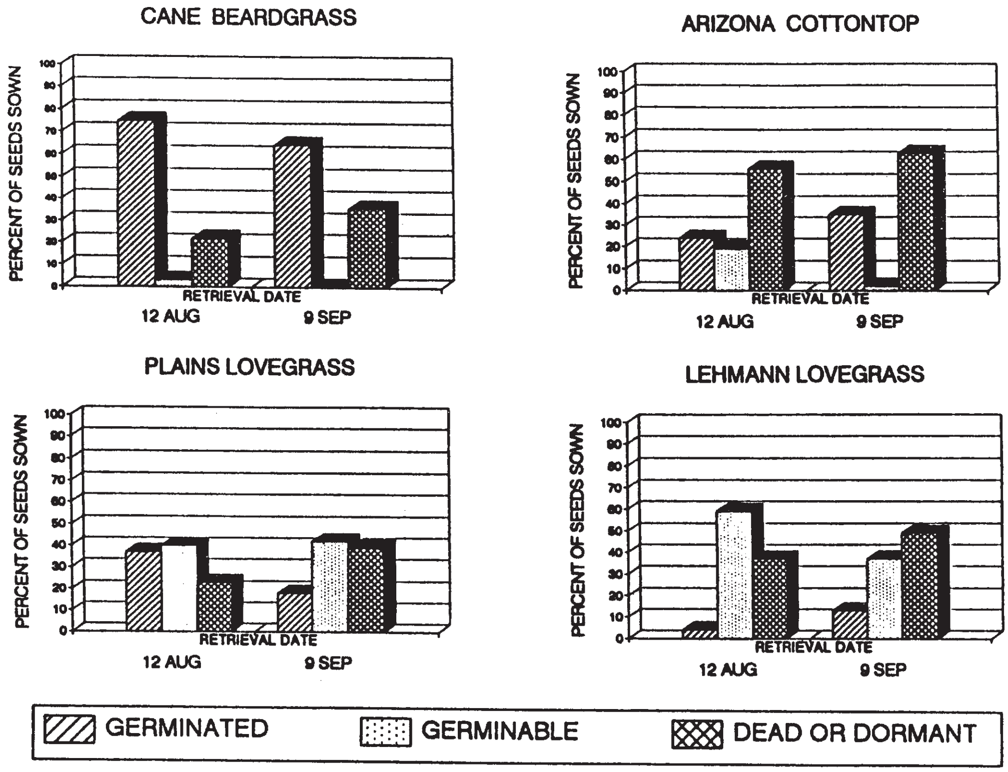

Figure 7—Seed fate responses of cane beardgrass, Arizona cottontop, plains lovegrass and Lehmann lovegrass following the 30 July 1992 planting on a loamy upland range site in southern Arizona.

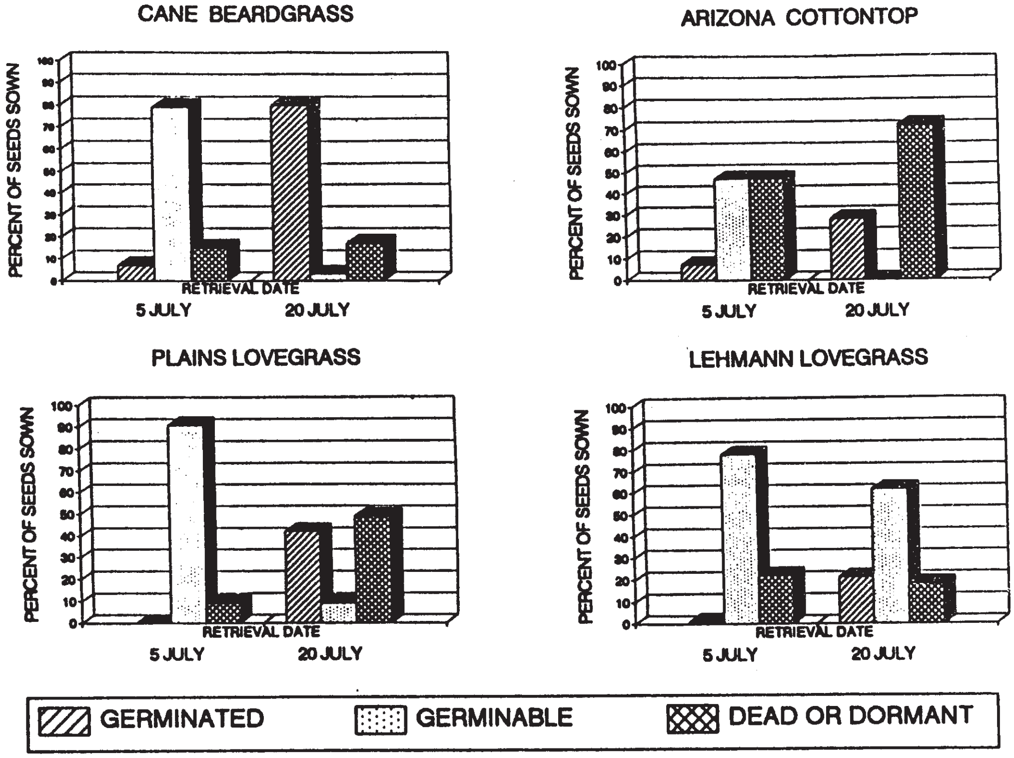

Figure 8—Seed fate responses of cane beardgrass, Arizona cottontop, plains lovegrass and Lehmann lovegrass following the 15 June 1993 planting on a loamy upland range site in southern Arizona.

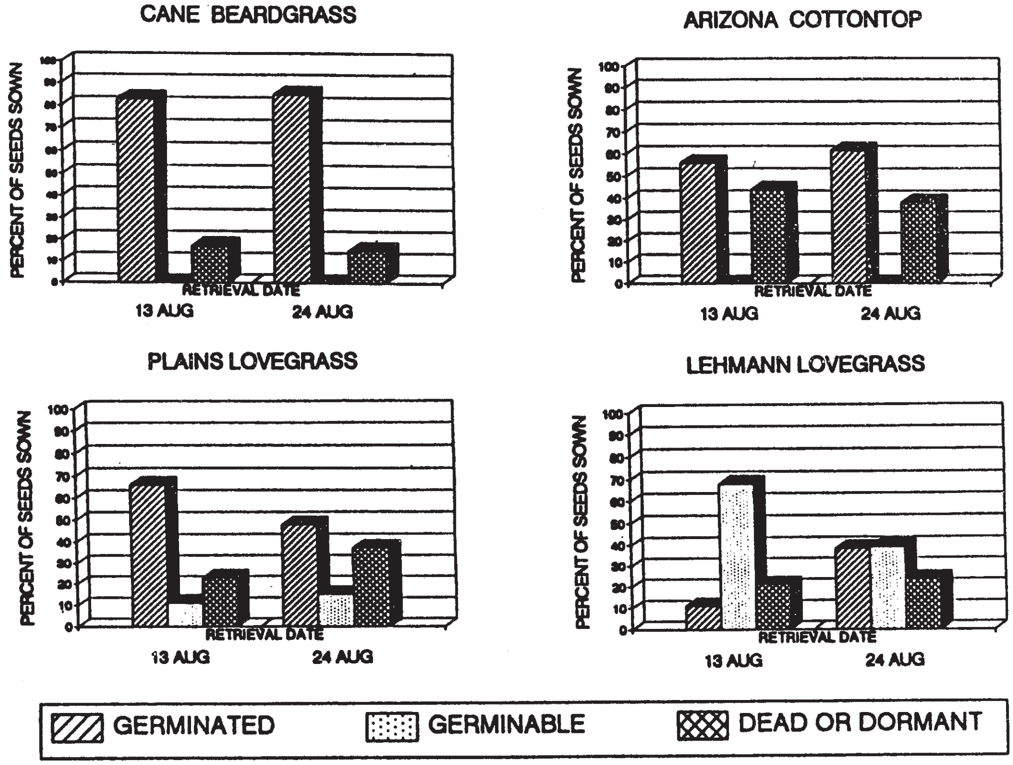

Figure 9—Seed fate responses of cane beardgrass, Arizona cottontop, plains lovegrass and Lehmann lovegrass following the 2 August 1993 planting on a loamy upland range site in southern Arizona.

first rain reduces its susceptibility to infrequent rains at the beginning of the summer rainy season. Species that produce both early- and late germinating seeds tend to be favored in variable environments (Venable, 1989). This pattern of delayed germination is a probable factor in the successful establishment of Lehmann lovegrass in revegetation projects in southern Arizona.

Acknowledgments

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Natural Methods of Establishing Native Plants on Arid Rangelands

Jerry R. Barrow
Kris M. Havstad

Abstract—Desertification of native rangelands is a global problem. Mechanical and chemical approaches to remediate these lands are not universally suitable or appropriate, and often times induce disturbances that escalate rather than resolve the trend. Therefore, we are proposing to utilize natural systems such as wind, water, or animals to disperse seeds of desirable native plant species. These methods would have minimal disturbance on native landscapes. Concepts of water and animal seed dispersal on arid rangelands are discussed.

In the last 120 years there has been a significant conversion of grasslands to shrublands in the northern Chihauhuan Desert. This change is thought to be driven by a combination of natural and anthropomorphic disturbances (Buffington and Herbel 1965). Principle causes have been attributed to overgrazing and drought; however, other important factors influence the dynamics of native plant communities. This transition is described as desertification and may have negative implications for global climate (Schlesinger and others 1990). Vegetation conversions to shrub dominated states are generally regarded as pernicious from several view points such as wildlife habitat, watershed hydrology, aesthetic conditions, livestock grazing land, or recreational aspects. In many cases, removing the causes of disturbance will not reverse this transition, and current shrubland states may be permanent without considerable intervention (Friedel 1991). Gibbens and others (1992) reported that recent rates of honey mesquite, *Prosopis glandulosa* Torr., establishment in the northern Chihuahuan Desert are sufficient to further change many remaining grassland areas to mesquite dominated rangelands. Unfortunately, natural resource managers are not presently equipped to repair desertified lands. Current intervention technologies such as chemical and mechanical brush control and reseeding with both native and introduced plant species require substantial inputs of capital, labor and fossil fuels, and could not be regarded as universally suitable or appropriate (Barbier 1989). A general consensus is that it is extremely difficult to restore grasslands to their original condition.

Israeli scientists are developing an approach to repair desertified lands called “savannization” (Gillis 1992). Their philosophy focuses on selecting specific regions within the desert landscape that are most suitable for renovation. They consider less than 5% of the desert to be suitable for these revegetation efforts. This is an extension of the resource island concept proposed by others, more recently by Schlesinger and others (1990).

Our parallel concept of savannization is based on the premise that resources, primarily water and soil nutrients are distributed heterogeneously across a landscape resulting in some sites being more favorable for reestablishment of native species. These relatively favorable microenvironments would be logical sites for remediation of desertified conditions.

Successful native plant species have evolved mechanisms and strategies that utilize natural systems such as wind, water and animals to disperse their seed (Barrow and Havstad 1992). We propose that these systems should be exploited in remediation efforts. For example, the successful invasion of mesquite in the southwestern United States can be attributed largely to the dispersal of its seeds by animals and humans.

The rationale for this research approach resulted from recent observations on root plowed plots previously established on gently sloping creosote sites on the Jornada Experimental Range by Herbel and others (1973). Vegetation patterns on the original seeded plots remains very similar to the descriptions given at the time of establishment. However, increase of the grasses and fourwing saltbush, *Atriplex canescens* (Pursh) Nutt., resulting from natural downstream seeding from these plots is many times greater than the original seeded plots. Our objective is to develop low input, minimal disturbance revegetation technologies that rely on endemic abiotic and biotic forces to promote autogenic succession within these favorable sites.

Materials and Methods

Water Dispersal of Seed

Target areas were selected at strategically located upstream sites along gently sloping arroyos now occupied principally with creosotebush, *Larrea tridentata* (DC.) Coville, and tarbush, *Flourensia cernua* DC. These sites receive regular inputs of water, nutrients and organic matter. Our intent was to establish permanent seeding blocks of native perennial grasses and shrubs selected for their competitive ability and productivity, which by their

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downstream establishment would improve productivity, habitat and hydrology both longitudinally and laterally along the arroyo.

Four seeding blocks were established by scraping the surface of undesirable shrubs from an area 10 meters wide and 30 meters long. Each block crossed a shallow gully, and blocks were established just prior to the anticipated summer rainy season. Four dikes approximately 30 cm high were constructed every 6 to 7 meters along the gully within each seeding block to slow and trap water during flooding. We seeded black grama, *Bouteloua eripoda* Torr., fourwing saltbush, and sideoats grama, *Bouteloua curtipendula* (Michx.) Torr., above the dikes where water was trapped. A portable fence to exclude livestock and rabbits was placed around the site. A portable sprinkler irrigation system was installed and a water tank truck was used to apply approximately one inch of water in each application as needed to supplant inadequate precipitation.

Gully Seeders

Gully seeders as described by Barrow (1992) were installed along gently sloping gullies during three successive summer rainy seasons.

Animal Dispersal

Barrow and Havstad (1992) inserted encapsulated seeds of several grass and shrub species directly into the digestive tract of cattle to determine animal-related effects upon viability and germination. Seed collected from the feces and undigested seed was analyzed and compared for germinability. Seed bearing fecal pats were also placed on rangeland sites to observe germination responses.

Results and Discussion

These studies were established to determine long term effects of the tested practices; therefore, we are only reporting the initial phase. Precipitation was below normal from July through September of 1992. Supplemental irrigation was applied every two to three weeks during this period and good stands of young plants of black grama, sideoats grama and fourwing saltbush were obtained. Protection from small rodents for emerging saltbush seedlings was provided by .5 cm mesh x 30 cm high and 30 cm in diameter wire circles. Fourwing saltbush also emerging in the spring of 1993 after favorable winter precipitation and also after favorable summer precipitation in 1993 were not disturbed by rodents because of either their absence or the abundance of other vegetation. In the fall of 1993 the grass plants produced seed and fourwing saltbush plants ranged from 25 to 75 cm in height.

No flooding occurred during 1991 and 1992 to activate gully seeders, but they were tripped five times during July 1993, each time dispersing seed into the flood waters. Seeds of alkali sacaton, *Sporobolus airoides* Torr., blue panicgrass, *Panicum antidotale*, and fourwing saltbush passed through cattle with minimal loss of germination and also germinated well in fecal pats. Sideoats grama seeds were digested and did not survive passage. Some seeds of blue panic germinated after three years in fecal pats when precipitation was favorable. Under arid conditions, for animal dispersal to be effective, seed must be selected for ability to survive the digestive tract and in the pat until favorable conditions for germination are met. Hot dry conditions occurring immediately after the pat is dropped cause severe crusting and prevention of seedling emergence. Animal dispersal of seed could be an effective means of seeding some remote or inaccessible locations if proper selection of seed, timing and animal management practices were followed.

The increase of productive shrubs and grasses along arroyos would be expected to increase fertility and water infiltration and would subsequently improve numerous habitat values. Such remediation technologies used on a regular basis provide low input efforts at strategic locations and would have long term benefits with minimal biological disturbance. It is unlikely that any single approach would assure complete success. Therefore, removal of pernicious shrub species by chemical or mechanical means may aid these natural processes if applied strategically or in a timely manner within a total management system.

Long-term responses will be further quantified by measurements of vegetation responses to applied technologies. The goal is to remediate deteriorated conditions rather than to restore prior vegetation. The latter may be neither feasible nor desirable.

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Reestablishing Cold-Desert Grasslands: A Seeding Experiment in Canyonlands National Park, Utah

Jayne Belnap
Saxon Sharpe

Abstract—Eighteen different treatments were applied to an area seeded with the native grasses *Stipa comata* and *S.* (*Oryzopsis*) *hymenoides*. Plots received supplemental water up to annual rainfall levels. Treatments included 30% cover of native grass mulch (*Hilaria jamesii*); nitrogen and phosphorus fertilizer; cyanobacterial inoculant from an adjacent, undisturbed area; sugar (to stimulate microbial activity); no water; and various combinations of these treatments. Plots were evaluated one year later for number of grass seedlings established, number of grass seedlings eaten, and cover and biomass of the exotics *Salsola kali* and *S. iberica*. Different treatments resulted in strikingly different establishment rates of the seeded grasses, with any treatment using mulch having only 15 to 25% as many seedlings as the most successful treatment. Fertilized plots tended to have fewer seedlings as well. Sugar, by limiting nitrogen availability, was effective at reducing *Salsola* biomass and cover, as well as in encouraging perennial seedling establishment. *Salsola* cover had a small negative effect on total *Stipa* plants present. However, herbivory was significantly reduced for *Stipa* plants growing in *Salsola* canopies. Consequently, biomass was enhanced in plots with *Salsola*. In spite of precipitation during the growing season being below the 50-year average, plots without supplemental water did as well as those with supplemental water. As measured by overall native plant establishment, the most successful treatments were seed only (with and without supplemental water), the combination of sugar and spring-spread cyanobacteria, and native grass straw mixed in with fall-spread cyanobacterial inoculant.

Perennial bunch-grass communities have been heavily impacted in the western United States. Once widespread and free from annual exotics, these communities have been decimated by anthropogenic activities over the past two hundred years, especially livestock grazing (Gleason & Cronquist 1964; Sampson 1918; Smith 1899). In addition, most bunch-grass communities have been invaded by exotic annuals such as *Bromus tectorum* (cheatgrass) and *Salsola* sp. (tumbleweed). Resultant displacement of native species, whether through competition or fire, now threatens remaining native communities (Billings 1990; McArthur et al. 1990).

Successful revegetation of these grasslands in semi-arid lands has been limited and, in spite of a great deal of money and effort (S. Monsen, personal communication), no successful restoration has been documented. Most of these failures are ascribed to competition from exotic annuals (Kay et al. 1981).

Nitrogen availability influences species composition in a number of disturbed ecosystems (Heil & Bruggink 1987; Parrish & Bazzaz 1982; McLendon & Redente 1992). Perennial species, generally having lower potential growth rates (Bazazz 1979), are competitively favored in nitrogen-limited situations (Heil & Bruggink 1987; McGraw & Chapin 1989). Consequently, limitation of nitrogen availability in a system should favor later seral, perennial plants, while increased nitrogen availability should favor early seral annual species. Greater nitrogen immobilization can be achieved through increasing soil microbial biomass, since these decomposers compete with plants for nitrogen (Hunt et al. 1988; Lamb 1980). Stimulation of microbial biomass is done by the addition of a readily usable source of energy such as sucrose (sugar) (McLendon & Redente 1992) to the soils.

This study examines the efficacy of 18 different treatments (sugar, fertilizer, mulch and cyanobacterial inoculant, and no water) on 1) the establishment and survival of two seeded perennial bunch-grasses; 2) the cover and biomass of two exotic annual species, *Salsola iberica* and *S. kali* (Welsh 1994); and 3) the influence of the exotic annuals on the survival of the seeded native perennials.

Methods

The Needles district of Canyonlands National Park is located in southeastern Utah in the Colorado Plateau biogeographic province. Precipitation averages 23 cm yearly. Precipitation is spread fairly evenly throughout the year, although June is an extremely dry month, and October is very wet. Late summer and fall monsoons (August-October) provide 31% of yearly rainfall. This area is a cold desert, with an elevation of 1,370 m; annual high temperatures average 28 °C; annual low temperatures average –2 °C. The growing season is generally March to October. Undisturbed soils in this district are Begay fine sandy loams, with clay contents averaging 8 to 10% and silt 11 to 14%. Average NO3-N content of soils in this area was 2.3 ppm; phosphorus was 5.9 ppm; pH ranged from 7.9 to 8.1.

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Construction activities in summer and fall of 1991 resulted in a denuded 4.8-km long, 10-m wide strip through a *Stipa* (*Oryzopsis*) *hymenoides*-*S. comata* (Welsh 1994) perennial bunchgrass community. The strip was driven on repeatedly. The presence of buried water and electrical lines precluded ripping; instead, a tractor-pulled disc was used to break up the surface to a depth of 30 cm. The topsoil from the disturbed area was windrowed for 18 months before replacement. However, during replacement, the topsoil was mixed with subsoil. Resultant surface soils in the revegetated area still had a texture, pH and bulk density similar to adjacent undisturbed soils, but less soil structure, and therefore probably less water infiltration, than the adjacent area. Seed was collected on-site in summer, 1991 and spread in October, 1991. *S. hymenoides* seed was drilled to 40 mm (9 pounds/acre), while *S. comata* seed, with awns intact, was hand broadcast (9 pounds/acre).

A sprinkler system was installed along the corridor. Sprinkler heads were carefully placed to insure even water coverage over plots receiving supplemental water. Natural rainfall was monitored biweekly, and if less than the 50-year monthly average of rain was received, supplemental watering was done to reach that average. Rainfall was 22% below average over the March to November growing season. March through June had average or slightly above average rainfall, while July was down 31%, August was down 38%, September was down 46%, and October was down 43%. The sprinkler system was used 5 times for water supplements during these times.

The corridor was assessed for slope, soil depth, soil texture and adjacent vegetative communities. A homogenous portion was then designated for experimental treatments. A randomized block/plot design was used, with 18 treatments replicated in 7 blocks. Plots were 5 m by 10 m. Only the interior 3 m x 6 m area was used for sampling to avoid edge effects of neighboring treatments. Fertilizer treatments, applied in spring and fall, included nitrogen at 100 pounds/acre/yr and phosphorus at 50 pounds/acre/yr to increase fertility of the plots. Native grass straw was mixed into the soil before seeding to provide a slowly decomposing substrate for microbial populations (0.5 bale/plot). Sugar was applied to provide a readily available carbon source for microbial populations to stimulate their growth, thus reducing nitrogen availability to plants (636 pounds/acre/yr, applied every 2 months except December-January). Mulch, applied in the spring, consisted of a 50% cover of native grass straw to help conserve moisture in the plots. Cyanobacterial-lichen soil crusts were salvaged from a nearby area (by scalping the top 20 cm of soil) and spread 50 mm deep on the plots in order to inoculate the plots with nitrogen-fixing microorganisms. All treatments were applied in the fall, with the exception of mulch and spring crusts, which were applied in the early spring. Treatments are listed in Table 1.

Plots were sampled in fall, 1992. Five 1 m^2 quadrats were assessed in each plot. Data collected included numbers of established *Stipa*, evidence of herbivory on *Stipa*, and cover and biomass estimates of the exotic annuals *Salsola kali* and *S. iberica*. Soil bulk density in the plots was compared with an adjacent, undisturbed area. Data collected as percentages were arc-sine transformed before analysis. Results were analyzed using ANOVA, Duncan's multiple range test and one-way regression analysis.

Table 1—Treatments applied to experimental plots.

1. FC:	Fall-applied cyanobacteria
2. FC/S:	Fall cyanobacteria, sugar
3. FC/F:	Fall cyanobacteria, fertilizer
4. FC/M:	Fall cyanobacteria, mulch
5. FC/F/M:	Fall cyanobacteria, fertilizer, mulch
6. FC/S/M:	Fall cyanobacteria, sugar, mulch
7. FC/H:	Straw mixed in with fall cyanobacteria
8. S/M:	Sugar, mulch
9. F/M:	Fertilizer, mulch
10. M:	Mulch
11. SC:	Spring-applied cyanobacteria
12. SC/S:	Spring cyanobacteria, sugar
13. SC/F:	Spring cyanobacteria, fertilizer
14. SC/M:	Spring cyanobacteria, mulch
15. F:	Fertilizer
16. SD:	Seed
17. SD/NW:	Seed, no water
18. SC/S/NW:	Spring cyanobacteria, sugar, no water

Results and Discussion

Average numbers of total *Stipa* plants observed in each treatment are shown in Figure 1. These numbers include all *Stipa* that survived the first growing season, regardless of their condition. Treatments fell into three groups. The four most successful treatments included seed only without water; native grass straw mixed in with fall-spread cyanobacterial inoculant; sugar plus spring-spread

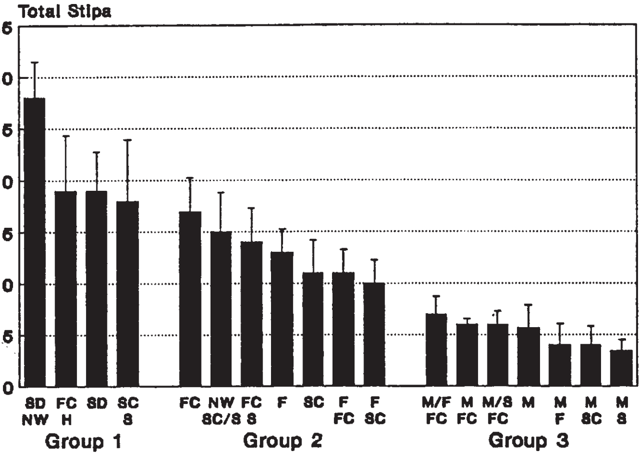

Figure 1—Total number of *Stipa* sp. present in each treatment, regardless of condition. FC = Fall applied cyanobacteria; SC = Spring applied cyanobacteria; F = Fertilizer; M = Mulch; S = Sugar; SD = Seed only; NW = No water; and H = Straw mixed in. Group 1 (a) was statistically different from Group 3 (b; p < 0.01); Group 2 was not different from 1 or 3.

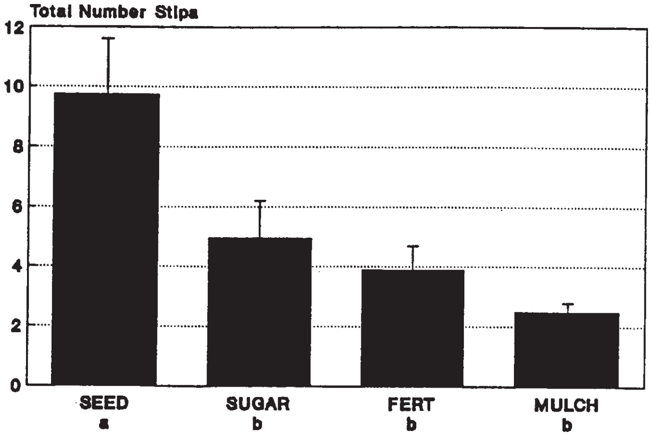

Figure 2—Total number of *Stipa* present, regardless of condition, lumped by common treatments. Statistical differences are denoted by different letters. Seed-only treatments had the fewest plants eaten when compared to the other treatments (p < 0.01). Other treatments were not statistically different among themselves.

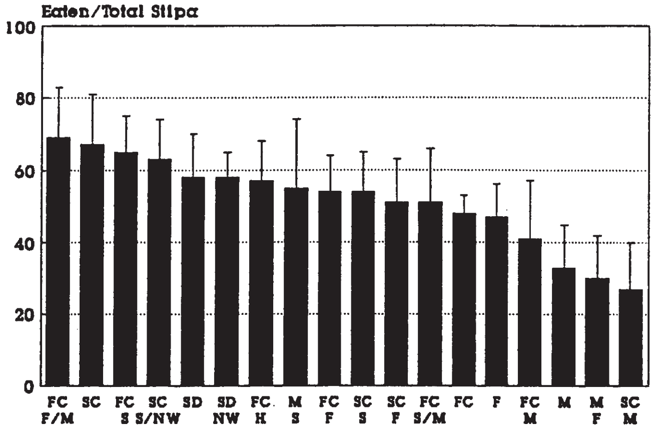

Figure 3—The ratio of eaten to total *Stipa* sp. in each treatment. FC = Fall applied cyanobacteria; SC = Spring applied cyanobacteria; F = Fertilizer; M = Mulch; S = Sugar; SD = Seed-only; NW = No water; and H = Straw mixed in. Due to high variability, no differences were statistically significant.

cyanobacterial inoculant, and seed only with water. This first group had significantly higher numbers of *Stipa* than the third group, which consisted of all treatments with mulch. Fertilized treatments were found in the lower half of the treatments, with some averages statistically lower than the first group. Three noteworthy results can be seen from these data. First, mulch clearly had a detrimental effect on seedling survival for the first year in this experiment. Plots with mulch had fewer seedlings present when compared to the most successful plots, regardless of whether the mulch was applied alone or mixed with other treatments. Secondly, two of the four most successful treatments, measured by plant survival, were those plots that were seeded only, with no additional treatment. And thirdly, lack of additional watering did not adversely affect seedling survival during a growing season with below-average rainfall.

Common treatments were combined into four categories: seed-only, sugar, fertilizer, and mulch (cyanobacterial inoculant was excluded, as it crossed most treatments). When averages for these categories were compared, the seed-only treatment had a statistically greater number of seedlings present than the rest of the treatments (Fig. 2). The other three categories (sugar, fertilizer and mulch) were not statistically different from each other. These categories did show the same trends as in the uncombined data: seed-only had the greatest establishment, followed by sugar, fertilizer and then mulch.

Herbivory by rabbits and mice was intense during the first year of this experiment. Plants counted as "eaten" were those that had been chewed to less than 5 cm in height. Plants that were completely removed were not counted. "Uneaten" were plants that showed either no herbivory, or herbivory was slight. Figure 3 presents the number of plants eaten as a percentage of total plants in the plots. Due to high variability, there was no statistical difference among treatments, although herbivory ranged from 27% to 69% of the plants present. Average numbers of total uneaten *Stipa* plants are presented in Figure 4. This figure is similar to the one showing total *Stipa* density. Indeed, there is a significant correlation between the total number of plants in the plot, and the number of plants eaten (r = 0.85; p < 0.01). Consequently, those plots with the greatest number of established plants were also those with the greatest amount of herbivory. Fertilized plots, with higher levels of available nitrogen and phosphorus, might have been expected to have more palatable plants, and consequently suffer higher herbivory rates. Concomitantly, sugared plots, with less available nitrogen, might be expected to show the reverse. However, this was not the case, as there was no difference between combined fertilized, sugared or mulched treatments (Fig. 5). Fertilized

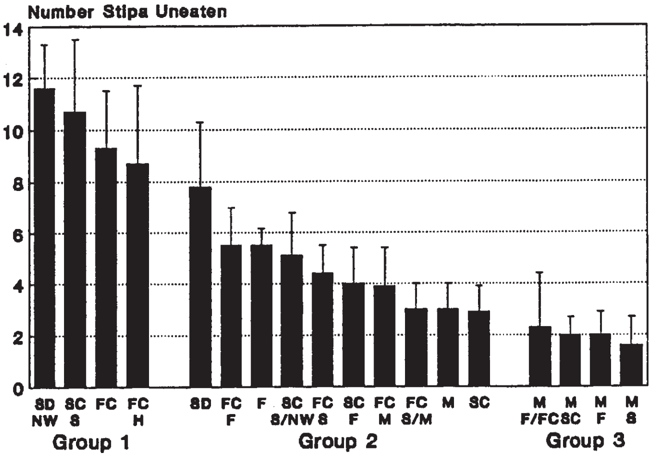

Figure 4—Total *Stipa* sp. uneaten in each treatment. FC = Fall applied cyanobacteria; SC = Spring applied cyanobacteria; F = Fertilizer; M = Mulch; S = Sugar; SD = Seed-only; NW = No water; and H = Straw mixed in. Group 1 (a) was statistically different from Group 3 (b; p < 0.01); Group 2 was not different from 1 or 3.

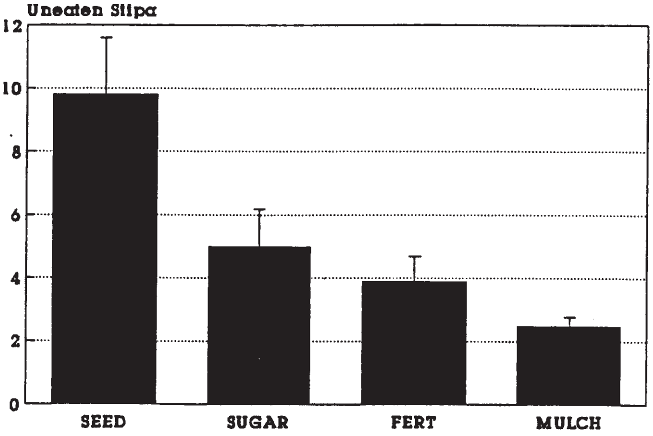

Figure 5—Total *Stipa* uneaten, with common treatments lumped. Seed-only treatments had the fewest plants eaten when compared to the other treatments ($p < 0.01$). Other treatments were not statistically different among themselves.

treatments showed an herbivory average of 50%, while sugared plots averaged 57%. Seed-only had significantly less herbivory than the other treatments.

Herbivory on *Stipa* was most often explained by the placement of the grass relative to *Salsola* canopies. Numbers of grasses growing outside the canopy of a *Salsola* were highly correlated with numbers of plants eaten ($r = 0.82$; $p < 0.01$); plants under *Salsola* were eaten 47% less often than those in the open. Numbers of grasses inside the canopy of the tumbleweed showed no correlation with herbivory events ($r = 0.22$; $p > 0.05$). However, there was also a high and significant correlation between total number of *Stipa* present and the number growing in the open ($r = 0.91$; $p < 0.01$). This may indicate seeded grasses were better able to establish outside *Salsola* canopies.

The two species of *Salsola*, *S. iberica* and *S. kali*, were combined for biomass and cover estimates. Average *Salsola* biomass ranged from 15 to 90 grams per plot in the different treatments, with 5 of the 6 lowest biomasses found in the sugared treatments (Fig. 6). However, the tremendous amount of variability among plots resulted in no statistical differences between treatments. When common treatments were lumped for *Salsola* biomass (Fig. 7), sugared plots had significantly less biomass than other treatment categories. Fertilized plots had 3 times the tumbleweed biomass of sugared plots, while the watered plots had 5 times the biomass of sugared plots. Fertilized, seed-only and mulch treatments were not different from each other.

Cover estimates for *Salsola* are presented in Figure 8. Although average cover values ranged from 23 to 42%, no statistical differences were seen. This may have been due to the high variability found. Some trends were apparent, however. Fertilized treatments were all at the high end of the cover estimates, while seed-only and sugared plots showed a tendency towards reduced *Salsola* cover. Combining treatment categories (Fig. 9) showed fertilized treatments with significantly greater cover than sugar or seed-only treatments. Mulched treatments were not statistically different from any other treatments.

Regression analysis was used to determine whether *Salsola* biomass or cover affected either total numbers of *Stipa* present in a plot, or the percentage of *Stipa* eaten in a plot. *Salsola* biomass showed no significant effect on the total *Stipa* in a plot ($r = -0.18$), although removal of one data point resulted in $r = -0.33$, which was statistically significant. There was no effect of *Salsola* biomass on the percentage *Stipa* eaten ($r = -0.23$). *Salsola* cover did not have a significant effect on the percentage eaten ($r = -0.24$), but did have some effect on the total *Stipa* present in the plot ($r = -0.37$; $p < 0.05$), though the "r" value was small.

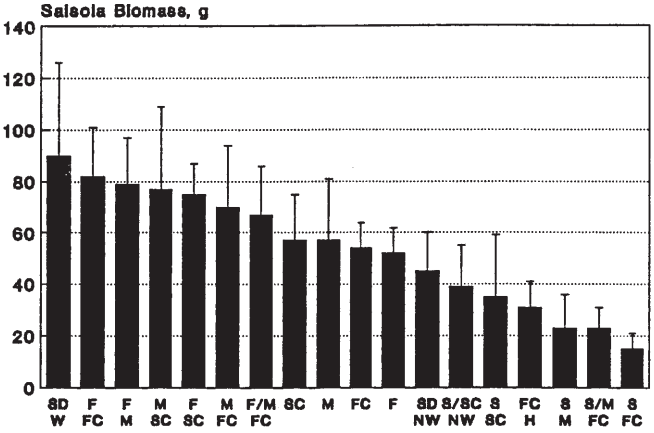

Figure 6—Total *Salsola* biomass in each treatment. FC = Fall applied cyanobacteria; SC = Spring applied cyanobacteria; F = Fertilizer; M = Mulch; S = Sugar; SD = Seed-only; NW = No water; and H = Straw mixed in. No differences were statistically significant, probably due to the high variability.

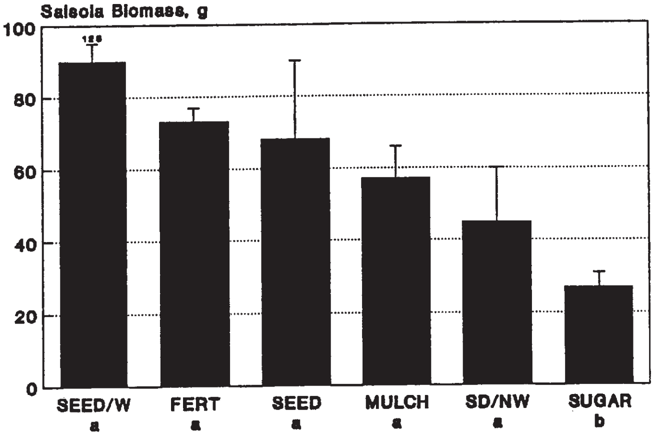

Figure 7—*Salsola* biomass, lumped by common treatments. Statistical differences are denoted by different letters. Sugar treatments had significantly less *Salsola* biomass when compared to the other treatments ($p < 0.01$). Other treatments were not statistically distinguishable.

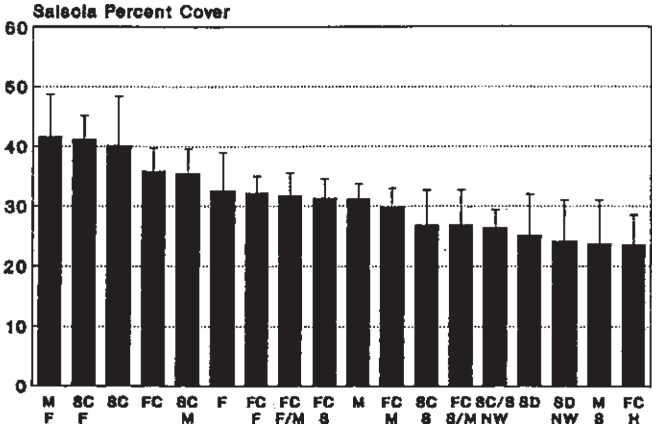

Figure 8—*Salsola* cover in each treatment. FC = Fall applied cyanobacteria; SC = Spring applied cyanobacteria; F = Fertilizer; M = Mulch; S = Sugar; SD = Seed-only; NW = No water; and H = Straw mixed in. No differences were statistically significant, probably because of high variability in the samples.

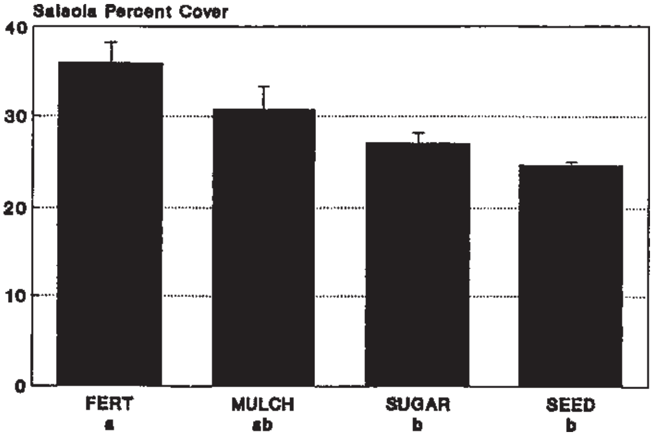

Figure 9—*Salsola* cover, lumped by common treatments. Statistical differences are denoted by different letters. Fertilized treatments showed greater cover than sugar or seed-only treatments ($p < 0.03$). Mulched treatments were not statistically different from any other treatment.

Conclusions

This seeding experiment calls into question several assumptions often made by restoration ecologists. First, mulch is generally assumed to be beneficial, especially in arid and semi-arid regions. In this study, straw mulch applications reduced the survival of seedlings compared to non-mulched treatments. Similar results have been reported from a project near Grand Junction, CO (J. Lance, personal communication). This may be a result of using dry straw. Both species of *Stipa* generally grow in loose, sandy soils. Since water percolates easily through these soils, long-lasting soil moisture in the upper horizons would not naturally occur unless the entire soil profile was charged with water. Straw, on the other hand, may hold water in the upper soil layer regardless of water levels in lower soil profiles. This may "fool" seeds into germinating at an inappropriate time and/or concentrating their roots in surface soils, instead of deploying these roots in deep soils.

In addition, rainfall patterns in this area may make straw mulch a liability for seedlings. Storms in the spring often produce small, short bursts of rainfall, and straw mulch may absorb the entire rainfall event, preventing much moisture from reaching the soil. Since temperatures are high, this surface moisture could evaporate before ever becoming available to plant roots.

A second commonly held belief is that establishment of native plants takes place in semi-arid lands only during years when rainfall is well above average. This study demonstrates that this is not always true. Plant establishment in the non-watered plots was as successful as in any other treatment during a growing season of below-average rainfall. The fact that spring had average or slightly above-average rainfall may have been more important than an overall below-average growing season. Other factors may be equally important as rainfall to the success of seedling survival, including soil conditions, herbivory, and mechanisms that increase water availability such as reduced air temperatures or plant microclimates.

The presence of exotic annuals in a perennial-dominated community is generally assumed to be a liability, especially where water resources are limiting (Hunter 1990; Mack 1981). The ability of annual seedlings to outcompete perennial seedlings has been demonstrated repeatedly (Bartolome & Gemmill 1981; Hull and Miller 1977; Kay et al. 1981; Young et al. 1972). Annual plants are generally at a competitive advantage in relatively high water and high nutrient situations (Romney et al. 1978). These factors are often not taken into account in revegetation efforts, as evidenced by the many projects that use fertilizers and water. The effects of water and nutrients on annual plants can be seen clearly in this study. Increasing levels of water, even only to imitate average annual rainfall, favored the establishment and growth of the exotic annual *Salsola*. Comparing the seed-only, no water treatments with the seed-only with water treatments, we can see that the biomass of this plant increased by over 70%. Low nutrient availability, induced by sugar applications that stimulated microbial biomass production, significantly reduced *Salsola* biomass and cover. Consequently, limiting water and nutrient availability should be considered in areas where annual exotics are a problem.

Exotic annuals may not always be a problem, and may actually aid in revegetation efforts. As demonstrated by this study, *Salsola* biomass and cover had no, or little, effect on *Stipa* survival or percentage eaten, though more *Stipa* plants were found outside than within *Salsola* canopies. However, growth under a *Salsola* canopy clearly protected the native grasses from herbivory. During data collection for this study, non-quantified observations were made that *Stipa* plants growing in the canopy of *Salsola* plants were much larger than plants growing in the open, often having 5 to 6 blades and being 20 to 30 cm tall, compared to plants with 1 to 5 blades that were 5 to 20 cm tall in the open. It is not known whether such severe herbivory will significantly affect long-term survival of these plants, though it seems likely. When biomass, not just number of established plants of desired species is considered, the protection offered by a *Salsola* canopy may outweigh the negative effect that increasing *Salsola* cover has on the desired perennial species in years of average rainfall. It is not known whether the negative impacts of these annual species would be greater in years of more limited water. *Salsola* populations did quite well in a recent 5-year drought in this area, and may compete effectively with perennial grass species when water is scarce.

Though much was learned about ways to hasten revegetation of disturbed semi-arid grasslands in this study, levels of herbivory and other environmental stressors prevented any of the treatments from being judged successful in terms of overall plant establishment. This may be true even when factors controlling plant germination and establishment are better understood. Consequently, we should be careful not to overestimate our ability to revegetate these areas in a short time frame (10 years), and certainly should refrain from claiming that true restoration of these areas is possible until more supporting data are available.

Acknowledgments

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Replacing Lehmann Lovegrass with Native Grasses

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L. Abbott

Abstract—This study determined the effects of Lehmann lovegrass (*Eragrostis lehmanniana*) stand manipulations on establishment of Lehmann lovegrass and seven native grasses. Grasses were sown in June and again in August into stands of Lehmann lovegrass that had been left intact, burned, sprayed with herbicide and left standing, or sprayed and mowed. In 1992 the June-sown mow treatment and in 1993 the August-sown burn treatment produced the most native grass seedling establishment for cane beardgrass (*Bothriochloa barbinodis*) and green sprangletop (*Leptochloa dubia*), respectively. Summer rainfall was most frequent in July in 1992 and most frequent in August in 1993. Lehmann lovegrass seedling density from sown seeds and from the residual seedbank was highest for the burn treatment.

Lehmann lovegrass (*Eragrostis lehmanniana*) was introduced from Africa during the 1930's to revegetate degraded Arizona rangelands (Cable 1971; Jordan 1981; Cox and others 1987). It has great value for erosion control, particularly in areas with altered site potential which are no longer capable of supporting native species. It also provides nutritious and palatable forage for livestock production. However, managers of wildlife sanctuaries, nature preserves, and wilderness areas are interested in controlling the spread of Lehmann lovegrass and restoring native grasses. Lehmann lovegrass spreads aggressively beyond the boundaries of seeded stands and can invade and displace native grasses (Kincaid 197l; Cable 1971; Anable and others 1992; McClaran and Anable 1992). Where exotic grasses dominate, the biodiversity of plant and animal communities may be decreased (Bock and others 1986). In addition Lehmann lovegrass has the potential to alter fire regimes by producing much more aboveground biomass than native grasses (Cox and others 1990). Fire enhances its germination, putting a cycle in motion which can perpetuate Lehmann lovegrass (Ruyle and others 1988; Sumrall and others 1991; Anable and others 1992). The purpose of this study was to determine the effects of Lehmann lovegrass canopy manipulations on the establishment of Lehmann lovegrass and seven seeded native grasses to assess the potential of canopy manipulation for re-establishment of native grasses in existing stands of Lehmann lovegrass.

The study was conducted on the Santa Rita Experimental Range in southeastern Arizona. The research plots are located on an alluvial fan at an elevation of about 1075 m. The vegetation type is Chihuahuan desert shrub dominated by an overstory of mesquite (*Prosopis juliflora* var. *velutina*) and an understory of Lehmann lovegrass. Lehmann lovegrass and seven native warm-season perennial grasses were seeded: cane beardgrass (*Bothriochloa barbinodis*), sideoats grama (*Bouteloua curtipendula*), Arizona cottontop (*Digitaria californica*), plains lovegrass (*Eragrostis intermedia*), green sprangletop (*Leptochloa dubia*), bush muhly (*Muhlenbergia porteri*), and plains bristlegrass (*Setaria leucopila* and *S. macrostachya*). These species are adapted to the environmental conditions on the Santa Rita Experimental Range and are present as individuals in Lehmann lovegrass stands or in areas which have not been seeded with or invaded by Lehmann lovegrass.

Methods

The Lehmann lovegrass stand was manipulated using four different treatments applied on three blocks in a randomized complete block design. For the burn treatment, Lehmann lovegrass stands were burned to remove the mature canopy and kill adult plants prior to seeding. For the mow treatment Lehmann lovegrass canopies were sprayed with glyphosate in spring and mowed prior to seeding into the mulch. For the dead standing treatment, Lehmann lovegrass was sprayed with glyphosate and the species seeded into the standing dead canopy. For the control treatment, species were seeded directly into intact stands of Lehmann lovegrass. These manipulations affected the seedbed environment by altering light, temperature, and moisture relations. Lehmann lovegrass seed germination is enhanced by red light and fluctuating diurnal temperatures (Roundy and others 1992). For these reasons the mow and dead standing treatments were expected to suppress the expression of the Lehmann lovegrass seedbank. Lehmann lovegrass germination from the seedbank increases after fire (Ruyle and others 1988; Sumrall and others 1991). Native grasses may require longer periods of available soil moisture than Lehmann lovegrass in order to establish, conditions which could be provided by the mow or dead standing treatments.

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The research plots were instrumented in order to relate seedling establishment to environmental conditions. Meteorological variables included precipitation, relative humidity, wind speed, air temperature, and solar radiation. Soil temperature at 1 cm soil depth was measured by thermocouple probes. Soil water tension was measured at 1-3, 6-8, and 12-14 cm by gypsum blocks. Hourly averages of the variables were recorded by microloggers.

There were two planting dates, early June and early August, and the experiment was repeated for 2 years. June is the traditionally recommended seeding date for southern Arizona, prior to the summer rains. However, late summer rains might be more reliable than those occurring early in the summer. Some native grasses may germinate rapidly in response to initial light rains and then desiccate and die during ensuing dry periods. Lehmann lovegrass, on the other hand, tends to delay germination until moisture conditions are adequate for establishment (Abbott and others 1994). Seeds were sown in 10-meter rows at a depth of 0.6 cm and at a rate of 1 pure live seed per cm of row.

Results

Rainfall patterns for the summer of 1992 were atypical in that rainfall was relatively well distributed in July but not in August (Figure 1). As a result, seedlings emerged in July after the June seeding, but very few emerged after the August seeding. There was little difference in soil water tension among treatments at 1-3 cm, just below the sowing depth, although the burn treatment dried out somewhat more quickly than the other treatments (Figure 2). At 6-8 and 12-14 cm soil depths, the mow and the dead standing treatments retained moisture somewhat longer than the burn and the control treatments (Figure 2).

June-sown seeds received initial rains in early July, 3 weeks after planting. Soil water tension remained low for approximately 7 days, then increased for 7 days before it rained again in late July (Figure 2). August-sown seeds were planted into a moist seedbed created by rains at the end of July and beginning of August. However, the seedbed dried out within 3 to 5 days and remained dry until late August. Only a few seedlings established from the August seeding.

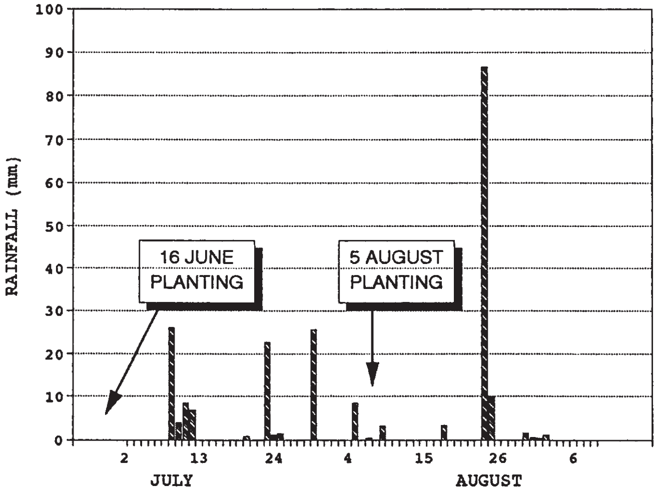

Figure 1—Precipitation from July through August 1992 at the Santa Rita Experimental Range.

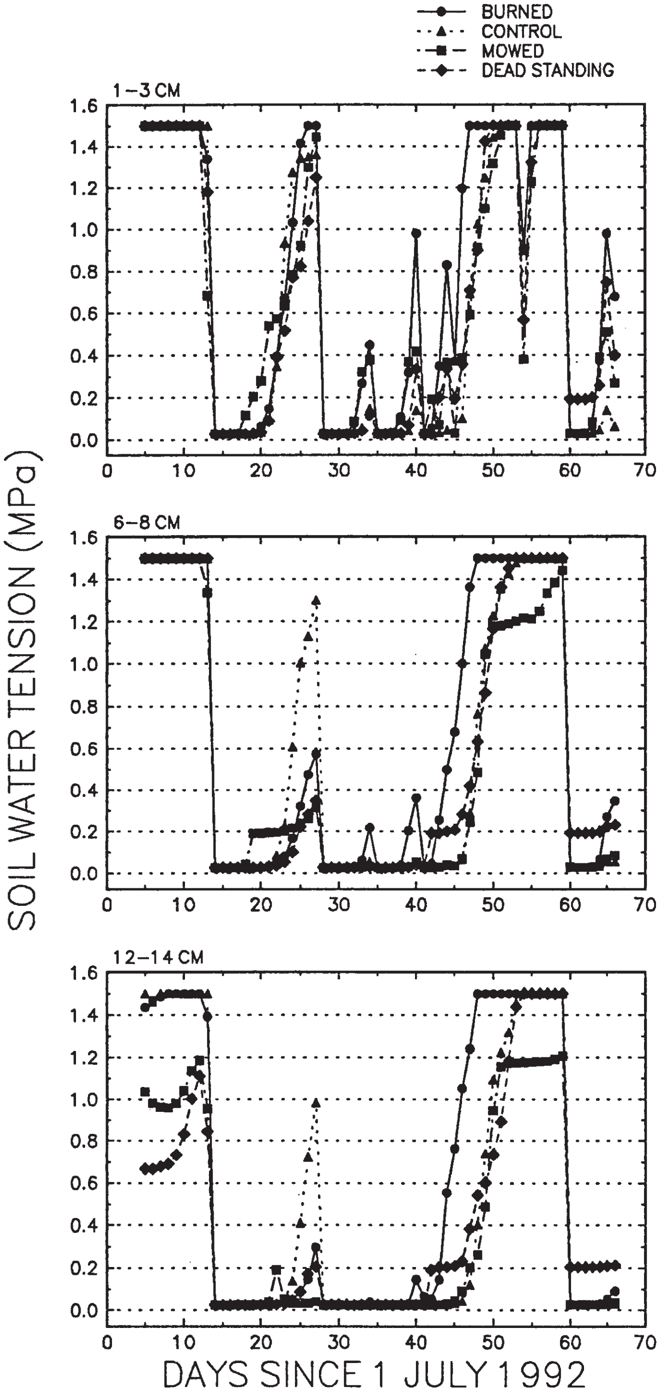

Figure 2—Soil water tension in 1992 at 1-3, 6-8, and 12-14 cm soil depth in relation to various Lehmann lovegrass canopy manipulations.

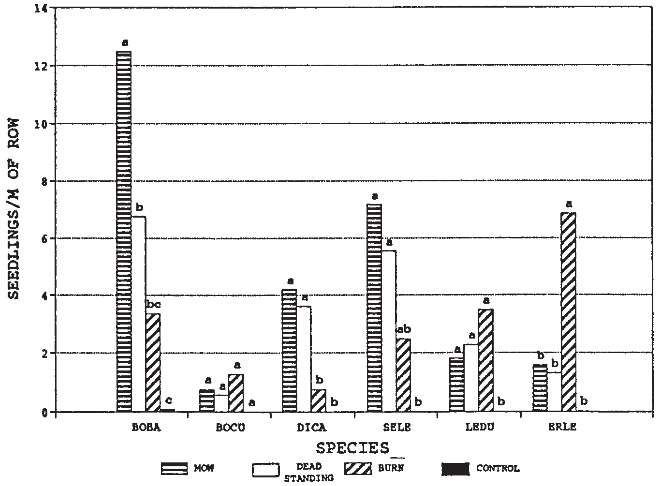

Figure 3—June 1992 sown native grass and Lehmann lovegrass seedling densities at the end of the summer growing season in relation to various Lehmann lovegrass canopy manipulations. *Bothriochloa barbinodis* = BOBA; *Bouteloua curtipendula* = BOCU; *Digitaria californica* = DICA; *Setaria leucopila* = SELE; *Leptochloa dubia* = LEDU; *Eragrostis lehmanniana* = ERLE.

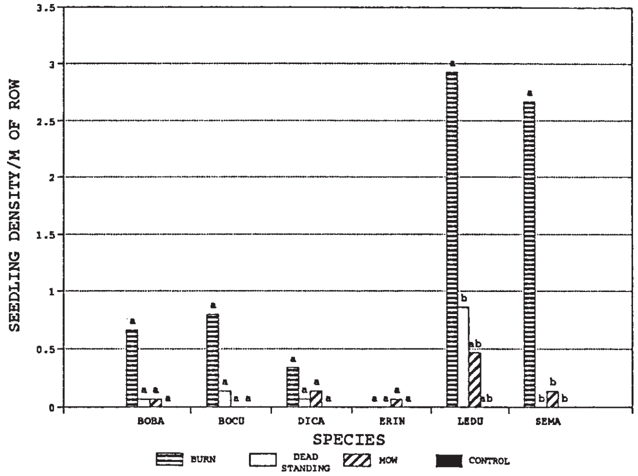

Figure 5—June 1993 sown native grass seedling density at the end of the summer growing season in relation to various Lehmann lovegrass canopy manipulations. *Bothriochloa barbinodis* = BOBA; *Bouteloua curtipendula* = BOCU; *Digitaria californica* = DICA; *Eragrostis intermedia* = ERIN; *Leptochloa dubia* = LEDU; *Setaria macrostachya* = SELE.

Seedling density for the 1992 June planting measured at the end of the growing season (Figure 3) showed significant treatment by species interactions ($p < 0.05$). Five native species emerged. The mow treatment had greater seedling density than the burn and control treatments for cane beardgrass, Arizona cottontop, and plains bristlegrass. The dead standing treatment also had greater density than the burn and the control treatments for Arizona cottontop. Lehmann lovegrass seedling density from sown seeds and the residual seedbank was highest on the burn treatment. Emergence of all species was limited on the control treatment, where species were seeded into living Lehmann lovegrass stands, even though soil water tension at 1-3 cm differed little from the other treatments. Native seedling height for the June planting was also measured at the end of the first growing season. Overall, the tallest seedlings were found in the mow treatment, but there was no statistical difference in seedling height between the mow and the dead standing treatments. There were no significant differences among the dead standing, burn, and control treatments. Seedling heights averaged 4.0, 12.9, 9.5, and 0.1 cm for the burn, mow, dead standing, and control treatments, respectively.

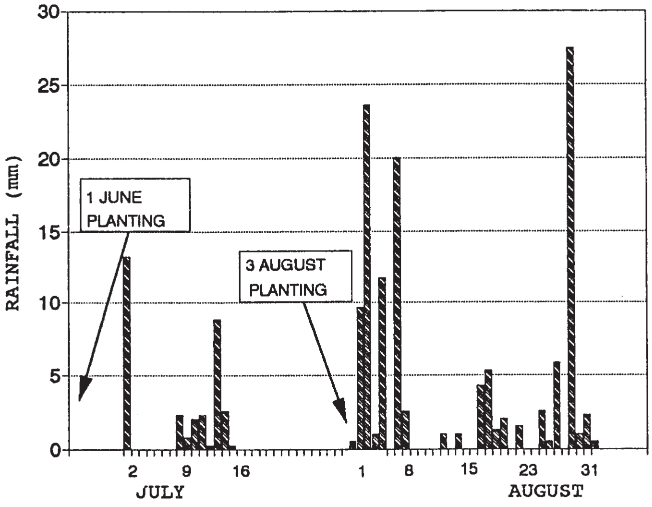

Figure 4—Precipitation from July through August 1993 at the Santa Rita Experimental Range.

In 1993 precipitation patterns were more typical (Figure 4). Seeds sown in early June received 13 mm of rain on 1 July, then experienced 6 dry days followed by 8 more days of rain, then 2 dry weeks. Few seedlings established from the June planting and many seedlings which emerged suffered mortality (Figure 5). Seeds sown in early August received 7 days of rainfall, 4 dry days, then frequent and consistent precipitation through the month of August. Many seedlings emerged and survived from the August planting (Figure 6). Soil water tension, like in 1992, showed little difference between treatments at 1-3 cm except that the burn treatment dried out somewhat faster than the other treatments (Figure 7). June-sown seeds experienced alternating wet and dry conditions in early July and a long dry period from mid-July to early August. August-sown seeds also experienced alternating wet and dry conditions, but the length of the periods between rains was shorter.

For the June planting in 1993, there were no significant treatment differences ($p < 0.05$) in seedling density for cane beardgrass, sideoats grama, Arizona cottontop, and plains lovegrass (Figure 5). Green sprangletop and plains

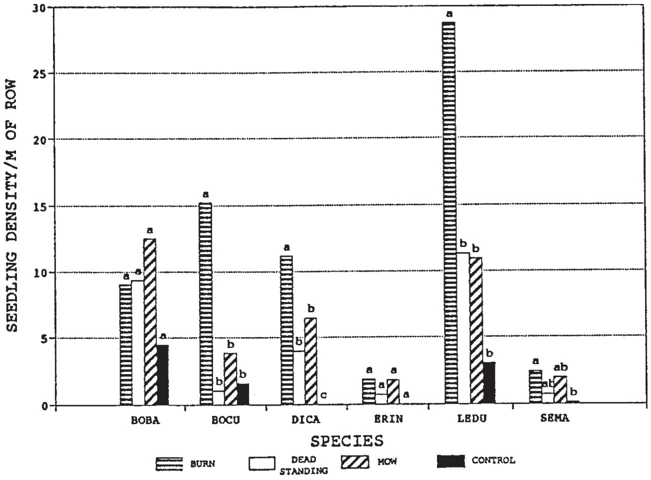

Figure 6—August 1993 sown native grass seedling density at the end of the summer growing season in relation to various Lehmann lovegrass canopy manipulations. *Bothriochloa barbinodis* = BOBA; *Bouteloua curtipendula* = BOCU; *Digitaria californica* = DICA; *Eragrostis intermedia* = ERIN; *Leptochloa dubia* = LEDU; *Setaria macrostachya* = SEMA.

bristlegrass had significantly greater establishment on the burn treatment. However, the average density was fewer than three seedlings per meter of row. For the August planting (Figure 6), average seedling density was 10 times the magnitude of the June seeding. There were no significant treatment differences for cane beardgrass and plains lovegrass, but the burn treatment produced significantly more sideoats grama, Arizona cottontop, and green sprangletop seedlings. The control treatment had the lowest seedling density, but it was only significantly less than the mow and the dead standing treatments for Arizona cottontop. However, the vigor of seedlings in the control treatment was extremely low.

As expected, Lehmann lovegrass emerged in significantly greater numbers from the burn treatment, and seedling emergence was suppressed by the mow, the dead standing, and control treatments (Figure 8). Density of mature Lehmann lovegrass plants was reduced by the burn treatment, but lovegrass density on the mow and the dead standing treatments was not significantly different than the control treatment, indicating that the herbicide application was not effective in killing mature Lehmann lovegrass plants. Forbs were most numerous in the control treatment, followed by the burn treatment, and lowest in the dead standing and mow treatments.

Conclusions

In terms of native species responses, there were significant species-by-treatment interactions. In 1992 cane beardgrass had the highest seedling establishment and it established best on mow plots. In 1993 green sprangletop had the highest establishment, and it performed best on burn plots. These differences can be attributed to the different rainfall patterns seen in the 2 years. Neither plains lovegrass nor bush muhly successfully established in either year. Sideoats grama showed no significant difference in establishment among treatments for 1992 and

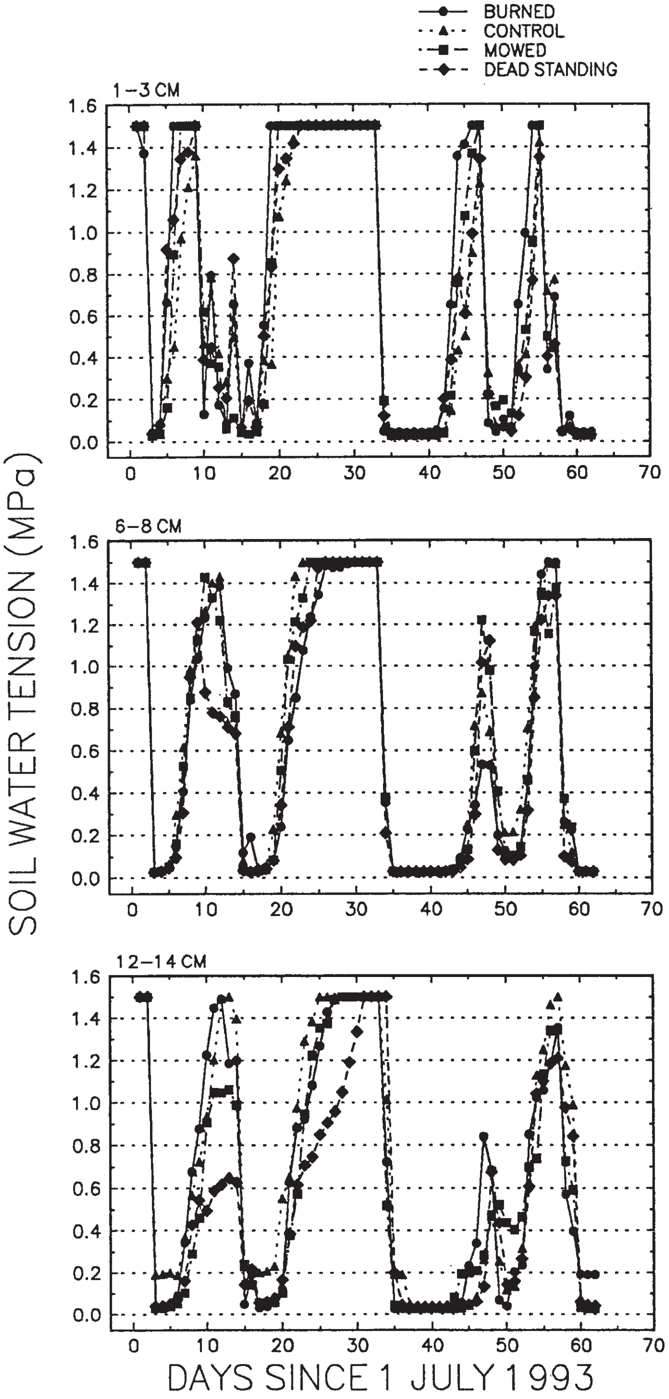

Figure 7—Soil water tension in 1993 at 1-3, 6-8, and 12-14 cm in relation to various Lehmann lovegrass canopy manipulations.

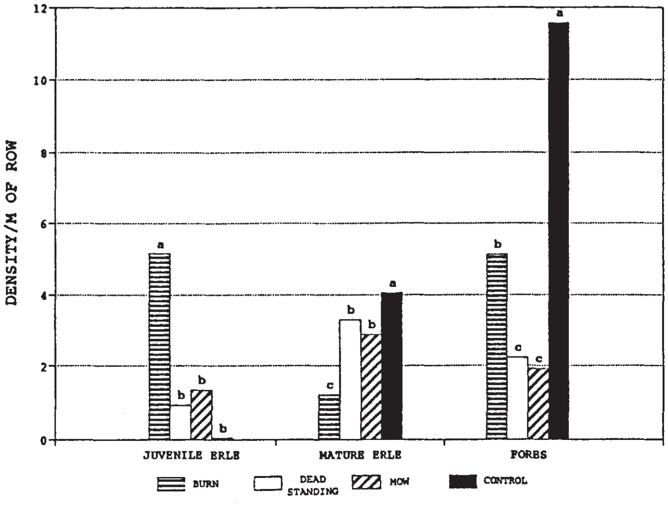

Figure 8—Juvenile and mature Lehmann lovegrass (ERLE) and forb seedling densities on August 1993 plots at the end of the summer growing season in relation to various Lehmann lovegrass canopy manipulations.

1993. Arizona cottontop established better on the mow and dead standing treatments than the burn and control treatments in 1992, but showed no significant difference among treatments in 1993. In 1992 plains bristlegrass did not establish on the control treatment and showed no significant differences among the other treatments; in 1993 it established significantly better on the burn treatment than on the others.

In 1992 the mow treatment and in 1993 the burn treatment had the best overall native seedling establishment. Lehmann lovegrass seedling emergence was suppressed by the mow and dead standing treatments and enhanced by the burn treatment. The control treatment had the lowest establishment overall for seedlings of all species.

Because Lehmann lovegrass has tremendous seedling establishment potential from seedbanks, controlling and replacing Lehmann lovegrass will probably require a two-step plan. The first step would be a treatment to force the expression of the seedbank, such as burning, then a follow-up treatment to kill juveniles and surviving adult lovegrass plants, such as an herbicide treatment, prior to seeding the desired species.

Ultimately, precipitation patterns and amounts are the most important factors in determining seedling establishment for revegetation in semi-arid climates. Precipitation is variable and unpredictable from year to year. However, examination of climatic records for a region may reveal patterns which could indicate optimum seeding dates for maximizing the chances of revegetation success.

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Effects of Soil Quality and Depth on Seed Germination and Seedling Survival at the Nevada Test Site

Kevin W. Blomquist
Glen E. Lyon

Abstract—A study was developed to test the effects of soil quality and depth on seedling emergence and survival. Fifty-six plots were established and two treatments were tested. The first treatment compared native topsoil to subsoil imported from a borrow pit. The second treatment compared four different depth ranges of both soil types. All plots received identical seeding treatments. Seedling density was measured after emergence. Overall seedling densities averaged 10.3 ± 8.8 (SD) plants/m^2. Statistical analysis revealed a significant interaction between the two treatment factors. The subsoil had increasing densities from the deep soil depths to the shallow depths while the topsoil had increasing densities from the shallow soil depths to the deep depths.

As part of its commitment under the Nuclear Waste Policy Act 1983, as amended in 1987, the U.S. Department of Energy (DOE) has developed an environmental program (DOE 1989) that is to be implemented during site characterization at Yucca Mountain. A portion of this environmental program deals with reclamation of disturbed sites. The goal of reclamation is to return land disturbed by site characterization activities to a stable ecological state with a form and productivity similar to the predisturbed state.

Since limited information exists pertaining to Mojave Desert reclamation, DOE has implemented a series of feasibility studies to investigate the success of various reclamation techniques for the Yucca Mountain area. The most successful techniques will be used for stabilizing and revegetating temporary topsoil stockpiles, and reclaiming sites released for final reclamation.

Many of the sites disturbed in the early years of site characterization did not have topsoil salvaged for later use during reclamation. Topsoil is an important component of the desert environment. It serves as a nutrient source for plants (Great Basin Naturalists Memoirs 4 1980; Ostler and Allred 1987) and the top 5-10 cm (2-4 in) of soil contains the majority of the seed-bank and a large percentage of the organisms associated with nutrient cycling (Foth and Turk 1972). Therefore, soil may have to be imported to these sites in order to meet the reclamation goals set by DOE. Because importing soil to a site is expensive, data needs to be collected to assess the minimum amount of soil necessary for reclamation.

The effects of topsoil depth have been studied by mining operations in semi-arid regions. Croft and others (1987) tested soil thicknesses of 0, 10, 20, 30, and 46 cm (0, 4, 8, 12, 18 in) and reported that plant cover and biomass did not appear to be affected by topsoil depth. However, Schuman and others (1985) tested soil depths of 0, 20, 40, and 60 cm (0, 8, 16, 24 in) and reported that production was greater for the 40 (16 in) and 60 cm (24 in) depths. Chambers (1989) recommends that 30 cm (12 in) of topsoil be applied to fine or medium-textured spoils while coarse-textured or rocky spoils may require up to 60 cm (24 in) of topsoil. Power (1978) found that red spring wheat yields increased as pure topsoil thickness increased up to 60-75 cm (24-30 in), at which point yields plateaued. Research conducted in California's San Joaquin Valley found that as little as 15 cm (6 in) of topsoil produced a 19-fold increase in production and a 4-fold increase in percent cover over a no-topsoil control (Anderson 1987).

Topsoil is a scarce resource in the desert so situations may arise where lower-quality soils may have to be used. The effects of topsoil quality on revegetation have not been studied extensively and findings have been mixed. Power (1978) concluded that red spring wheat yields were lowest on subsoil, followed by a subsoil and topsoil mix. Red spring wheat yields were highest for pure topsoil. Other experiments have shown that rough-graded subsoil can be superior to topsoil for grass and legume establishment, although subsoil moisture rather than the topsoil material was the primary factor responsible for the improved grass and legume establishment (Wright and others 1978). Information gained by studying soil depth and soil quality will aid in determining methods for reclaiming sites in the most cost-effective manner.

The objectives of this study were to determine the effects of soil quality and depth on emergence and survival of native plant species. The working hypotheses are: 1) seedling emergence will be higher in the topsoil in comparison to the imported subsoil; and 2) seedling emergence will be the same across all soil depths. This paper presents preliminary data. Field plots will be monitored for the next several years to determine plant survival as it relates to soil quality and depth. The working hypotheses for the long-term study are: 1) long-term plant density and survival will be higher in the native topsoil in comparison to the imported subsoil; and 2) long-term plant density and survival will have a direct relationship to soil depth.

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Materials and Methods

A disturbed area on the northern end of the Yucca Mountain crest was selected for this study due to the flat, homogeneous bedrock surface. Elevation at the site is approximately 1,450 m (4,750 ft). The undisturbed area surrounding the study site is dominated by blackbrush (*Coleogyne ramosissima*) and is characteristic of a transition desert shrub community between the lower elevation Mojave Desert and the higher elevation Great Basin Desert. In 1982, the area was scraped with a bulldozer and the soil was used in construction of a road. Minimal topsoil and subsoil remained on the exposed bedrock.

In November 1992, a road-grader was used to scrape off any remaining topsoil and subsoil and expose the bedrock at the study site. While most of the area was exposed bedrock, some soil remained in the cracks and undulations of the bedrock's surface. Fifty-six 5 x 7.5 m (16.4 x 24.6 ft) plots were marked out on the site in a completely randomized 2 x 4 factorial design with seven replications. The first factor, soil quality, had two levels: subsoil and topsoil. The subsoil originated from a borrow pit on the east side of Yucca Mountain. The topsoil was the material that remained on the site following the original disturbance. It was a mixture of topsoil and subsoil similar to material that would have been salvaged for future use. The second factor, soil depth, had four levels: 5 ± 5, 15 ± 5, 25 ± 5, and 35 ± 5 cm (2.5 ± 2.5, 6 ± 2.5, 10 ± 2.5, 14 ± 2.5 in) of soil. A front-end loader was used to spread the soil over each plot. Removal of large rocks and final leveling was accomplished by hand. Samples from both soil types were analyzed for the physical and chemical factors listed in Table 1.

Plots were seeded at a rate of 18.4 kg/ha pure live seed (PLS) (16.4 lb/ac PLS) with a mix of species native to Yucca Mountain (Table 2). All seed was drill-seeded except for winterfat (*Ceratoides lanata*) which was broadcast-seeded. Plots were mulched with wheat straw at a rate of 2,803 kg/ha (2,500 lb/ac). The straw was then tackified with a mixture of commercially available tackifier at a rate of 112 kg/ha (100 lb/ac) and wood fiber at a rate of 168 kg/ha (150 lb/ac). Approximately 0.64 cm (0.25 in) of supplemental water was applied to the plots after mulching.

Table 1—Median comparisons of selected soil properties for the subsoil and topsoil soil types. Letters denote differences at the $p < 0.05$ level. Differences were calculated using the Wilcoxon two sample test.

Soil property	Subsoil (n = 5)	Topsoil (n = 4)
Nitrogen (ppm)	2a	11b
Phosphorus (ppm)	0.1a	2.4b
Potassium (ppm)	604a	514a
Percent organic matter	0.2a	1.5b
Percent gravel > 2mm	57a	44.5b
Percent sand	88a	64b
Percent silt	2a	24b
Percent clay	10a	13a
Soil type	Loamy sand	Sandy loam
Percent water at 1/10 bar	15a	22b
Percent water at 15 bars	9.2a	15.3b
Cation Exchange Capacity (CEC)	10.6a	21b
pH	8a	8a
Electrical conductivity	1.38a	0.8b

Table 2—Seeded and unseeded species counted during spring (1993) seedling density measurements.

Common name	Scientific name	Identification code
Seeded Species:		
Anderson desert thorn	*Lycium andersonii*	LYAN
blackbrush	*Coleogyne ramosissima*	CORA
California buckwheat	*Eriogonum californica*	ERCA
common snakeweed	*Gutierrezia sarothrae*	GUSA
desert mallow	*Sphaeralcea ambigua*	SPAM
fourwing saltbrush	*Atriplex canescens*	ATCA
galleta grass	*Hilaria jamesii*	HIJA
spiny hopsage	*Grayia spinosa*	GRSP
Nevada ephedra	*Ephedra nevadensis*	EPNE
shadscale	*Atriplex confertifolia*	ATCO
sticky leaf rabbit-brush	*Chrysothamnus viscidiflorus*	CHVI
white burrow-brush	*Hymenoclea salsola*	HYSA
white bursage	*Ambrosia dumosa*	AMDU
winterfat	*Ceratoides lanata*	CELA
Unseeded Species:		
wheat	*Triticum aestivum*	TRAE
white clover	*Melilotus alba*	MEAL
storksbill	*Erodium cicutarium*	ERCI
red brome	*Bromus rubens*	BRRU

The site received approximately 20.7 cm (8.1 in) of precipitation during the period of November, 1992 through March, 1993, which postponed seeding until the end of March. Approximately 2.0 cm (0.8 in) of natural precipitation occurred between the time of planting (March, 1993) and when seedling density data was collected in June, 1993.

Seedling density data by species was obtained on June 3, 1993, by counting all seedlings (seeded and annual) within 1-m^2 quadrats. Ten quadrats were located along a transect centered within each replicate plot. Seedling density was calculated for each species as the number of seedlings/m^2.

Treatment differences and interactions were determined nonparametrically with an extension of the single factor Kruskal-Wallis method (Zar 1984), using ranked sums to determine sum of squares. Species differences according to treatment effect were determined with the single factor Kruskal-Wallis method (Zar 1984). Multiple comparisons within treatments and species were determined with a nonparametric analog to Student-Newman-Keuls mean comparison test (Zar 1984).

Results

Soil Analysis

Ten of the 13 soil properties analyzed were different between the topsoil and subsoil (Table 1). The topsoil's chemical properties were generally more conducive for plant growth and establishment, since it had higher amounts of nitrogen, phosphorus and organic matter. The topsoil also had a higher water-holding capacity at both –1/10 and –15 bar pressure.

Seedling Density of Seeded Species

Seedling densities across all treatments were low and variable, averaging 10.3 ± 8.8 (SD) plants/m^2. Replicates within the same treatment combination (soil type x soil depth) often had large ranges of means. Of the 14 species seeded, seven species did not emerge or had fewer than 12 individuals counted in all 560 sample quadrats. Two species, California buckwheat (*Eriogonum californica*) and winterfat made up 88.5% of the entire seeded species response.

Analysis showed the data to have a nonnormal distribution. Log$_{10}$ and square root transformations were unsuccessful in normalizing the data, so nonparametric methods were used for data analysis. Seedling densities were not different for the main treatments, soil type ($p > 0.50$) and soil depth ($p > 0.10$). The interaction of the two main treatments, however, was highly significant ($p < 0.0001$). For this reason, the remaining analyses of seedling density for each main treatment effect is presented within the levels of the other treatment factor as recommended by Sokal and Rohlf (1981).

Median seedling densities in the subsoil were high in the shallowest depths and low in the deeper depths (Figure 1A). Median densities in the 5 cm (2.5 in) and 15 cm (6 in) soil depths were different from each other ($p < 0.005$), and from the median densities in both the 25 cm (10 in) and 35 cm (14 in) depths ($p < 0.001$). The median densities in the 25 cm (10 in) and 35 cm (14 in) depths were not different from each other ($p > 0.05$). The median density trend for the topsoil was opposite (Figure 1B). The 25 cm (10 in) and 35 cm (14 in) depths had higher median densities than the two shallow depths ($p < 0.01$), but the 25 cm (10 in) and 35 cm (14 in) depths were not different from each other ($p > 0.05$).

Seedling densities were different between soil types within the same soil depth categories (Figure 1A and 1B), a result of the significant interaction. A minimum two-fold magnitude difference ($p < 0.0005$) is seen in median seedling densities between soil type for all soil depth levels.

Comparisons of individual species shows that the same six species responded best in both the subsoil and topsoil treatments (Figure 2A and 2B). Because the median values were mostly zeroes on the species level, the mean was used to see trends. The mean is an overestimation of the central point of the data because the data is positively skewed. For this reason the mean rank scores are also provided and multiple comparisons were determined from the mean rank scores. The response of individual species to soil type was generally the same; mean differences were never greater than one plant/m^2.

Seedling Density of Non-seeded Annual Species

Thirty-three non-seeded annual species were identified and counted within the seedling density quadrats. Three common desert perennials: rubber rabbitbrush (*Chrysothamnus nauseosus*), needle leaf rabbitbrush (*Chrysothamnus teretifolius*) and Indian rice grass (*Oryzopsis hymenoides*) were also counted but were not included in the analysis. Non-seeded annual species responded differently to soil type ($p < 0.005$) but not soil depth ($p > 0.25$). The interaction was also significant ($p < 0.001$).

For both soil types, median annual species' densities in the two shallow soil depths were different than the densities in the two deeper soil depths (subsoil $p < 0.001$; Figure 3A and topsoil $p < 0.005$; Figure 3B), but the median density trends for the two soil types were opposite. This response is very similar to that seen from the seeded species. Annual species densities across soil types were not different ($p > 0.05$) for the two shallow depths as they were for the seeded species. Only in the two deeper soil depths were annual species densities different for soil type ($p < 0.0001$).

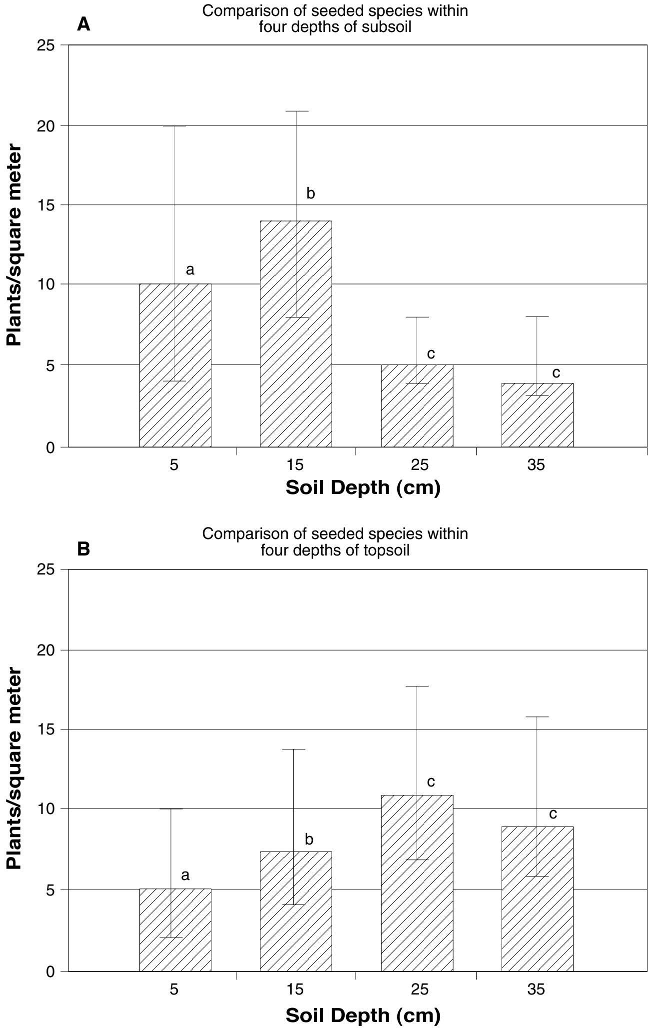

Figure 1—Median plant densities of all seeded species for two soil types, subsoil (A) and topsoil (B) at four soil depths. Differences among soil depths were measured using the Kruskal-Wallis method (Zar 1984). Multiple comparisons were determined using a nonparametric analog to the Student-Neuman-Keuls test (Zar 1984). Letters denote differences ($p < 0.05$). Vertical bars represent the 25%-75% quartile range. Sample size (n) equals 70.

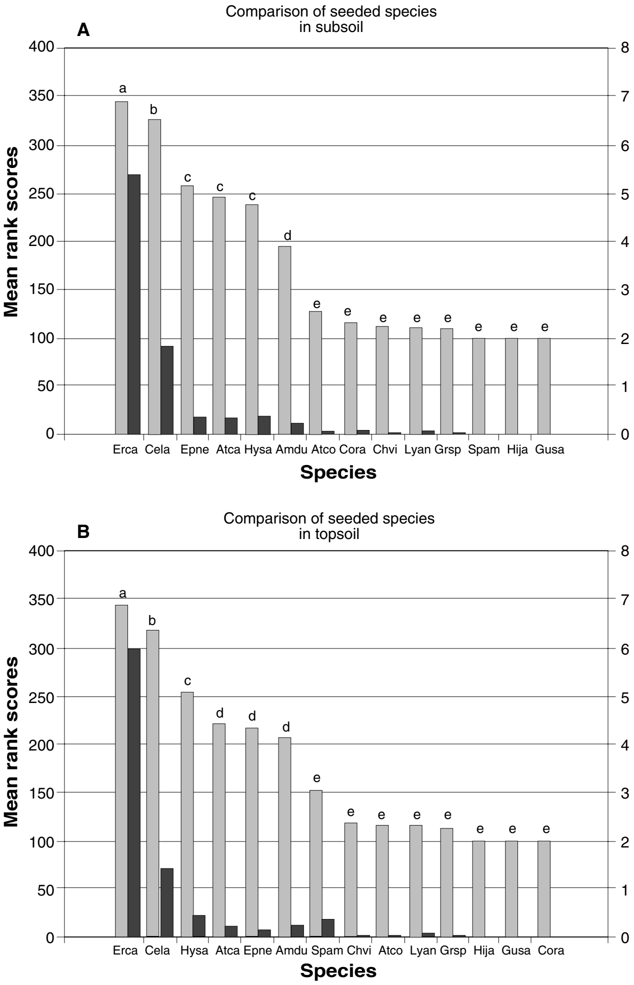

Figure 2—Response of 14 seeded species in two soil types, subsoil (A) and topsoil (B). The left bar is the mean rank score and the right bar is plant density/m^2. Differences among species were measured using the Kruskal-Wallis method (Zar 1984). Multiple comparisons were determined with a nonparametric analog to the Student-Neuman-Keuls test (Zar 1984). Letters denote differences ($p < 0.05$). Sample size (n) equals 280. Plant codes are defined in Table 2.

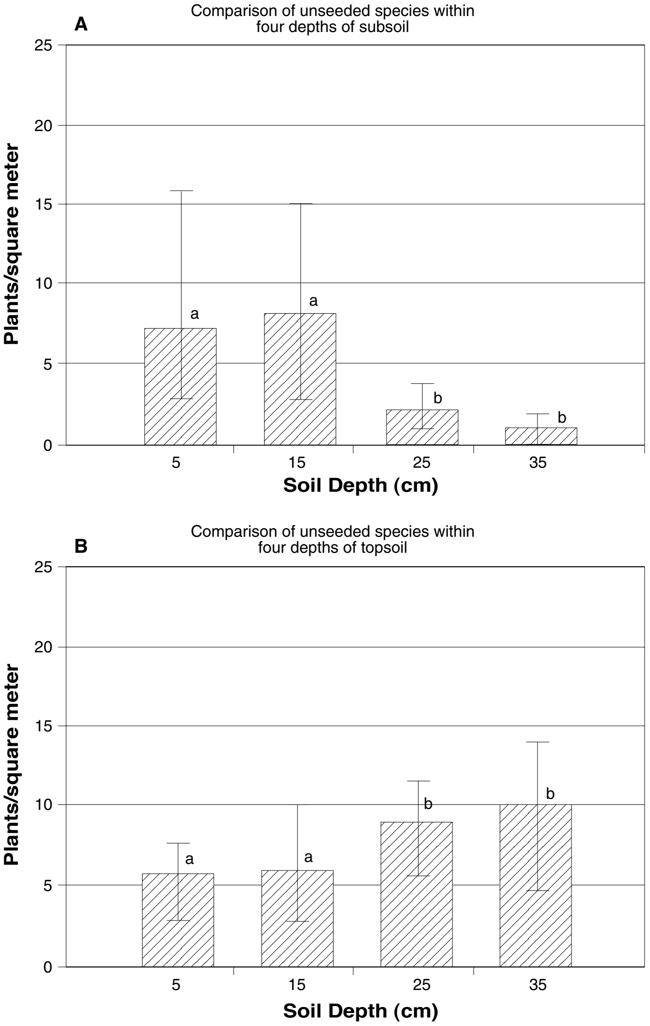

Figure 3—Median plant densities of all unseeded annual species for two soil types, subsoil (A) and topsoil (B) at four soil depths. Differences among soil depths were measured using the Kruskal-Wallis method (Zar 1984). Multiple comparisons were determined using a nonparametric analog to the Student-Neuman-Keuls test (Zar 1984). Letters denote differences ($p < 0.05$). Vertical bars represent the 25%-75% quartile range. Sample size (n) equals 70.

The response of annual species to soil type and depth was determined for the most abundant species. The densities of annual species varied. Twenty of the 33 annual species identified in the 560 sample quadrats were counted fewer than 10 times, while some species were counted more than 500 times. An annual species was considered separately if it was found in greater than 25% of the plots and more than 100 individuals were counted. Five species, storksbill (*Erodium cicutarium*), red brome (*Bromus rubens*), wheat (*Triticum aestivum*), white clover (*Melilotus albus*) and an unknown grass met this criteria. The remaining species were grouped together. Wheat and white clover were the most common annual species in both soil types (Figure 4A and 4B). Both wheat and white clover were also non-native annual species.

Discussion

The low seedling densities measured during this study could have been a result of several factors. Wester (1991) summarized 212 different papers that covered 11 different factors influencing seed germination. Most of these studies focused on three main factors, moisture, light, and air temperature. Germination requirements for many species indicate that a combination of factors affect seed germination and that these requirements sometimes conflict between species. For example, the germination profile of common snakeweed (*Gutierrezia sarothrae*) suggests that this species germinates best at cooler temperatures (<70° Fahrenheit) under low moisture stress (Kruse 1970). In contrast, spiny hopsage (*Grayia spinosa*) collected from the Mojave

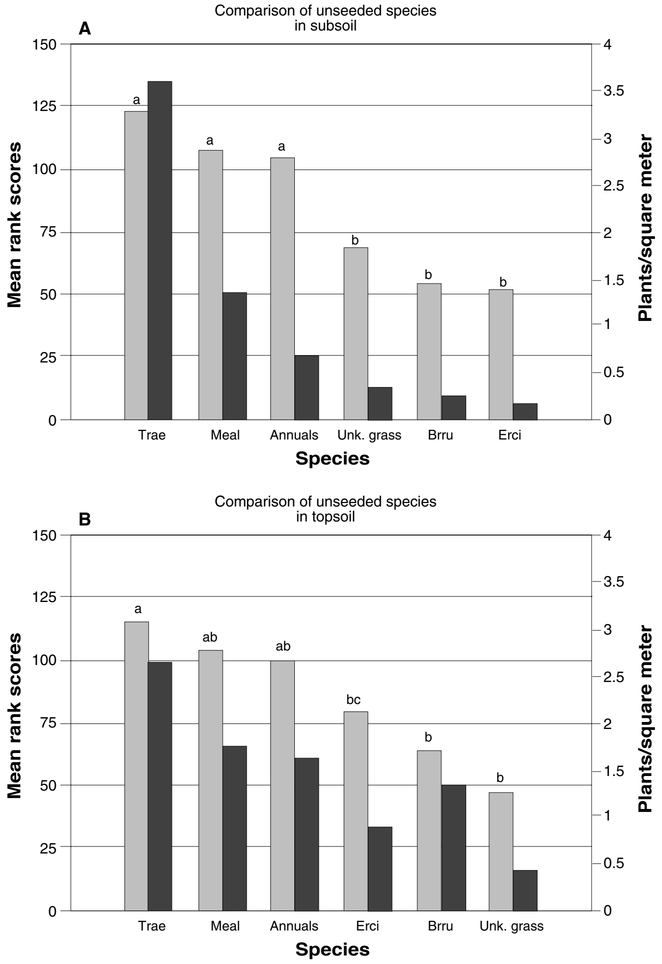

Figure 4—Response of 5 separate unseeded annual species and the pooled species (Annuals) in two soil types, subsoil (A) and topsoil (B). The left bar is the mean rank score and the right bar is plant density/m^2. Differences among species were measured using the Kruskal-Wallis method (Zar 1984). Multiple comparisons were determined with a nonparametric analog to the Student-Neuman-Keuls test (Zar 1984). Letters denote differences ($p < 0.05$). Sample size (n) equals 280. Plant codes are defined in Table 2.

Desert appeared to germinate best in warmer temperatures (>86° Fahrenheit) but wasn't affected by moisture stress down to –12 bars (Wood 1976). The late planting date for this study may have been one reason why seedling density was low. Not all germination requirements may have been met for all species. Although overall densities were low, the response of California buckwheat was good, averaging over 5 plants/m^2. This favorable response would suggest that the germination requirements of California buckwheat were present.

The observed interaction between soil type and soil depth is difficult to explain. Although California buckwheat's response may have been the greatest contributor to the interaction, the response of five other seeded species and the annual species also follow a similar trend. This indicates that there was a consistent effect across all plots that caused seedling emergence of most species to react similarly.

The first working hypothesis stated that soil type would affect seedling emergence. It was anticipated that the topsoil may have slightly higher densities than the subsoil. Two variables may be responsible for creating differences in seed germination and seedling emergence across soil types: 1) soil water-holding capacity (created by differences in soil texture) and 2) the seed's ability to absorb available water (created by differences in soil chemistry). Soil chemical properties such as salt content affect this by creating an osmotic pressure that inhibits the seed's ability to absorb water. Both water-holding capacity and salt content based on electrical conductivity are different between soil types; however, the electrical conductivities of both soils are probably not high enough to affect soil water availability to the seed. Soil water-holding capacities of the two soil types may have been different enough to cause differences in seedling emergence; however, the bedrock tended to hold water near the surface of the shallow subsoil plots providing adequate moisture for germination and thus overcoming the main treatment effect of soil type.

The second hypothesis stated that the different soil depths would not influence seedling emergence. Differences in seedling emergence across soil depth for a soil type can only be attributed to different amounts of soil water being held by different volumes of soil because both soil chemistry and soil particle size are identical. It was anticipated that the seedlings would not grow fast enough to be limited by soil water even at the shallowest depth. Although the topsoil showed a direct relationship between seedling density and soil depth, it is not likely that soil water depletion is the cause because the subsoil with a lower water-holding capacity showed higher density in the shallower plots. The data suggest that shallow subsoils and deep topsoils are the combinations that give the highest seedling emergence. However it seems reasonable that another variable may be responsible for the result seen.

One possible explanation results from a shallow bedrock surface's influence on soil water movement when rainfall occurs. Precipitation events prior to planting were observed to saturate the shallow soils (both in the experimental plots and in undisturbed areas) while the deeper soils were able to absorb water without becoming saturated. The topsoil in the deeper plots also seemed to hold this moisture for quite a long time while the subsoil in the deeper plots had dried 20 to 25 cm below the soil surface. Because the study was located on exposed bedrock, the shallow soils would naturally reach water-holding capacity more quickly than the deep soils during a precipitation event. This may have caused seedling germination in the shallow topsoil to be limited by anaerobic conditions or seed rot caused by a saturated soil profile. Although the shallow subsoil also reached the saturation point quickly, due to its larger particle size distribution, soil saturation may not have lasted long enough to cause anaerobic conditions or seed rot, thus allowing seeds to germinate. Conversely, water in the deep subsoil infiltrated and may have drained away so quickly that seeds did not have time to absorb water for germination. The native soils in the deeper plots may have held the water in the seed zone long enough for germination to occur but not long enough for germination to be limited. To determine if the combined effects of a shallow bedrock surface and rainfall actually caused the results found, daily soil moisture data would have been required before and during the time of germination and emergence.

Conclusions

Preliminary results show an interaction of the two main treatments, soil type and soil depth for both seeded perennial species and non-seeded annual species. The cause of this interaction is not known; however, it may result from the shallow bedrock surface's influence on soil water movement when rainfall occurs. This study will continue for the next several years so that a final determination can be made.

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Evaluating Degraded Riparian Ecosystems to Determine the Potential Effectiveness of Revegetation

Mark Briggs

Abstract—Revegetation is often limited in its ability to improve the condition of degraded riparian ecosystems. In some cases, revegetation was implemented in riparian areas that were fully capable of coming back naturally. In other instances, plantings were placed in riparian sites where they could not survive.

To use riparian revegetation most effectively, the causes of site decline and the current ecological condition of the site need to be understood. This can best be accomplished by evaluating the condition of the degraded riparian ecosystem from a watershed perspective that takes into consideration how perturbations in surrounding ecosystems may be affecting site conditions.

Riparian ecosystems are declining throughout the Southwest; many have disappeared completely. The rapid decline of these valuable ecosystems has made riparian conservation a focal issue for many federal, state, and private organizations. Nevertheless, progress toward checking the decline of riparian ecosystems has been marginal. This is due, in part, to the fact that the "science" of repairing damaged riparian ecosystems is relatively young, and some of the fundamental questions on riparian ecosystem processes and how human activities are affecting the ecological condition of riparian areas are still being investigated. In addition, the results of only a relatively small number of riparian mitigation efforts have been evaluated for the benefit of future projects (mitigation is defined here as any project that is performed to improve the ecological condition of an area.) Consequently, we have learned only marginally from past mitigation efforts and are just beginning to understand how to effectively repair degraded riparian ecosystems.

The objective of this paper is to discuss the limitations of using revegetation to improve the condition of degraded riparian ecosystems. This paper also reviews riparian site characteristics that play a significant role in determining the effectiveness of riparian revegetation to improve the condition of degraded riparian ecosystems in arid environments. These issues are discussed in greater detail in a guidebook—Repairing Degraded Riparian Ecosystems—being prepared by the Rincon Institute in cooperation with the University of Arizona, Arizona Game & Fish Department, U.S. Fish and Wildlife Service, and other agencies. The guidebook also reviews approaches to evaluating degraded riparian ecosystems so that effective mitigation strategies can be developed.

The information presented in this paper is based on the results of two studies on improving the condition of degraded riparian ecosystems. The first study was funded by the U.S. Fish and Wildlife Service, and evaluated the results of 25 riparian revegetation projects and two alternative mitigations in Arizona (Briggs 1992). The second study, funded by World Wildlife Fund, investigated methods for evaluating the condition of degraded riparian ecosystems so that the potential effectiveness of revegetation can be determined (Briggs 1993).

Riparian Revegetation

Riparian revegetation (planting trees, shrubs, forbs, and grasses to replace lost vegetation) is probably the most widely used of the strategies that have been employed to repair degraded riparian ecosystems. Revegetation has been used to improve degraded riparian conditions along many of the major drainageways in the southwestern United States, including the Colorado River, Santa Cruz River, Gila River, and the Rio Grande. When used in appropriate situations, revegetation can produce dramatic results by helping to replace lost riparian vegetation and stabilize deteriorating conditions, thereby initiating recovery of the ecosystem (Maddock 1976; Miller and Borland 1963; Porter and Silberberger 1961).

The Limitations of Riparian Revegetation

Despite the wide use of revegetation, results are often marginal. In many cases, revegetation could have been used more effectively in other locations, or other mitigation strategies should have been used instead of revegetation (Briggs 1992).

Although 19 out of 27 riparian revegetation projects evaluated by Briggs (1992) achieved their objectives, most did so despite low survival rates of planted vegetation. Out of this group of projects, almost a third experienced natural regeneration so prolific that plantings were completely obscured by regrowth, while over one-half of the projects experienced less than 20% survival of the vegetation that was planted (Fig. 1). Many of the revegetation projects that did achieve their objectives did so primarily by using mitigation techniques that addressed the causes of site degradation, while others succeeded because of prolific natural regeneration at the site (Briggs 1992).

One of the principal reasons why riparian revegetation often produces only marginal results is that the factors

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In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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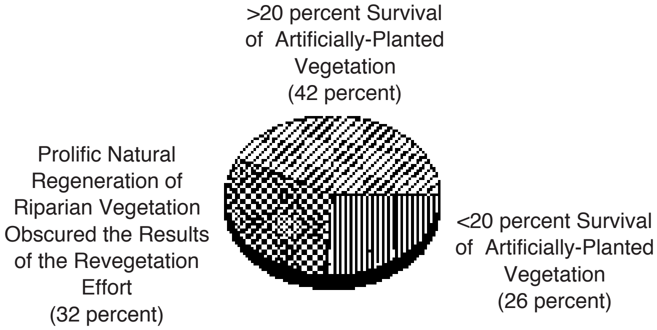

Figure 1—Classification of successful projects by percent survival of artificially-planted vegetation for 19 riparian sites in Arizona.

responsible for the initial degradation of the site often hamper or prevent establishment of artificially planted vegetation as well. In a group of successful riparian revegetation projects evaluated by Briggs (1992), the majority addressed the causes of site degradation (either indirectly or directly) by including secondary mitigation such as bank stabilization structures, check dams, irrigation, and/or improved land management strategies in their overall project design. The ability of these secondary mitigations to overcome the causes of site degradation appeared to have a more significant impact on the overall results of the projects than did revegetation.

Determining the Causes of Riparian Decline from a Watershed Perspective

One of the most important lessons learned from the experiences of past riparian mitigation efforts is the importance of evaluating site conditions to identify the causes of degradation (Briggs 1992). Only after the causes of degradation are identified can mitigation strategies be developed that will directly address the causes, not just the symptoms, of degradation. Evaluating site conditions will provide the information needed to better understand the potential effectiveness of revegetation to improve degraded riparian conditions.

Evaluating only isolated components of a watershed (e.g., a specific stream reach) will be ecologically incomplete and will often fail to provide the information needed to fully understand why the riparian ecosystem has become degraded. Therefore, evaluating degraded riparian ecosystems from a watershed perspective can determine the success of mitigation efforts. More than any other type of ecosystem, the structure and processes of lotic ecosystems are determined by their connection with adjacent ecosystems (Gregory and others 1991). (Lotic environments are areas, such as rivers and streams, that are influenced by running water that is unidirectional; these environments therefore differ from lakes and oceans which are characterized by water flow in more than one direction.) A disturbance in any part of a watershed will create disequilibrium that will be felt through rippling effects by many ecosystems within the watershed. Since riparian ecosystems are in the bottomlands of a watershed, changes in the way that sediment and water run off of surrounding lands impact them most. Riparian ecosystems are affected by perturbations (e.g., timber harvesting, livestock grazing, urbanization, etc.) along upstream and downstream reaches, tributaries, and surrounding uplands.

Resource managers must therefore avoid the myopic approach of developing mitigation strategies that are based solely on an evaluation of the immediate degraded riparian site. It is likely that mitigation based on such a narrow evaluation will not be very effective because the factors that initially caused degradation may continue to affect the site. The evaluation process should include a significant amount of the riparian ecosystem's watershed, taking into consideration the condition of surrounding uplands, upstream and downstream reaches, and tributaries.

The evaluation process should also be broadened from a time perspective. Broadening one's time frame from the present to include historical information may significantly help to determine the extent to which a riparian area has changed, the reasons for the change, and the types of mitigation strategies that may be effective in improving the condition of a degraded ecosystem.

Determining the Potential Effectiveness of Riparian Revegetation

Riparian revegetation is most effectively used in sites where conditions will allow plantings to survive and where natural regrowth will not overrun plantings after they have established. Four site characteristics play a particularly important role in determining whether or not plantings will survive: water availability, channel stability, intensity of direct impacts, and soil salinity. The role that natural regeneration and the above four factors play in determining the potential effectiveness of riparian revegetation is discussed below.

Natural Regeneration

Riparian revegetation is used most effectively in riparian areas that are not likely to experience natural regrowth. This does not imply that natural regeneration is a negative result. On the contrary, natural regeneration is often the restorationist's strongest ally, and fostering natural regrowth should be the aim of most riparian mitigations. The extent and rapidity of natural recovery can be a "concern" when revegetation is being considered as a way of improving the condition of a degraded riparian area. Riparian revegetation can be misused when the area is fully capable of coming back naturally.

The results of several riparian revegetation projects indicate that in some situations natural regeneration can meet or exceed the revegetation objectives established by resource managers. In short, natural regeneration occurred so strongly at some sites that, after a number of years, the manager's careful plantings and site manipulations became difficult or impossible to locate.

Revegetation projects that experienced prolific natural regeneration were not unique. All told, 32% of the successful riparian revegetation sites evaluated by Briggs (1992) experienced prolific natural regeneration that completely obscured the results of artificial planting efforts. It is therefore important for resource managers to recognize the potential for dramatic natural regeneration in riparian ecosystems and consider the possibility that artificial revegetation may not be necessary.

This point is valid even if a riparian site is characterized by low diversity and volume of vegetation. The health of a riparian ecosystem should not be determined solely by changes in vegetation components. A riparian ecosystem may be "healthy" even if it is characterized by low vegetation density, diversity, and volume, as long as all the components required for natural regeneration are intact.

Of the numerous factors that determine natural regeneration in riparian ecosystems, there are a few that appear to have an overriding role in determining the extent, location, and timing of natural regeneration. Of the revegetation sites evaluated by Briggs (1992), those that experienced prolific natural regeneration had three characteristics in common:

1. Riparian sites were not characterized by a decline in groundwater, channel instability, high soil salinity, or a high frequency of direct impacts. These four factors are the same factors that play an important role in determining the effectiveness of riparian revegetation. This should not be surprising. Whether a plant is placed in the ground naturally or artificially, the likelihood that it will establish and survive is determined by many of the same factors;
2. Seed sources were located in or near the riparian sites; and,
3. The majority of sites experienced large flood events. Large flood events (floods large enough in magnitude to remove streamside vegetation and rework and deposit alluvium on upper flood plain surfaces) produce the site conditions suitable for natural establishment of many riparian species.

Water Availability

In arid climates, the amount of water that is available for plant use is probably the single most important characteristic for determining where phreatophytes can establish. Riparian vegetation communities are commonly composed of phreatophytes that exist only in areas where they can develop root systems to saturated soils (Campbell and Green 1968; Stromberg and others 1992). Groundwater conditions therefore play an important role in determining how much water is available for phreatophytes.

The riparian water table is the primary source of water for most phreatophyte trees (Busch and others 1992), and when the water table drops below the root zone it becomes very difficult for these species to survive (Fenner and others 1984; McBride and Strahan 1984). Many phreatophytes develop relatively shallow root systems that often spread out great distances laterally, but frequently do not penetrate more than 3 m below the soil surface.

This characteristic makes riparian species vulnerable to changes in subsurface water. Not only does water have to be available in the shallow subsurface for phreatophytes to survive, but flood plain areas also must be inundated for certain periods of the year to produce moisture conditions necessary for germination and seedling establishment (Fenner and others 1984; Stromberg and others 1991).

Just as groundwater decline can affect the overall health of riparian ecosystems, a decline in groundwater can also have a tremendous influence on the effectiveness of artificial revegetation. Artificially planted phreatophytes will not survive if their root systems cannot reach the water table. Over 80% of the unsuccessful revegetation projects evaluated by Briggs (1992) experienced low survival rates of planted vegetation (0% in some cases) due to low water availability. For the purposes of this paper, areas described as having low water availability are those areas where the saturated part of the soil profile frequently drops to 3 meters or more beneath the soil surface.

Determining the current depth to groundwater is therefore an important step for understanding the potential effectiveness of riparian revegetation. Comparing current groundwater conditions in degraded riparian areas to past groundwater conditions will provide resource managers with a good sense of groundwater stability, and how and to what extent groundwater characteristics have changed.

If information describing the current condition of groundwater in the degraded riparian ecosystem is insufficient, resource managers will need to collect their own hydrogeologic data. A description of current groundwater conditions should include depth to groundwater, how depth to groundwater varies within the revegetation site, and how groundwater conditions vary throughout the year. Such information will allow resource managers to choose vegetation species, plan irrigation schedules, and develop planting designs tailored to the specific area, greatly improving overall effectiveness of revegetation.

Channel Stability

Including the drainageway that passes through the degraded riparian ecosystem in the evaluation process is integral to understanding the condition of bordering vegetation communities. Here the focus turns to issues associated with repairing riparian ecosystems bordering unconfined alluvial stream channels, particularly methods for evaluating their general stability.

Revegetating near unconfined alluvial channels is inherently risky because there is often a fine line between planting in areas that are too dry and planting in areas that are too unstable. Even when these channels are "stable," they are still prone to dynamic changes that can affect the results of revegetation (or any other type of mitigation, for that matter).

Reichenbacher (1984) described riparian communities as a continuum. The continuum is most unstable closest to the stream channel where floods are common, and most stable in areas further removed from the stream channel (e.g., flood plain terraces) where flood disturbances are relatively infrequent. Planting further away from the channel may provide the newly planted vegetation with the stability it needs to establish and grow. However, increased distance from the stream channel is often accompanied by increased depth to the riparian water table. This may produce a dilemma for revegetation planners, particularly if phreatophytes are being used in the revegetation project (Fig. 2).

Channels that have incised into their beds epitomize this dilemma. In such a situation, revegetation may be limited to two choices: planting in a narrow and deep channel, where vegetation can be removed by even minimal flow events, or planting on abandoned terraces, where water availability can be greatly reduced.

When an unconfined alluvial channel falls out of equilibrium and becomes unstable, it can alter its dimensions (e.g., channel width) quite rapidly (Schumm and others 1984; Wallace and Lane 1976). In general, revegetating near alluvial stream channels that are characterized by instability should be avoided because abrupt changes in channel dimensions can be disastrous to streamside revegetation projects.

Emphasized throughout this paper is the concept of evaluating degraded riparian ecosystems from a watershed perspective that includes upstream and downstream reaches, tributaries, and surrounding uplands. This broad evaluation approach is especially relevant to evaluating drainageway stability. The reach of the drainageway that passes through the degraded riparian ecosystem cannot be evaluated in isolation from the rest of the drainage system. Instability along one part of the drainage system can spread to other areas as the various reaches attempt to reestablish stability. This means that channel reaches not characterized by obvious signs of instability at the time of revegetation can exhibit unstable characteristics years after rehabilitation work is completed as a result of disturbances in other parts of the drainage system. For example, Schumm and others (1984) cautioned that renewed instability can quickly return to a channel reach if downstream nickpoints are present. Nickpoints downstream from a revegetation site can work their way upstream during succeeding years, ultimately affecting site stability and the effectiveness of revegetation.

A broad evaluation approach will more accurately define the causes of degradation and trends in channel stability. Such an understanding will allow resource managers to better predict the direction, type, and magnitude of channel adjustment so that mitigation strategies will work in harmony with natural stream processes, rather than against them (Brookes 1985; Harvey and Watson 1986; Heede 1981; Keller and Brookes 1984; Leopold 1977; and Schumm and others 1984).

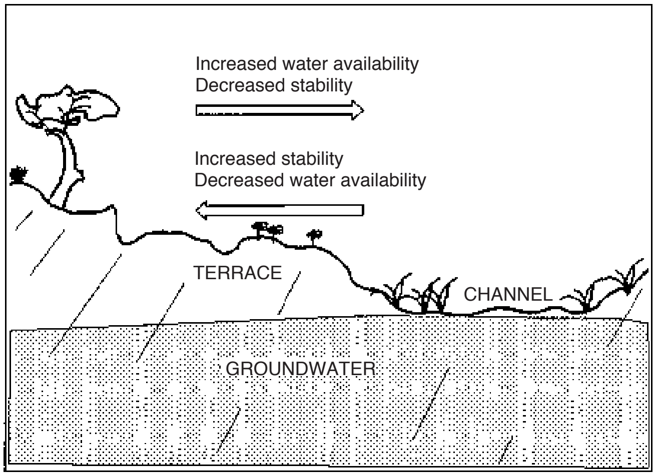

Figure 2—A riparian revegetation dilemma. Increased water availability often means decreased stability for planted vegetation.

Direct Impacts

Land use activities can affect the ecological condition of riparian ecosystems both directly and indirectly. Direct impacts are the results of those activities that occur in the immediate riparian ecosystem. Common examples of activities that directly impact riparian ecosystems are removal of riparian vegetation (e.g., to make way for urban or agricultural expansion), livestock grazing, and recreational activities. Indirect impacts result from activities occurring outside the immediate riparian ecosystem. Activities on remote parts of the watershed, such as timber harvesting and urbanization, can indirectly impact bottomland ecosystems by altering the way sediment and water run off of upper watershed surfaces.

It is important to evaluate how land use activities are affecting the condition of a riparian site before using revegetation. Two of the more common direct impacts on wildland riparian ecosystems are the results of livestock grazing and recreation activities. Competition from nonnative vegetation species and wildlife activities can also directly impact the results of revegetation and should also be considered before planting vegetation in riparian ecosystems.

Soil Salinity

High soil salinity affected the results of several riparian revegetation projects in Arizona (Briggs 1992). It is therefore important for resource managers to recognize the potential that riparian soils may contain abnormally high levels of salts and include an analysis of soil salinity in the evaluation.

For most wildland riparian ecosystems, high soil salinity will not be a problem. Salts are unlikely to build up in healthy, lotic riparian ecosystems, where annual spring floods remove excess salts. However, human impacts have altered natural flow regimes and water quality in many river systems to the point where salinity is contributing to the decline of riverside ecosystems. In the southwestern United States, agricultural practices within the Colorado Basin have greatly impacted the quality of the Colorado River, which picks up roughly 10 million tons of salt per year as it traverses the seven basin states (Hedlund 1984).

Unfortunately, the Colorado River is not the only drainage system in the United States with salinity problems. The Rio Grande and Pecos Rivers, as well as the closed river systems in the Great Basin, the Arkansas River, areas of Texas and Oklahoma, and tributaries of the Upper Missouri River, have problems with increased salinity levels (Hedlund 1984).

Anderson (1989) noted that soil salinity can reach high levels in riparian areas where groundwater is near the soil surface and where stream waters are high in total dissolved solids (TDS). These characteristics unfortunately fit several rivers in the United States. Salt accumulation in flood plain soils can be especially rapid along drainages whose flood patterns have been artificially altered by impoundment. Along reaches of the Lower Colorado River (after the river has been subjected to the effects of 3 large dams), buffered spring flows are no longer capable of flushing accumulated salts from many parts of the formerly active flood plain. This greatly increases the likelihood that salts will accumulate to the extent that salinity will negatively affect establishment and growth rates of riparian species.

Conclusions

Revegetation is limited in its ability to improve the condition of degraded riparian ecosystems. Revegetation efforts are misused in riparian ecosystems that are capable of coming back naturally; revegetation is also misused in riparian ecosystems where plantings cannot survive. Four riparian site characteristics play a particularly important role in determining establishment success of plantings in desert riparian areas: groundwater characteristics, channel stability, direct impacts, and soil salinity.

To design mitigation efforts that will be effective in improving the condition of degraded riparian ecosystems, the causes of riparian decline must be understood. Understanding these causes can best be accomplished from a perspective that considers how the riparian ecosystem is being affected by perturbations in surrounding ecosystems in its watershed. Evaluating only isolated reaches of a stream system will often fail to provide the information required to understand why the riparian ecosystem became degraded, the severity of the decline, and what types of mitigation strategies will be most effective in improving its condition.

To assist in evaluating the condition of riparian ecosystems, the Rincon Institute, in concert with other agencies, has developed a guidebook that reviews strategies for evaluating the condition of degraded riparian ecosystems so that revegetation, and other mitigation techniques, can be used more effectively.

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Evaluating Roadside Revegetation in Central Arizona

Margaret A. Brooks

Abstract—The objective of this study was to evaluate the success of revegetation on highway cuts and fills in a warm desert environment. Revegetation goals were mitigation of visual impacts and soil stabilization. Research methods included surveys of plant cover and density, visual quality, and documentation of erosion and site attributes. Results indicated that revegetation for visual impact mitigation was unsatisfactory on 72% of the cut slopes. Plant cover was the only measured variable that explained variability in "aesthetic satisfaction"; cover was judged as satisfactory to mitigate visual impacts when it reached approximately 20%. Plant cover was significantly higher on fills than on cuts, and erosion was less on fills (although fills were flatter). It was concluded that revegetation was successful only on fill slopes, in terms of meeting the specified goals.

Nationwide, the cuts and fills resulting from highway construction have been cited as one of the largest and most visible types of drastically disturbed lands (Box, 1978). The highway building program in this country has been called "staggering" (Johnson and Lees, 1988) in the wake of over a half century of road building to serve transportation needs as well as driving as a leisure activity (Hottenstein, 1970; Box, 1978). As travel speeds have increased, so has the amount of land disturbed in order to accommodate flatter roads with gentler, safer curves (Gallup, 1974). Advances in earth-moving machinery have made it possible to move mountains and alter stream courses (although today, one would have to question these alignments), and with this ability has come an unprecedented amount of roadside ground disturbance placed prominently before the public's eye.

It has been suggested that these scars may be accepted by the public as an accompaniment to progress (Box, 1978), but there are many notations in the literature of society's reprehension toward leaving ravaged landscapes to heal on their own (Leopold, 1949; Randall and others, 1978; McKell, 1978; Box, 1978; Jensen, 1980; Johnson and Lees, 1988). The consequences of leaving denuded cut faces and barren roadway fills are not only detrimental to scenic values; accelerated erosion by wind and water can degrade aquatic ecosystems, reduce air quality and visibility, and pose safety concerns along the highway (NAS, Hwy. Res. Bd., 1973; Toy and Hadley, 1987).

In arid and semi-arid wildlands, denuded ground is difficult to revegetate due to low amounts and high variability of precipitation, temperature extremes, low soil fertility, and a high evaporation/precipitation ratio (Cook and others, 1974; Mortenson, 1979; Bainbridge and Virginia, 1990). Steep slopes (50% to 67% are common) of highway cuts and fills and exposure of subsurface soils result in additional challenges when revegetating these sites. Although these soils are often similar to those encountered in mining reclamation, they cannot be mixed or regraded to reduce the gradient (Andrews and Jackobs, 1966; Hodder, 1977).

Identification of long-term management goals and the capabilities and/or restrictions of the site are important first steps in the any revegetation process (Bache and MacAskill, 1984; Diamond, 1987). For a roadside project, considerations might include: What will future uses of the roadside area be? Are there scenic considerations? Does the roadside have value as habitat? What is the proximity to water bodies and drainages? Site inventory and analysis prior to construction should include a review of existing vegetation, soils, wildlife, drainage patterns, views, geology, and other pertinent features (ASCE, 1980; Cook and others, 1974). In some instances, existing conditions may indicate the potential for revegetation success (Jordan, n.d.; Fischer, 1986).

In general, roadside revegetation should produce plants in sufficient numbers and patterns to provide effective erosion control and to mitigate undesirable impacts to the scenic quality of the surrounding landscape (Hottenstein, 1970; Wright et al., 1978; Miller, 1979; Mortenson, 1978; Bradshaw and Chadwick, 1980). Species selection, plant density, and plant cover necessary to meet these objectives will, of course, vary in response to the surrounding landscape and the ability of the site to support vegetation.

This research project sought to evaluate the success of revegetation projects on highway cuts and fills in the middle-elevation deserts of central Arizona. The approach used was to sample vegetation on roadside cuts and fills and analyze how well this vegetation met the specified goals for revegetation established by the USDA Forest Service (the land manager) and the Arizona Department of Transportation (the highway builder). The principal revegetation goals of both agencies are mitigation of visual impacts and soil stabilization.

Methods

Site Selection

The study area selected for this project lies within the Tonto National Forest in central Arizona, below the

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Mogollon Rim. Elevations surveyed were between 640 and 1158 m (2100 and 3800 ft.) above sea level. Average annual precipitation ranges from 30 to 51 cm (12 to 20 in.), but is highly variable from year to year (NOAA, 1991). The surrounding terrain is mountainous, with numerous streams, ephemeral drainages, small mesas and plateaus. The scenery is described as "outstanding" (USDA, 1985).

Seven recent construction projects on state highways crossing the Tonto National Forest were selected on which to evaluate revegetation of cuts and fills. A total of 55 sites were sampled within these 7 projects. The projects selected ranged in age (time since seeding) from 1 to 7 years. Construction projects were typically 4.8 to 9.6 km (3 to 6 mi.) long and were spread over a distance of about 144 km (90 mi.) on State Routes 87, 88, and 188. Seeding methods were similar for all projects; seed was applied using a hydroseeder and covered with blown-on straw and a vegetative tackifier (Arizona D.O.T., 1985, 1990, 1992). Little seedbed preparation was done prior to seeding (personal observation). Table 1 lists the seeded species and seeding rates for all 7 projects.

Vegetation Sampling and Documentation of Site Conditions

Vegetation was sampled in December of 1992 and January of 1993. All perennial species were recorded, even those dormant; annual species were not recorded. Cover was estimated for each species occurring within square quadrats placed at 2-meter intervals along a randomly located 50-meter transect stretched across the cut or fill slope. Where vegetation had established in distinct stripes across the slope, the transect was skewed at an angle to ensure a representative sample.

Quadrat size was dictated by plant density; the objective was to have from 3 to 10 plants occurring within each quadrat. Where different species exhibited different densities, "nested" quadrats were used to minimize variability between samples and to minimize the number of plants to be counted. Both 50 x 50 cm and 1 square meter quadrats were used; widely dispersed shrubs were tallied using a 1 m x 50 m belt transect. All densities were converted to plants per square meter prior to data analysis.

The soil surface across each transect was observed for signs of erosion (rilling, pedestaling of rocks and plants, pocked soil surface). Initially, the number and depth of rills crossing each quadrat were recorded, in an attempt to provide a quantifiable measure of erosion for this "point in time" survey. However, it was acknowledged early in the data collection process that this method was insufficient to accurately record the erosion that had occurred on many of the sites, as much of the surface soil that had been lost was not transported in rills. Instead, many of the sites had an uneven or pocked appearance, with heavy soil deposition on the uphill side of plants and rock. Thus the decision was made to describe the evidence of soil loss on each data sheet, resulting in a less-quantifiable but presumably more accurate description of past erosion.

Slope gradient, elevation, and project age were also documented on each site for use as independent variables in the analyses.

Visual Quality Surveys

Each cut slope was photographed using color slide film to record the view of the revegetated slope from the motorist's vantage point. The camera was held at eye-level in the travel lanes of the adjacent highway with the cut slope positioned in the foreground of each slide. Varying amounts of the surrounding terrain were visible in each slide due to variations in roadway profile and alignment, but the natural vegetation beyond the edge of the disturbance could be seen in all slides.

In lieu of a professional visual analysis (an "expert opinion"), non-design students at the University of Arizona rated the appearance of the revegetated cuts using the color slides in their classroom. This method was used to obtain a measure of how the general public might view these sites and whether or not the revegetation was satisfactory in aesthetic terms. This approach assumes that public acceptance of revegetation is generally based on

Table 1—Seeded species, seeding rates (pounds/acre), and year of seeding.

	Seeding Rates by Project						
Species	**A**	**B**	**C**	**D**	**E**	**F**	**G**
Lehmann lovegrass (*Eragrostis lehmanniana*)	1	1	.5	.5	1	.5	
Cochise lovegrass (*Eragrostis trichopora*)	1	1	.5	.5	1	.5	.5
Crested wheatgrass (*Agropyron cristatum* "Ephraim")			3	3			
Sideoats grama (*Bouteloua curtipendula*)							3
Mediterranean grass (*Schismus barbatus*)	1	1				1	1
California buckwheat (*Eriogonum fasciculatum*)			1	1	1		
Fourwing saltbush (*Atriplex canescens*)			3	3		4	4
Fairy duster (*Calliandra eriophylla*)					2		
Brittlebush (*Encelia farinosa*)	1	1			2		
Desert marigold (*Baileya multiradiata*)	1	1					
Madrid yellow sweetclover (*Melilotus officinalis*)			1	1			
Mexican gold poppy (*Eschscholzia mexicana*)						2	
California poppy (*Eschscholzia sparsiflorus*)	3	3	2	2	3		2
Arizona lupine (*Lupinas sparsiflorus*)	1	1			2		
Year seeded:	1988	89	86	87	91	85	90

appearance, and not the ability of the vegetation to meet less visible, functional goals (such as soil stabilization), as suggested by Thornburg (1982).

A Likert Rating Scale (see Daniel and Boster, 1976; Daniel, 1977; and Schroeder 1984) was prepared for the students to use in rating the appearance of the vegetation on each cut slope. The scale ranged from 1 (unsatisfactory) to 5 (very satisfactory), with 3 labeled as neutral. The students were told that the slope in the foreground had been completely cleared of vegetation during the road construction process and had since been revegetated. Twenty-five slides were shown; the slides were placed in random order before viewing. Prior to rating the slides, the students were shown one slide for regional context. Next, they were quickly shown all of the slides they would be rating, to give them a sense of the range of conditions. They were then shown the slides again and allowed 15 seconds to rate the appearance of the revegetated cut slope shown in each slide.

Participants were also asked to respond to statements regarding revegetation issues and the overall success of the projects used in the survey. A Likert Scale was used to record responses, with a range from 1 (disagree) to 5 (strongly agree).

Data Analysis

Ratings assigned to each site by survey participants were tallied and a mean score calculated for each study site. This mean was used as a dependent variable representing the participants' degree of satisfaction with the appearance of vegetation on each site. Mean density and percent cover (by species and total) were also calculated for each study site.

Plant cover, species richness, and project age were selected as variables that were likely to be positively correlated with high "satisfaction scores." A scatter diagram of plant cover plotted against these satisfaction scores was used to examine the relationship between cover and satisfaction with appearance of the sites (Figure 1). Stepwise multiple regression was used to further define what appeared to be a positive correlation, and to examine the roles played by species richness and age in the variability observed in the satisfaction scores.

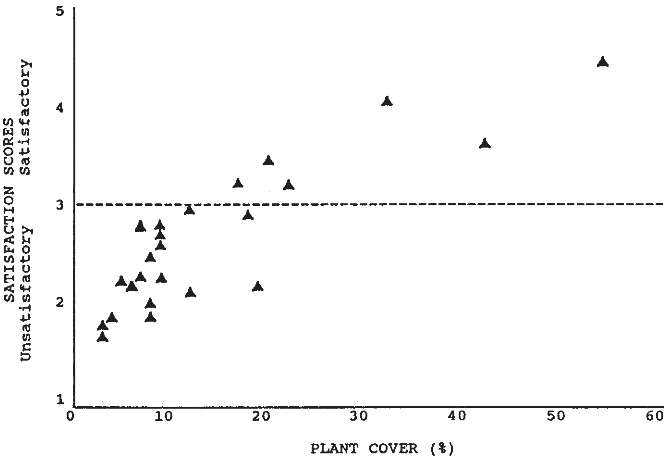

Figure 1—Relationship between aesthetic satisfaction and plant cover on revegetated road cuts in central Arizona.

To assess the degree of soil stabilization which had been attained, the sites were divided into 2 groups according to observed soil condition: those with little or no evidence of erosion, and those with evidence of moderate to severe erosion. Mean plant cover and slope gradient were calculated for each group; each group was also reviewed to determine common attributes (i.e. prevalence of cuts or fills). The objectives were to determine the number of sites on which soils appeared to have stabilized, and to identify conditions under which erosion was more likely to occur.

Results and Discussion

Six of the 25 sites for which appearance of revegetation was rated received scores in the satisfactory range (mean score above 3.00). All others were rated as being unsatisfactory in appearance. The mean score for all cut slopes reviewed by the participants was 2.65, which is in the unsatisfactory range. A positive relationship was found between plant cover and satisfaction.

Common attributes of the most highly rated sites include age (those receiving the 3 highest ratings were all 6 years old), relatively high plant cover (17 to 54%), and relatively high diversity of species and/or life-forms.

Sites receiving the lowest visual satisfaction scores had low plant cover (3 to 8%), low species and/or life-form diversity, and often were lovegrass monocultures. A noticeable visual element present at most sites receiving low scores was also the presence of large areas of bare ground. Also, sites having moderate amounts of plant cover (12 to 17%) received low scores if vegetation distribution was "patchy", thus exposing larger areas of bare ground than on sites with evenly-distributed vegetation.

Regression of satisfaction scores against total plant cover, species richness, and project age revealed that only cover explained variability in satisfaction. The regression equation between satisfaction (S) and cover was: $S = 1.97 + 0.051$ (total cover). This equation explained 76% of the variability in satisfaction, and was highly significant ($P<0.0001$).

While species richness was not correlated with participants' satisfaction with the appearance of revegetated slopes, observation of the vegetation communities receiving high ratings suggests that life-form diversity is positively correlated with these ratings. This could be a result of the participants' preference for visual complexity, or it could be linked to the character of vegetation beyond the limits of the disturbance, which was a complex mixture of shrubs, half-shrubs, and grasses. At locations where this natural vegetation abuts roadsides which were revegetated with mostly grass species, there is a distinct edge and sharp visual contrast between the two communities; the limits of disturbance are still very evident. At locations where shrubs have been used in the revegetated area, there is usually much less contrast between the two zones.

Opinions regarding aesthetic and biodiversity issues in revegetation were obtained by asking survey participants to respond to the following statements:

1. "Plants used to revegetate the areas cleared during highway construction should look like the plants growing naturally beyond the cleared area."
2. "Plants used to revegetate the areas cleared during highway construction should be the same species as those growing naturally beyond the cleared area."

Recalling that the response scale ranged from 1 (disagree) to 5 (strongly agree), the mean scores for these questions were 4.425 and 4.250, respectively, indicating strong agreement with the statements and perhaps explaining the higher ratings for the shrub-covered sites. While native species were rarely used on the projects surveyed, the presence of similar life-forms may have been adequate to result in satisfactory ratings. The overwhelming preference for the species used in revegetation to actually be the same provides support for the argument in favor of using species that are native to the site or local area.

To answer one of the central questions of this research, whether or not revegetation of the study sites was effective in mitigating negative impacts on the area's scenic resources, three sets of data produced similar results. The mean satisfaction rating for all cut slopes used in the visual survey was 2.65, in the unsatisfactory range. Furthermore, 72% of the slides received mean ratings in the unsatisfactory range (below 3.00). And finally, participants were asked to agree or disagree with the following statement:

> "In general, revegetation of the roadsides shown in the slides has been done very well."

The responses to this statement averaged 2.325, indicating general disagreement.

These findings indicate that participants in this study felt that revegetation of the cut slopes was unsatisfactory in appearance at this point in time. However, as satisfaction was positively correlated with plant cover, and cover with age (confirmed in additional studies), it can be expected that satisfaction (i.e., aesthetic "success") will increase over time. Land managers must decide what is an acceptable time period to wait. Data obtained in this study suggest that satisfactory mitigation occurs on some sites in this region 6 years after seeding; yet half of the sites this age and older still were not aesthetically acceptable.

In any case, it must be recognized that reduction of visual impacts through revegetation is never instantaneous mitigation, regardless of whether planting is done by seeding or with container stock. The dynamic nature of plant communities must be considered; as the structure and composition of these communities change, so does their effectiveness in meeting specific management objectives (e.g., restoring scenic resources, providing habitat, protecting water quality). Understanding plant community dynamics is essential for advance planning and to ensure that revegetation objectives are met. Other management tools can also help meet some objectives during periods when vegetation may be inadequate in doing so. One example is the use of erosion control blankets to protect soils until plants establish and grow to provide adequate soil cover.

This study also sought to evaluate the success of revegetation in terms of protecting slopes from erosion. The results of this inquiry were less definitive than those obtained in the quest for evaluating aesthetic success, but offer some insight.

Fifty-eight percent of the sites surveyed (cuts and fills) were described as having little or no erosion; 42% had moderate to severe erosion. On moderately to severely eroded sites, the average slope was 50% (2:1); 87% of these were cut slopes. Mean plant cover was 15.6% with a range from 2% to 55%. On the less-eroded sites, the average slope was 39% (2.5:1); 62% were fills. Mean plant cover on these sites was 35% with a range from 5% to 98%. Confidence limits set at 95% indicated that there was less plant cover on moderately/severely eroded sites than on those with little or no erosion.

Observations also revealed that factors other than plant cover may contribute to soil protection. Sites with high lovegrass cover tended to have substantial litter. Many sites had good soil protection provided by red brome (*Bromus rubens*) litter. Soils on some sites were well-armored by small rock fragments; this appeared to be a result of cutting the slope through fractured, rocky material, rather than the washing away of fine particles.

In summary, plant cover, slope gradient, and whether a site was in cut or fill were factors that appeared to influence erosion. Ideally, it would have been desirable to quantify the degree of erosion which had occurred on each site, to allow regression against plant cover and other measured environmental variables. Even if this had been possible, it may have produced an inaccurate picture, as it was difficult to discern if erosion was recent or had occurred prior to plant establishment. In general, soil conditions observed in this study supported the suppositions that soil losses are greater on sites with low plant cover than on sites with higher cover, and that soil loss increases with increasing slope.

It was more difficult to assess whether revegetation had met the agencies' goal of soil stabilization, due to both the time factor noted above and an inexact definition of the term soil stabilization. Does this mean no increase in soil loss over pre-disturbance conditions? Does it allow for a short term increase in erosion until vegetation reestablishes? If so, how long will increased levels of soil loss be tolerated? Answers to these questions are necessary to properly evaluate soil stabilization; they will, of course, need to be site specific, and will need to consider factors such as site potential and the sensitivity of surrounding resources.

Conclusions and Suggestions for Future Research

The results of this study indicate that revegetation of fill slopes was often successful in meeting the specified goal of soil stabilization. Furthermore, although the appearance of fill slopes was not rated, plant cover on fills was at a level which was rated as being satisfactory in aesthetic terms on cuts, thus we might conclude that mitigation of scenic impacts has been successful on fills.

In contrast, the results from this study indicate that revegetation on cut slopes has not been successful. Sixty-five percent of the cut slopes surveyed were moderately to severely eroded, plant cover was significantly less on cuts than on fills, and participants in the study rated the revegetation on most cuts as unsatisfactory in appearance.

The results of visual quality surveys indicated that revegetated cut slopes in this region were satisfactory when plant cover reached about 20%; although sites with unevenly distributed plant cover received lower ratings than sites with the same amount of evenly distributed plant cover. As this is presumed to be the first study of its kind, additional research is certainly desirable to support these findings and provide a well-researched basis for future revegetation evaluations and/or performance specifications.

Finally, while the flatter fill slopes had higher plant cover and less evidence of erosion, it must be recognized that flatter gradients require wider cuts and fills, thus more ground disturbed and increased area needing revegetation. Additional research might be best aimed toward pursuing aggressive revegetation techniques on moderate slope gradients, as suggested in the literature (Hawaii D.O.T., 1976; Kay, 1978 and 1984; Brammer, 1978; Theison, 1988; and Klemens, 1990). Specific methods recommended include deep ripping of cuts, topsoil plating, use of deep-rooted container plants, a variety of effective mulching techniques, and temporary irrigation to improve plant establishment and growth.

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Restoration of Big Sagebrush Habitat in Southeastern Washington

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Abstract—Recent wildfires have removed big sagebrush (*Artemisia tridentata*) from large portions of the Hanford Site in southeastern Washington. Loss of sagebrush habitat may have rendered the site unsuitable for western sage grouse. Although sage grouse historically inhabited the site, none have been found in the past three years. To determine the feasibility of restoring big sagebrush through broadcast seeding, we compared germination and seedling establishment through seed dispersal from isolated parent plants with establishment after artificial seeding trials. Sagebrush seedling establishment was evaluated on 1) undisturbed plots, 2) plots where plant competition was reduced through selective herbicide application and 3) plots where the soil surface was mechanically disturbed during late winter/early spring. Herbicide application in early spring reduced competition from native bunchgrasses and appeared to best accelerate sagebrush seedling establishment.

The western subspecies of sage grouse (*Centrocercus urophasianus* subsp. *phaios*) is declining in the sagebrush steppe regions of both Washington and Oregon (Pederson 1981; Crawford and Lutz 1985). Loss of quality sagebrush habitat is most likely responsible for the decline (Roberson 1986; Yokum 1956; Welch and others 1990). Concerns about the status of sage grouse in Washington have prompted efforts to identify areas where habitat restoration and/or species reintroductions may be feasible.

Sage grouse were at one time relatively common on the Hanford Site in southeastern Washington, but have disappeared from the site over the past decade. Coincident to their disappearance were wildfires in 1981 and 1984 that removed big sagebrush from large land areas on the site. Sage grouse rely heavily on sagebrush as a food source during winter months, switching to succulent forbs during the summer months (Roberson 1986). Sagebrush also provides preferred nesting sites, protection from the elements, and escape cover for the birds.

We are currently evaluating the extent and status of big sagebrush habitat on the Hanford Site in relation to sage grouse. Lands of the Hanford Site were set aside in 1943, and stands of native vegetation have been protected from development, agriculture, and grazing for the past 50 years. Much of the best potential habitat for sage grouse lies in the Fitzner/Eberhardt Arid Lands Ecology (ALE) reserve (Fig. 1) at upper elevations (400 to 1,700 m). Native bunchgrasses, especially bluebunch wheatgrass (*Pseudoroegnaria spicata*), and Sandberg's bluegrass (*Poa sandbergii*) dominate the vegetation of the deep silt loam soils on the lower slopes of the Rattlesnake Hills since sagebrush stands were removed by wildfire. Canopy cover of grasses ranges from 30 to 60% depending on elevation and aspect. Cryptogamic crusts are often contiguous in the interplant spaces (Rickard and others 1988). Sagebrush recolonization of burned areas over the past decade has been extremely slow. The lack of recovery led us to question whether artificial seed dispersal would be successful in increasing big sagebrush establishment or whether some method of reducing competition from existing herbaceous species is needed to improve sagebrush seedling establishment.

Goals of this study were to provide information on restoration techniques appropriate to use in restoring big sagebrush to areas that have potential to provide nesting and brood-rearing habitat for sage grouse. That is, methods that will enhance recovery of big sagebrush without adversely affecting the succulent forbs of the plant community that provide spring and summer forage for sage grouse. Specific objectives were to 1) determine whether seeding into established bunchgrass stands could accelerate sagebrush establishment, and 2) compare germination and establishment with natural reinvasions of sagebrush into grassland areas.

This paper presents preliminary results from monitoring both seedling establishment of big sagebrush around parent plants and seeding trials under three conditions: undisturbed soil surfaces, mechanically disturbed soil surfaces, and herbicide-treated surfaces.

Study Area and Methods

The 560-mi^2 Hanford Site lies within the shrub-steppe ecoregion, and the climate is characterized by hot, dry summers and cold winters. Most precipitation falls between October and April (Thorp and Hinds 1977). Rattlesnake Mountain (1,150 m), which receives approximately 30 to 35 cm of precipitation annually, falls steeply to about 500 m elevation, where slopes become more moderate and annual precipitation ranges from 20 to 25 cm. The topography continues to descend to approximately 150 m in Cold Creek Valley and eastward to the Columbia River, where annual average precipitation is 12 cm (Rickard and others 1988).

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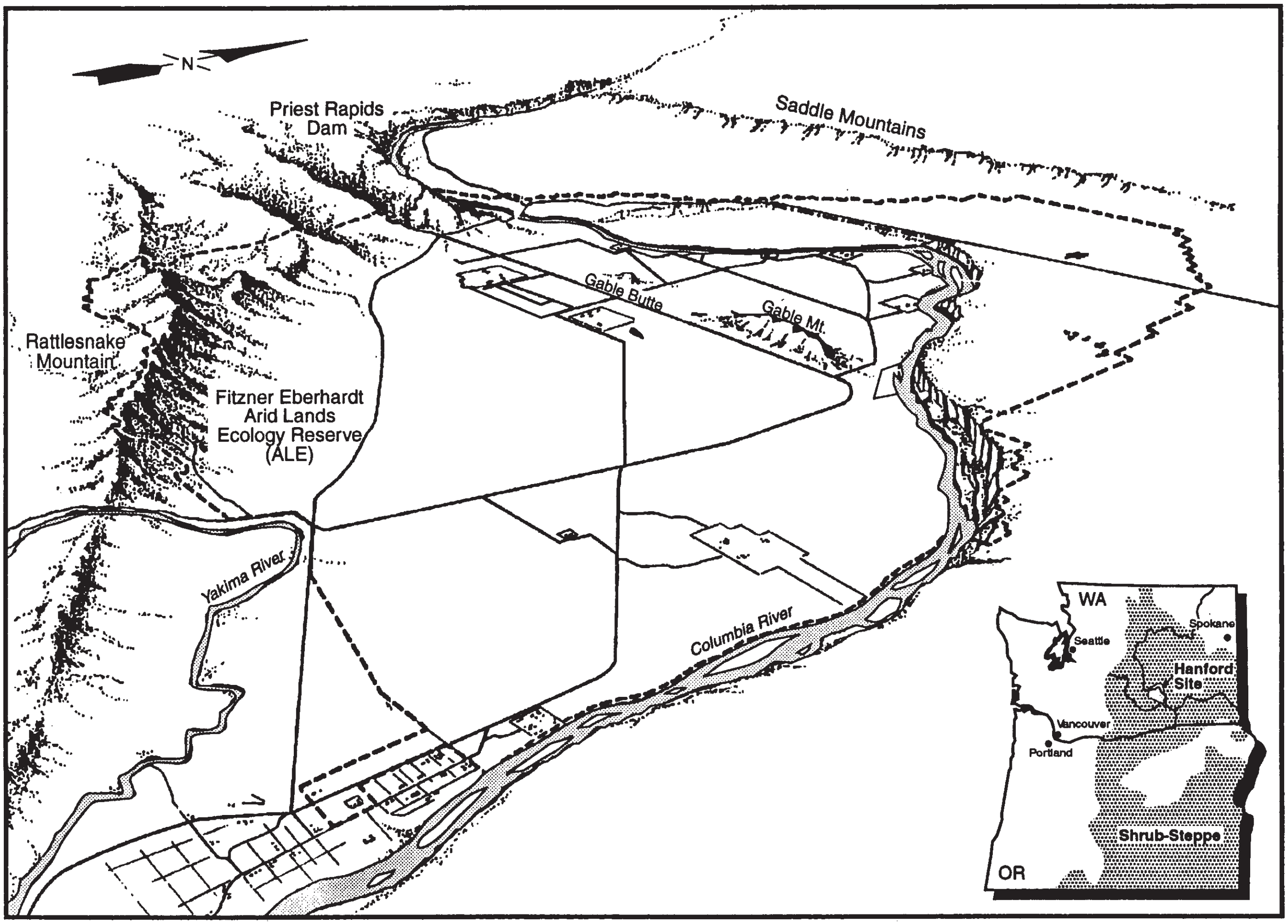

Figure 1—Location and major features of the Hanford Site within the shrub-steppe ecoregion.

The vegetation association at the study sites is a big sagebrush-bluebunch wheatgrass community (Daubenmire 1970). Wildfires burned through the area in 1981 and again in 1984, effectively removing big sagebrush as a component of the plant community. Scattered big sagebrush plants remain along firebreak lines and along old roadways.

Seeds were collected from a remnant big sagebrush stand at 400 m elevation on ALE in early December 1992 to use in seeding trials. Seeds were air dried, cleaned by screening through brass sieves, and then refrigerated at 40 °F for at least 30 days to ensure stratification.

Plots for seeding trials were also located at the 400 m elevation as were plots surrounding isolated parent plants of big sagebrush. Seeding trials were conducted in 1 m wide x 5 m long plots and were surrounded by a 1-m buffer zone. These plots were located upslope and upwind from any remnant big sagebrush plants. Plots to monitor seedling establishment around parent plants were established in a circle with a 2-m radius around isolated big sagebrush plants, taller than 0.75 m. The three treatments—undisturbed control, mechanically disturbed soil surface, and herbicide-treated surface—were assigned in a randomized block design for five replicates (15 plots) for the seeding trials. Treatments were randomly assigned to each of the 15 plots established around parent plants.

Plots were treated in late February 1993. We disturbed the soil surface using a weighted spring-tooth harrow pulled behind a garden tractor. Using a hand-held sprayer, we applied herbicide, Roundup (active ingredient 18% glyphosate) at a concentration of 31.3 ml/L (4 oz/gal) of water, completely wetting the foliar surface of vegetation. Using a hand-spreader, we seeded plots the first week of March 1993 with a mixture of sawdust and big sagebrush seed at a ratio calculated to provide 1 seed per square centimeter of ground area.

Plots were analyzed in August 1993 by counting the number of sagebrush seedlings and determining the condition of forbs and grasses. The entire area of each plot was visually inspected to locate and tally sagebrush seedlings. The condition of forbs and grasses was evaluated by visually estimating percent cover of forbs and grasses in each plot using four 1-m diameter subplots. The numbers of forbs and forb seedlings in each 5-m^2 seeded plot were also counted. Numbers of forbs on plots with parent shrubs were counted in a 5-m^2 area on the leeward side of each parent shrub.

Mean values were calculated for the canopy cover of grasses and forbs and the numbers of forbs in each treatment type. Treatment differences were compared by testing for significant differences in mean values at the 5% level using analysis of variance and Dunnett's t-test.

Table 1—Number of shrub and forb seedlings in seeded plots and plots around parent plants.

	Seeded plots			Parent plants		
Plants	Control	Disturbed	Herbicide treated	Control	Disturbed	Herbicide treated
Big sagebrush	0	0	2	0	2	17
Forbs	14	25	15	42	70	44

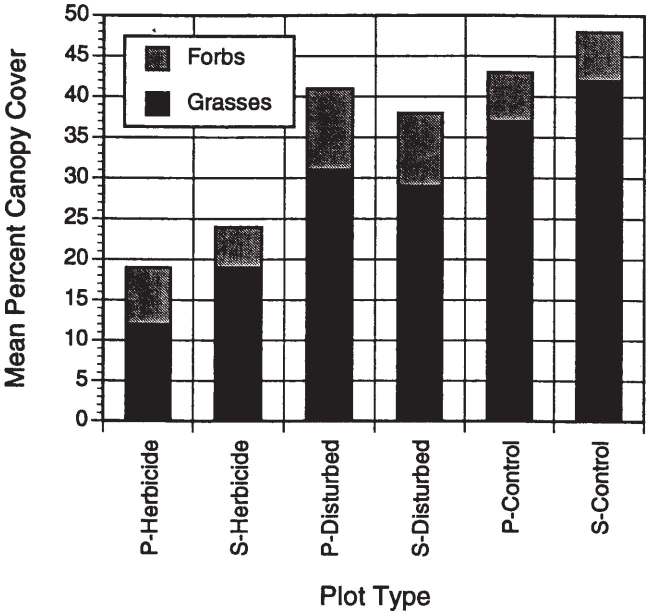

Figure 2—Mean percent canopy cover of grasses and forbs on seeded plots (S) and around parent shrubs (P).

Results

Viability and germination of big sagebrush seeds collected after the 1991 growing season were low. Few sagebrush seedlings established in any of the seeded plots or in the plots around parent big sagebrush. In both seeded plots and plots around big sagebrush parent plants, the number of seedlings that established in herbicide-treated plots was greater than in mechanically disturbed plots (Table 1). No big sagebrush seedlings established in any of the control (undisturbed) seeded plots, and none established within 2 m of big sagebrush plants where the soil was undisturbed.

The application of herbicide significantly increased the recruitment of big sagebrush seedlings around parent plants. Sagebrush seedlings were found in all five herbicide-treated plots around parent plants; no sagebrush seedlings were found in control (undisturbed) plots around parent shrubs. Two out of five of the mechanically disturbed plots around parent plants contained big sagebrush seedlings.

Use of herbicides affected the canopy cover of grasses on both the seeded and parent shrub plots, but did not significantly decrease either the canopy cover of forbs or total numbers of forbs counted on the plots (Fig. 2 and Fig. 3). Decreases in the canopy cover of grasses growing on all herbicide-treated plots were attributable to the loss of Sandberg's bluegrass after spraying.

Total numbers of forbs and forb seedlings counted on plots on the leeward side of parent shrubs were at least twice the number counted in seeded plots (Table 1, Fig. 3). Disturbed plots around parent shrubs contained significantly greater numbers of forbs and forb seedlings than the numbers of forbs in herbicide-treated and control plots around parent shrubs. Numbers of forbs in mechanically disturbed seeded plots were greater than those found in control plots, but the difference was not significant.

Discussion

The extremely low levels of germination and establishment for seed produced in 1992 may be a result of adverse climatic conditions during the growing season. Variability in rates of sagebrush germination and establishment has been documented previously (Daubenmire 1970; Harniss and McDonough 1976). Harniss and McDonough (1976) reported ranges from 22 to 88% germination for basin big sagebrush seeds from 10 plants over a 3-year period. In comparison, germination was 85 to 98% for seeds collected from big sagebrush growing in other stands on the ALE reserve after the 1993 growing season. Reasons for the low rates of seed viability and germination for the 1992 seeds are not known, but climatic conditions and subsequent soil water availability may have adversely affected seed development.

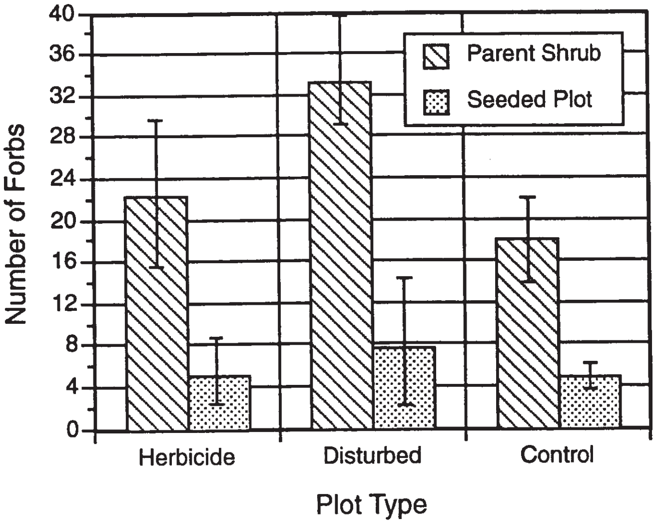

Figure 3—Numbers of forbs counted on plots around parent plants and on seeded plots (error bars are ± 1 standard error).

March through September 1992, although not drier than normal months, were significantly warmer than in previous years. Average spring temperatures were the highest recorded since 1945, and average summer temperatures in 1992 were the fourth highest recorded since 1945.

Germination and establishment of seedlings occurred in significant numbers in herbicide-treated plots around parent plants. Whether seeds that germinated were from the 1992 seed crop or originated from the seed bank in the soil could not be discerned in our study. However, reducing competition with native bunchgrasses through herbicide application enhanced sagebrush seedling establishment around parent shrubs. Seedling establishment in seeded plots appears to support this premise. The number of seedlings that established in herbicide-treated seeded plots was too few to provide significant information, but these were the only seedlings that established in any of the seeded plots.

The application of herbicide affected only the Sandberg's bluegrass, which is an early season grass and was actively growing at the time of herbicide application. Neither bluebunch wheatgrass nor perennial forbs were affected by applying Roundup. Most perennial and annual forbs native to the shrub-steppe ecoregion had not emerged and/or germinated at the time we applied herbicide and did not appear to be significantly affected by herbicide application. Roundup is a contact herbicide with no residual or pre-emergence effectiveness.

Mechanical disturbance did not enhance the germination and establishment of big sagebrush, but may have increased the establishment of forbs. Numbers of perennial forb seedlings in mechanically disturbed plots were twice the number of those found in control plots and in herbicide-treated plots. No measurements were made of forb occurrence or seedling establishment during previous years on these plots. Mechanical disturbance of the soil surface and the cryptogamic crusts may create larger numbers of safe sites for forb seed germination.

Neither mechanical disturbance of the soil surface nor herbicide application in February increased percent cover or number of invasive aliens, such as tumble mustard (*Sisymbrium altissimum*) and cheatgrass (*Bromus tectorum*), on the plots. Invasion by aggressive aliens would be expected after disturbance in most shrub-steppe communities (Daubenmire 1970; Mack 1981); however, few seed sources for these species exist in the areas surrounding the study plots, and these invasive annuals germinate primarily in the fall.

The greater numbers of forbs and forb seedlings found around parent shrubs is notable with regard to sage grouse habitat requirements. Shrubs provide shading and wind protection as well islands of fertility that may enhance forb establishment and diversity in the herbaceous component of the community (McAuliffe 1988; McKell 1989). Big sagebrush then may be an important component of sage grouse habitat in providing 1) leaf material for winter forage, and 2) microclimatic conditions that enhance forb germination, establishment, and diversity.

Conclusions

Selective herbicide applications in early spring reduced Sandberg's bluegrass cover and increased the number of big sagebrush seedlings that established compared to mechanically disturbed and control treatments. Mechanical disturbance significantly increased establishment of forb seedlings. Herbicide treatment and mechanical disturbance did not increase the occurrence of invasive alien species, probably because seed sources for alien plants were lacking.

Acknowledgments

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Health of Plants Salvaged for Revegetation at a Mojave Desert Gold Mine: Year Two

Raymond L. Franson

Abstract—At Viceroy Gold's Castle Mountain Mine in the East Mojave Desert, Joshua trees and barrel cacti are salvaged before disturbance and maintained in two nurseries for later outplanting to revegetation sites. The plants are assessed each year on a qualitative scale. In the 1993 survey, 7,941 plants were rated. Joshua trees that were salvaged by hand showed only 4% mortality in the nursery each of the first two years. A comparison of Joshua tree health in the two nurseries showed that the Joshua trees in the south nursery had a higher percentage rated as being in poor health. This is attributed to problems with the irrigation system in the south nursery. Barrel cacti had 9% mortality in the first year and 7% mortality in the second year. Barrel cactus plots in undisturbed areas were established in 1993 to compare death rates in the nursery to death rates under natural conditions. Joshua trees and barrel cacti can both be transplanted by bare rooting in large numbers and maintained in nurseries in high densities for at least two years. The data on these nurseries is useful for anyone attempting salvage of *Yuccas* or barrel cacti for restoration or landscaping purposes.

Even under the most favorable conditions, seedling establishment for most plant species in desert systems is a rare event. This poses a problem for reclamation efforts in desert systems. In recognition of this, Viceroy Gold Corporation salvages Joshua trees (*Yucca brevifolia*), barrel cacti (*Ferocactus acanthodes*) and several other plant species ahead of disturbance to land at the Castle Mountain Mine in the East Mojave Desert in southeast California. To date, over 10,000 live plants have been salvaged and are being maintained in two nurseries at the mine. In September 1992 and June 1993 the health of plants in the nurseries was assessed on a qualitative scale. The health of 7,941 plants that were salvaged in 1991 and 1992 were assessed in 1993 (Table 1).

Very little is known about the growth of Joshua trees (Rowlands 1978) and barrel cacti. Even less is known about transplantability of these plants. Franson and Bernath (1993) reported on the health of about 45% of the salvaged plants one year after transplanting and focused on the health of Joshua trees by season of salvage and salvage methods. Joshua trees transplanted with a tree spade during winter had the best health rating. Joshua trees treated with Superthrive to promote root growth showed no improvement over trees transplanted without Superthrive.

This paper reports on the death rate of Joshua trees and barrel cacti, transplanted by bare rooting, two years after transplanting, providing the first large data set on survival of both species after salvage. *Yucca* sp. and barrel cacti are salvaged in the Mojave desert before a variety of disturbances and for various landscaping projects. Data collected at the Viceroy Gold nurseries will be useful to anyone attempting to salvage these plants

Methods

Salvage

Joshua trees between 3 and 8 feet tall with few branches are salvaged by hand digging. The bare roots are dusted with sulfur powder to minimize infection from airborne microbes. The trees are then planted in rows in the nurseries. The soil at the nurseries is better than most of the soils on site. Each row has a drip irrigation line for summer watering. Soil moisture in the rows is monitored by gypsum block soil moisture sensors. The Joshua trees are watered because their density in the nursery is much higher than their density in nature.

Barrel cacti small enough to be lifted by one person (up to about 15 inches in diameter) are salvaged by hand digging. The plants with bare roots are left to cure in the sun to minimize root infections. After several days of curing the cacti are planted in rows in the nurseries and grown without supplemental watering.

Plant Health

Plants are located by row and sequential position in the row and rated as being in excellent, poor or dead condition. By this method, improvement and decline in individual plants can be followed. For Joshua trees, an excellent rating is given if there is no yellowing of the leaves and they are rated as dead if they have no green leaves. For barrel cacti, an excellent rating is received if there is no yellowing of the tissue and they are rated as being dead if they have become hollow. Two plots in undisturbed areas, each containing 100 barrel cacti, were established in 1993 to compare the death rates in the nurseries to barrel cacti in the wild.

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Table 1—Health of salvaged plants by species.

Species	Common name	Health			Total
		Excellent	Poor	Dead	
Ferocactus acanthodes	barrel cactus	3,718	368	709	4,795
		(78)[1]	(8)	(15)	
Yucca brevifolia	Joshua tree	523	811	113	1,447
		(36)	(56)	(8)	
Opuntia erinacea	old man cactus	80	25	8	113
		(71)	(22)	(7)	
Echinocactus polycephalus	cottontop cactus	250	33	21	304
		(82)	(11)	(7)	
Opuntia basilaris	beavertail cactus	39	23	23	85
		(46)	(27)	(27)	
Yucca schidigera	Mojave yucca	623	150	166	939
		(66)	(16)	(18)	
Yucca baccata	blue yucca	160	34	32	226
		(71)	(15)	(14)	
Opuntia chlorotica	pancake cactus	20	10	2	32
		(63)	(31)	(6)	
	Total	5,413	1,454	1,074	7,941
		(68)	(18)	(14)	

[1] Numbers in parentheses are percentages.

Results

Joshua Trees

The 1992 survey of 713 Joshua trees showed that 4% of the trees had died (Table 2). This number is much lower than was expected at the start of the salvage operation. How much of this 4% was due directly to transplant shock could not be determined from this single assessment. The same rows of Joshua trees were assessed in 1993. At the end of two years the total percent dead was 9%. Since Joshua trees are tallied by location, dead Joshuas are tallied each year. So, the 9% number means that 5% died in the second year, or approximately the same number as the first year. The similarity of the death rate in both years suggests that transplant shock was not a major cause of death.

The 1993 survey tallied 1,447 Joshua trees. In the north nursery 41% of the Joshua trees were rated as being in excellent condition (Table 3). This percentage dropped to 29% for Joshua trees in the south nursery. There were two major differences between the two nurseries during the first two years. The soil in the north nursery is better (deeper and less rocky) and the irrigation system worked better in the north nursery.

Table 2—Health of salvaged barrel cacti (*Ferocactus acanthodes*) by nursery.

Nursery	Health			Total
	Excellent	Poor	Dead	
North	2,978	203	582	3,763
	(79)[1]	(5)	(15)	
South	740	165	127	1,032
	(72)	(16)	(12)	

[1] Numbers in parentheses are percentages.

Barrel Cacti

The 1992 survey of 3,295 barrel cacti showed that 9% of the cacti had died (Table 4). At the end of the second year the same rows showed 16% mortality (9% the first year and 7% the second). As with the Joshua trees, barrel cacti showed similar mortality in the first and second year.

The 1993 survey tallied 4,795 barrel cacti. The plants in the north and south nurseries showed similar health ratings (Table 5). This result suggests that the poor rating of the Joshua trees in the south nursery was due to lack of water and not soil since the barrel cacti were in the

Table 3—Health of salvaged Joshua trees (*Yucca brevifolia*) by nursery.

Nursery	Health			Total
	Excellent	Poor	Dead	
North	348	432	66	846
	(41)[1]	(51)	(8)	
South	175	379	47	601
	(29)	(63)	(8)	

[1] Numbers in parentheses are percentages.

Table 4—Health of salvaged barrel cacti (*Ferocactus acanthodes*) by year.

Years after transplanting	Health			Total
	Excellent	Poor	Dead	
1	2,796	203	297	3,296
	(84)[1]	(7)	(9)	
2	2,539	198	508	3,245
	(78)	(6)	(16)	

[1] Numbers in parentheses are percentages.

Table 5—Health of salvaged Joshua trees (*Yucca brevifolia*) by year.

Years after transplanting	Health			Total
	Excellent	Poor	Dead	
1	246	437	30	718
	(35)[1]	(61)	(4)	
2	303	375	65	743
	(41)	(50)	(9)	

[1] Numbers in parentheses are percentages.

Table 6—Health of barrel cacti at undisturbed sites.

Location	Health			Total
	Excellent	Poor	Dead	
North of Hart	93	0	7	100
Green and Gold	87	0	13	100
Total	180	0	20	200

same soil but not watered. The irrigation system problems have been remedied for the 1994 summer season.

To determine whether the barrel cacti death rate is similar to plants in the wild, plots were established in two areas that will not be disturbed by mining. In each plot 100 barrel cacti in the same size class as those in the nursery were marked and their health was assessed (July 1993). In the initial survey, all plants were either rated excellent or dead (Table 6). These plots will be assessed each year when the nurseries are assessed.

Conclusions

Joshua trees and barrel cacti can be transplanted by bare rooting in large numbers and maintained in high density nurseries for at least two years with a very low death rate (4% for Joshua trees and 8% for barrel cacti). This allows both affordable salvage of areas that will be disturbed and the use of large numbers of plants up to 50 years old in revegetation and landscaping.

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Characterizing Rare Plant Habitat for Restoration in the San Bernardino National Forest

Michael P. Gonella
Maile C. Neel

Abstract—Surface mining of limestone in the San Bernardino Mountains has caused loss of native vegetation and of habitat for four carbonate-endemic plant taxa. This paper characterizes features of carbonate substrates and of habitat occupied by two of these species: Cushenbury milkvetch (*Astragalus albens*) and Cushenbury buckwheat (*Eriogonum ovalifolium* var. *vineum*) to assist in developing revegetation success criteria for mined lands.

Carbonate substrates in the San Bernardino Mountains were vegetationally and floristically distinct from non-carbonate substrates. In addition to the endemic plant species, we found five indicator taxa and 15 characteristic taxa for carbonate. At the same time, 36% of the taxa on non-carbonate soil did not occur on carbonate. Habitats occupied by Cushenbury milkvetch and Cushenbury buckwheat were distinguished from general carbonate substrate by higher percentage soil calcium, different slope angles, surface soil characteristics, and floristic composition.

As human populations and subsequent demands on natural resources increase, native species and plant communities are disappearing at an alarming rate (Ehrlich 1992, Franklin 1993). Habitat loss is the leading cause of species decline (Ehrlich 1988, p. 21). On public lands, timber harvest, cattle grazing and surface mining are leading causes of habitat loss and modification (Losos and others 1993). The decline and extinction of many plant species has led to increased listing activities under the Federal Endangered Species Act (16 U.S.C. 1531 *et seq.*).

On the San Bernardino National Forest in southern California, surface mining of limestone has caused loss and degradation of native vegetation in general and of habitat for four plant taxa endemic to carbonate substrates (limestone and dolomite). These species are Cushenbury milkvetch (*Astragalus albens*), Cushenbury buckwheat (*Eriogonum ovalifolium* var. *vineum*), Parish's daisy (*Erigeron parishii*) and Parish's oxytheca (*Oxytheca parishii* var. *goodmaniana*). One additional species, San Bernardino bladderpod (*Lesquerella kingii* ssp. *bernardina*), is threatened primarily by ski area development on public land and housing development on private land. All five of these taxa have been proposed for listing under the Federal Endangered Species Act (USFWS 1991).

Over 1,600 acres of potential habitat for these taxa has already been lost to mining activities including road construction, mineral extraction, processing plant construction and deposition of waste material. Additional degradation has resulted from erosion and from deposition of windblown dust. Restoration of these disturbed areas provides the only hope of re-creating habitat for these taxa. Reclamation of mined lands has been required since 1974 (USFS 1974). Unfortunately, most of the existing disturbance predates these requirements and thus will never be reclaimed. On many sites where reclamation is legally required, revegetation is not feasible due to physical conditions of the post-mining landscapes (for example, lack of topsoil, steep slopes or inaccessibility) and the cost of such efforts. The arid climate of the region further complicates the picture and limits restoration potential. Also, until recently requirements have been very general and the limited amount of revegetation that has been accomplished has focused on erosion control activities. Most often only a few species were planted and these most often were not native to the planting sites. These plantings in no way reflect predisturbance ecosystems or recreate the ecosystems on which the rare species depend. Where revegetation of new disturbance is undertaken, SBNF mine reclamation standards now require establishment of 50% of the predisturbance cover and 15% of the predisturbance species richness on a site (USFS 1991). Obviously, detailed baseline descriptions of pre-disturbance conditions are necessary to establish success criteria and to meet these standards. Such descriptions are important for restoring native ecosystems in general; they are even more important when dealing with endangered species habitat. Unfortunately, such descriptions are most often lacking.

The purpose of this research was to characterize vegetational and abiotic features of carbonate substrate and of habitat occupied by two of the five carbonate-endemic plants species mentioned above: Cushenbury milkvetch and Cushenbury buckwheat. This research is part of a larger study that will also include the other carbonate endemic plant species. While the focus of this paper is restoration, quantitative descriptions of rare plant habitats can be important in identifying potential but previously unknown habitat, developing integrated conservation strategies (Falk 1992), assessing and prioritizing sites for protection (DeVelice and others 1988; Lesica 1993) and evaluating sites for potential reintroduction or introduction of the target species into suitable but unoccupied habitat (Falk 1992, p. 414-415).

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Study Area

The San Bernardino Mountains lie at the eastern end of the Transverse Mountain Ranges of southern California. Wedged between coastal southern California to the south and west, the Mojave Desert to the north and the Sonoran Desert to the southeast, the San Bernardino Mountains support a high degree of vegetational and floristic diversity (Minnich 1976). There is also a relatively high degree of endemism, with at least 20 plant taxa entirely restricted to the mountain range (Krantz 1987 and 1990; Smith and Berg 1988).

Cushenbury milkvetch and Cushenbury buckwheat are found on the north slope of the San Bernardino Mountains, on carbonate substrate. The portion of the mountain range occupied by these taxa borders the Mojave Desert. Elevations range from approximately 1,300 to 2,500 meters. Dominant vegetation types in the study area include blackbrush scrub, piñon woodlands, piñon-juniper woodlands and yellow pine woodlands; piñon woodlands and piñon-juniper woodlands are the most extensive types. Precipitation ranges from 1 to 4 cm per year, falling primarily as winter rain. Snowfall is common but does not persist through the winter. Summer thunder showers occur infrequently in most years, accounting for no more than 20% of the annual precipitation. Temperatures in the study area range from winter nighttime lows of –1.4° to summer daytime highs of 28 °C.

Methods

Sampling Design

The study area was stratified into carbonate substrate, non-carbonate substrate, occupied Cushenbury milkvetch habitat and occupied Cushenbury buckwheat habitat. Plots were selected as follows:

Carbonate Plots (n=88)—Plots were located on carbonate substrate by randomly selecting two points within each cadastral section of land that had more than 5% coverage of carbonate surface deposits (Geo/Resource Consultants, Inc. 1981; Brown 1992). All plots were located more than 200 m from a mapped boundary between carbonate and non-carbonate substrates to avoid edge effects and map error. A total of 88 carbonate plots were sampled; nine of these plots supported Cushenbury milkvetch and 19 supported Cushenbury buckwheat.

Non-Carbonate Plots (n=73)—Within each section sampled for carbonate plots, two random points that occurred off of mapped carbonate substrate were randomly selected. If a section had 100% carbonate surface deposit coverage, non-carbonate plots were located in adjacent sections of land. All plots were located more than 200 m from a mapped boundary between carbonate and non-carbonate substrates to avoid edge effects and map error.

Plant-Centered Plots (n=58)—One to two plots were randomly located within each section containing at least one occurrence of either Cushenbury milkvetch (n=30) or Cushenbury buckwheat (n=28). To qualify as a Cushenbury milkvetch sample, the plot had to contain a minimum of 20 Cushenbury milkvetch plants. Cushenbury buckwheat samples needed at least 15 Cushenbury buckwheat plants to qualify.

The results presented here are preliminary. We sampled approximately one-half of the available carbonate substrate and two-thirds of the occupied habitat for both Cushenbury milkvetch and Cushenbury buckwheat in 1992 and 1993. We will sample the remaining carbonate substrate and remaining populations of all five rare taxa during 1994 and 1995.

Data Collection

Each random point served as the center of a 0.04 hectare plot. Aspect, slope (degrees) and elevation (m) were recorded in each plot. A northness index was calculated as (sin(slope in degrees) x cos (aspect in degrees)). A soil sample was taken in the center of each plot to approximately 30 cm depth; pH, total extractable calcium and total extractable magnesium were determined for each soil sample. Percentage cover was estimated for surface coverage of outcrop, boulder, rock, cobble, gravel, soil and litter. Percentage cover of each overstory species, shrub layer species and perennial bunchgrass was recorded. Total canopy and shrub cover were then calculated for each plot. In 1992 percentage cover was recorded in classes while absolute cover was recorded in 1993. Mean values of percent cover of variables for each group were calculated and compared using only plots in which absolute cover was recorded. Abundances of all herb layer species were recorded in the following categories: 1) rare, 2) occasional, 3) frequent, 4) abundant, 5) dominant; only presence-absence data were used in comparisons. Densities of Cushenbury milkvetch, Parish's daisy, Cushenbury buckwheat and Parish's oxytheca were also recorded. Species richness and Shannon's diversity index were calculated for each plot. Additionally, total species richness was calculated for each comparison group. Nomenclature follows Munz (1974) for all genera except *Cryptantha* and *Phacelia* which follows Hickman (1993).

Data Analysis

The following comparisons were made:

1) Carbonate (n=88 for frequency; n=40 for cover) vs. non-carbonate plots (n=73 for cover and frequency).
2) Cushenbury milkvetch-centered (n=30 for frequency; n=15 for cover) vs. carbonate plots not occupied by Cushen-bury milkvetch (n=79 for frequency; n=38 for cover).
3) Cushenbury buckwheat-centered (n=28 for frequency and cover) vs. carbonate plots not occupied by Cushenbury buckwheat (n=69 for frequency; n=31 for cover).

Species frequency data were used to determine characteristic and indicator species for each group. Characteristic species were those with high fidelity (greater than 80% of the occurrences within one group and occurring in greater than 5% of the plots in that group) and/or high constancy (occurrence in more than 25% of the plots in a group). Indicator species were species with both high fidelity and high constancy and that also had significant differences in percent cover between comparison groups.

The Mann-Whitney U test was used to compare groups for all sampled environmental variables, percentage cover of characteristic overstory species, shrub species and perennial bunchgrasses, densities of rare species, species richness per plot, Shannon's diversity index per plot, total overstory cover and total shrub cover height. The non-parametric Mann-Whitney U test was chosen due to the non-normal nature of the data. Differences were considered significant if p was less than 0.01.

Results

Comparison of Carbonate and Non-Carbonate Substrates

Carbonate plots ranged in elevation from 1,440 m to 2,374 m; non-carbonate plots were between 1,304 m and 2,401 m. Carbonate plots had significantly higher mean values of pH (U=1,670, p<0.0001), percentage extractable calcium (U=683, p<0.0001) and percentage extractable magnesium (U=1,630, p<0.0001). Carbonate plots also occurred on significantly steeper slope angles (U=2,085, p<0.001; Table 1).

Total species richness was greater in non-carbonate plots (226 species) than in carbonate plots (189 species). Mean species richness per plot and Shannon's diversity index did not differ significantly between groups (Table 1). In this comparison, 48 species were found only in carbonate plots and 81 were found only in non-carbonate plots.

Two overstory species (singleleaf pinyon pine, *Pinus monophylla*, and Joshua tree, *Yucca brevifolia*), five shrub species (Great Basin sagebrush, *Artemisia tridentata*; mormon tea, *Ephedra viridis*; sticky snakeweed, *Guttierrezia microcephala*; beavertail cactus, *Opuntia basilaris*; and antelope bitterbrush, *Purshia glandulosa*) and four bunchgrass species (Fendler's bluegrass, *Poa fendleriana*; bottlebrush squirreltail grass, *Sitanion hystrix*; coronate needlegrass, *Stipa coronata* ssp. *depauperata*; and desert needlegrass, *Stipa speciosa*) were characteristic of both carbonate and non-carbonate substrates (Table 2). Only one herb species, *Gilia austro-occidentalis* was characteristic of both groups (Table 3). Total overstory cover and total shrub cover did not differ between groups (Table 2).

No indicator species were identified for non-carbonate substrates. One overstory species (shrub live oak, *Quercus turbinella*), seven shrub species (false indigo, *Amorpha californica*; California buckwheat, *Eriogonum fasciculatum* var. *pollifolium*; goldenbush, *Haplopappus linearifolius*; prickly phlox, *Leptodactylon pungens*; Parry's nolina, *Nolina parryi*; grizzly bear cactus, *Opuntia erinacea*; and *Salvia dorrii*) and one bunchgrass species (bluegrass, *Poa secunda*) were characteristic of non-carbonate substrates (Table 2). An additional 20 herbs were also characteristic of non-carbonate plots (Table 3). All of these species were either completely absent or were infrequently encountered on carbonate substrate. While its occurrence was characteristic of both substrate types, bottlebrush squirreltail grass had significantly higher mean percentage cover in non-carbonate plots.

Carbonate plots supported five indicator taxa: Utah juniper (*Juniperus osteosperma*), mountain mahogany (*Cercocarpus ledifolius*), yellow rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *stenophilus*), San Bernardino buckwheat (*Eriogonum microthecum* var. *corymbosoides*),

Table 1—Mean values of environmental variables, species richness and diversity and densities of rare plant species in carbonate and non-carbonate plots. An asterisk denotes a significant difference between the two substrate types as determined by the Mann-Whitney U test.

	Carbonate			Milkvetch-centered		
Variable	n	Mean	SD	n	Mean	SD
pH*	88	6.0	0.3	73	5.5	0.6
% Calcium*	88	16.6	8.7	73	2.6	6.3
% Magnesium*	88	2.6	2.8	73	0.9	1.4
Slope (°)	88	29.9	10.8	73	13.8	10.6
Northness	88	0.09	0.5	73	–0.0001	0.5
Elevation (m)	88	1917.0	217.0	73	1905.0	222.0
% Outcrop cover	40	5.1	10.5	73	4.9	9.7
% Boulder cover	40	1.5	2.6	73	6.9	13.0
% Rock Cover	40	5.8	5.7	73	6.2	5.7
% Cobble Cover	40	9.9	7.0	73	8.1	8.0
% Gravel Cover	40	5.0	5.9	73	8.0	7.0
% Soil Cover	40	5.8	5.4	73	11.0	11.0
% Litter Cover	40	5.4	7.2	73	6.8	11.8
Species Richness	88	20.5	5.6	73	19.3	5.8
Shannon's Diversity Index	88	0.9	0.2	73	0.9	0.2
Cushenbury Milkvetch Density[1]	88	4.6	26.7	73	1.1	9.0
Parish's Daisy Density	88	0.1	0.5	73	0.0	0.0
Cushenbury Buckwheat Density	88	3.8	11.9	73	0.0	0.0
Parish's Oxytheca Density	88	14.2	62.0	73	0.0	0.0

[1] Two plots mapped as non-carbonate substrate supported Cushenbury milkvetch. However, one of these plots had an extractable calcium content of 7.5% and the other had an extractable calcium content of 29.8%. Cushenbury milkvetch did not occur in plots that did not have calcium in the soil.

Table 2—Frequency and mean percentage cover values for overstory, shrub and bunchgrass species characteristic of carbonate and non-carbonate substrates. High fidelity and high constancy species are designated by "F" or "C", respectively. Indicator species (I) are those with high fidelity, high constancy and a significant difference in mean percentage cover between the sample groups. For frequency, carbonate n=88 and non-carbonate n= 73. For cover, carbonate n= 40 and non-carbonate n=73.

	Carbonate			Non-carbonate		
Species	**Mean**	**SD**	**Freq**	**Mean**	**SD**	**Freq**
Overstory Layer						
Juniperus osteosperma	3.9	6.2	53^{I}	0.9	2.6	10
Pinus monophylla	17.5	12.4	81^{C}	16.1	17.5	57^{C}
Quercus turbinella	0.0	0.0	0	2.6	7.0	10^{F}
Yucca brevifolia	0.7	1.8	34^{C}	1.2	3.2	24^{C}
Total Overstory Cover	23.2	17.0	—	28.6	21.0	—
Shrub Layer						
Amorpha californica	0.1	0.8	1	0.2	1.0	7^{F}
Artemisia tridentata	1.7	4.0	26^{C}	5.9	10.5	34^{C}
Cercocarpus ledifolius	11.3	12.1	47^{I}	1.0	3.6	8
Chrysothamnus viscidiflorus ssp. *stenophilus*	3.3	3.4	64^{I}	1.0	2.2	8
Echinocereus engelmannii	0.01	0.1	16^{F}	0.1	0.3	3
Ephedra viridis	2.5	3.5	69^{C}	1.5	2.5	33^{C}
Eriogonum fasciculatum var. *pollifolium*	0.2	0.5	14	1.8	3.8	27^{C}
Eriogonum microthecum var. *corymbosoides*	1.9	2.4	31^{I}	0.0	0.0	0
Forsellesia nevadensis	1.2	3.8	13^{F}	0.0	0.0	0
Guttierrezia microcephala	0.5	1.2	25^{C}	1.9	5.3	19^{C}
Haplopappus linearifolius	0.3	1.1	8	2.0	4.1	29^{C}
Leptodactylon pungens	0.0	0.0	0	0.2	0.7	12^{F}
Nolina parryi	0.0	0.0	0	0.3	1.2	6^{F}
Opuntia basilaris	0.4	0.7	32^{C}	0.01	0.8	36^{C}
Opuntia erinacea	0.0	0.0	0	0.2	0.7	7^{F}
Purshia glandulosa	1.0	2.5	31^{C}	3.4	4.7	40^{C}
Salvia dorrii	0.0	0.0	0	0.5	3.2	9^{F}
Salvia pachyphylla	0.9	2.4	22^{C}	0.3	1.1	9
Yucca whipplei	0.1	0.4	5^{F}	0.0	0.0	0
Total Shrub Cover	36.2	17.5	—	39.1	24.6	—
Bunchgrass						
Oryzopsis hymenoides	0.5	0.5	49^{I}	0.1	0.2	5
Poa fendleriana	0.4	0.5	33^{C}	0.3	0.5	22^{C}
Poa secunda	0.02	0.2	2	0.1	0.3	8^{C}
Sitanion hystrix	0.5	0.5	42^{C}	0.7	0.5	50^{C}
Stipa coronata ssp. *depauperata*	1.1	1.5	70^{C}	2.1	1.2	39^{C}
Stipa speciosa	0.3	0.5	30^{C}	0.5	0.5	37^{C}

and Indian ricegrass (*Oryzopsis hymenoides*). Mean percentage cover of each of these taxa differed significantly from their cover in non-carbonate plots (U=960, p<0.01, U=622, p<0.0001, U=813.5, p<0.001, U=949, p<0.01, U=914.0, p<0.01, respectively). Carbonate plots supported four characteristic shrub species (Engelmann's hedgehog cactus, *Echinocereus engelmannii*; Nevada greasewood, *Forsellesia nevadensis*; rose sage, *Salvia pachyphylla*; and our Lord's candle, *Yucca whipplei* var. *caespitosa*) and 11 characteristic herb species (Tables 2 and 3). Four of these herbs (Shockley's rock cress, *Arabis shockleyi*; desert paintbrush, *Castilleja chromosa*; Eaton's penstemon, *Penstemon eatonii*; and southern mountain phlox, *Phlox austromontanum*) had both high constancy and fidelity in carbonate plots. While its occurrence was characteristic of both substrate types, desert needlegrass had significantly higher mean percentage cover in carbonate plots.

Cushenbury milkvetch was found in nine carbonate plots, *Erigeron parishii* was found in 2 plots, Cushenbury buckwheat was found in 19 plots and Parish's oxytheca was found in 9. San Bernardino bladderpod was not found in any plots because sampling completed thus far is below the elevational limits of this taxon. Of these species only Cushenbury milkvetch was found in any plots that were mapped as non-carbonate. However, percentage extractable calcium for the two "non-carbonate" plots in which Cushenbury milkvetch was found was 7.5% and 29.8%, indicating that these plots were mapped incorrectly.

Cushenbury Milkvetch

Carbonate plots ranged in elevation from 1,440 to 2,374 m; Cushenbury milkvetch plots were between 1,469 and 2,011 m. Cushenbury milkvetch-centered plots had significantly higher values of percentage extractable calcium (U=818.5, p<0.01) and on the average they occurred at lower elevations (U=574.0, p<0.0001) and on signifi-

Table 3—Frequency of herbaceous species characteristic of carbonate and non-carbonate substrates. High fidelity and high constancy species are designated by “f” or “c”, respectively.

Species	Carbonate n=88 Frequency	Designation	Non-carbonate n=73 Frequency	Designation
Abronia nana-covillei	5	f	0	
Arabis dispar	0		5	f
Arabis shockleyi	26	c,f	4	
Arenaria macradenia	19	f	0	
Artemisia ludoviciana	0		6	f
Castilleja chromosa	40	c,f	6	
Caulanthus major	27	c	13	
Chaenactis santolinoides	1		9	f
Cryptantha confertiflora	5	f	0	
Cryptantha utahensis	1		4	f
Descurainia pinnata	32	c	19	
Draba corrugata	7	f	0	
Draba cuneifolia	5	f	0	
Dudleya abramsii	1		4	f
Eriastrum densifolium	1		6	f
Eriastrum sapphirinum ssp. *sapphirinum*	0		13	f
Erigeron aphanactis	0		6	f
Eriogonum inflatum	5	f	0	
Eriogonum kennedyi	1		4	f
Eriogonum ovalifolium var. *vineum*	20	f	0	
Eriogonum saxatile	1		11	f
Eriogonum umbellatum var. *munzii*	1		5	f
Eriogonum wrightii var. *subumbellatum*	1		11	f
Eriophyllum lanatum	0		14	f
Gayophytum diffusum	1		4	
Gilia austro-occidentalis	58	c	24	c
Linanthus breviculus	0		9	f
Lotus strigosus	0		7	f
Machaeranthera canescens	1		7	f
Mentzelia mojavensis	1		4	f
Monardella linoides	1		5	f
Oxytheca parishii var. *goodmaniana*	9	f	0	
Penstemon eatonii	24	c,f	5	
Penstemon labrosus	0		4	f
Phacelia fremontii	42	c	18	
Phlox austromontanum	28	c,f	4	
Senecio bernardinus	0		4	f

cantly shallower slope angles than randomly located plots on carbonate (U=613, p<0.0001; Table 4). Cushenbury milkvetch-centered plots also had significantly lower percentage cover of litter (U=148.0, p<0.01).

Total species richness was greater in carbonate plots without Cushenbury milkvetch (181 species) than in Cushenbury milkvetch-centered plots (136 species). While total species richness was lower, mean species richness per plot (U=452, p<0.000001) and Shannon’s diversity index (U=418, p<0.00001) were both significantly greater in Cushenbury milkvetch-centered plots (Table 4). In this comparison, 19 of the species sampled were restricted to Cushenbury milkvetch plots while 64 species were found only in carbonate plots that did not support Cushenbury milkvetch.

Three overstory species (Utah juniper, singleleaf pinyon pine, and Joshua tree), six shrub species (Great Basin sagebrush, yellow rabbitbrush, Mormon tea, sticky snakeweed, beavertail cactus, and antelope bitterbrush) and three bunchgrass species (Fendler’s bluegrass, coronate needlegrass, and desert needlegrass) were characteristic of both groups (Table 5). Six herb species, *Arabis pulchra*, Shockley’s rock cress, desert paintbrush, tansey mustard, (*Descurainia pinnata*), *Gilia austro-occidentalis* and Fremont’s phacelia (*Phacelia fremontii*) were also characteristic of both groups (Table 6). Total overstory cover and total shrub cover did not differ between groups (Table 5).

Two overstory species (mountain juniper, *Juniperus occidentalis* var. *australis,* and canyon live oak, *Quercus*

Table 4—Mean values of environmental variables, species richness and diversity and densities of rare plant species in Cushenbury milkvetch-centered plots and carbonate plots that did not support Cushenbury milkvetch. An asterisk denotes a significant difference between the two substrate types as determined the by Mann-Whitney U test.

	Carbonate			Milkvetch-centered		
Variable	n	Mean	SD	n	Mean	SD
pH	79	6.0	0.4	15	6.1	0.2
% Calcium*	79	16.2	9.0	30	21.3	6.8
% Magnesium	79	2.7	2.9	30	3.0	6.0
Slope (°)*	79	20.8	10.8	30	12.1	5.7
Northness	79	0.098	0.497	30	–0.009	0.570
Elevation (m)	79	1929.0	223.0	30	1737.0	150.0
% Outcrop Cover	38	5.3	10.7	15	5.3	8.4
% Boulder Cover	38	1.5	2.6	15	0.4	0.7
% Rock Cover	38	5.7	5.8	15	2.9	3.0
% Cobble Cover	38	9.6	7.0	15	7.1	4.6
% Gravel Cover	38	5.2	6.0	15	6.2	6.5
% Soil Cover	38	5.7	5.6	15	4.0	2.9
% Litter Cover*	38	5.5	7.4	15	2.3	3.6
Species Richness*	79	20.0	5.4	30	28.5	8.3
Shannon's Diversity Index*	79	0.9	0.2	30	1.1	0.2
Cushenbury Milkvetch Density*	79	0.0	0.0	30	87.1	69.4
Parish's Daisy Density	79	0.1	0.5	30	1.0	3.0
Cushenbury Buckwheat Density	79	4.2	12.5	30	2.5	8.0
Parish's Oxytheca Density	79	15.8	65.2	30	0.0	0.0

chrysolepis) and nine shrub species (service-berry, *Amelanchier utahensis*; big berry manzanita, *Arctostaphylos glauca*; Mojave ceanothus, *Ceanothus greggii* var. *vestitus*; mountain mahogany; Engelmann's hedgehog cactus; San Bernardino buckwheat; Nevada greasewood; prickly pear cactus, *Opuntia littoralis*; Mexican paperbag bush; *Salazaria mexicana;* and rose sage) and two bunchgrass species (Indian ricegrass and bottlebrush squirreltail grass) were characteristic of carbonate plots that did not support Cushenbury milkvetch. Three of the shrub layer species (mountain mahogany, San Bernardino buckwheat and rose sage) and the two bunchgrass species had both high constancy and fidelity. However, only mountain mahogany was a true indicator species in that it had a significantly higher mean percentage cover than was found in Cushenbury milkvetch-centered plots (U=121, p<0.01). Five herb species, including Cushenbury buckwheat and Parish's oxytheca were also characteristic of carbonate based plots (Table 6).

Cushenbury milkvetch-centered plots did not support any indicator species. These plots did support four characteristic shrub species (blackbrush, *Coleogyne ramosissima*; Mojave mound cactus, *Echinocereus triglochidiatus* var. *mojavense*; desert almond, *Prunus fasciculatus*; and Mojave yucca, *Yucca schidigera*), one characteristic bunchgrass (sand dropseed, *Sporobolus cryptandrus*) and three characteristic herb species (*Allium* sp., *Eriastrum sapphirinum* ssp. *sapphirinum* and *Phacelia douglasii*) (Tables 5 and 6). Both blackbrush (U=112.5, p<0.001) and Mojave yucca (U=140.5, p<0.01) had significantly higher cover in Cushenbury milkvetch-centered plots. While their occurrences were characteristic of both groups, Joshua tree (U=127.5, p<0.01) and desert needlegrass (U=154, p<0.01) had significantly higher mean percentage cover in Cushenbury milkvetch-centered plots.

Cushenbury Buckwheat

Carbonate plots that did not support Cushenbury buckwheat ranged in elevation from 1,506 m to 1,927 m; Cushenbury buckwheat-centered plots were between 1,426 m and 2,390 m. Cushenbury buckwheat-centered plots had significantly higher mean values of percentage extractable calcium (U=449.5, p<0.0001) and on the average they occurred on sites where rock outcrop cover was significantly higher (U=245.5, p<0.01; Table 7).

Total species richness was greater in carbonate plots without Cushenbury buckwheat (185 species) than in Cushenbury buckwheat-centered plots (107 species). Neither mean species richness nor Shannon's diversity index differed between groups (Table 7). In this comparison, 25 species were restricted to Cushenbury buckwheat plots while 82 species were found only in carbonate plots that did not support Cushenbury buckwheat.

Three overstory species (Utah juniper, singleleaf pinyon pine and Joshua tree), nine shrub species (Great Basin sagebrush, mountain mahogany, yellow rabbitbrush, Mojave mound cactus, Mormon tea, San Bernardino buckwheat, sticky snakeweed, beavertail cactus and antelope bitterbrush) and four bunchgrass species (Indian ricegrass, Fendler's bluegrass, coronate needlegrass and desert needlegrass) were characteristic of both Cushenbury buckwheat-centered plots and carbonate plots without this species (Table 8). Six herb species, *Arabis pulchra*, desert paintbrush, jewelflower (*Caulanthus major*), tansy mustard, *Gilia austro-occidentalis,* (*Penstemon eatonii*),

Table 5—Frequency and mean percentage cover values for overstory, shrub and bunchgrass species characteristic of Cushenbury milkvetch-centered plots and carbonate plots that did not support Cushenbury milkvetch. High fidelity and high constancy species are designated by "F" or "C," respectively. Indicator species (I) are those with high fidelity, high constancy and a significant difference in mean percentage cover between the sample groups. For frequency, Cushenbury milkvetch plots n=30 and carbonate n=79. For cover, Cushenbury milkvetch=15 and carbonate n=38.

	Carbonate			Milkvetch-centered		
Species	**Mean**	**SD**	**Freq**	**Mean**	**SD**	**Freq**
Overstory Layer						
Juniperus occidentalis var. *australis*	1.6	4.7	5^{F}	0.0	0.0	0
Juniperus osteosperma	3.6	6.1	47^{C}	4.6	6.8	19^{C}
Pinus monophylla	17.9	12.6	74^{C}	10.5	8.0	29^{C}
Quercus chrysolepis	3.7	7.3	16^{F}	<0.001	<0.001	1
Yucca brevifolia	0.8	1.8	29^{C}	2.8	4.3	25^{C}
Total Overstory Cover	23.6	17.7	—	22.2	15.4	—
Shrub Layer						
Amelanchier utahensis	0.4	1.1	9^{F}	0.0	0.0	0
Arctostaphylos glauca	3.5	8.2	18^{F}	3.2	11.6	4
Artemisia tridentata	1.8	4.1	22^{C}	0.8	1.4	8^{C}
Ceanothus greggii var. *vestitus*	3.0	8.7	15^{F}	<0.001	<0.001	1
Cercocarpus ledifolius	11.4	12.4	46^{I}	0.2	0.5	4
Chrysothamnus viscidiflorus ssp. *stenophilus*	3.2	3.5	58^{C}	3.0	3.4	23^{C}
Coleogyne ramosissima	1.1	5.7	12	15.4	11.7	16^{C}
Echinocereus engelmannii	0.01	0.1	13^{F}	<0.001	<0.001	3
Echinocereus triglochidiatus var. *mojavense*	0.1	0.3	18	0.3	0.4	10^{C}
Ephedra viridis	2.4	3.6	62^{C}	2.0	2.4	24^{C}
Eriogonum microthecum var. *corymbosoides*	1.1	2.5	$27^{C,F}$	0.1	0.4	6
Forsellesia nevadensis	1.2	3.9	12^{F}	0.4	1.1	3
Guttierrezia microcephala	0.5	1.3	24^{C}	1.0	1.9	8^{C}
Lepidium fremontii	0.1	0.6	5	0.4	0.5	9^{C}
Opuntia basilaris	0.4	0.7	29^{C}	0.5	0.6	19^{C}
Opuntia littoralis	0.1	0.7	12^{F}	0.03	0.1	2
Prunus fasciculatus	0.3	0.9	12	1.4	3.3	9^{C}
Purshia glandulosa	1.0	2.6	25^{C}	3.7	5.6	18^{C}
Salazaria mexicana	0.1	0.5	5^{F}	0.0	0.0	0
Salvia pachyphylla	1.0	2.4	$22^{C,F}$	0.2	0.6	3
Yucca schidigera	0.03	0.2	9	1.9	2.4	14^{C}
Total Shrub Cover	36.1	17.9	—	40.0	15.8	—
Bunchgrasses						
Aristida fendleriana	0.1	0.2	13	0.5	0.8	14^{C}
Oryzopsis hymenoides	0.6	0.8	$44^{C,F}$	0.3	0.6	10^{C}
Poa fendleriana	0.7	1.0	31^{C}	0.5	0.7	8^{C}
Sitanion hystrix	0.2	0.4	$36^{C,F}$	<0.001	<0.001	2
Sporobolus cryptandrus	0.01	0.1	1	0.03	0.1	4^{F}
Stipa coronata ssp. *depauperata*	1.2	1.3	64^{C}	1.7	2.8	20^{C}
Stipa speciosa	0.3	0.5	29^{C}	1.0	1.1	20^{C}

and Fremont's phacelia were also characteristic of both groups (Table 9). Total overstory cover and total shrub cover did not differ between groups (Table 8).

Carbonate plots without Cushenbury buckwheat supported one characteristic overstory species (mountain juniper), seven characteristic shrub species (service-berry; Engelmann's hedgehog cactus; winter fat, *Eurotia lanata*; goldenbush; silver cholla, *Opuntia echinocarpa*; prickly pear; and Mexican paperbag bush, *Salazaria mexicana*) and one characteristic bunchgrass species (bottlebrush squirreltail grass, Table 8). None of these were indicator species. The herbs Nevin's birdbeak (*Cordylanthus nevinii*), *Cryptantha nevadensis, Draba corrugata*, western wallflower (*Erysimum capitatum*), rattlesnake weed (*Euphorbia albomarginata*), common muilla (*Muilla maritima*), southern mountain phlox, *Stephanomeria myrioclada*, and *Stephanomeria virgata* were characteristic of carbonate plots alone (Table 9). Only four of the species above had both high constancy and high fidelity: bottlebrush squirreltail grass, tansy mustard, Fremont's phacelia, and southern mountain phlox. While its occurrence was characteristic of both substrate types, Fendler's bluegrass (U=260.0, p<0.01) had significantly higher mean percentage cover in carbonate plots that did not support Cushenbury buckwheat.

Cushenbury buckwheat-centered plots also did not support any indicator species. This group had five characteristic shrub species (big berry manzanita, rubber rabbitbrush, blackbrush, rose sage and mojave yucca) and four herb species (desert sandwort, *Arenaria macradenia*;

Table 6—Frequency of herbaceous species characteristic of Cushenbury milkvetch plots and carbonate plots that did not support Cushenbury milkvetch. High fidelity and high constancy species are designated by "f" or "c," respectively.

	Carbonate n=79		**Milkvetch-centered n=30**	
Species	**Frequency**	**Designation**	**Frequency**	**Designation**
Allium campanulatum	0		2	f
Allium sp.	2		8	c,f
Arabis pulchra	37	c	10	c
Arabis shockleyi	24	c	11	c
Arenaria macradenia	18		9	c
Brickellia oblongifolia	16	f	1	
Castilleja chromosa	34	c	16	c
Caulanthus major	26	c,f	1	
Cordylanthus nevinii	13	f	1	
Cryptantha angustifolium	0		3	f
Cryptantha muricata	0		2	f
Cryptantha nevadensis	11		8	c
Cryptantha watsonii	0		2	f
Descurainia pinnata	27	c	18	c
Draba cuneifolia	5		8	c
Eriastrum sapphirinum ssp. *sapphirinum*	0		8	c,f
Eriogonum inflatum	5		8	c
Eriogonum parishii	0		3	f
Eriogonum maculatum	0		4	f
Eriogonum nidularium	0		5	f
Eriogonum ovalifolium var. *vineum*	17	f	4	
Festuca octoflora	4		8	c
Galium parishii	5	f	0	
Gilia austro-occidentalis	52	c	25	c
Nemacladus longiflorus	0		3	f
Nemacladus sp.	3		11	c
Oxytheca parishii var. *goodmaniana*	9	f	0	
Parishella californica	0		7	f
Penstemon eatonii	23	c,f	2	
Phacelia douglasii	0		8	c,f
Phacelia fremontii	37	c	21	c
Phlox austromontanum	26	c,f	0	f

Table 7—Mean values of environmental variables, species richness and rare plant densities in Cushenbury buckwheat-centered plots and carbonate plots that did not support Cushenbury buckwheat. An asterisk denotes a significant difference between the two substrate types as determined by the Mann-Whitney U test.

	Carbonate			**Buckwheat-centered**		
Variable	**n**	**Mean**	**SD**	**n**	**Mean**	**SD**
pH	69	6.0	0.3	28	6.1	0.3
% Calcium*	69	15.4	8.7	28	22.9	4.3
% Magnesium	69	2.3	2.5	28	1.8	1.6
Slope (°)	69	18.6	10.8	28	19.6	10.3
Northness	69	0.05	0.51	28	0.08	0.49
Elevation (m)	69	1927.0	224.0	28	1861.0	219.4
% Outcrop cover*	31	5.0	11.9	28	6.7	7.2
% Boulder cover	31	1.4	2.8	28	2.2	3.8
% Rock Cover	31	5.7	6.2	28	6.3	4.5
% Cobble Cover	31	8.4	5.7	28	10.2	6.7
% Gravel Cover	31	5.7	6.7	28	4.0	2.1
% Soil Cover	31	6.1	6.0	28	3.8	2.8
% Litter Cover	31	6.4	8.1	28	2.7	1.5
Species Richness	69	20.7	5.9	28	22.9	7.1
Shannon's Diversity Index	69	0.9	0.2	28	1.0	0.2
Cushenbury Milkvetch Density	69	5.4	30.2	28	1.4	1.2
Parish's Daisy Density	69	0.1	0.5	28	1.4	4.3
Cushenbury Buckwheat Density	69	0.0	0.0	28	49.3	45.0
Parish's Oxytheca Density	69	7.1	38.3	28	0.6	1.9

Table 8—Frequency and mean percentage cover values for overstory, shrub and bunchgrass species characteristic of Cushenbury buckwheat-centered plots and carbonate plots that did not support Cushenbury buckwheat. High fidelity and high constancy species are designated by "F" or "C," respectively. Indicator species (I) are those with high fidelity, high constancy and a significant difference in mean percentage cover between the sample groups. For frequency, Cushenbury buckwheat plots n=28 and carbonate n= 69. For cover, Cushenbury buckwheat n=28 and carbonate n=31.

	Carbonate			Buckwheat-centered		
Species	**Mean**	**SD**	**Freq**	**Mean**	**SD**	**Freq**
Overstory Layer						
Juniperus occidentalis var. *australis*	2.0	5.2	5^{F}	0.0	0.0	0
Juniperus osteosperma	3.4	6.2	39^{C}	7.8	7.5	23^{C}
Pinus monophylla	18.9	13.2	63^{C}	17.3	9.4	28^{C}
Yucca brevifolia	0.9	2.0	28^{C}	1.1	1.4	15^{C}
Total Overstory Cover	26.2	17.5	—	28.5	14.5	—
Shrub Layer						
Amelanchier utahensis	0.4	1.2	9^{F}	0.0	0.0	0
Arctostaphylos glauca	3.9	8.8	13	2.4	5.4	7^{C}
Artemisia tridentata	2.2	4.4	26^{C}	1.4	3.2	11^{C}
Cercocarpus ledifolius	9.0	11.9	32^{C}	7.5	10.1	17^{C}
Chrysothamnus nauseosus	0.61	1.3	10	0.4	0.9	7^{C}
Chrysothamnus viscidiflorus ssp. *stenophilus*	3.0	3.4	48^{C}	4.6	4.5	27^{C}
Coleogyne ramosissima	1.4	6.4	7	2.2	5.5	7^{C}
Echinocereus engelmannii	0.05	0.1	13^{F}	0.02	0.1	1
Echinocereus triglochidiatus var. *mojavense*	0.1	0.3	14^{C}	0.3	0.5	8^{C}
Ephedra viridis	2.3	3.8	50^{C}	2.3	3.8	28^{C}
Eriogonum microthecum var. *corymbosoides*	1.3	2.7	28^{C}	0.8	1.0	14^{C}
Eurotia lanata	0.1	0.5	4^{F}	0.02	0.1	1
Guttierrezia microcephala	0.5	1.2	20^{C}	1.2	2.1	9^{C}
Haplopappus linearifolius	0.4	1.3	8^{F}	0.0	0.0	0
Opuntia echinocarpa	0.4	0.1	5^{F}	0.0	0.0	0
Opuntia basilaris	0.8	0.4	28^{C}	0.3	0.4	10^{C}
Opuntia littoralis	0.2	0.7	11^{F}	0.0	0.0	0
Purshia glandulosa	1.0	2.6	28^{C}	2.1	4.0	10^{C}
Salazaria mexicana	0.1	0.5	4^{F}	0.0	0.0	0
Salvia pachyphylla	0.5	1.2	14	0.8	1.9	8^{C}
Yucca schidigera	0.03	0.2	8	0.4	0.8	8^{C}
Total Shrub Cover	34.6	17.9	—	38.2	11.4	—
Bunchgrasses						
Oryzopsis hymenoides	0.5	0.8	36^{C}	0.5	0.7	12^{C}
Poa fendleriana	0.8	1.0	30^{C}	0.2	0.4	8^{C}
Sitanion hystrix	0.3	0.5	40^{C,F}	0.0	0.0	0
Stipa coronata ssp. *depauperata*	1.1	1.5	51^{C}	2.1	1.2	25^{C}
Stipa speciosa	0.2	0.5	25^{C}	0.5	1.1	9^{C}

Shockley's rock cress; brickellbush, *Brickellia oblongifolia* and *Phacelia douglasii*, Tables 8 and 9). Only *Phacelia douglasii* had both high constancy and high fidelity. While their occurrences were characteristic of both substrate types, Utah juniper (U=234.5, p<0.01) and coronate needlegrass (U=216.5, p<0.001) had significantly higher mean percentage cover in Cushenbury buckwheat-centered plots.

Discussion

It is clear from our results that carbonate substrates in the San Bernardino Mountains support vegetation that is distinct from vegetation found on adjacent non-carbonate substrates. Thus, carbonate soils contribute substantially to the native floristic and vegetational biodiversity of this portion of the mountain range. In addition to the five rare plant species that are endemic to carbonate, we found five indicator and 15 characteristic taxa for carbonate substrates as compared to non-carbonate substrates. A total of 48 species were entirely restricted to randomly located carbonate plots. An additional 14 species were restricted to carbonate substrate in either random carbonate, Cushenbury milkvetch-centered or Cushenbury buckwheat-centered plots. At the same time, 36% of the taxa found on non-carbonate soil did not occur on carbonate at all, resulting in an overall lower species richness on carbonate. While total species richness was lower on carbonate, mean species richness per plot was not different between the groups. This pattern indicates that generally species characteristic of carbonate occurred on that substrate with relatively high constancy. On the other hand, species characteristic of non-carbonate had high fidelity to the substrate but more often occurred with low frequency.

Table 9—Frequency of herbaceous species characteristic of Cushenbury buckwheat plots and carbonate plots that did not support Cushenbury buckwheat. High fidelity and high constancy species are designated by "f" or "c," respectively.

	Carbonate n=69		Buckwheat-centered n=29	
Species	Frequency	Designation	Frequency	Designation
Arenaria macradenia	14		10	c
Arabis pulchra	36	c	12	c
Arabis shockleyi	14		13	c
Brickellia oblongifolia	11		6	c
Castilleja chromosa	29	c	16	c
Caulanthus major	10	c	10	c
Cordylanthus nevinii	12	f	2	
Cryptantha nevadensis	8	f	1	
Descurainia pinnata	29	c,f	7	c
Draba corrugata	4	f	0	
Erysimum capitatum	5	f	1	
Euphorbia albomarginata	7	f	0	
Gilia austro-occidentalis	43	c	24	c
Muilla maritima	4	f	0	
Penstemon eatonii	19	c	11	c
Phacelia douglasii	0		11	c,f
Phacelia fremontii	34	c,f	7	c
Phlox austromontanum	24	c,f	6	
Stephanomeria myrioclada	7	f	1	
Stephanomeria virgata	5	f	1	

Because plots in each group did not differ in terms of elevation, northness or slope angle, vegetational and floristic differences are thought to most likely be related to the carbonaceous nature of the soil. Limestone and dolomite soils have long been recognized for supporting unique species assemblages (Kruckeberg 1969; Major and Bamberg 1963; Whittaker 1975, p. 275-276; Whittaker and Niering 1968), endemic species (Barbour and others 1993, p. 138; Raven 1988, p. 122; Kruckeberg 1969 and 1991), and disjunct occurrences of species that are common in other regions (Major and Bamberg 1963; Kruckeberg 1991). Species richness has also often been found to be lower on carbonate soils (Wentworth 1981; Kruckeberg 1969). Mechanisms resulting in these patterns are complicated and are not always clear. Parent material plays a large role in physical and chemical soil properties (Kruckeberg 1969; Barbour and others 1993). Soils derived from limestone are known to generally be poorly developed, alkaline in pH, deficient in available nutrients and to have decreased water holding capacity (Barbour and others 1993; Whittaker 1975, p. 275-276). Some have suggested that differences in ionic contents of soil solution and soil exchange complexes between carbonate and non-carbonate substrates influence species distributions (particularly iron, manganese, phosphorous and potassium; Kruckeberg 1991 and 1969; Hutchinson 1967; Grime and Hodgson 1968; Marchand 1973). Others have related vegetational differences to physical properties such as higher reflectance and thus lower surface temperatures on carbonate (Wright and Mooney 1965). Neely and Barkworth (1984), Wentworth (1981), Goldin (1976), Noy Meir (1973), and Whittaker and Niering (1968) found that carbonate substrates were generally more exposed and xeric than non-carbonate substrates. The insular nature of carbonate outcroppings may also contribute to reduced species richness (Ashton 1992; Kruckeberg 1991). Determining the extent to which any of these mechanisms might be operating in our study area was beyond the scope of this study. Certainly the observed lower species richness is at least in part a result of the fact that a wider range of plant communities (for example riparian woodlands, yellow pine woodland and Great Basin sagebrush scrub) were sampled only on non-carbonate substrates. These communities supported many species that were found nowhere else in the study area. Additional sampling will reveal whether these communities are actually not found on carbonate substrates or whether they are just uncommon.

Cushenbury Milkvetch Habitat

Habitat occupied by Cushenbury milkvetch was generally similar to random sites on carbonate in terms of physical characteristics and dominant overstory and shrub layer species. Cushenbury milkvetch habitat did have higher percent calcium, shallower slope angles and less litter cover than carbonate sites that did not support this species. Occupied habitat was primarily distinguished by the lower frequency or absence of species generally found on carbonate, though a number of characteristic species were identified. It is interesting to note that Cushenbury buckwheat and Cushenbury milkvetch co-occurred only infrequently, and thus primarily occupied different microsites. Parish's daisy and Parish's oxytheca also rarely occurred with Cushenbury milkvetch, indicating different habitat requirements for these taxa.

Cushenbury Buckwheat Habitat

Occupied Cushenbury buckwheat habitat was also basically similar to random carbonate sites, differing physically only by having higher percent calcium in the soil and also higher surface exposure of rock outcrop. Dominant species were primarily similar. For both of these rare species, sampling may have been too coarse to detect microhabitat characteristics. Parish's daisy and Parish's oxytheca also rarely occurred with Cushenbury buckwheat, indicating different habitat requirements for these taxa.

Restoration Implications

The results presented above provide baseline data on environmental and vegetational characteristics of carbonate substrate, non-carbonate substrate, Cushenbury milkvetch habitat and Cushenbury buckwheat habitat. These parameters may be ecologically important to the rare species and to the functioning of the ecosystem as a whole. Replication of these characteristics in a revegetation program would thus be essential to returning ecosystem functions to a site. While our results may be used as broad scale restoration guidelines, there was sufficient environmental heterogeneity within the study area to warrant more detailed sampling. Such sampling could entail site specific studies detailing microhabitat characteristics to be restored. Alternatively, success criteria could be made more specific by developing a plant community classification and establishing criteria for each community. Such a classification will be developed once data collection is completed throughout the range of carbonate soils. Environmental features and characteristic and indicator species will be determined for each recognized community and this will refine knowledge of baseline species occurrences and percentage cover. We will then compare these data with data from site specific sampling to determine their application to individual sites or conditions. Even if site specific sampling remains a necessity, this data set will provide a framework for understanding how the vegetation of a particular site fits into that found in the whole range of carbonate substrate.

Notwithstanding the environmental heterogeneity, our results have several immediate applications, especially in terms of soil texture and chemistry characteristics. Assume you are restoring a limestone quarry and want to return species characteristic of carbonate soils to that site. You would need to apply topsoil that had a pH between 5.7 and 6.3 and a calcium content of between 7% and 25% (Table 1). Clearly based on the evidence presented here, application of a non-carbonate soil would be inappropriate. If you were specifically restoring Cushenbury milkvetch or Cushenbury buckwheat habitat you would want an even higher percentage of calcium in the soil, though the pH of general carbonate is adequate. The significantly higher pH in the three groups on carbonate substrates has implications for addition of soil amendments or mulches that would acidify the soil. Similarly, the relatively low percentage cover of litter found in these areas indicates that heavy mulching or other addition of organic matter to the soil would not likely be appropriate.

Based on our results, species used in revegetation efforts would also vary greatly depending on whether carbonate or non-carbonate areas were being revegetated. However, because of the heterogeneity discussed above, it is not possible to directly develop vegetation success criteria from the data presented here.

Attempting to develop success criteria from the existing mine revegetation standards (USFS 1991) has uncovered several shortcomings in the existing standards. First the species richness requirement of 15% of the predisturbance species richness is vague and is a low percentage. There is no stipulation for the area that needs to be included in sampling or surveying for species richness. This point is critical as species richness is known to vary greatly with the area sampled (Magurran 1988). For example, assume you are going to develop success criteria for revegetation of an old limestone quarry. If you used the total richness we found on carbonate (189 species) as the pre-disturbance guideline for reclaiming the quarry, 28 species would need to be planted. Clearly though, not all 189 species that occurred on carbonate substrates would occur on any one site. Thus total richness for carbonate represents an inflated richness measure for this purpose. Alternatively if you used the mean species richness per 0.04 hectare plot as the standard (20.5 species), only three species would meet the standard. Clearly, meeting the standard in this case would result in a very depauperate site. Granted these examples are extremes, but they illustrate the wide range of potential outcomes that would meet the letter of the reclamation standards as they are written now. An additional problem stems from the fact that there is no provision for which species are used to meet the species richness, cover or density standards. In general it would be preferable to focus on characteristic or indicator species as such taxa are likely to be more important in ecosystem functioning due to their higher cover and abundance in the ecosystem. An exception to this generality would be maintaining biodiversity through inclusion of any species that were found on a site that were not common elsewhere in the range.

Several recommendations can be made to improve the existing mine revegetation standards (USFS 1991). Adopting the following changes would greatly strengthen the standards and improve their utility in restoring ecosystems disturbed by mining in the San Bernardino Mountains.

1) Pre-disturbance species richness will be determined in one of two ways. If the site is small enough, a complete floristic survey will be conducted by a qualified botanist at times of year when all taxa can be properly identified. For larger sites that cannot feasibly be completely surveyed, sampling will be acceptable. Samples will be 0.04 hectare, circular plots. A sufficient number will be sampled such that when successive plots are sampled, species richness is not increased by more than 2%.
2) All overstory species will be represented in approximately the same proportion of density and cover as they occur naturally. Cover will be returned to 50% of the pre-disturbance overstory cover. Densities will be equal to the pre-disturbance densities.

3) 25% of the pre-disturbance shrub species will be returned to a site in approximately the same proportion of cover as they occur naturally. Priority in species selection will be placed on species characteristic of the habitat that was disturbed. Total shrub cover will be at least 50% of pre-disturbance cover.
4) 15% of the herb species will be returned to the site. Priority in species selection will be placed on species characteristic of the habitat that was disturbed.

Summary and Conclusions

In summary, documentation of natural vegetation and associated environmental characteristics is critical for setting restoration or revegetation success criteria. Such criteria are especially important where specialized edaphic conditions support unique vegetation or rare species. Even with such criteria, the difficulty of replicating unique edaphic conditions, the arid climate of the region and the unsuitability of post-mining conditions for revegetation make potential for successful restoration low and potential for great expense high. This limited restoration potential illustrates the importance of conserving intact ecosystems, especially those that support the proposed endangered plant species.

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Reseeding Four Sensitive Plant Species in California and Nevada

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Abstract–The Kern River Gas Transmission pipeline was constructed in 1991 to supply natural gas to be used in the thermally enhanced recovery of crude oil in Kern County, California, as well as to distribute natural gas in Utah, Nevada, and southern California. Populations of nine sensitive plant species were observed during surveys conducted prior to construction of the pipeline. Mitigation measures for this project included avoidance of identified populations, and reseeding of Rusby's desert mallow (*Sphaeralcea rusbyi* ssp. *eremicola*), Parish's phacelia (*Phacelia parishii*), rosy twotone beardtongue (*Penstemon bicolor* ssp. *roseus*) and yellow twotone beardtongue (*Penstemon bicolor* ssp. *bicolor*). Revegetation success varied within species. The number of Parish's phacelia plants in 1992 that germinated in adjacent seeded and unseeded plots was 706 and 10, respectively. In 1993, the number of plants increased to 2,702 in the seeded plot and 245 plants in the non-seeded plot. During an inventory in 1992, 216 Rusby's desert mallow plants were observed in 73 of 128 standard seeded plots (57 percent), and 300 rosy twotone beardtongue plants were found in the 11 seeded plots.

The Kern River Gas Transmission pipeline (KRGT) was constructed in 1991 to deliver new supplies of natural gas to be used in the thermally enhanced recovery of heavy crude oil in Kern County, California, and also to distribute natural gas in Utah, Nevada, and southern California. The pipeline route extended from a point near Opal, Wyoming, through Utah and Nevada to Daggett, California. Total pipeline length was 596 miles, which included 119 miles in Nevada and 95 miles in California.

The Final Environmental Impact Report/Environmental Impact Statement (Chambers Group 1987) identified potential habitat for several rare plant species along the proposed pipeline route. Additional information regarding rare plants in Nevada and California was acquired during 1989 and 1990 field surveys (Dames & Moore 1990a, b). Those surveys followed a mitigation plan developed by Dames & Moore (1990c). Potential species of special concern included federal candidate species, state-listed species and species on the Northern Nevada Native Plant Society (NNNPS) and California Native Plant Society (CNPS) lists of rare plants (United States Fish and Wildlife Service 1990; NNNPS 1989; Smith and Berg 1988). One sensitive plant species was found in April 1991, after construction began, and further mitigation measures were developed.

The objective of this paper is to document implementation of mitigation measures regarding reseeding of four taxa of sensitive plants along the Nevada and California portions of the Kern River pipeline route and the subsequent reestablishment of these sensitive populations.

Sensitive Plant Surveys and Mitigation Measures

During sensitive plant surveys conducted in 1989 and 1990 along the Kern River pipeline route in Nevada and California, populations of nine sensitive species were observed within the 200-foot wide survey corridor (Table 1). The pipeline was generally constructed in a 75-foot wide disturbance zone located within the survey corridor. These populations were described and mapped (Dames & Moore 1990a, b). Additional surveys were conducted in May 1991 to locate *Phacelia parishii*.

Mitigation measures for this project to facilitate reestablishment of sensitive plants included avoidance, minimization of disturbance to the extent practicable, salvage of topsoil, use of an imprinter during reclamation, and reseeding. Seedbank material, including seeds of sensitive plants saved along with the topsoil, assisted in reestablishment of rare plants. Similarly, the use of an imprinter aided in the retention of precipitation, which assisted the revegetation of both common and sensitive plants.

Active revegetation measures were evaluated for their appropriateness in reestablishing sensitive plants. The methods evaluated for potential use included reseeding of sensitive species, and transplanting bearclaw poppy (*Arctomecon californica*). Mormon needle grass (*Stipa arida*) and scaly cloak fern (*Cheilanthes cochisensis*) plants were located at or adjacent to the 200-foot wide corridor, and avoidance of plants was considered more appropriate than reseeding. The same consideration applied for the annual species three corner milk vetch (*Astragalus geyeri* var. *triquetrus*) and sticky buckwheat (*Eriogonum viscidulum*) which were observed outside of the standard 75-foot-wide disturbance zone and work spaces. In anticipation of possible transplantation efforts, a permit to collect 50 bearclaw poppy plants was obtained from the Nevada Division of Forestry. However, because reseeding and transplanting

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Table 1—Sensitive plant species observed along the Kern River pipeline route, Nevada and California, 1989 to 1991.

Taxon name	Common name	Protection status
Sphaeralcea rusbyi ssp. *eremicola*	Rusby's desert mallow	C2, CNPS 1B
Phacelia parishii	Parish's phacelia	C2, CNPS 1B*
Penstemon bicolor ssp. *roseus*	Rosy twotone beardtongue	C2
Penstemon bicolor ssp. *bicolor*	Yellow twotone beardtongue	C2
Stipa arida	Mormon needle grass	CNPS 2
Cheilanthes cochisensis	Scaly cloak fern	CNPS 2
Astragalus geyeri var. *triquetrus*	Three corner milkvetch	C2, Nevada CE, NNNPS T
Eriogonum viscidulum	Sticky buckwheat	C2, Nevada CE, NNNPS T
Arctomecon californica	Bearclaw poppy	C2, Nevada CE, NNNPS T

*Currently reclassified to CNPS 2; CNPS = California Native Plant Society; NNNPS = Northern Nevada Native Plant Society.

of this species has not been successful in the past (Knight 1990), those methods were not implemented. The remaining four sensitive plant taxa were located within the pipeline zone and could not be avoided during construction of the pipeline. These species were Rusby's desert mallow (*Sphaeralcea rusbyi* sp. *eremicola*), Parish's phacelia (*Phacelia parishii*), rosy twotone beardtongue (*Penstemon bicolor* ssp. *roseus*) and yellow twotone beardtongue (*Penstemon bicolor* ssp. *bicolor*). Reseeding of these species appeared to be appropriate and the methods are described below.

Reseeding Methodology

Seed Collection and Storage

Reseeding efforts were accomplished for Rusby's desert mallow, Parish's phacelia, rosy twotone beardtongue, and yellow twotone beardtongue. Ripe seeds of Rusby's desert mallow were collected on 20-21 June, 1991. This species is located near Keany Pass on the east and west sides of the Clark Mountains, San Bernardino County, California, approximately 10 miles west of the Nevada/California border and Interstate 15. Seed collections for this species were segregated as east and west side samples to maintain local gene pools. Seed material for Parish's phacelia was collected on 21 May, 1991. Seeds were gathered from a larger population located less than one mile north of the population that intercepted the pipeline near the Manix Trail, approximately 12 miles northeast of Yermo, California. Collections of seeds of the two subspecies of twotone beardtongue were accomplished during July 1990, within and adjacent to locations along the proposed pipeline construction zone in which the subspecies were observed during the initial plant surveys. Rosy twotone beardtongue seeds were collected near Apex, Clark County, Nevada, at the intersection of the pipeline and State Highway 93. Yellow twotone beardtongue seeds were collected in a wash about 0.5 mile northeast of Wilson Tank in the Bird Spring Range, approximately 8 miles north of Goodsprings, Nevada.

Seeds of all taxa were air dried and stored at constant temperature (approximately 65 to 70 °F). Seed material of Rusby's desert mallow and Parish's phacelia was not cleaned and contained capsules, small leaves and some stems, but seeds of the two subspecies of twotone beardtongue were cleaned by removing most of the extraneous plant matter.

Seed viability of the four taxa was tested by either the Ransom Seed Laboratory in Carpinteria, California, or the Colorado Seed Laboratory at Colorado State University in Fort Collins, Colorado. The following tests were performed to obtain the percentage of total live seed. Germination tests resulted in 1 to 2 percent germination within 21 days for Rusby's desert mallow seeds, and 0 to 6 percent within 14 days for Parish's phacelia seeds. The remaining seeds were treated with gibberellic acid and 5 to 50 percent of the seeds germinated (percent hard seed, as shown in Table 2). Ungerminated Parish's phacelia seeds were then evaluated for viability with tetrazolium. The two subspecies of twotone beardtongue were only tested with tetrazolium, resulting in 83 to 87 percent total live seed (Table 2).

Reseeding Rusby's Desert Mallow

Rusby's desert mallow, a perennial herb, was reseeded in late October and early November, 1991. Seventy-two reseeding plots (designated as E-1 through E-72) were placed in the disturbance zone on the east side of Keany Pass. Plots E-1 to E-8 were 6-foot diameter circles, and the remaining sites were 8 feet in diameter. Seven or eight plots each were placed within 10 of 11 drainages in that portion of the right-of-way. For the purpose of placing the sample plots, a drainage was defined as the area from hilltop to hilltop. West of Keany Pass, 52 plots were placed within approximately a one-mile stretch of pipeline (plots W-1 to W-52), and 5 plots were placed in the area of a disjunct population (plots W-53 to W-57) approximately 2.25 miles west of Keany Pass. Sample plots W-1 to W-20 were 8 feet in diameter, and the remaining plots each covered a 4-foot diameter circle. The 5 plots in the area of the disjunct population were placed on a west-facing slope; the other 52 sample plots were placed within 11 drainages on both east- and west-facing slopes. Each plot was marked with rebar and metal tags.

Because of pipe repair, the seed material in sample plots E-5 and E-8 was salvaged subsequent to reseeding. Topsoil and seed material were removed from those two sample sites in November 1991, and new plots were established 2 weeks

Table 2—Results of germination tests for seeds collected along the Kern River pipeline route in Nevada and California, 1991.

Species	Sample number	% Germination	% Hard seed	% Tetrazolium	% Total live seed
Rusby's desert	#1	1	44	—	45
mallow	#2	2	50	—	53
(east side)					
Rusby's desert	#1	1	9	—	10
mallow	#2	1	5	—	6
(west side)					
Parish's phacelia	#1	3	39	17	59
	#2	6	17	51	74
	#3	0	22	55	77
Rosy twotone	#1	—	—	85	85
beardtongue					
Yellow twotone	#1	—	—	83	83
beardtongue	#2			87	87

later. The soil was deposited within a new 4-foot diameter circular area in the vicinity of the old plot sites.

Each plot was raked prior to reseeding to loosen compacted soils. Seed material (0.5 ounce) was broadcast by hand in each sample plot and the ground was raked again to cover seeds with a small amount of soil. Seed material was estimated to contain approximately 1,190 Rusby's desert mallow seeds per 0.5 ounce. Thirty-six ounces of material were broadcast on the east side of Keany Pass, and 29 ounces on the west side. Overall, it was estimated that approximately 155,000 seeds were dispersed in the Clark Mountain area.

Reseeding Parish's Phacelia

Before reseeding the annual Parish's phacelia, special preparation of the reseeding plot was implemented. This species generally grows on desert alkaline flats, specifically in desiccation cracks of thick clay accumulations. A reseeding plot of 270 by 30 feet was chosen on the spoilside of the pipeline within the 75-foot wide disturbance zone. The plot was sprayed with 4,000 gallons of water on 3 December, 1991. Then the site was allowed to dry and crack. An equally large unwatered control plot was chosen on the workside of the pipeline within the disturbance zone. After 2 weeks, the soil had dried and cracked and the habitat of the reseeding plot approached nearly natural conditions. Transects were walked width-wise, and the seed material was evenly broadcast in 25 subsamples. Seeds were distributed for an additional 10 feet beyond the disturbed area, to compensate for depletion of plants during seed collection. It was estimated that approximately 1,300,000 Parish's phacelia seeds were broadcast during reseeding. The plot was marked with rebar and metal tags. To reduce motor vehicle travel through the plot, orange wooden stakes were placed across the width of the plot.

Reseeding Twotone Beardtongue

Reseeding of the two perennial subspecies of twotone beardtongue was accomplished in early November 1991. Reseeding areas were selected according to the general location of collection to maintain local gene pools. In addition, existing populations were located near the pipeline before reseeding within the disturbance zone.

Rosy twotone beardtongue was reseeded near the intersection of the pipeline and Highway 93. Five sites were chosen within the 0.5-mile stretch west of the highway. Seeds were dispersed within 11 three-foot diameter subplots. At Site 1, which is located at the greatest distance from the highway, 1 subplot was established at the southern edge of the pipeline disturbance. Site 2 was established in a prominent wash approximately 0.4 miles from the highway. Three subplots were placed across the disturbance zone, with additional plots east of the wash. One subplot each was placed at the northern edge of the pipeline disturbance at Sites 3 and 4, located approximately 2,000 and 1,800 feet from the highway, respectively. Site 5 consisted of 2 subplots at the northern edge of the disturbance zone and a broad wash adjacent to Highway 93. Approximately 30,600 rosy twotone beardtongue seeds were broadcast in the 11 subplots.

Yellow twotone beardtongue was reseeded in a small wash dissecting the disturbance zone approximately 0.5 miles northeast of Wilson Tank in the Bird Spring Range. An approximately 115-by-53-foot plot was established and marked at the corners. The equivalent of 45 subplots of 9 to 16 square feet was established within the large plot. Individual subplots were raked and a small amount of seed was spread within the subplot. The subplots were then raked to cover the seed. Approximately 17,400 seeds were broadcast.

Reseeding Results

Reseeding success was evaluated by inventorying plant establishment the first season after reseeding activities. One species was evaluated for a second season. The survey methods and the results of reestablishment of each species are described below.

Rusby's Desert Mallow

The 57 plots located on the west side of the Clark Mountains were inventoried on 21 June and 9 August, 1992.

Table 3—Results of follow-up surveys of Rusby's desert mallow, Clark Mountains, San Bernardino County, California, June, August 1992.

	Side of Keany Pass			
	Standard plot		Expanded plot	
	East	West	East	West
Plots surveyed	71	57	71	57
Total plants observed	69	147	84	237
Plants/Plot	1.0	2.6	1.2	4.5
Frequency (%)	46	70	46	72
Density (plants/100 ft^2)	2.0	3.8	—	—

Seventy-one of 72 plots on the east side of the Clark Mountains were inventoried on 20 June, 1992. Locations of these plots were identified by markers that had been installed during reseeding. The boundaries of the plots were determined by observing the rake marks that were still discernible, and by measuring from the center stake. Plot E-5 was not found during the inventory.

Many Rusby's desert mallow plants were observed, sometimes in greater densities in areas adjacent to the reseeded plots. It was speculated that seeds were transported outside of the reseeded plots by wind and rain erosion of the seedbed. As a result, counts were made in the original reseeded plot as well as in an expanded plot of approximately 40 feet in diameter.

The total number of plants counted in the original plots was 69 plants on the east side of the Clark Mountains and 147 plants on the west side (Table 3). The east-side plots contained an average of 1.0 plants, and 33 of the 71 plots contained at least 1 plant. The average number of plants per plot of the west side was 2.6 plants. Growth of at least 1 plant occurred in 40 of 57 plots. The average densities of plants in the east side and west side plots were 2.0 per 100 square feet and 3.8 per 100 square feet, respectively.

In the expanded plots, 84 plants were counted on the east side of the Clark Mountains and 237 plants on the west side. The average number of plants per plot was 1.2 (east) and 4.5 (west), respectively. The number of plots that contained at least 1 plant was almost the same as in the original plots, as shown in Table 3. Frequency of the original and expanded plots was 46 percent in the east side plots, and 70 and 72 percent on the west side.

Parish's Phacelia

Reestablishment of Parish's phacelia was evaluated on 18 April, 1992, and during April 1993. In addition to the reseeded plot, two additional plots were inventoried as control sites. One control site was located within the disturbance zone of the pipeline; it had not been reseeded in 1991. The other control plot was located in an undisturbed area outside the disturbance zone. Each plot measured 270 by 30 feet. The number of Parish's phacelia plants observed in each plot was counted. The first year after reseeding, 706 Parish's phacelia had germinated in the reseeded plot, and only 2 plants in the control plot within the disturbance zone (Table 4). In the adjacent non-reseeded plot, a total of 10 plants was found. In 1993, approximately 2,702 plants were found in the reseeded plot, which represented a density of 33.4 per 100 square feet. In the non-reseeding plots in and adjacent to the disturbance zone, 245 plants and 1,014 plants were counted, respectively.

Rosy Twotone Beardtongue

The 5 reseeding sites were inventoried on 6 October, 1992. Locations of the plots were identified by markers that had been installed during reseeding activities. Although many of the sites had been disturbed by off-road vehicle traffic, 10 of the 11 subplots contained small plants, ranging from 3 to 68 per subplot (Table 5), with a total of 300 plants. In the following year, no counts were made. However, cursory observation indicated that plants were flowering and covered the entire surface of one three-foot diameter subplot. Other subplots were less prolific.

Yellow Twotone Beardtongue

During the October 1992 inventory, the reseeding plot and surrounding area contained a moderate to dense cover of species of a wild horse seed mix, including *Penstemon* sp. seedlings. Subsequent to the sensitive species reseeding effort in 1991, the pipeline disturbance zone in that area was reseeded with a different seed mixture. The second reseeding effort was completed at the request of the Bureau of Land Management with the objective of enhancing the wild horse habitat in that area. The yellow twotone beardtongue reseeding area was included in the second reseeding effort. The wild horse seed mix contained Palmer's

Table 4—Results of follow-up surveys of Parish's phacelia, San Bernardino County, California, April 1992 and April 1993.

	Within disturbance zone		Adjacent to disturbance zone
	Reseeded	Non-reseeded	Non-reseeded
1992			
Number of plants	706	2	10
Density (plants/100 ft^2)	8.7	<0.1	0.1
1993			
Number of Plants	2,702	245	1,014
Density (plants/100 ft^2)	33.4	3.0	12.5

Table 5—Results of follow-up surveys of rosy twotone beardtongue, Clark County, Nevada, October 1992.

Site	Number of subplots	Number of plants observed/subplot
1	1	45
2	6	0-45
3	1	55
4	1	68
5	2	3-26
Total	11	300

penstemon (*Penstemon palmeri*). Yellow twotone beardtongue could not be distinguished from Palmer's penstemon at this morphological stage, and reseeding efforts were not determined.

Discussion and Conclusions

Review of this project indicated successful mitigation for impacts to sensitive plant species. Avoidance and minimization of disturbance zones is still considered the preferred method, but active revegetation in the form of reseeding can be an effective mitigation alternative for some species if avoidance is not possible.

Early planning is important for successful reestablishment of sensitive plant species. Several points need to be considered. These are: site analysis of habitat prior to disturbance; biotic and physical requirements of each taxon; optimal time for seed collection; specific site preparation to create an environment favorable for reestablishment; and developing methods of monitoring.

Reseeding of Rusby's desert mallow required no specific seedbed preparation. This species appears to be adapted to disturbed areas; many of the seeds collected came from plants found on old powerline spur roads. Other factors, however, may have influenced the difference in reestablishment between the east and west populations (2.0 plants versus 3.8 plants per 100 square feet, respectively). Specifically, the one-time seed collection was apparently suboptimal. Seeds appeared to be at a late stage of seed dispersal; the west side population was further advanced than the east side population. In addition, the east side material contained 50 percent hard seeds compared to 10 percent in the west side population. Since afterripening may break dormancy over time (Young and Young 1986), a second year of monitoring may have been beneficial. Also, seed collections should have occurred over a period of time to obtain high quality seeds.

Some species require special methods for seedbed preparation. For instance, the disturbance zone was graded and leveled at the end of construction. Parish's phacelia specifically grows in desiccation cracks of thick clay accumulations, and re-creating this microenvironment was critical for reestablishment. Because rain is unpredictable in desert environments, application of 4,000 gallons of water was essential for re-creating desiccation cracks. During the second year after reseeding, natural seed dispersal and subsequent rains to create desiccation cracks in the control plots apparently increased seed germination in both the reseeding and control plots.

Frequently, provisions are not made for monitoring the success of reestablishment projects, for both sensitive and common species. Hall (1987) reported that 7 of 15 mitigation projects failed because of lack of maintenance and monitoring. No monitoring was required for this project, neither of the sensitive plant taxa nor of the imprinting success and natural revegetation of the common species. Monitoring the reseeding results of these four taxa was only due to a voluntary effort of the authors. Valuable information could be gained from revegetation projects, if monitoring the success rate would be a condition of project approvals by the responsible governmental agencies.

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New Arid Land Revegetation Techniques at Joshua Tree National Monument

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Abstract—Joshua Tree National Monument's nursery created methods for using native desert vegetation on disturbed areas in the desert southwest; most notable is our "tall pot", a 30 inch tall PVC pipe that allows deep tap root development. We continue to research other methods of arid land restoration. Although direct seeding shows little success in the desert, a site preparation method called imprinting improves success of direct seeding. Another modification to existing technology is Joshua Tree's use of containers smaller than our tall pot. Being lighter and more economical to grow and plant, these containers offer benefits for use in remote areas, such as abandoned mine sites.

Joshua Tree National Monument conceived its native plants nursery and revegetation program to mitigate impacts to the park's vegetation systems from historic and current activities. The nursery grows over 80 species of desert plants, used along roadsides following road improvements, on closed dirt roads and jeep trails, abandoned mine sites, as well as for facilities landscaping, and historic plant restoration. Joshua Tree's work has attracted the attention of a number of outside agencies and we have entered into cooperative work with a number of these: Death Valley National Monument, Lake Mead National Recreation Area, Anza-Borrego Desert State Park (plants for landscaping, roadside work, and mitigating off-highway vehicle damage), the USDA Forest Service and the U.S. Bureau of Mines (growing plants for mine restoration projects), and the USDA Soil Conservation Service (species ecotype and direct seeding trials).

Through our work and contact with others we have collected information on the restoration of vegetation in deserts. To this end, in cooperation with UNESCO's Man and the Biosphere Program we created the Center for Arid Lands Restoration, a clearinghouse for information and consultation on desert revegetation.

Joshua Tree has developed methods and materials well suited to successful propagation and planting of desert plants. However, these methods are not always economically or logistically feasible and we have researched new techniques for our work. For instance, larger disturbed areas requiring restoration may become expensive to plant. Direct seeding is an economical means of reestablishing vegetation, but has proven ineffective in deserts due to the harsh environment. Smaller nursery material is more economical for larger sites, but rarely hardy enough to survive the harsh environment. Joshua Tree has used variations on these methods which may prove successful for the desert.

Imprinting

The desert does not afford a favorable environment for the establishment of vegetation. The climate is harsh—high winds, extremes in temperature and sparse rainfall hamper seedling survival. Disturbance in desert areas compound these conditions. In many cases, the thin top organic layer of soil containing seeds and protective cryptobiotic organisms has been stripped away. Soil compaction is also a problem: a sealed interface between the air and soil impedes water infiltration and causes surface run-off and erosion.

While there is little restorationists can do about the desert climate (save irrigation), one strategy for restoration is proper site preparation. Ripping is often used to break up soil compaction; however, rainfall can quickly recompact soil and reseal the surface. A method of site preparation that has shown success in the desert is imprinting, which roughens a smooth, closed soil surface. The benefits include providing favorable microsites for seed establishment and concentrating scarce site resources, namely water and organic matter. This process was developed by Robert Dixon following applied research at the USDA's Agricultural Research Service in Tucson, AZ, and has continued with Dixon's Tucson-based Imprinting Foundation.

Imprinting forces depressions into the soil surface. The depressions are wedge, cone, or pyramid shaped, made by hand or foot-attached implements or specially designed tractor-towed rollers. By their shape, the imprints can infiltrate rainwater rapidly and funnel limited seed, topsoil and finely-divided plant litter to a common point or line at the bottom the depressions. This helps germinate seeds and establish seedlings with a minimal amount of rainfall. Thus, compacted soil is roughened, opened, mulched, and stabilized (Dixon, 1989).

Results have been favorable on grasslands and shrub lands of the Sonoran and Chihuahuan deserts and in the sagebrush-bunchgrass areas of the Great Basin desert. Imprinting has proven superior to other methods, especially where low precipitation is the main limiting factor to seedling establishment. The process has not been used to a great extent in the Mojave desert.

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We wanted to test the effectiveness of imprinting as a means of site restoration. If successful, it could prove more economical for revegetation on larger disturbed areas than using nursery grown plants. We chose three disturbed sites within Joshua Tree National Monument: an inactive borrow pit near the park's west entrance, a section of closed dirt road (both in the Mojave desert), and a second inactive borrow pit in the Mojave/Colorado desert interface.

We devised four treatments; half the treatment areas were ripped, the other half ripped and imprinted. Treatments included sowing with native seed (seed sown by hand at approx. 6 lbs./acre); sowing with a sterile wheat as a cover crop (Yecora Rojo Wheat, 99.0% sterile, sown at 40 lbs./acre); sowing native seed and sterile wheat together (sown at 6 lbs./acre and 20 lbs./acre, respectively); and no seed or wheat. The National Park Service Denver Service Center advised us on the seeding rate for the wheat cover crop; the amount of native seed sown was dictated by the amount collected and available for sowing. Treatment plots measured 6 x 12 feet; our response variable is the germination and survival of native seedlings on each plot.

We collected the native seed within the monument during summer 1992. These were collected, dried, cleaned, weighed, and stored in refrigeration until needed for the project. We used the following species: needle grass (*Achnatherum speciosum*), burrobush (*Ambrosia dumosa*), coyote melon (*Cucurbita palmata*), jimson weed (*Datura meteloides*), brittlebush (*Encelia farinosa*), goldenbush (*Ericameria* spp.), cheesebush (*Hymenoclea salsola*), bladderpod (*Isomeris arborea*), white ratany (*Krameria grayi*), creosote bush (*Larrea tridentata*), galleta grass (*Pleuraphis rigida*), paperbag bush (*Salazaria mexicana*), chia (*Salvia columbariae*), desert senna (*Senna armata*), jojoba (*Simmondsia chinensis*), globe mallow (*Sphaeralcea ambigua*), and desert aster (*Xylorhiza tortifolia*) (Jepson, 1993).

We imprinted in January 1993; Robert Dixon supplied the imprinter, and was also on hand during the imprinting process. Before imprinting, Joshua Tree's Maintenance Division used a road grader to rip the soil on all sites to break up and decompact the soil and make the surface amenable for holding the imprints. The teeth on the grader penetrated to approximately 18 inches. We seeded each plot by hand, then towed the imprinter roller over the plots. The imprints depressed the soil approximately 4-6 inches.

Following the imprinting treatment, normal winter rainfall was lower than average, and we have seen little germination of the native species. We plan to monitor the plots in spring 1994 following the winter rains to assess germination and growth for each treatment, and will continue to monitor for a number of years.

Recommendations from Dixon and Wendell Hassell (National Park Service, Denver Service Center) for the use of imprinting in the Mojave include slight variations on the original process. Dixon states the three factors that affect imprinting in any environment are good seeds, good rains, and good imprints.

A good mix of both annuals and perennials is thought to be the best for returning the range of natives to a site. Native plants are best adapted to local site conditions; the National Park Service requires use of locally collected propagules and genetic material. Of course, viable seed is required for best germination. Dixon and Hassell state a sterile cover crop provides cover for newly emerging seedlings, acts as mulch, increases soil organic matter, and improves soil aggregation. A sterile or non-returning species reduces competition for resources with native seedlings. Another tactic is sowing the cover crop the first year, waiting for at least 70% mortality, then sowing native seeds the second year.

Imprinting is best done in the fall, or just after the first rain: damp soil will hold imprints better, and sown seed can take advantage of the remainder of the season's precipitation. This is especially important in the Mojave where most precipitation falls in the winter months, unlike the regular summer and winter precipitation in the Sonoran desert.

For good imprints, Dixon recommends using the imprinter on lighter (sandier) soils. On heavier (clayey) soils, there may be a need to weight the imprinter, or wait for right soil moisture. Clayey soils may also have a tendency to stick to the roller, pulling up the top soil layer. Ripping or disking first may be beneficial on heavier soils. Besides being more economical than planting on larger disturbed areas, imprinting may also be more successful because of the reduced edge effect. Adjacent undisturbed perimeter provides cover for herbivores, who prefer to browse close to protection. Hence, the larger a disturbed area, the smaller the perimeter to area ratio. Newly emerging seedlings, highly palatable to herbivores, may be safer because of the distance from cover. Dixon also counsels patience when waiting for results; a few seasons may be required until all conditions to be right for germination.

Experimental Containers

Joshua Tree's native plants nursery has provided containerized plant material for roadside revegetation projects since 1988. We developed the containers specifically for growing native desert plants. These plants must survive the rigors of the Mojave desert life (extreme air and soil temperatures and low average rainfall) virtually unassisted, and indeed they have. Our "tall pot" is a PVC cylinder 6 inches in diameter, 30 inches deep, and weighs about 40 lbs. when filled. In our largest revegetation project to date, we planted 1509 plants in early spring of 1990, 1991 and 1992. As of spring 1993, our monitoring showed 77% planting survival. Just to be alive in that environment is deemed successful; however, a large percentage of nursery stock had already set flowers and fruit within the first year in the field.

Revegetation techniques developed by Joshua Tree may prove troublesome to restorationists not working on a roadside. Not only are our tall pots difficult to transport to remote sites, but a power auger is necessary to drill the planting holes. Finally, plants grown in this manner are fairly expensive ($10 to $12 each) and larger projects may not be cost effective.

In the summer of 1992 the U.S. Bureau of Mines came to us with a proposal to revegetate an abandoned mine site within our park boundaries. This project afforded us the chance to try to answer two questions: were containerized plants able to survive on such heavily disturbed arid sites; and what kinds of results could we get from pots of smaller size and varying designs? We chose the Silver Bell Mine as project location, an abandoned silver mine 22 miles south of the town of Twentynine Palms, .6 miles by air from the nearest paved road and more than 3/4 mile overland with a moderately difficult climb to the mine. Smaller, lighter containers were called for but how small could we go and still ensure survival in the harsh environment?

A few years earlier the nursery grew desert plants in 10 cubic inch super cells for a cooperator; we felt these containers were too small for desert planting. We also propagated plants for the University of California at Riverside using Stuewe & Sons "Tall One" citrus pots (4 inches x 4 inches x 14 inches tall). The university reported these plants grew successfully in their experimental plots. In 1991 we tested three different plant species in 36 citrus pots planted in conjunction with our regular roadside revegetation. When monitored in 1992 we found 76% survival. In May 1993, after three months of very low precipitation, we planted 60 citrus pots containing nine species in another small test plot. The summer continued with little or no rainfall. When we returned to the site in mid-September, we found 52 of the 60 plants were alive and in various stages of vigor. Because of the positive results of those two trials, we chose this as the smallest container size to use for the mine revegetation project.

Looking for a container size between the citrus pot and our PVC tall pot, we selected another Stuewe & Sons pot, the "Treepot" (5½ inches square at the top x 7¾ inches square at the base x 18 inches tall). We made changes to both the citrus pot and the treepot to facilitate the way we plant containerized stock. When using the PVC tall pot we snip the bailing wire at the bottom of the pot, pull off the hardware cloth circle that holds the soil in place, place the pot in the augered hole and pull the pot up and over the plant, back-filling and watering as the pot is removed. With this method there is no disturbance to the plants root-ball. The Stuewe & Sons pots are wider at the top than the bottom; in order to pull the pot over the plant, we invert it. We make the wide top the new bottom, and install hardware cloth and bailing wire which holds the soil in place.

We created a third pot size when we ran out of hardware cloth for the bases of the treepots. We had pre-cut pot bottoms to fit our 6 inch diameter tall pots. We cut tall pots in half enabling us to use the pre-cut wire circles in a shorter container, the "half-tall" pot (6 inches in diameter x 15 inches tall).

Once we established container sizes we began propagating the plants. When using the tall pot for revegetation, germinated seed is first planted into a rolled newspaper cylinder (the paper pot) and grown for 12-14 weeks. Once roots appear at the bottom of the cylinder we transplant the seedling into the tall pot where in continues growing for another 9-12 months. The treepot and the half-tall pot seedlings require the intermediate paper pot stage but total growing time is shortened by 6 or 7 months. The citrus pot is too small for a paper pot transplant so germinated seed is planted directly into the container. The citrus pot seedling is treated the same as the paper pot for the first two weeks but many labor hours have been eliminated by avoiding a transplant stage. The citrus pot seedling is ready for planting in less that 4 months.

The smaller containers weigh less than tall pots. A mature plant in a tall pot can weigh 40 lbs. as mentioned earlier. The ready-to-plant smaller containers weigh as follows: the treepot, 23 lbs.; the half-tall pot, 18 lbs.; and the citrus pot, 7 lbs. We appreciated the reduced weight each time we lifted a pot and when we transported the pots to the mine site. Lastly, the shorter the pot, the shallower the planting hole. The workers running the auger attest to the benefit of digging 15 inches or less in the mine's rocky substrate, rather than 30 inches or more.

In February 1994 we began the Silver Bell Mine revegetation project. A helicopter transported the plants, the auger and other planting tools, wire and rebar for caging, a portable water tank, and 1,500 gallons of water to the mine site. The reduced weight of the smaller containers allowed the helicopter to carry more pots per trip, considerably reducing air time.

The rocky substrate of the mine's 7,500 square feet of benches and tailings created difficult planting conditions. Rocks (up to melon-sized) frequently stopped the auger from digging to the prescribed depth and often the hole could not be dug at all. The crew then used hand trowels to dig the holes on the tailings slopes. If these problems weren't enough, the plants may have a difficult time getting established due to extremely fine soil particles coupled with the rocks. The combination of these results in air pockets that dry roots, a major inhibitor of plant survival.

The shallow soil depth hampered planting of all but the citrus pots. A lip around the top (now bottom) of the treepots hindered slipping the pot up around the plants. Despite the problems and difficult conditions, the planting crew planted 382 plants of 24 different species on the site in 74 treepots, 77 half-tall pots, and 231 citrus pots. We will continue to monitor plant survival and growth at the Silver Bell Mine site.

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Regeneration of Cold Desert Pine of N.W. Himalayas (India)—A Preliminary Study

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Abstract—The cold desert pine of India, *Pinus gerardiana* (Wall.) has been subjected to overexploitation because of the commercial value of its edible seeds and ethnic uses. Regeneration is deficient. Preliminary studies conducted by inoculating the seedlings with mycorrhiza show great promise in establishment and performance of the seedlings.

Pinus gerardiana, commonly and commercially known as 'chilgoza' and/or 'neoza' pine, is a forest tree restricted in India to dry inner valleys of the Northwest Himalayas (1,600 to 3,000 m elevation). It occurs in Kinnaur (Satluj Valley) and Pangi in Himachal Pradesh (Ravi and Chenab Valleys) extending westward to Kashmir, Afghanistan, and Northern Baluchistan.

Neoza pine grows gregariously, forming forests of a somewhat open type, though it sometimes forms moderately dense pole crops. It is mixed with deodar in varying proportions in the region outside the influence of monsoons. The annual precipitation (about 250 to 270 mm) is received mainly in the form of snow during winter. It endures severe winter cold. The summer temperature within its habitat, however, seldom exceeds 39 °C. The neoza pine makes little demand on the fertility of the soil and is capable of growing on very dry hillsides with shallow soils.

Pinus gerardiana is well known for its edible seed. The seed (chilgoza) is eaten as dry fruit which is rich in oil, starch, and albumenoids. Seeds are obtained from cones which are still green. The cones are gathered from the trees, heaped up, and burned to open them, after which the seeds are picked out. Much damage is apt to be done to the trees during cone collection.

The natural regeneration of this pine is deficient. There are a number of factors responsible for poor natural regeneration. First, since 'chilgoza' is a cash crop, the rights holders remove almost all the cones for seed collection leaving none for germination; second, whenever seeds are left, they are damaged by rodents, birds, and reptiles; third, there is high seed mortality during drought; fourth, the big seed does not embed into loose sandy soil with poor soil moisture; and fifth, heavy and unrestricted sheep and goat grazing causes a lot of damage to young seedlings (Chauhan 1986). All these factors reduce the chances of natural regeneration of this pine. Severe biotic interference and lack of regeneration in this pine may result in the extinction of this species (Kumar 1986; Sehgal and Chauhan 1989).

For regeneration, it has been suggested that areas bearing chilgoza pine should be closed for a period of 30 years for rights holders. Artificial regeneration has been achieved at a number of places both by sowing and planting of nursery raised plants at Kalpa, Ralli (Kilba Range), Akpa (Morrand Range), Shongtong, and Purbani (Kalpa Range) (Chauhan 1986).

However, no attention has ever been paid to the use of mycorrhiza for artificial inoculation of chilgoza pine seedlings. Saplings are usually planted after they attain a height of about 5 to 10 cm and are 3 to 4 years old. This article reports the first attempts of artificial mycorrhizal inoculation of *Pinus gerardiana* seedlings.

Materials and Methods

The mycobiont was isolated from the natural mycorrhizal roots following Marx et al. (1982) and pure cultures were raised following Mikola (1973).

For raising cultures, Martins (1950), White's modified (Vasil 1959), and Potato Dextrose Peptone-Agar (Rawlings 1933) media were used. For artificial inoculation, two inoculum sources, forest soil (soil from the natural range of chilgoza pine) and pure culture of the mycobiont were used. The former involves the incorporation of about 10 to 20 percent of soil inoculum by volume in the experimental pots prior to transplanting. In the latter case mycobiont was isolated from the ectomycorrhiza itself.

After four weeks, when seedlings reached the cotyledon stage, they were picked up from the experimental beds and planted in sterilized plastic pots containing thermally sterilized soil. A sufficient amount of inoculum was taken from the culture tubes and mixed with sterilized soil. A thin layer of inoculum was spread on the topsoil. The inoculum was also put at the planting hole as an additional safeguard to ensure that every seedling receives the inoculum (Mikola 1969). When mixing inoculum with potting mixture, care was taken to secure even distribution of the inoculum. After inoculation, roots were sampled periodically to estimate the number of mycorrhiza. The inoculated pots were kept in temperature- and moisture-controlled chambers in the greenhouse. The seedlings' characteristics, like green luster on the foliage, height, growth, and root development, were noted during the course of experiments. Shoot height was recorded at the end of the experiments. The

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seedlings were harvested, taking care that all root ends remained intact. Data on root lengths, number of laterals, total short roots (including both uninfected and mycorrhizal) and total mycorrhizal roots were recorded for individual seedlings. Since mycorrhizal roots exhibit repeated dichotomy in this plant, the branch was counted as one mycorrhiza. Ten-power magnification was used to classify short roots as mycorrhizal or uninfected.

The mycobiont was isolated from the rhizoplane of *Pinus gerardiana* seedlings and seedlings were inoculated with the culture. The development and estimation of mycorrhiza in inoculated seedlings are presented in table 1.

The seedlings inoculated with the mycobiont attained better shoot height, root length, stem diameter, total root shoot, fresh weight, and high shoot-root fresh weight ratio. The shoot height, root length, and fresh weight shoot-root ratio was significantly greater (at the 0.01 level) in the inoculated seedlings; the stem diameter was also significantly higher (at the 0.05 level). Development of mycorrhiza in inoculated seedlings results in green luster on the foliage; they are easily distinguished from uninoculated control seedlings which remained pale green.

There was a significant difference (at the 0.05 level) in the mycorrhizal counts between inoculated and uninoculated control seedlings. The mycorrhizal counts show that all the seedlings which were inoculated developed ectomycorrhizal infection. None of the plants in the uninoculated controls developed any mycorrhizal short roots. Seedlings inoculated with mycobiont had 67.60% mycorrhizal short roots and 32.40% uninfected short roots. The total number of short roots (144 maximum) was higher in inoculated seedlings than in the uninoculated seedlings (96 maximum).

Discussion

The seedlings of *Pinus gerardiana* inoculated with mycorrhizal symbiont showed a 67.6% increase in mycorrhizal development. The inoculated seedlings were highly ectomycorrhizal. The number of bifurcate roots which developed four months after inoculation showed a threefold increase. Shoulders (1972) observed that inoculated slash pine seedlings had four times as many bifurcate roots at lifting as uninoculated seedlings. Trappe (1967) and Harley (1969) pointed out that bifurcate or dichotomously branched short roots are not irrefutable evidence of mycorrhizal infection, nor is their absence concrete proof that roots are not infected.

Inoculation markedly increased the intensity of infection and also enhanced the survival. The abundance of bifurcated roots on seedlings appeared to be a useful index of transplanting survival. Nonmycorrhizal seedlings (table 1) grew pale and remained stunted in contrast to mycorrhizal seedlings, which grew vigorously and acquired bright green luster. Similar observations have been reported from various parts of the world following inoculation of soil with pure cultures of ectomycorrhizal fungi (Fassi et al. 1969; Theodorou and Bowen 1970; Theodorou 1971; Vozzo and Hacskaylo 1977; Lamb and Richards 1974). Kormanik et al. (1977) also reported that inoculation of plants with mycorrhizal fungi normally caused a striking increase in growth.

There was a significant increase in the shoot height of mycorrhizal seedlings compared to nonmycorrhizal seedlings (table 2). The fresh weight as well as dry weight of shoots and roots of mycorrhizal plants was higher than compared to nonmycorrhizal plants (table 3). It is clear

Table 1—Effect of mycorrhizal inoculation on seedlings of *Pinus gerardiana* Wall. after 6 months of inoculation (mean of five readings).

Soil infestation treatment	Shoot height	Root length	Stem diameter	Fresh weight			Shoot/root ratio	Foliage luster
				Shoot	Root	Total		
	cm	*cm*	*mm*	*gm*	*gm*	*gm*		
Control	12.5	8.6	4.2	12.0	8.1	20.1	1.48	Pale
	11.6	8.3	4.6	13.5	7.9	21.4	1.70	
	13.0	8.5	4.5	13.0	7.8	20.8	1.54	
Basidiomycetous mycelium	21.2**	14.0**	4.8*	18.0*	11.0*	29.0*	1.63*	Green
	20.3*	13.6*	4.7*	19.5**	10.8**	30.3**	1.80**	
	20.6*	13.2*	5.0*	19.8**	10.5*	30.3**	1.88**	

	Mycorrhizal Counts			
	Number of uninfected short roots	Number of mycorrhizal short roots	Total number of short roots	mycorrhizae development
				percent
Control	80	0	80	0
	96	0	96	0
	92	0	92	0
Basidiomycetous hyphae	48 (37%)	82 (63%)	130	100
	46 (32.40%)	96 (67.69%)	142	100
	54 (39.89%)	88 (61.11%)	144	100

*P 0.05 = significant; **P 0.01 = highly significant.

Table 2—Shoot height of 8-month-old mycorrhizal and nonmycorrhizal seedlings of *Pinus gerardiana* Wall.

Sample	Mycorrhizal (Mean ± SE)	Nonmycorrhizal (Mean ± SE)	't' value (df = 8)
	- - - - - - - - - - - *cm* - - - - - - - - - - -		
1	17.2 ± 0.28	12.1 ± 0.28	2.65*
2	16.8 ± 0.32	11.2 ± 0.32	2.65*
3	16.4 ± 0.31	10.2 ± 0.31	3.00*
4	14.7 ± 0.32	8.2 ± 0.32	2.25*
5	17.4 ± 0.36	8.4 ± 0.36	3.00**
6	16.8 ± 0.28	9.2 ± 0.28	2.65*
7	16.2 ± 0.30	8.8 ± 0.30	2.65**
8	17.2 ± 0.31	8.6 ± 0.31	1.75**
9	17.4 ± 0.28	9.1 ± 0.28	3.00**
10	16.6 ± 0.34	8.5 ± 0.34	2.25*

SE = standard error about mean; df = degree of freedom; *P 0.05 = significant; **P 0.01 = highly significant.

Table 4—Shoot/root ratio per plant of 8-month-old mycorrhizal and nonmycorrhizal *Pinus gerardiana* Wall. seedlings.

Sample	Mycorrhizal (Mean ± SE)	Nonmycorrhizal (Mean ± SE)	't' value (df = 8)
	Fresh weight shoot/root ratio		
1	6.28 ± 0.21	4.54 ± 0.21	2.17*
2	5.91 ± 0.26	5.21 ± 0.26	2.65*
3	6.28 ± 0.24	5.16 ± 0.24	2.35**
4	5.82 ± 0.18	3.86 ± 0.18	1.75 NS
5	6.78 ± 0.22	4.42 ± 0.22	3.00*
6	6.36 ± 0.24	4.36 ± 0.24	1.65*
7	6.14 ± 0.23	4.08 ± 0.23	2.35**
8	6.36 ± 0.24	4.62 ± 0.24	1.75*
9	6.52 ± 0.25	4.15 ± 0.25	1.65 NS
10	6.64 ± 0.24	4.36 ± 0.24	2.60*
	Dry weight shoot/root ratio		
1	3.98 ± 0.20	2.82 ± 0.20	2.25**
2	4.38 ± 0.17	3.16 ± 0.17	2.65**
3	4.32 ± 0.18	3.26 ± 0.18	2.40*
4	4.28 ± 0.21	2.17 ± 0.21	1.50 NS
5	4.36 ± 0.24	3.67 ± 0.24	3.25*
6	4.08 ± 0.22	2.87 ± 0.22	3.00*
7	3.68 ± 0.21	2.67 ± 0.21	2.54*
8	4.28 ± 0.24	2.64 ± 0.24	3.75**
9	4.26 ± 0.21	3.07 ± 0.21	2.65*
10	4.17 ± 0.18	2.94 ± 0.18	3.00*

SE = standard error; df = degree of freedom; *P 0.05 = significant; **P 0.01 = highly significant; NS = nonsignificant.

from table 4 that the shoot/root ratio for both fresh weight and dry weight was significantly higher in mycorrhizal plants.

However, there were no obvious differences in soil nutrients (organic carbon percentage, total nitrogen percentage, available phosphorus and available potassium) and pH of the soils. The soils were low in nitrogen, available phosphorus and available potassium. The pH of unsterilized soil was more acidic as compared to sterilized soil (table 5).

Significant differences were obtained in the percentage of nitrogen, phosphorus, potassium, calcium, and magnesium accumulated in needles of the mycorrhizal and nonmycorrhizal seedlings. Needles of the mycorrhizal seedlings generally showed the higher concentration of these elements (table 6). The percentage of nitrogen accumulation in the needles varied from 0.95 to 0.98 in mycorrhizal seedlings and from 0.72 to 0.76 in the nonmycorrhizal seedlings. The difference was significant at the 0.05 probability level.

The gain in phosphorus by the needles of mycorrhizal seedlings was three times that of nonmycorrhizal seedlings. Phosphorus levels in the mycorrhizal needles varied from 1.27 to 1.28 percent, whereas in nonmycorrhizal needles phosphorus varied from 0.39 to 0.43 percent. The difference was significant at the 0.01 probability level (table 5). The level of potassium, calcium, and magnesium in the needles of mycorrhizal seedlings was significantly higher compared to nonmycorrhizal seedlings.

The total nutrient percentage in shoots and roots was higher in mycorrhizal seedlings compared to nonmycorrhizal seedlings (table 7). The difference in accumulation of phosphorus in mycorrhizal and nonmycorrhizal seedlings was threefold; the difference was significant at the 0.01 level. Nitrogen, potassium, calcium, and magnesium are significantly higher in the roots and shoots of mycorrhizal plants at the 0.05 probability level.

Inoculation of seedlings with mycorrhizal fungi clearly increases overall growth and development. In these isolations

Table 3—Fresh weight and dry weight of 8-month-old mycorrhizal and nonmycorrhizal seedlings of *Pinus gerardiana* Wall.

	Mycorrhizal				Nonmycorrhizal			
	Fresh weight		Dry weight		Fresh weight		Dry weight	
Sample	Shoot	Root	Shoot	Root	Shoot	Root	Shoot	Root
	- *gm* -							
1	1.76	1.15	0.66	0.46	1.62	0.96	0.36	0.21
2	1.84	0.98	0.47	0.37	1.71	0.72	0.29	0.19
3	1.90	0.86	0.61	0.42	1.58	0.64	0.40	0.24
4	1.86	0.95	0.86	0.38	1.38	0.82	0.32	0.26
5	1.56	1.20	0.94	0.46	1.48	0.86	0.32	0.23
6	1.64	1.16	0.96	0.51	1.62	0.78	0.36	0.21
7	1.75	0.88	0.90	0.32	1.70	0.98	0.32	0.27
8	1.82	0.96	0.65	0.46	1.56	0.96	0.31	0.26
9	1.58	1.05	0.70	0.42	1.35	0.94	0.28	0.21
10	1.72	1.22	0.98	0.42	1.68	0.72	0.36	0.24

Table 5—Nutrient content of sterilized and unsterilized soils in which nonmycorrhizal and mycorrhizal seedlings of *Pinus gerardiana* Wall. were raised. Each figure is the mean of five readings.

Treatment	Soil pH	Organic carbon	Total nitrogen content	Available soil nutrients	
				P_2O_5	K_2O
		Percent		*lb/acre*	
Unsterilized soil	6.4	0.54	0.32	48	128
Sterilized soil	6.2	0.57	0.34	49	132

Table 6—Elemental compostition of needles of 6-month-old mycorrhizal and nonmycorrhizal seedlings of *Pinus gerardiana* Wall. Each figure represents the mean of five readings.

Nutrient elements	Mycorrhizal (Mean ± SE)	Nonmycorrhizal (Mean ± SE)	't' value (df = 8)
	Percent		
Nitrogen	0.98 ± 0.04	0.74 ± 0.04	0.80*
	0.96 ± 0.06	0.72 ± 0.06	0.85*
	0.95 ± 0.03	0.76 ± 0.03	1.00*
Phosphorus	1.28 ± 0.02	0.41 ± 0.02	3.25**
	1.27 ± 0.05	0.43 ± 0.05	2.80*
	1.28 ± 0.03	0.39 ± 0.03	3.00**
Potassium	0.63 ± 0.04	0.43 ± 0.04	2.58
	0.67 ± 0.04	0.44 ± 0.04	2.25**
	0.72 ± 0.05	0.49 ± 0.05	2.65**
Calcium	0.36 ± 0.06	0.32 ± 0.06	2.60*
	0.39 ± 0.03	0.36 ± 0.03	2.48**
	0.37 ± 0.04	0.38 ± 0.04	1.90*
Magnesium	0.30 ± 0.02	0.21 ± 0.02	3.25**
	0.28 ± 0.02	0.22 ± 0.02	3.00*
	0.28 ± 0.04	0.26 ± 0.04	3.20*

SE = standard error about mean; df = degree of freedom; *P 0.05 = significant; **P 0.01 = highly significant.

the inoculum was from the excised mycorrhizal roots. There is need to collect associated fungi and try their pure cultures for mycorrhizal synthesis; it has been reported that different fungi and their strains differ in their capacity to form mycorrhiza. Nevertheless, it is conclusively proven that in inoculated seedlings the transplanting period will be reduced almost by a year or so, which if calculated in terms of time, money, and energy is a lot of saving.

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Table 7—Nutrient content of shoots of 6-month-old mycorrhizal and nonmycorrhizal seedlings of *Pinus gerardiana* Wall. Each figure is the mean of five readings.

Nutrient	Mycorrhizal			Nonmychorrizal			't' value df = 8
	Shoot	Root	Total ± SE	Shoot	Root	Total ± SE	
	Percent						
Nitrogen	0.98	0.76	1.74 ± 0.02	0.68	0.50	1.18 ± 0.02	1.65*
	0.96	0.82	1.78 ± 0.03	0.72	0.53	1.25 ± 0.02	2.65*
	0.98	0.81	1.71 ± 0.02	0.64	0.54	1.18 ± 0.02	1.75*
Phosphorus	1.17	0.98	2.15 ± 0.06	0.39	0.26	0.65 ± 0.06	2.00**
	1.18	0.93	2.11 ± 0.05	0.32	0.27	0.59 ± 0.05	3.65**
	1.11	0.89	2.00 ± 0.07	0.36	0.30	0.66 ± 0.07	3.25*
Potassium	0.54	0.46	1.00 ± 0.01	0.24	0.18	0.42 ± 0.01	2.30*
	0.52	0.50	1.02 ± 0.02	0.26	0.21	0.47 ± 0.02	3.25**
	0.57	0.54	1.11 ± 0.01	0.25	0.20	0.25 ± 0.01	2.65*
Calcium	0.32	0.30	0.62 ± 0.03	0.24	0.22	0.46 ± 0.04	2.65*
	0.34	0.32	0.66 ± 0.04	0.21	0.18	0.39 ± 0.04	2.65*
	0.31	0.33	0.64 ± 0.01	0.23	0.21	0.44 ± 0.01	3.00**
Magnesium	0.28	0.26	0.54 ± 0.02	0.18	0.16	0.34 ± 0.02	1.65 NS
	0.24	0.23	0.47 ± 0.02	0.20	0.17	0.37 ± 0.02	2.65*
	0.23	0.21	0.44 ± 0.03	0.18	0.13	0.31 ± 0.03	2.65*

SE = standard error; df = degree of freedom; *P 0.05 = significant; **P 0.01 = highly significant; NS = nonsignificant.

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Lessons from the Past—Gilbert L. Jordan's Revegetation Research in the Chihuahuan and Sonoran Deserts

Bruce A. Roundy

Abstract—From 1963 to 1973, Gilbert L. Jordan at the University of Arizona conducted numerous native and exotic grass revegetation trials at four sites in central and southeastern Arizona. Lehmann lovegrass A68 initially established best. Initial establishment was highest for most species from broadcast sowing in March after rootplowing and pitting. Grasses did not persist at the Congress and Pima sites and density of species decreased substantially at the Bowie and San Simon sites 12 to 15 years after sowing. Revegetation projects on arid and semiarid grass/shrublands should be evaluated over time to determine which species are adapted to persist under the long-term climatic conditions of the site.

Over the last part of the 1800's and the first half of the 1900's, grasses decreased and woody plants increased on desert grassland in the southwestern United States and northern Mexico. Early recognition of the loss of grass by scientists and stockmen led to an interest in developing appropriate range management practices, including grazing management, brush control, and revegetation to restore the grass. Numerous field trials were conducted to determine successful species to seed and to develop techniques to control undesirable vegetation and to catch and hold rainwater for improved revegetation (Roundy and Biedenbender, in press).

Erosion associated with cultivation and abandonment and with uncontrolled grazing of semiarid and arid lands led to the development of a strong national consciousness for soil conservation. Scientists and others sought innovative approaches and possible "miracle plants" to successfully revegetate severely eroding watersheds.

In the Southwest, exotic lovegrasses (*Eragrostis* spp.), especially Lehmann lovegrass (*E. lehmanniana*), showed great promise for revegetation of desert grassland sites (Crider 1945). In the 1940's Lytle Adams, a retired dentist and inventor-aviator, proposed reseeding western rangelands by broadcasting pelleted seeds from airplanes (Roundy and Biedenbender, in press). This inexpensive approach to revegetation occurred to him in southern California, where he had observed small cactus plants spring up from rabbit droppings. In 1945, he interested Congress in the idea of aerially distributing pelleted seed. The idea was that seed could be compressed in earthen pellets with fertilizers, fungicides, and insect and rodent repellents. The weight of the pellets would allow even distribution and penetration into the soil from inexpensive aerial seeding (Jordan 1967).

This idea was appealing compared to the alternate methods of broadcasting seeds without pellets, where success was usually limited by lack of soil coverage, or mechanical seedbed preparation and sowing on the ground, which was slow and expensive considering the large acreages involved. Dr. and Mrs. Adams actively promoted the pelleted seeding program at the local and national level. Mrs. Adams made hats with Lehmann lovegrass and devil's claw (*Proboscidea* spp.), which she presented to such prominent ladies as Mrs. Morris Udall and Jacqueline Kennedy.

Pelleted seeding research was conducted in many western states from 1945 into the 1960's (Hull and others 1963; Jordan 1967). At the University of Arizona, Gilbert L. Jordan began what was to become over 20 years of intensive, field-oriented, revegetation research by conducting pelleted seeding studies.

Jordan's (1967) findings on a Chihuahuan desert shrub site were similar to those of other studies. Pelleted seeding produced similar or less establishment than aerially broadcasting non-pelleted seed. Mechanical seedbed preparation and sowing on the ground produced successful stands of lovegrass while pelleted seeding did not, even in years with favorable precipitation. Pelleted seeding failed partly due to a decrease in germination associated with the pelleting process (Jordan 1967). When Adam's advocate in Congress, Representative Ben F. Jensen from Iowa, learned that pelleted seed research money had been used to make comparisons with other methods, he accused the University of Arizona of sabotaging the program. The pelleted seeding story is interesting because it shows the interest and concern at the local and national level in revegetating the range, and it demonstrates the need to do careful comparative research to test apparently easy solutions.

It is also interesting to note the unquestioned acceptance of introduced species, at this period in time, and that the main controversy was how, not what to seed. For Jordan and many others, it forcefully demonstrated that reseeding of lower elevational desert grassland/shrubland sites required appropriate seedbed preparation.

Appropriate seedbed preparation should be designed to increase water availability to seeds and seedlings by

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controlling competing species, covering seeds at a shallow depth, and creating depressions to catch and hold water from intense thundershowers (Roundy and Call 1988). After the pelleted seeding studies, Jordan conducted revegetation research from 1963 to 1973 on species, seedbed preparation, and sowing methods on former desert grassland and desert shrubland sites in the San Simon and Gila Valleys, as well as near the base of the Date Creek Mountains near Congress, Arizona, and on the Arizona Strip. The primary objective in southeastern Arizona was to determine successful revegetation techniques for rehabilitating the badly eroded San Simon watershed (Jordan and Maynard 1970a,b). The seeding sites are transitional between the Sonoran and Chihuahuan deserts and averaged about 250 mm annual precipitation (Table 1). Funded by the Bureau of Land Management (BLM), Jordan's studies were representative of an extensive approach to revegetation research. He tested chemical and mechanical means of brush control and seeding techniques: seeding in fall, late spring, or summer, drilling versus broadcasting seeds, seeding at different rates, and treating seeds with fungicides. He tested at least 14 species of native grasses and seven exotic grasses, as well as a number of exotic experimental selections developed by L. Neal Wright of the Agricultural Research Service. At the peak of his research activity, Jordan was annually seeding dozens of plots on five different sites, as well as evaluating density and forage yield of hundreds of plots from previous years. He did this for 10 years, often with a small field crew, which included a series of student employees. He also faithfully produced annual reports documenting his progress for the BLM. The current study summarizes findings from this exhaustive revegetation research effort and analyzes the long-term success of techniques and plant materials tested by Dr. Jordan.

Sites and Methods

Characteristics for the San Simon, Bowie, and Pima sites are shown in Table 1 (Roundy and Jordan 1988). The Congress site is approximately 21 km west of the town of Congress at the base of the Date Creek Range in west-central Arizona. Soils are deep sandy loams. Average annual precipitation is 257 mm, elevation is 914 m, and dominant vegetation includes mesquite (*Prosopis juliflora)*, creosotebush (*Larrea tridentata*), Joshua tree (*Yucca brevifolia*), and wolfberry (*Lycium californicum*). The Pima, Bowie, and San Simon sites are transitional between the Sonoran and Chihuahuan Deserts (Cox and others 1982). Summer precipitation, often as intense thundershowers, is 50 to 60% of the total annual precipitation on these sites.

Revegetation trials from 1963 through 1973 on these sites focused primarily on various methods of mechanical brush control (discing and rootplowing), seedbed preparation (roller, furrow, and disc pitting), sowing methods (broadcasting, drilling), sowing time (March, June), sowing rate (1, 1.5, and 2 times the standard sowing rate of 1.2 million seeds per ha), and plant materials (Table 2). Root plowing was generally at a 35 to 55 cm depth and pits were generally less than 20 to 30 cm deep. Experimental design was a randomized block, with generally three to four replications per treatment. Individual plots ranged from 10 to 30 m wide and 30 to 60 m long. Density and dry matter yield of seeded species the year of seeding and 2 to 4 years later were recorded in 10 to 20, 0.3- by 1.5-m quadrats randomly placed along the diagonal of each replication. Density of plants seeded in 1969 through 1972 were recorded 12 to 15 years later in 1984 in two belt transects, 2 m wide by 30 m long in each replication. Basal cover of seeded species was estimated in 1984 by measuring basal diameter of five plants per belt transect. Mean basal area was calculated using the formula for the area of a circle and multiplied by mean plant density to give a total plot basal area. This was divided by total plot area to give an estimated basal cover percentage. Analysis of variance was used to determine significant treatment and species differences ($P \leq 0.05$) for different years. Results are based on Jordan's progress reports and on 1984 persistence data.

Table 1—Characteristics of three sites where Gilbert L. Jordan conducted revegetation studies in southeastern Arizona (Roundy and Jordan 1988).

	Study site		
Location	**25km SW San Simon**	**13 km NE Bowie**	**11 km NW Pima**
Elevation (m)	1,230	1,080	990
Mean annual temperature (°C)	17	17	17
Average percipitation 1968-1984 (mm)			
Winter (November-March)	72	100	79
Summer (July-October)	152	160	137
Total annual	248	284	222
Dominant vegetation	*Flourensia cernua*, *Prosopis juliflora* var. *glandulosa,* *Larrea tridentata,* *Gutierrezia sarothrae*	*Larrea tridentata*	*Prosopis juliflora* var. *glandulosa,* *Haplopappus tenuisectus*
Soils	Eba gravelly sandy loam, mixed, thermic Typic Haplarids (Vogt 1980)	Dona Ana fine-loamy, mixed, thermic Typic Haplargids (Vogt 1980)	Sandy loam to loamy sand

Table 2—Names and symbols of some of the grass species sown in revegetation trials by Gilbert Jordan in southern Arizona.

Symbol	Common name	Scientific name
A68	Lehmann lovegrass	*Eragrostis lehmanniana*
L11	Lehmann lovegrass	*E. lehmanniana*
L19	Lehmann lovegrass	*E. lehmanniana*
L28	Lehmann lovegrass	*E. lehmanniana*
L38	Lehmann lovegrass	*E. lehmanniana*
A84	Boer lovegrass	*E. curvula* var. *conferta*
ERAT	Cochise lovegrass	*E. lehmanniana* x *E. trichophora*
CAT	Catalina Boer lovegrass	*E. curvula* var. *conferta*
BOIS	Yellow bluestem	*Bothriochloa ischaemum*
SEMA	Plains bristlegrass	*Setaria macrostachya*
PAAN	Blue panic	*Panicum antidotale*
ERSU	Wilman lovegrass	*E. superba*
SPCR	Sand dropseed	*Sporobolus cryptandrus*
BOCU	Sideoats grama	*Bouteloua curtipendula*

Results and Discussion

Seedbed Preparation

Rootplowing in March, pitting and broadcasting grass seeds into disturbed seedbeds was the most effective revegetation method, especially for small-seeded lovegrasses. Not only did rootplowing effectively control the woody species, but it also loosened the soil, increased infiltration, and helped bury seeds broadcast after plowing. Jordan built a Nisbet rotary shaft seeder to permit controlled sowing rates of small-seeded species with the rangeland drill, but broadcasting into a disturbed seedbed produced similar emergence as drilling. Jordan considered that seeding in March was better than seeding in June because the small amount of residual moisture in the soil helped retain soil structure during rootplowing. Jordan concluded that pitting generally increased stand density and yield from 20 to 25% over nonpitted seedbeds and could prevent seeding failure on some sites once in every five seedings. He observed that the value of pitting for catching and holding water from intense summer thundershowers was additive to the benefits of rootplowing. Consequently, Jordan built a disc pitter that could be attached behind a rootplow to permit plowing, pitting, and broadcast sowing in one pass.

For the years 1969 and 1970, pitting increased initial density of all sown grasses at San Simon, Pima, and Bowie, but density 14 to 15 years later was generally similar on pitted and unpitted seedbeds (Fig. 1). For the small-seeded Lehmann lovegrass, pitting increased initial density on only one out of eight site-years for which data were available for the San Simon, Pima, and Bowie sites between 1969 and 1972. Pitting did not increase persistence of Lehmann lovegrass for any sites or years measured.

Sowing Rates

Higher sowing rates increased initial seedling density on three of seven site-years tested between 1970 and 1972 at San Simon, Pima, and Bowie. However, established plant densities measured 12 to 13 years after initial sowing were similar for different sowing rates (Fig. 2).

Summer Precipitation Amount and Pattern

Summer precipitation for this area of the Southwest is highly variable from year to year (Cox and Jordan 1983). Also, the pattern of rainfall in time and space within a given summer rainy season is highly variable (Osborn

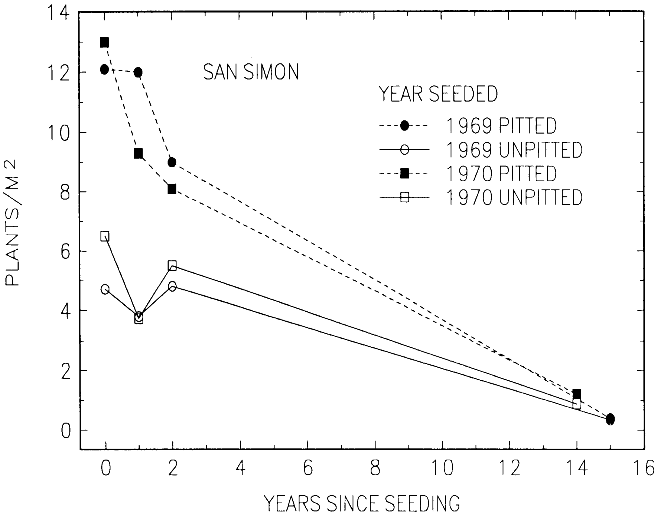

Figure 1—Density of warm-season grasses seeded on pitted and unpitted seedbeds near San Simon, Arizona. Densities are significantly different (P ≤ 0.05) for pitted and unpitted treatments for all years sampled except at 15 years since seeding.

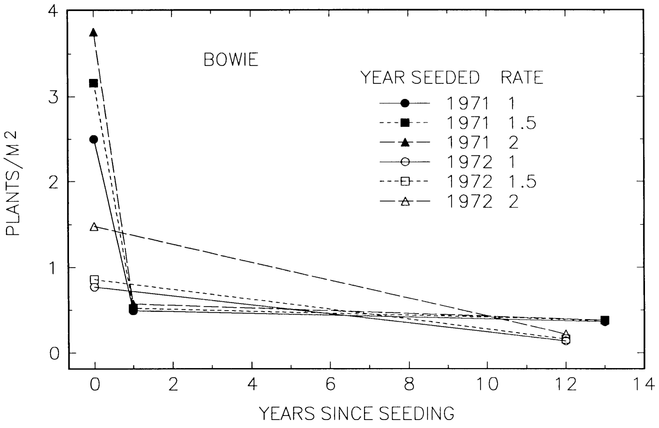

Figure 2—Density of warm-season grasses seeded at various rates near Bowie, Arizona. Densities are significantly different (P ≤ 0.05) among rates only during the year of sowing. Rates are 1, 1.5, and 2 times the standard rate of 1.2 million seeds per hectare.

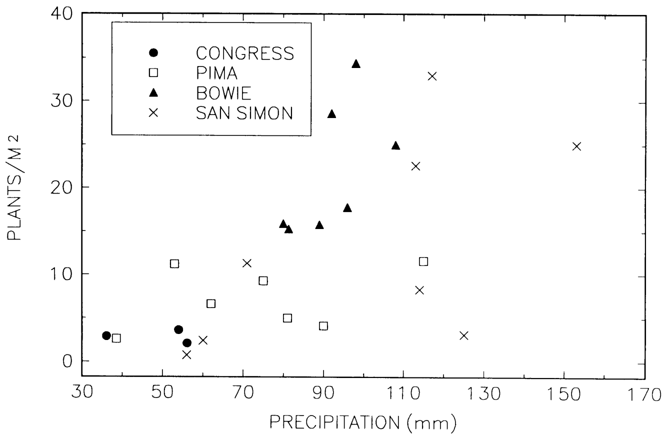

Figure 3—Initial seedling density of Lehmann lovegrass sown at four sites in central (Congress) and southeastern Arizona in relation to total summer precipitation.

1983). Lehmann lovegrass A68 had consistently higher establishment than other plant materials. However, its initial establishment varied greatly with total precipitation in July through August or July through September (Fig. 3). Although there is a general correlation of increased initial seedling density with increased precipitation, this correlation varied among sites and did not hold for some sites and years (Fig. 3). For example, initial establishment at San Simon was much higher in 1968 and 1969 than in 1966 and 1972, even though total summer precipitation was similar for these years. Initial rainfall followed by a 10- to 15-day dry period may have germinated but later desiccated seedlings in 1966 and 1972.

Species and Sites

In the initial years of his studies, Jordan evaluated a number of native grasses. On exceptionally wet years he observed successful establishment of a number of grama grasses—blue, black, hairy, and sideoats grama (*Bouteloua gracilis*, *B. eriopoda*, *B. hirsuta*, and *B. curtipendula*), as well as other natives such as spike and sand dropseed (*Sporobolus contractus*, *S. cryptandrus*). However, since the introduced lovegrasses established more consistently from year to year, and at higher densities, he quit testing most native grasses by 1970. Perhaps it was also difficult for him to obtain quality native grass seeds. Jordan suggested that plains bristlegrass (*Setaria macrostachya*) had the highest potential of the native grasses to establish, but that most native grasses adapted to the San Simon area, for example, would establish only once in 10 years.

Due to lack of initial establishment and persistence, Jordan quit seeding the Congress site after 1966. He felt that lack of summer precipitation (40% of annual precipitation) limited potential for revegetation of this site. Jordan (1983) later developed a method of using average annual temperature, seasonality of precipitation, and total annual precipitation to describe the boundary between arid and semiarid, with arid sites not being suitable for revegetation.

Seedling establishment and persistence varied among sites. Seedlings initially established at high densities at the Pima site, but little persistence was observed by 1984. Seedlings initially established at generally similar densities at the San Simon and Bowie sites, depending on the year, but persisted better at San Simon (Figs. 4 and 5). Lehmann lovegrass A68 consistently established at higher densities than the other grass species, including drought-tolerant Lehmann lovegrass selections of Neil Wright of the Agricultural Research Service (L-11, L-19, L-28, L-38). All species and selections decreased substantially in density over time (Figs. 4 and 5). These decreases occurred in

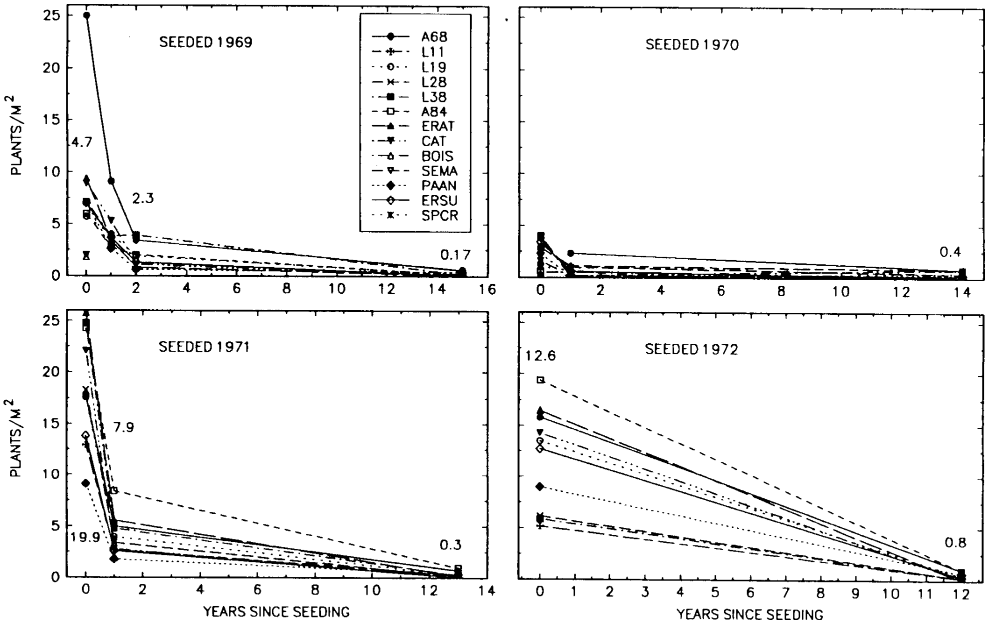

Figure 4—Density of warm-season grasses sown near Bowie, Arizona. Species names for legend symbols are in Table 2. Numbers indicate LSD (P ≤ 0.05) for a given year since seeding.

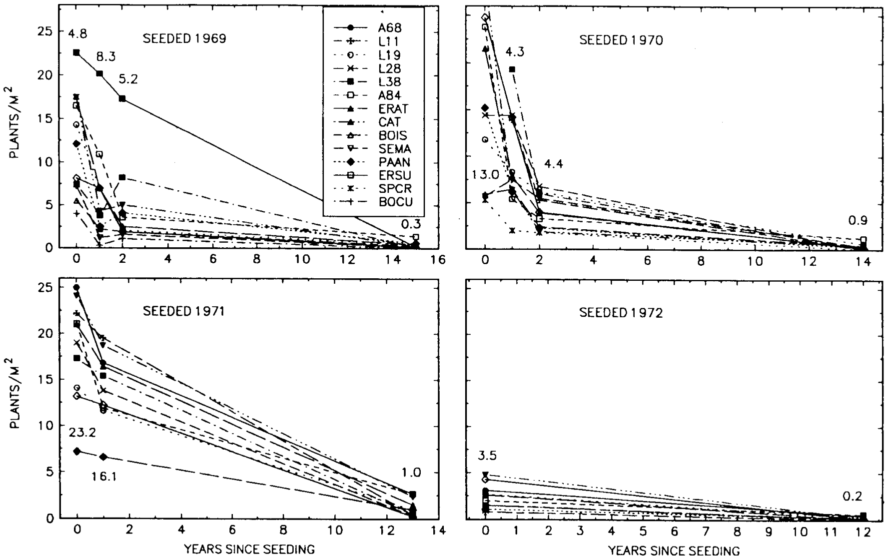

Figure 5—Density of warm-season grasses sown near San Simon, Arizona. Species names for legend symbols are in Table 2. Numbers indicate LSD ($P \leq 0.05$) for a given year since seeding.

the absence of cattle grazing, since the original exclosures were still functional during the 1984 evaluations. Plant density varied more among species at initial establishment than 12 to 15 years later. Decreases in forage yield 12 to 13 years after seeding at San Simon indicate that revegetation for increased livestock production may not be economical (Cox and Jordan 1983). However, in some cases, grass basal cover persistence may justify revegetation for watershed protection. Grass basal cover of some seeded areas at San Simon was still high (up to 19% on some plots) and seeded species had spread to adjacent small arroyos by 1984.

Lehmann lovegrass A68 had greater persistence in terms of density than all other species at Bowie while A84 Boer lovegrass (*E. curvula* var. *conferta*) had greatest persistence at San Simon (Fig. 6). In terms of basal cover, blue panic (*Panicum antidotale*) had highest persistence at Bowie (Fig. 7). Seedings at Congress, Pima, and on the creosotebush site at Bowie would be considered failures after 12 to 15 years, while some seedings at San Simon could be considered successful, but not necessarily profitable. Seedings on a sand dune mesquite (*Prosopis juliflora* var. *glandulosa*) site at Bowie also had high persistence, but were not evaluated in 1984 due to difficulty in determining plot borders.

Rootplowed and seeded plots with limited grass persistence at Bowie were relatively bare, while those at Pima and San Simon were dominated by burroweed (*Haplopappus tenuisectus*) and snakeweed (*Gutierrezia sarothrae*), respectively, in 1985 (Roundy and Jordan 1988). Native grasses such as bush muhly (*Muhlenbergia porteri*) occur at very low densities at these sites and have not invaded rootplowed and seeded areas. The paradox of this is that bush muhly is adapted to persist on these sites but rarely establishes new plants.

Some important lessons learned from this exhaustive field research are:

- Initially successful revegetation in summer rainfall areas doesn't necessarily indicate long-term success. It's important to evaluate persistence in revegetation studies overtime;

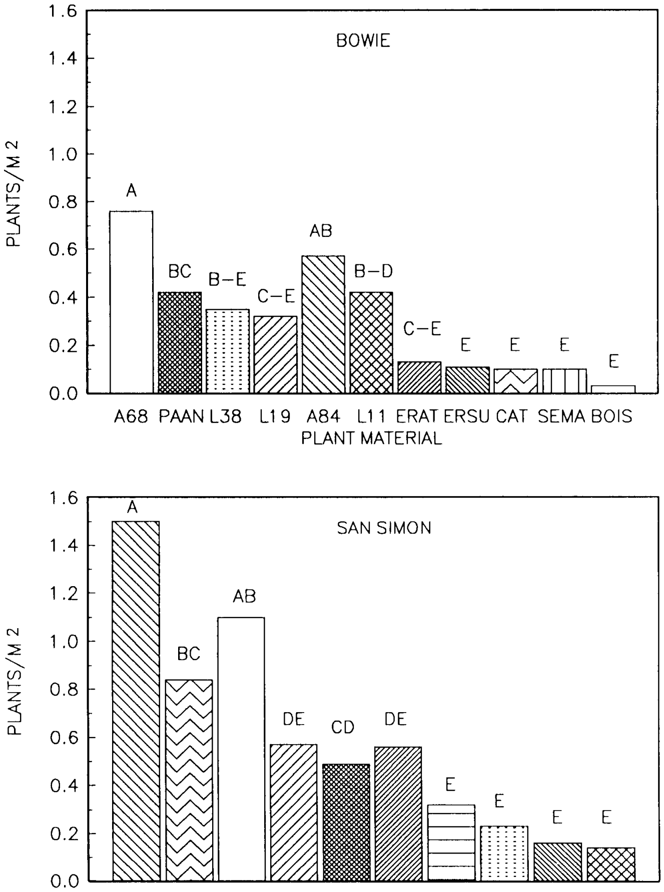

Figure 6—Mean density in 1984 of warm-season grasses sown during 1969-1972 near Bowie and San Simon, Arizona. Species names for symbols are in Table 2. Species are ordered from highest to lowest mean rank (left to right) over the 4 seeding years. Similar letters above bars indicate no significant difference ($P \leq 0.05$).

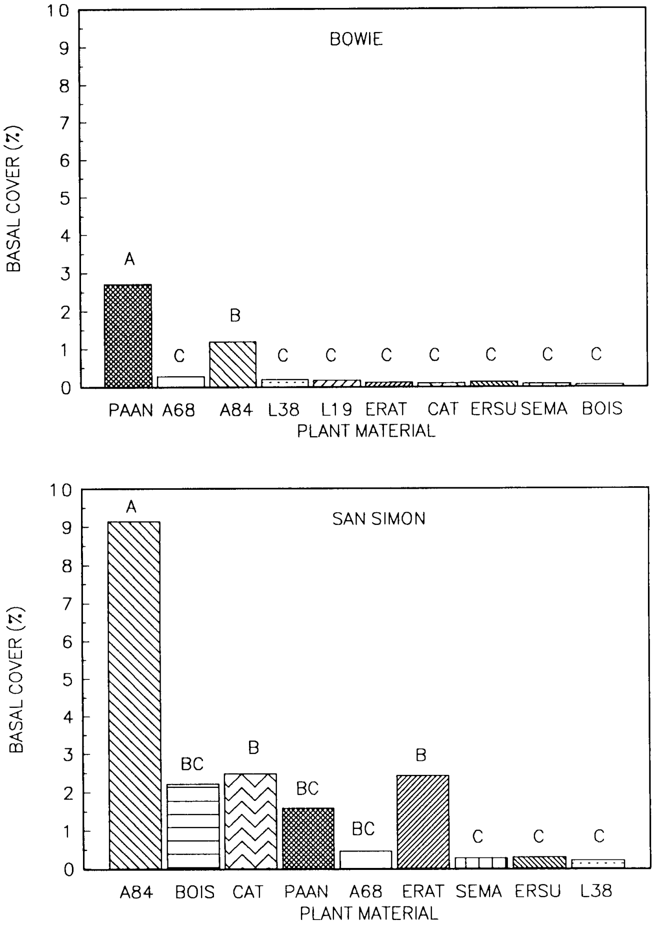

Figure 7—Mean basal cover in 1984 of warm-season grasses sown during 1969-1972 near Bowie and San Simon, Arizona. Species names for symbols are in Table 2. Species are ordered from highest to lowest mean rank (left to right) over the 4 seeding years. Similar letters above bars indicate no significant difference ($P \leq 0.05$).

- Native grasses are more difficult to establish on these sites than exotic grasses, but some natives might persist better than exotics on certain sites;
- Conversion of semiarid and arid shrublands back to grasslands is difficult.

Perhaps we should consider revegetation with desirable shrubs to control erosion and provide forage on these lands. At any rate, we should remember and honor Gilbert L. Jordan for conducting one of the most extensive and intensive revegetation research projects in the West.

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Restoring Mojave Desert Farmland with Native Shrubs

Robert D. Slayback
Walter A. Bunter
L. Robert Dean

Abstract—This 2,500 acre project on abandoned farmland in the Antelope Valley, Los Angeles County, was instigated by the February 1991 severe dust storms and hazardous conditions in Lancaster, Palmdale, Rosamond and nearby Edwards Air Force Base. The project administered by the USDA, Soil Conservation Service and promoted by the local Dust Busters Task Force was completed in late May, 1992. 'Seco' barley and furrowing provided initial erosion control and greatly reduced the dust blowing from the project area. California buckwheat was the most successful shrub with fourwing saltbush and desert saltbush almost equal in stand. California poppy provided a splash of color the first year. Aerial seeding during windy weather affected the proper distribution of the seed.

Wind blown dust has been a serious problem in the Antelope Valley of eastern Los Angeles County, California, for many years. The February 1991 severe dust storms caused damage, poor air quality and hazardous driving conditions in the Lancaster, Palmdale, Rosamond and nearby Edwards Air Force Base areas and brought the efforts of a local group into focus. This local group called the "Dustbusters Task Force" was spearheaded by the Antelope Valley Resource Conservation District. They are composed of Federal, State, County and local government agencies, civic organizations and private citizens. One of their prime concerns has been the wind blown dust from abandoned farmland, especially upwind from the more populated areas. This condition was aggravated by five years of drought. Farms have been abandoned due to the lowering of water tables and the higher cost of irrigation water.

After the February 1991 storms, it was decided to apply for assistance through the Emergency Watershed Protection (EWP) program administered by the U.S. Department of Agriculture, Soil Conservation Service. An aerial survey by the Los Angeles County Fire Department showed about 4,800 hectares (12,000 acres) needing treatment upwind from the above populated areas. It was decided to treat about 1,000 hectares (2,500 acres) that were more severely denuded and prone to severe wind erosion. One area was adjacent to Antelope acres, a rural housing development. Rainfall averages 17.5 to 25 centimeters (7 to 10 inches) and occurs during the fall-winter season. Soils were identified as Hesparia sandy loam and Rosamond fine sandy loam, sandy loam, loamy fine sand, loamy sand, and loam. They are very erosive and very droughty, which presents problems in revegetation with natural rainfall. This was the first time EWP funding was used to reduce wind erosion.

Methods

Effective methods to treat this denuded and erosive farmland to control wind erosion have not been tried due to cost and non-use of the land. After discussing farming problems with the local people on the Dust Busters Task Force, it was decided that deep-furrowing and planting native, adapted species would be the best short- and long-term solution to reducing the severe wind erosion. A sand fence would also be installed along a major roadway and next to a housing development.

Preparation

To prepare the land for furrowing, islands of Russian thistle (*Salsola tragus*) were gathered and burned or burned in place and the area smoothed with graders. Underground irrigation pipelines were not disturbed unless they would interfere with the ripping and furrowing operations. It was decided to furrow, rip and plant in one operation in order to eliminate further breakdown of the soil structure and to lower the cost of operations. Ripping was done to a minimum depth of 30 centimeters (12 inches) with rippers spaced not less than 60 centimeters (24 inches) nor more than 100 centimeters (40 inches) apart.

Furrowing and Drilling

All furrows were constructed with a minimum depth of 20 centimeters (8 inches) below the mean natural grade. Spacing between furrows was 87.5 centimeters (35 inches) to 100 centimeters (40 inches).

'Seco' and 'Arivat' barley (*Hordeum vulgare*) and Indian ricegrass (*Oryzopsis hymenoides*) were drilled into the bottom of each of the furrows at about 2.5 centimeters (1 inch) deep. Drilling was done in the same pass with the furrowing. The barley was planted at 11.4 kilograms per hectare (10 pounds per acre) and the Indian ricegrass was

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drilled 2.42 kilograms per hectare (2.2 pounds per acre). The furrowing and drilling started in early February 1992 and was completed at the end of March 1992.

Aerial Seeding

The Los Angeles County Fire Department applied the following species with a helicopter and suspended bucket seeder:

Species	Application Rates
Fourwing saltbush (*Atriplex canescens*)	6.4 kg/ha (5.8 lbs/acre)
Desert saltbush (*Atriplex polycarpa*)	6.1 kg/ha (5.5 lbs/acre)
California buckwheat (*Eriogonum fasciculatum*)	4.9 kg/ha (4.4 lbs/acre)
California poppy (*Eschscholzia californica*)	0.8 kg/ha (0.7 lbs/acre)

Aerial seeding was started in late February 1992 and completed in late May 1992. The wind blew most days that were scheduled for aerial seeding. Seeding was halted when winds reached 16 kilometers per hour (10 miles per hour). Light winds affected the proper distribution of seed on the ground.

Sand Fencing

A double-row, four-foot sand fence was installed along Avenue 110 West. Two double rows were installed upwind of the Antelope Acres housing development. Green, high density polyethylene fabric was installed on six-foot steel posts with three ties per post. Spacing between fence rows was 9.1-meters (30 feet) and posts were installed 1.7 meters (6 feet) apart. Due to the potential of the desert tortoise occurring in the area, 1.7-meter-(6 foot) wide-angled openings in the fence were installed every 60.6 meters (200 feet). Sand fencing was completed in late May, 1992.

Results

Overall, the furrowing and planting operations were very successful in reducing the blowing dust and the wind erosion on this 2,500-acre project area. Because Russian thistle seed was resident in the planted area, it also took advantage of the excellent seedbed and moisture conditions and produced scattered to heavy stands over the project area. This severe competition from the thistle reduced overall stands of the forb and shrub species. The only planted species not affected by the thistle was the barley, which provided good initial wind erosion cover. Rodents were probably the next serious deterrent in establishing the forb, grass and shrub species. They did major damage to the barley and California buckwheat plants, which they seemed to prefer. Two years of above average rainfall in the area have provided the excellent establishment and growing conditions for the seeded plants. There were scattered areas that were devoid of any vegetation including Russian thistle, which was probably due to soil extremes such as loamy sand or gravelly sandy loam. The deposition of blowing soil on the upwind outer edges of the project could have buried the seed too deep and resulted in poor to no stands of planted species.

Evaluations were made on June 23, 1992, November 24-25, 1992, April 13, 1993 and September 21, 1993.

Barley

Due to its fast germination and initial establishment, this was the most successful species planted. Drilling seed into the bottom of the furrow provided good growing conditions and initial germination was excellent. Two varieties, ‘Seco’ and ‘Arivat’, were planted due to a short supply of ‘Seco’ barley. ‘Seco’ was superior in providing more growth and seed production. However, the rodents liked the barley and seed and grazed some areas down to the ground. Some volunteer reseeding was evident the second season, but very scattered. Where rodent activity was very heavy, there was little reseeding. One area south of Avenue C looked like a planted field with plants up to 0.6 meters (2 feet) tall with mature seed. No Russian thistle or other planted species were identified in this volunteer stand of ‘Seco’ barley. The main reason to plant barley, a non-native, was to give a fast, initial cover to aid in the reduction of wind erosion and establishment of the native shrub species. It was very successful in this aspect.

California Buckwheat

Next to barley, this was the most successful species over the total seeded area of 2,500 acres. It was also preferred by the rodents that grazed it severely. In a walking transect over the northeast and southeast sections of the large planting area north of Highway 138 on April 14, 1993, California buckwheat showed about 5.3 plants per square meter (0.5 plants per square foot) with an average height of 14 centimeters (5.6 inches). More new plants were identified in the bottom of the furrows, especially where barley had not reseeded. In reviewing the areas containing droughty phases of Rosamond and Hesparia soils, very few plants were identified. Barley was about the only planted species found in these droughty soils.

Fourwing Saltbush

On September 21, 1993, 2-year old plants were up to 1.5 meters (60 inches) high, while first-year seedlings were 10-20 centimeters (4-8 inches). As with the California buckwheat, there were many new plants down in the furrows. Initial germination was on top of the furrows. This species along with desert saltbush showed very spotty stands, which could have been due to the seed dispersal caused by wind conditions at time of aerial seeding. Fourwing seemed to prefer the better soils having higher moisture content.

Desert Saltbush

This shrub was better adapted to the droughty phases of the soils and sometimes was the only seeded plant found under the heavy stands of Russian thistle. The rodents did graze this plant, but only slightly. Stands seem to be very scattered, which could have been due to the lower seed germination and the seed dispersal problem in aerial seeding. However, some stands of the four-wing and desert saltbushes were good to excellent, which again points to the application success.

California Poppy

Scattered stands of poppy came on early and displayed colorful bands of gold. By November 24, 1992, most plants had winter-killed, but some mature seed had been produced. Second-year stands of poppy were not quite as good due to higher competition from seeded species and Russian thistle. Again, the aerial seeding of this species provided uneven distribution and scattered stands.

Indian Ricegrass

Initially, only a few scattered plants were identified in the bottom of the furrows. More plants continue to show up from this highly dormant seed. Plants ranged from 15 to 45 centimeters (6 to 18 inches) high with larger plants showing mature seed heads. This plant was the only one found in the area where the furrows had filled in from blowing soil. This species is well adapted to these sandy soils and can germinate from deeper depths. It will be interesting to follow the progress of this plant.

Sand Fencing

The double-row sand fence seemed to be very effective in collecting the wind-blown Russian thistles and an average of one foot of soil on the windward side. Thistles had completely filled the area between the fences and the Desert tortoise openings. On April 14, 1993, several ties had broken loose and portions of the fence were flapping in the wind. Ninety feet of fence along Avenue 100 West had been removed which eliminated the buildup of Russian thistle on each side of the fencing. Overall, it looks like the fence reduced the wind erosion hazard from Avenue 100 West and the housing development at Antelope Acres. Seedings between the fences showed poor establishment due to the heavy concentrations of Russian thistles, either growing or blown there. At the end of two seasons, this polyethylene fabric has stretched from the weight of thistles and in several areas has broken loose from original ties.

Conclusions

Revegetation of abandoned farmland in the Mojave Desert can be accomplished with proven cultural techniques and conservation and native plant materials. Antelope Valley is an area of low rainfall and two seasons of above precipitation provided good moisture conditions for establishing the grass, forb and shrub species. In the past, we have had poor results in coming up with feasible methods in reducing wind erosion on these types of soils. The cost of this project exceeded $750 per hectare ($300 per acre), but we know now it would have been cheaper to apply all the seed with ground equipment. Aerial seeding is usually more economical on large acreages, but with the light and fluffy seed being applied, the prevailing winds prevented an even distribution of seed and adequate stands of seeded species in some areas. The species applied aerially could have been applied in the same operation with the drilling of barley and Indian ricegrass.

Barley was very effective in providing initial wind erosion control, except where the soils were extremely sandy and plants were covered up by the blowing soils. Even though the area received a lot of rodent depredation, most of the shrub species were established in varying stands. California buckwheat was the most successful species to be seeded on the total area. Fourwing and desert saltbushes were almost equal in establishment, with fourwing saltbush preferring the heavier soils and desert saltbush doing well on the drier soils. If a splash of color is needed, California poppy provides this, but the species fades out when competition becomes severe. Ultimate stands of the native grass and shrubs will show this method is feasible to revegetate these prior farmlands to a remnant of native plants.

The native shrub seed used on this project was provided from several seed companies that collected seed from similar growth regions, but was not too specific in vegetative type, which was not required. In a large planting such as this, large amounts of desired species are hard to locate and seed from similar areas is usually acquired. Geneticists have stated this is not the proper method in restoring natives to an area such as this, but that erosion control plants be planted until a native source of seeds are collected or grown.

The double-row sand fence provided good initial protection to a major road and a portion of the Antelope Acres housing development. Desert tortoise openings in the fence became clogged with Russian thistle and were not very functional after that time.

This project was financed mainly by Emergency Watershed Protection funds and cosponsored by the Los Angeles County Fire Department. It was successful in reducing wind erosion on highly erodible soils in the Antelope Valley. Revegetation and restoration of these abandoned farmlands will alleviate the serious health and vehicle hazard problems in the area. This work has stimulated the development of a 3-5 year study that will include research and demonstration projects. These projects will provide effective best management practices for abandoned farmland in Antelope Valley and other similar arid regions.

Ecosystem Restoration: Theory, Practice, and Evidence

Wayne Tyson

Abstract—"Garbage in, garbage out," applies to almost everything but ecosystem restoration. Nature is so forgiving that on all but the worst sites, regardless of the quality of the theoretical foundation, the hyperbole, and the practice applied, something is bound to happen eventually.

Another dictum, "gold in, garbage out" does apply, however. Elaborate and expensive programs do not guarantee performance. We are tempted to take full credit when Nature compensates for our inadequacies and blame her whenever performance fails to meet expectations. Sound theory, integrity in practice, and evidence in proof of previously predicted performance (feasibility) can, like a good cutting horse, ultimately improve the stock of theory, practice, and performance.

Given a sound theoretical foundation and corresponding practice, ecosystem restoration should be a snap. Why, then, are there so many failures and disappointments? What distinguishes sound from flawed theory, good practice from poor, successful from unsuccessful ecosystem restoration?

A sculptor, asked how he was able to create such fine works, once said, "I just cut away the ugly part." If theory, practice, and evidence of performance are parts of a feedback continuum, the first step in improving results is to identify the ugly parts, the flaws, over which we have some control. Flaws in theory feed flaws in practice which produce disappointing results.

Flaws in performance or in our interpretation of evidence can be due to poor theory and practice, but also to unrealistic expectations, as in mitigation requirements. So a realistic determination of what is feasible must be part of the picture. Wishing—demanding a specific level of performance not supported by the capabilities and limitations of the site and technology—creates an illusion of failure. Conversely, failing to demand what is feasible allows flawed performance to masquerade as successful.

If we are to reduce the number of failures and disappointments in ecosystem restoration, we must find a practical course toward betterment. Working with the wrong paradigm will not achieve this. Therefore, a paradigm-shift will be needed.

Evidence—Successful Ecosystem Restoration Defined

Before we can grapple with these issues, we need a definition of a restored ecosystem. Better men than I have proposed a pretty good one. St. John (1989) has modified Ewel's (1987) criteria, and I really can't improve upon these efforts. Ewel and St. John define what a restored ecosystem is, and in so doing, establish the criteria for evaluating evidence which can be used to judge the validity of the theory and practice employed on any one project.

I will quote or paraphrase from St. John (1989), who quotes Ewel (1987) and adds his own comment. Ewel suggests that sustainability, low invasibility, productivity, nutrient retention, and biotic interactions define a successful restoration project ecosystem.

Sustainability

Ewel and St. John agree that the restored community must be capable of perpetuating itself without outside subsidy. For example, a restored ecosystem must not require fertilizer or irrigation.

Resistance to Invasion

Ewel concluded that because natural communities make complete use of resources, they resist invasion by alien species. "While some [alien] invasion always occurs," St. John points out, "especially following…disturbance…the community should progress toward reduced invasibility with time."

Productivity

Ewel considers the rate of production of biomass per unit time to be an integrating measure of several important ecosystem processes. St. John agrees with him that the restored community should equal the pre-disturbance community in productivity; he points out that allowances will have to be made for stage of development and for species composition.

I would add that productivity cannot exceed the productive potential of the restored site. If productivity is to be related solely to the pre-disturbance community, a restored community may be capable of more or less productivity than the original site (pre-disturbance or comparable site).

Nutrient Retention

Ewel states that the conservation of nutrients is relatively greater in natural than disturbed communities. St. John cites the difficulty and expense of direct methods of measurement, but describes indirect techniques that are more feasible.

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Biotic Interactions

Ewel says that the entire range of critical biological components should be in evidence, emphasizing pollinators and symbionts.

This five-point approach is a means of providing ample evidence of ecosystem health, and St. John has pointed out that circumstances can alter cases. The complete restoration of any disturbed ecosystem takes time.

Completeness, at least in the near term, may not be as large an issue in restoration as many consider it to be. The initial reintroduction of those species which are able to maintain viable populations under site conditions as modified according to sound restoration theory may be sufficient—particularly if species diversity and productivity increase over time to a level approaching (sometimes exceeding) that of the pre-disturbance or comparable (example) habitat.

Function may be a more valid measure, since part of restoration planning consists of creating conditions by use of some organisms to produce habitat in the future for species for which suitable habitat does not yet exist. If that function is present under the applicable conditions of Ewel, normally the remaining conditions can be anticipated.

The degree to which a restored ecosystem resembles the pre-disturbance or exemplar system is a gross measure of its validity. But just as the constituents of undisturbed ecosystems vary, so do restored ecosystems, as do disturbed ecosystems which are not actively restored, from Mt. St. Helens to "old fields" of various kinds. Restoration may be more the management for acceleration of a powerful, inexorable process of nature than it is an expression of the creative genius of mankind. It may be that simply being on that acceleration curve is sufficient.

There is a continuum from very slow to very rapid post-disturbance recovery of damaged ecosystems, from years to centuries to millennia, depending upon whether we are thinking of the oil fields of Kuwait or a rich bottom-land post-flood environment—of whether the disturbance was total or slight, the site potential great or minimal.

Through simple logic, concluding that if results are consistently good the theory that drove the practice and the practice itself must be good, we can evaluate the validity of theory and practice. Similarly, we can conclude that theory and/or practice may have flaws if restoration projects founded on them are consistently flawed.

The concept of consistency is important. Anybody can be lucky or unlucky, more or less, fifty percent of the time. One could have an isolated, sterile site in a tough environment with a low budget, an indifferent client, and an uncooperative contractor. Or one could have good site conditions with excellent natural recruitment, a favorable weather pattern, a reasonable budget, and an enthusiastic contractor.

Theory and Practice

Theory and practice need not, and probably should not, be judged entirely upon direct empirical evidence. Theoretical foundations for theoretical structures and practices can be evaluated by disciplined logic in an atmosphere of intellectual integrity. The problem is that such conditions are difficult to achieve, particularly in a highly competitive academic environment. People despise boring detail; they like pictures.

Figure 1—A 1 1/2:1 road cut restored using a low-cost but technically adequate concept.

In Figure 1, a 1 1/2:1 road cut is shown, just after treatment according to "Restoration Theory A."

Figure 2 shows (photo is taken from a different position; use the tall pine tree and houses on the horizon for reference) the Theory A project site ten years later, just prior to re-grading and re-treatment according to "Restoration Theory B."

Figure 3 shows the same site ten years after treatment according to "Restoration Theory B."

Theory A was a low-cost but technically adequate concept which relied upon site modification and no irrigation or maintenance; Theory B employed a more costly, fairly standard hydraulically applied seed and fiber mulch, irrigation, and maintenance.

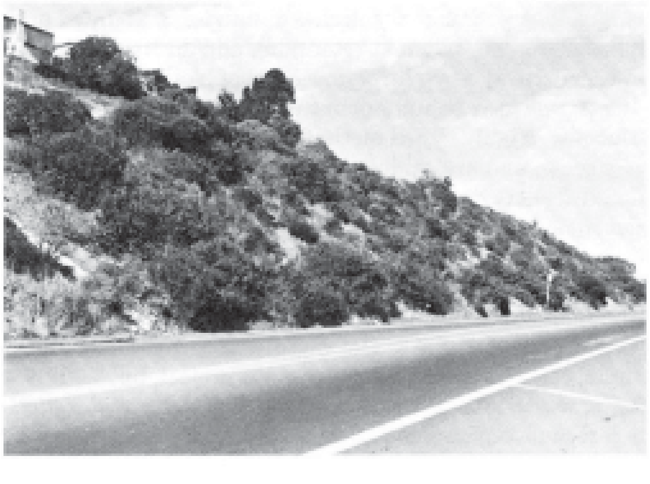

Figure 2—The same road cut 10 years later. The perspective of this picture differs from Figure 1. Use the tall pine tree and the houses on the horizon for reference.

Figure 3—The same road cut 10 years after a more expensive, more complicated, but less successful attempt at restoration.

Pictures don't tell everything, but in this case they tell quite a bit. Theory A produced a sequence of actions more or less consistent with what might be called "Theory A Practices." The result was not an exact duplication of the site's original vegetation, but a functional ecosystem comparable to the original was achieved immediately (this could not be validated for about three years, however). It was self-sustaining throughout the ten years of its existence, and still declining in invasibility, maintaining (subject to fluctuations in productive capacity) the level of productivity it reached after about five years, retaining nutrients, and increasing in diversity when it was re-graded and replaced by the "Theory B" restoration project.

Theory B produced a similarly consistent sequence of actions which, however, did not result in a functional ecosystem comparable to the original. An illusion of success was maintained until the irrigation system and maintenance program were phased out, but the artificially maintained vegetation quickly declined (no sustainability), the site remains dominated by alien species (little resistance to invasion), productivity declined, nutrients declined and remain low (poor nutrient retention), and diversity declined and remains at a low level (low level of biotic interaction).

This case may be unique but it illustrates a universal principle. Highly hyped methodologies are not always what they seem, and are seldom equally valid in all situations. Money doesn't guarantee success. Sound habitat restoration theory can work where highly hyped methodologies don't.

If the evidence is good, one can take credit; if bad, one can blame the Ides of March or other "slings and arrows of outrageous fortune." The vagaries of weather, for example, can be deadly to a restoration project, but within limits, weather is part of the context in which a restoration project must be designed to work. Although weather can't be predicted, climate can be understood and considered as the context in which the restoration project must function.

Each site has a potential, difficult to delineate precisely but simple enough to get a rough handle on, that can be called its productive capacity. Productive capacity also eludes precise description, but it can be determined within useful boundaries.

This "fuzzy" logic is a difficult pill for most scientists to swallow, because they have been trained to adore precision. But nature is sloppy. This infatuation with precision in dealing with a very ragged process may be at the root of many of our troubles. To compound the confusion, every factor in this equation is in a constant state of flux. Is it wise to attempt to describe, much less deal with, such a squishy and "unreliable" process using a system of thought tightly bounded by several decimal places of precision?

The other factor in this "maybe"-ridden equation is what we might call technical feasibility—that is, given the site and environmental, not to mention political, social, and psychological conditions of each project—what are the boundaries of what can be done? You guessed it, the boundaries of technical feasibility also elude precise definition, but they at least can be determined within useful limits.

The purpose of getting this rough handle on this jiggly process is to define our ignorance. This is what is known as "brilliance." It may be the soul of genius. It seems like a playful paradox, but lack of concern with his or her own brilliance has characterized every "genius" I have known or read about, and every "ordinary" person who has done extraordinary things. It's like Chinese handcuffs—the more you struggle, the more tightly you are held. To know, you must let go, relax. This is a tall order for most people of "western" cultures, but it came quite naturally to my native American ancestors and many eastern cultures.

In a very broad sense, ecosystem restoration may best be described as re-setting basic conditions so that natural systems can recover lost or interrupted functions faster. The world or regional subset ecosystems will eventually restore some kind of biological complex to any disturbed site, but it may take centuries or millennia. When we do finally grasp the importance of understanding our ignorance, we may come at last to the conclusion that it would have been far cheaper to leave it alone in the first place.

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Water Requirements for Establishing Native *Atriplex* Species During Summer in Southern Arizona

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Abstract—Germination and establishment characteristics of 11 perennial *Atriplex* accessions belonging to four species were determined during the summer of 1992 and 1993 under field conditions in southern Arizona. Meteorological, soil moisture, soil temperature, irrigation and plant performance data of seedlings or transplants were used to estimate water requirements for establishment under a line-source sprinkler irrigation gradient system. Under natural rainfall conditions during the summer, establishment of plants by transplanting was greater than that by direct seeding. Transplant survival varied within and among species and was generally lower in *A. linearis*, which was heavily grazed by rabbits. Germination and emergence of plants were greater at the highest irrigation level than under natural rainfall conditions. Supplemental irrigation increased the probability of seedling establishment both years.

Disturbed desert plant communities can be improved by reseeding forage-producing and soil-stabilizing grasses, forbs, shrubs or trees that are adapted to the environmental conditions of the area (Roundy and Call, 1988). Vegetation recovery on direct-seeded disturbed lands depends largely on the amount and seasonal distribution of precipitation during the period when temperatures are favorable for germination and establishment. Since soil moisture availability during establishment is a primary factor determining the success of plantings in arid and semiarid lands, revegetation projects have focused on the use of water catchment and mulching methods, and of supplemental irrigations. Jackson and others (1992) evaluated the establishment of perennial shrubs on disturbed lands in the lower Sonoran Desert that had shown no signs of natural recovery. They were able to establish *Atriplex polycarpa* and *A. canescens* on abandoned farmland in central Arizona under average to above-average winter rainfall by using organic mulches and water catchment methods. Supplemental irrigation has been a promising tool in revegetation of mine sites (Ries and Day, 1978) and of non-mine sites, such as abandoned farmlands. Thacker and Cox (1992) recommended that for the arid conditions in southern Arizona, a permanent vegetative cover be established on farmland before farmland is retired to take advantage of existing irrigation systems.

The line-source sprinkler irrigation gradient system (LSSIGS) has been utilized extensively to evaluate the effects of variable water deficits on crop plants and to screen cool-season grass and legume genotypes for responses to different levels of moisture stress under field or greenhouse conditions (Hanks and others, 1976; Johnson and others, 1982; Rumbaugh and others, 1984; Asay and Johnson, 1990; Johnson and others, 1990). This irrigation technology is designed to give uniform application at the same distance along the line-source and decreasing application with increased distance from the irrigation line. The LSSIGS has been mostly used to study post-establishment plant responses and has not yet been extended to measure water requirements during seedling establishment of desert-adapted plants.

The use of *Atriplex* shrub transplants may facilitate revegetation of rangelands where seed germination and seedling establishment may be low and in critical areas (Springfield, 1970; Aldon, 1972; Van Epps and McKell, 1980; McKell, 1986; Roundy and Call, 1988). In many instances, transplanting adapted shrubs may be the only viable revegetation strategy. Although the use of container-grown transplants provides more flexibility in timing of planting, supplemental water may be required to ensure survival. Aldon (1972) indicated that soil moisture availability after planting was a factor in successfully establishing *A. canescens* transplants.

Direct-seeding would generally be more economical in establishing perennial shrubs than using transplants. Studies have shown that the optimum temperature for germination and establishment of *Atriplex* shrubs native to the western United States is at relatively low temperatures and that high temperatures frequently suppress germination and survival. Although optimum germination temperatures may vary both among and within species (Mikhiel and others, 1992), the temperatures most favorable for germination of *A. lentiformis*, *A. polycarpa* and *A. canescens* range from 10 to 25 °C, 9 to 15 °C, and 13 to 24 °C, respectively (Cornelius and Hylton, 1969; Springfield, 1969; Sankary and Barbour, 1972; Young and others, 1980; Potter

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and others, 1986). In general, the best time for native *Atriplex* seedling establishment appears to correspond to the cooler winter periods in the southwestern and western U.S. arid and semiarid lands (Wilson, 1928; Parker and McGinnies, 1940; Cornelius and Hylton, 1969; Sankary and Barbour, 1972; Thacker and Cox, 1992; Munda, 1993).

Tucson, Arizona has a bimodal rainfall pattern which provides the opportunity to evaluate establishment under both summer and winter rainfall patterns. In the summer of 1992, field studies were initiated to measure water requirements for establishment and survival of desert-adapted grass, shrub, and tree species that were direct-seeded. Because high soil temperatures associated with summer conditions are potentially unfavorable for establishing *Atriplex* from direct seeding, transplants were evaluated as an alternate method of establishment. The main objectives of the summer field studies were to: 1) evaluate direct seeding and transplanting methods for establishing plants under a LSSIGS and, 2) utilize meteorological, soil temperature and moisture levels, irrigation amounts and plant performance data to determine water requirements for successful establishment.

Methods and Materials

Site Description and Plant Sources

The 1992 and 1993 summer experiments were conducted at the USDA-SCS Tucson Plant Materials Center (TPMC), Tucson, AZ. The soil was an Anthony sandy loam (coarse-loamy, mixed, calcareous, thermic typic Torrifluvent). For both years, the soil profile was wet from either natural rainfall or from supplemental irrigations prior to planting.

Grass, tree and shrub species were planted perpendicular to a line-source sprinkler into field plots with rows 16.5 m long spaced 41 cm apart. Plots were replicated six times, three on each side of the irrigation pipe. Six water application levels were designated within the 16.5 m distance from the irrigation line, with one level receiving only natural rainfall. The amount of water applied at each irrigation was measured with catch cans placed at 1.5, 4.5, 7.5, 13.5 and 16.5 m from the line-source sprinkler. An electronic weather station was installed to record windspeed, temperature, solar radiation, relative humidity and precipitation.

In three replicates, soil moisture and temperature sensors were buried at five depths (1-3, 8-10, 18-20, 38-40 and 58-60 cm below soil surface) and at four distances (1.5, 6, 10.5, 16.5 m) from the irrigation line. Soil temperatures were measured with thermocouples; gypsum blocks were used to measure soil water tension. Hourly averages of soil water tension and temperature, air temperature, relative humidity, total and net radiation and windspeed were recorded with Campbell CR-10 microloggers.

Species that were evaluated either as direct-seeded plants or as transplants are listed in Table 1. The three direct-seeded species and one of the transplant sources were cultivars or collections maintained at Tucson Plant Materials Center (TPMC). The remaining sources were from seed collections made during the fall and winter of 1992 and 1993 from populations in central and southern Arizona, and coastal northern Mexico. The subspecies classification of *A. canescens* accessions were based on descriptions and site information provided by S. Sanderson and H. Stutz (USDA, Shrub Lab and Brigham Young Univ., Provo, UT).

Direct Seeding

Germination was counted in four replicates of 25 seeds each placed on filter paper in petri dishes in a Conviron incubator under a gradual diurnal fluctuating temperature regime from 20 to 40 °C. Bulk seeding rates were based on mean percent purity, seed germination percentage and individual seed weight for each seed lot. A seeding rate of 33 pure live seed (pls) per meter was used for the direct-seeding trials when germination percentages were greater than 50%. Seeding rates were adjusted to 66 pls/m and a germination percentage of 10% was used to calculate bulk seeding rates when actual germination was <10%. Seed was sown using a Kincaid No-Till Plot drill at a depth of 1.3 cm on 14 July in 1992 and 20 July in 1993. Irrigation water was applied daily for 9 to 11 successive days to maintain high soil moisture in the upper 3 cm of the soil profile nearest the irrigation line. After initial seedling emergence, irrigation water applications

Table 1—*Atriplex* accessions evaluated under the line-source irrigation system during the summer of 1992 or 1993 at Tucson, Arizona.

Species	Subspecies/ cultivar	Collection locality/source
A. linearis	—	Toltec, AZ
A. linearis	—	Tucson, AZ
A. linearis	—	Puerto Penasco, MX
A. canescens	*angustifolia*	Tucson, AZ
A. canescens	*grandidentatum*	Puerto Penasco, MX
A. canescens	*occidentalis*	Willcox, AZ
A. canescens	cv. Santa Rita	Tucson Plant Materials Center, AZ
A. polycarpa	—	Tucson, AZ
A. polycarpa	—	Casa Grande, AZ
A. polycarpa	—	Tucson Plant Materials Center, AZ
A. lentiformis	cv. Playa	Tucson Plant Materials Center, AZ

were scheduled according to evapotranspiration data obtained from a AZMET weather station located approximately 3 km from the experimental site. Irrigations were then adjusted to maintain the mean cumulative catchment of water at the 1.5 to 4.5 m line source distance approximately equal to 75% of the cumulative reference evapotranspiration. Irrigation was conducted in the early morning to minimize wind interference.

Over a period of 3 months, seedling plant counts (plants per linear meter) were recorded at five to seven dates and at six distances from the line-source sprinkler (1.5-2.5, 4.5-5.5, 6.0-7.0, 7.5-8.5, 10.5-11.5, and 13.5-16.5 m). Within 28 days after sowing seed in 1993, the field planting was fenced to exclude rabbits.

Transplants

Seedlings were started under greenhouse conditions and juveniles were hardened-off in a lath-house for 2 weeks and cut back to approximately 18 cm height prior to transplanting. Transplants were of 3 months and 5 months of age for the 1992 and 1993 planting dates, respectively. In both years, spacing of the transplants within rows was 76 cm. Transplants were planted during the first 10 days of August, the root ball being placed within a 10 cm (1993) or 20 cm (1992) depth. The 1992 trial contained four rows of each accession in each plot and the 1993 trial contained one row of each accession per plot.

Transplant survival was determined approximately every 20 days until the end of November by counting the number of live plants in each row. Survival and persistence of the 1992-established plants that had received no supplemental irrigation over the winter season were evaluated at the beginning of the 1993 summer season. In the 1993 planting, mortalities were classified as being caused by rabbit predation, as determined by less than 2.5 cm of plant remaining above the soil line, or being due to natural causes, when plants were greater than 15 cm tall at time of death. Survival percentage data were arc sine transformed prior to analysis of variance.

Results and Discussion

Climatic Data and Irrigation Amounts

In both summers, mean air temperatures during the first month averaged 30 °C for the direct-seed planting and 29 °C for the transplants (Fig. 1). In 1993, most of the precipitation occurred within 40 days after seeding, while in 1992 most of the precipitation fell within a 25 day period after seeding. Total rainfall for the first 80 days after irrigation during 1993 (76.9 mm) was slightly less than that of 1992 (85.1 mm). In both summers, rain fell within 1 day after transplanting and was followed by a series of storms that essentially kept the soil profile wet.

The quantity of irrigation water applied was generally higher in 1992 than in 1993 (Fig. 2). During the 1992 and 1993 seasons, there were a total of 16 or 11 irrigation events, respectively, during the first 32 days after direct seeding. Transplants received two irrigations after planting in 1992 and no supplemental water in 1993.

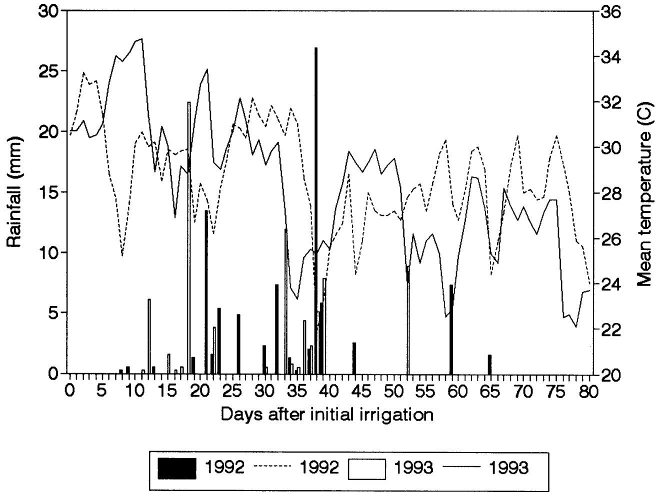

Figure 1—Daily rainfall (bars) mean daily air temperature (lines) for 80 days after commencement of line-source irrigation for direct seeding and transplant trials of *Atriplex* species at Tucson, Arizona.

Direct Seeding

Laboratory seed germination of *A. canescens*, *A. polycarpa* and *A. lentiformis* was 0%, 0 to 4% and 7 to 53% for the 1992 and 1993 trials, respectively.

Between the 1.5 to 10.5 m line-source distance, species plant counts 23 or 24 days after seeding were generally less than 1 plant per meter (Fig. 3). During the study period, none of the direct-seeded accessions became established with only natural precipitation. In general, seed germination and emergence of plants were greater at the highest irrigation level than under natural rainfall conditions. Direct-seeded plants established in 1992 survived the mild wet winter and persisted through the first year.

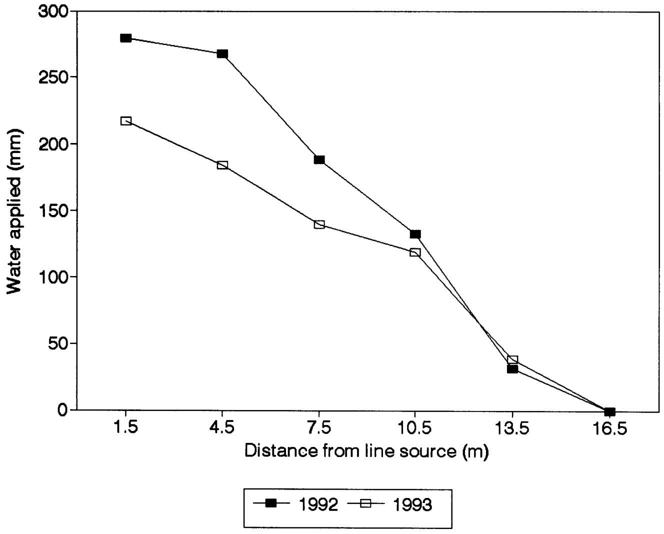

Figure 2—Total irrigation water applied at different distances from a line-source sprinkler during summer 1992 and 1993 revegetation trials of *Atriplex* species at Tucson, Arizona.

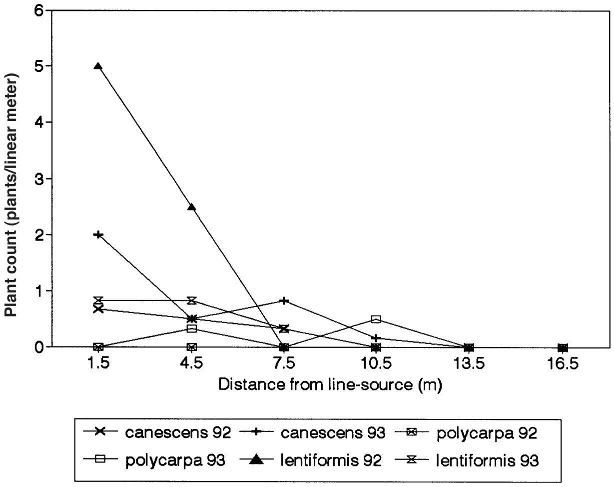

Figure 3—Plant counts of three *Atriplex* species at six distances from a line-source sprinkler 23 days after initial irrigation during the summers of 1992 and 24 days after initial irrigation during 1993 at Tucson, Arizona.

For the first 13 days (1993) and 21 days (1992) after seeding, soil moisture availability was high at all distances from the line-source sprinkler except for the non-irrigated area (Fig. 4). After the initial dry period, all positions had generally similar patterns of soil moisture availability as a result of continued storms. Between rainstorms, there were brief drying-out periods resulting in relatively high (greater than 0.3 MPa) soil water tensions, especially in 1993. After the initial dry period, soil moisture tensions were less than 0.4 MPa for at least 16 days in the non-irrigated area, but no germination occurred. Results of these studies indicate that except for an initial dry period, soil moisture levels were generally adequate for seed germination in the non-irrigated area. However, soil water tension at the depth of seeds may have been greater than that at the sensor depth of 1 to 3 cm as presented in Figure 4.

Until the rainy season began, daylight soil temperatures were 5 to 15 °C lower at the highest irrigation level (1.5 m) when compared to the non-irrigated area (Fig. 5). After a series of rainstorms, differences in temperatures between the two levels were not as extreme. Maximum germination rates for *A. canescens* occurred between –0.2 to –0.8 MPa

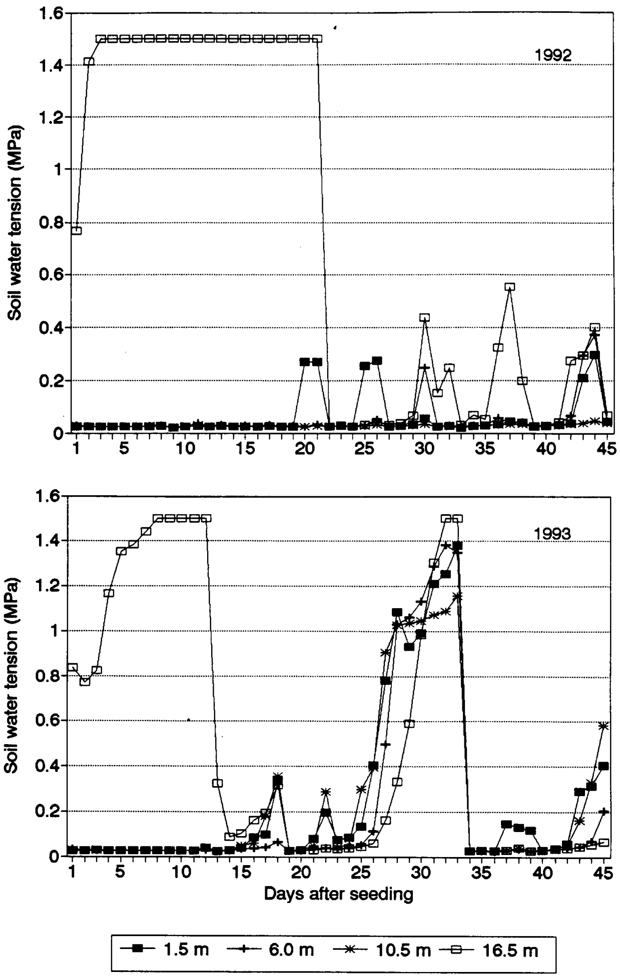

Figure 4—Soil water tensions (1-3 cm depth) at four distances from a line-source sprinkler after direct seeding *Atriplex* species during the summers of 1992 and 1993 at Tucson, Arizona.

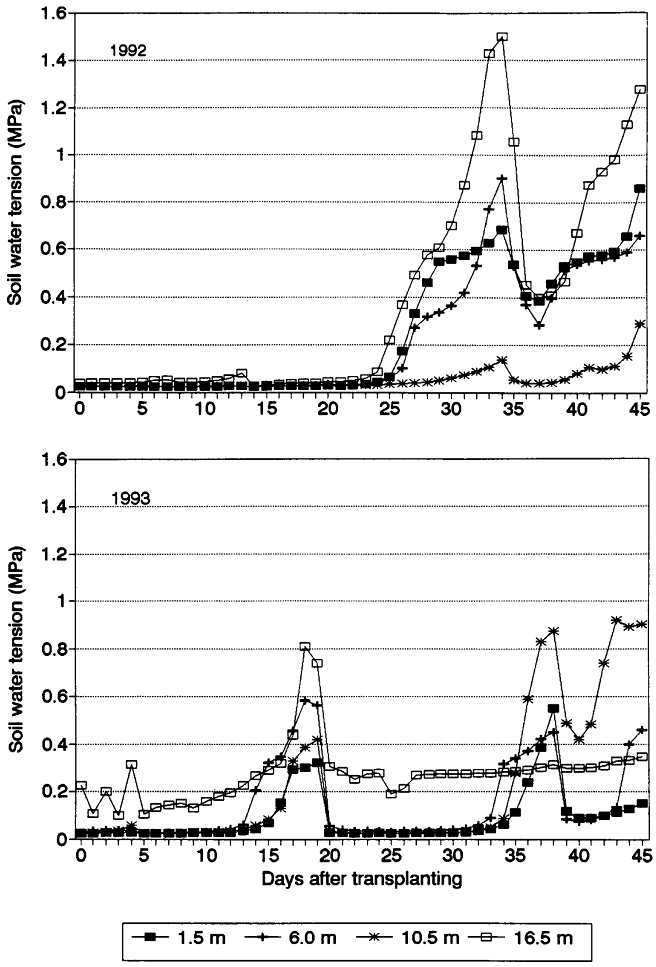

Figure 5—Soil water tensions (8-10 cm depth) at four distances from a line-source sprinkler after transplanting *Atriplex* species during the summers of 1992 and 1993 at Tucson, Arizona.

(Briede and McKell, 1992) and between –0.1 to –0.8 MPa osmotic potentials when temperatures were low (12-17 °C) (Potter and others, 1986). Springfield (1966) reported that limited water availability decreased and delayed germination of *A. canescens*, with an osmotic potential of –0.3 MPa being the effective limit for germination at high temperatures. In these studies, the relatively low plant counts in the irrigated areas and the absence of seedling establishment under natural rainfall conditions may have been caused by the combination of high soil temperature and low soil moisture availability.

Transplants

During 1992, irrigation applications after transplanting did not have an effect on survival since planting was followed by a series of rainstorms. Within 15 days after planting in 1992 and 1993, transplants had received 51 and 28 mm of rainfall, respectively, resulting in soil water tensions below 0.3 MPa (Fig. 6).

Aldon (1972) found that survival of *A. canescens* transplants was at least 80% when soil moisture tension was between 0.03 and 0.2 MPa. The recommended time for transplanting was when the probability for sizable summer thunderstorms exceeded 50%. Soil moisture conditions of this study were comparable to those suggested by Aldon (1972) for successful transplant survival. The occurrence of continued storms after transplanting allowed soil moisture to be relatively high during the first 15 days of establishment. In this study, the soil profile was wet at the time of transplanting. Transplant survival may have been much lower if the soil profile had been initially dry.

During both years, transplants became established with only natural rainfall (Table 2). Except for *A. linearis*, whose survival was generally low both years, survival rates were above 90%. During 1992, transplant survival was highest in *A. canescens* cv. Santa Rita compared to *A. linearis*, and by the next summer season, plant densities had not significantly declined. Most of the mortality in *A. linearis* accessions was due to rabbit predation, with the ecotype from Mexico being the most highly preferred. Although not monitored during 1992, it is likely that transplants of *A. linearis* were also affected by rabbit predation. Variations in the browsing preferences exhibited by rabbits to different collections of *A. canescens* have been reported (Nord

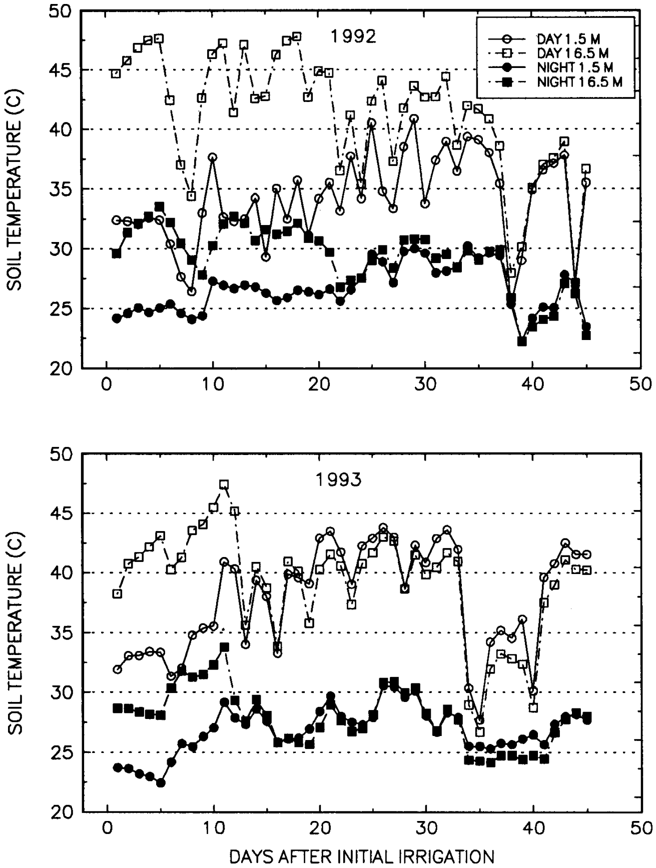

Figure 6—Soil temperature at 1 to 3 cm depth at 1.5 and 16.5 m from a line-source sprinkler during the summers of 1992 and 1993 at Tucson, Arizona.

Table 2—Transplant survival of *Atriplex* accessions on a sandy loam soil during summer of 1992 and 1993 at Tucson, Arizona.

Species	Subspecies/cultivar	Source	Survival (percent) Sept. 1992	June 1993	Sept. 1993	Rabbit predation % of mortalities
1992						
A. linearis	—	Mexico	74 a[1]	67 a	—	—
A. canescens	cv. Santa Rita	Tucson Plant Materials Center	93 b	88 b	—	—
1993						
A. linearis	—	Tucson	—	—	83 a	25 abc
A. linearis	—	Toltec	—	—	77 a	47 bc
A. linearis	—	Mexico	—	—	76 a	87 d
A. canescens	*grandidentatum*	Mexico	—	—	92 b	20 abc
A. canescens	*occidentalis*	Willcox	—	—	97 cd	0 ab
A. canescens	*angustifolia*	Tucson	—	—	99 d	17 abc
A. polycarpa	—	Tucson	—	—	94 c	0 ab
A. polycarpa	—	Casa Grande	—	—	98 d	17 abc

[1] Means within a column followed by the same letter are not significantly different (P<0.05).

Table 3—Summary of cumulative rainfall, applied irrigation and total rainfall plus applied irrigation at different distances from a line-source sprinkler for direct seeding and transplant revegetation trials with *Atriplex* species during the summer of 1992 and 1993 at Tucson, Arizona.

	Cumulative rainfall	Cumulative applied water		Total rainfall plus applied water		
		1.5 m	10.5 m	1.5 m	10.5 m	16.5 m
	mm					
Direct seeding						
1992						
23 days after seeding	18	236	109	254	127	18
30 days after seeding	28	280	139	308	167	28
60 days after seeding	84	280	139	364	223	84
1993						
24 days after seeding	35	217	118	252	153	35
60 days after planting	77	217	118	294	195	77
Transplant						
1992						
15 days after planting	51	29	17	80	68	51
30 days after planting	53	29	17	82	70	53
60 days after planting	62	29	17	91	79	62
1993						
15 days after planting	28	0	0	—	—	28
60 days after planting	71	0	0	—	—	71

and Stallings, 1975; Young and others, 1981; Sanderson and others, 1987). Springfield (1970) and Van Epps and McKell (1980) indicated that many successful seedings of *A. canescens* have been severely damaged or destroyed by rabbit predation.

Conclusions

Applied irrigation and rainfall amounts totaling a range of 223 to 364 mm for 1992 and 195 to 294 mm for 1993 resulted in at least some establishment of *Atriplex* seedlings (Table 3). These studies indicate that for a summer planting, supplemental irrigation will increase the probability of plant establishment after direct seeding. Results suggest that establishment of perennial *Atriplex* seedlings is restricted to those conditions when the environmental criteria of soil moisture availability and soil temperatures are met. Criteria for successful establishment of *Atriplex* from direct seeding during the summer include long periods of high soil moisture in combination with relatively low soil temperatures favorable for germination.

In contrast, transplants required only natural rainfall for establishment, with amounts ranging from 62 to 71 mm (Tables 2, 3). With the exception of *A. linearis*, transplant accessions which originated distant from the planting site were equally adapted for establishment when compared to the germplasm collected nearest to the site. Assuming that over a three month period soil moisture remains relatively high from natural rainfall, or irrigation, transplants may be a more efficient method of establishing plants than using seed. Available moisture at lower depths in the soil profile probably increased transplant establishment under natural rainfall conditions but had less effect on direct-seeding establishment. This study suggest that *Atriplex* transplants may be fairly easily established by irrigating to fill the soil profile prior to transplanting and by adding a minimal amount of supplemental irrigation water, even in the absence of precipitation.

Acknowledgments

This paper is dedicated to the late A. K. Dobrenz, Department of Plant Science, University of Arizona, Tucson.

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Beyond Twelve Percent Purity

Bruce L. Welch

Abstract—This study examines three myths of sagebrush (*Artemisia* spp.) seed technology. These myths are: (1) processing sagebrush inflorescences through a debearder will lower seed viability; (2) seeds of sagebrush cannot be cleaned economically beyond 12 percent purity; and (3) sagebrush achenes (seeds plus pericarps) retain viability longer than sagebrush seeds (achenes with pericarps removed). Evidence given in this paper support the conclusion that all three myths are false.

This paper explores the truthfulness of three myths of sagebrush seed technology. A myth is "a belief given uncritical acceptance by the members of a group, especially in support of existing or traditional practices." The myths referred to are: (1) processing sagebrush inflorescences through a debearder will lower seed viability; (2) seeds of sagebrush cannot be economically cleaned beyond 12 percent purity; and (3) sagebrush achenes (seeds plus pericarps) retain viability longer than sagebrush seeds (achenes without pericarps). Hypotheses tested are: viability of sagebrush seeds passed through a debearder is equal to the viability of seeds not passed through a debearder; sagebrush seed can be cleaned economically beyond 12 percent purity; and viability of stored sagebrush seeds is equal to the viability of stored achenes.

Materials and Methods

Five experiments were conducted to obtain the data presented in this study. Each experiment is outlined below.

Experiment 1

This experiment was designed to determine if passing sagebrush inflorescences through a debearder lowers seed viability. Inflorescences were obtained from a native Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) stand, clipped by hand, and dried to a moisture content of about 13 percent. Drying was accomplished using a forced air heater. The heater circulated dry air around and through the pile of inflorescences. Temperature of the air contacting the inflorescences never exceeded 32 °C.

Main stems were removed and the resulting mixture of achenes, seeds, seed bracts, leaves, and fine stems were placed in 30-gal plastic garbage cans. Samples were taken from each garbage can before the contents were run through a "Cripen Model DB-1524" debearder. Samples were taken of the material after it passed through the debearder. After cleaning to a purity of 56.7 percent (see experiment 3 for cleaning details), achenes, seeds, and trash were passed through the debearder a second time and samples taken. This yielded three treatments: no passage through the debearder, single passage through the debearder, and after cleaning, a second pass through the debearder. Each treatment was represented by six replications of 100 achenes or seeds. Also, the percentage of achenes per treatment was noted as an indicator of harshness of treatment. The lower the percentage of achenes the harsher the treatment.

Viability was determined by using the tetrazolium staining test (Grabe 1972) as outlined by Meyer and others 1987. "Tetrazolium viability was determined by piercing imbibed seeds (seeds setting 24 hours on a saturated filter pad inside of a petri dish) with a fine needle through the center of the cotyledon region of the embryo, immersing the seed in 1 percent buffered tetrazolium chloride solution for 6 hours (I saturated the filter pad with 1 to 2 ml of 1 percent buffered tetrazolium chloride solution and allowed the seeds to set on the pad for 24 hours) at ca. 25c, slitting the cotyledon end of the pericarp and seed coat with a needle, and squeezing out the intact embryos. Embryos stained a uniform bright red were classed as viable" (Meyer and others 1987).

Data, from the three treatments, were statistically analyzed ($P < 0.05$) by means of a one-way analysis of variance. For significant F tests, Newman-Keuls' multiple range tests were used to test for significant differences among treatment means.

Experiment 2

The objective for this experiment was the same as that outlined for experiment 1. Biological material for this experiment came from a 'Hobble Creek' (Welch and others 1986) mountain big sagebrush (*A. t.* ssp. *vaseyana*) seed increase garden. This experiment was conducted in the same manner as experiment 1, with the following exception: when the seeds, achenes, and chaff were run the second time through the debearder the exit door was tied so that the material could exit only a small opening (about 10 percent of the usual opening). Materials run through the debearder a second time were warm to the touch. This treatment exposed the seeds to the maximum harshness in the debearder.

Experiment 3

This experiment was designed to show that sagebrush seed can be cleaned economically beyond 12 percent purity. Biological material for this experiment came from

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In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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a ‘Hobble Creek’ mountain big sagebrush seed increase garden. Inflorescences were removed by hand then dried by a forced air heater to a moisture content of 12 percent. Main stems were removed and the resulting mixture of seeds, seed bracts, leaves, and fine stems were placed in 30-gal plastic garbage cans. Next, the content of the garbage cans were fed through a debearder set up as described in experiment 1. Then the material was cleaned by a two-screened Crippen model XV-242-LH seed cleaner with air lift. A 14-by-14 mesh screen was placed in the top screen position with a 36-by-36 mesh screen in the bottom position. Air lift was adjusted to maximum lift without picking up seeds. Weights were taken of all materials (seeds, seeds bracts, fine stems) that were passed through the debearder, carried over the 14-by-14 mesh screen, passed through the 36-by-36 mesh screen, and uplifted by the air lift. Materials carried over the 14-by-14 mesh screen, uplifted by air lift and passed through the 36-by-36 mesh screen were considered screenings and would normally be discarded. Materials passing through the 14-by-14 mesh screen, carried over the 36-by-36 mesh screen and not uplifted would be either the final product of cleaned seed or the materials used for reruns through the seed cleaner to obtain higher degrees of purity.

Experiment 4

This experiment had the same objective as experiment 3. After finishing experiment 3, I found that the starting seed purity of the biological material was 13.2 percent. This was unusually high for a field seed lot. I felt that I needed to test the cleaning procedure on field seed lots with lower starting purity. Three field seed lots with starting seed purity of 6.1, 7.5, and 9.4 percent were located and run through the debearder once and the seed cleaner four times.

Experiment 5

Because passing sagebrush seed through a debearder and a seed cleaner removes all of the pericarp from some of the sagebrush achenes, this experiment was designed to test the hypothesis that seeds in intact achenes retained higher viability in storage than seeds out of achenes. Biological material was obtained from ‘Hobble Creek’ mountain big sagebrush seed stored at the Shrub Sciences Laboratory in paper envelopes. Age of the seeds was 52, 76, and 88 months. Samples from each age group were separated into achenes with fully intact pericarps and seeds outside achenes (pericarps were removed). Tests included six replications of 100 achenes and 100 seeds per age group. Seed viability was determined for the two classes as outlined in experiment 1. Data were statistically analyzed by means of student’s tests of unpaired observations ($P < 0.05$) for each age group.

Results and Discussion

Results of experiments 1 and 2 are given in table 1. There were no significant differences in seed viability between seeds passed through the debearder once or twice or not at all. There was a significant increase in the percentage of seeds outside the achenes with repeated runs through the debearder. For experiment 2, there were no significant differences in seed viability between seeds before debearding and those run through the debearder once; however, with the second run through the debearder (with exit door tied nearly closed) seed viability dropped significantly. As with experiment 1, number of seeds outside the achenes increased significantly with the second run through the debearder. What these data sets tell us is that sagebrush seed can be put through a properly adjusted debearder without affecting seed viability. However, as shown in experiment 2, an improperly adjusted debearder will greatly reduce seed viability. Welch and others (1986) warned that this procedure “should be done rapidly so that seeds are not overheated.” Shaw and Monsen (1990) reported the use of debearders to facilitate sagebrush seed cleaning. Variables that need to be watched include: length of debearder, pressure on exit door, and rotational speed of debearder.

Table 1—Effects of debearder on sagebrush seed viability and percent of seeds outside achenes. Data expressed as a percent of live seeds for seed viability and percent of seeds outside achenes. Means and standard deviations sharing the same superscripts in columns of the same experiment are not significantly different ($P < 0.05$)

	Percent of viable seeds	Percent of seed outside achenes
Experiment 1		
Before debearder	93.3 ± 1.79^{a}	18.0 ± 3.08^{a}
After 1st debearder	93.0 ± 1.87^{a}	48.3 ± 4.76^{b}
After 2nd debearder and cleaning	93.0 ± 0.71^{a}	66.8 ± 1.79^{c}
Experiment 2		
Before debearder	87.8 ± 3.11^{a}	2.3 ± 1.48^{a}
After 1st debearder	89.0 ± 3.74^{a}	20.3 ± 5.76^{b}
After 2nd debearder and cleaning[1]	40.8 ± 8.26^{b}	79.3 ± 2.28^{c}

[1] Exit door tied nearly closed.

Results of experiment 3 are given in figure 1. Final product, after five runs through the seed cleaner, weighed 17.56 pounds with a purity of 65.9 percent. Seed viability as determined by the tetrazolium test was 93 percent. At four runs through the seed cleaner the purity was 53.3 percent. These purities are well above the 8 to 12 percent standards set in the literature (Steven and Meyer 1990). By pouring the 17.56 pounds of final product of experiment 3 in front of a greenhouse exhaust fan, I obtained a product that had a purity of 89.1 percent. I did experience a seed loss of 1.5 percent using this technique.

For runs III, IV, and V the purity of the materials carried over the 14-by-14 mesh screen was: 10.6, 17.6, and 15.8 percent, respectively. The producer may choose to rerun these lots through the seed cleaner and clean them up to at least 50 percent purity. About 80 percent of the seed can be recovered. The producer also can save the lots and sell them to an agency with lower standards.

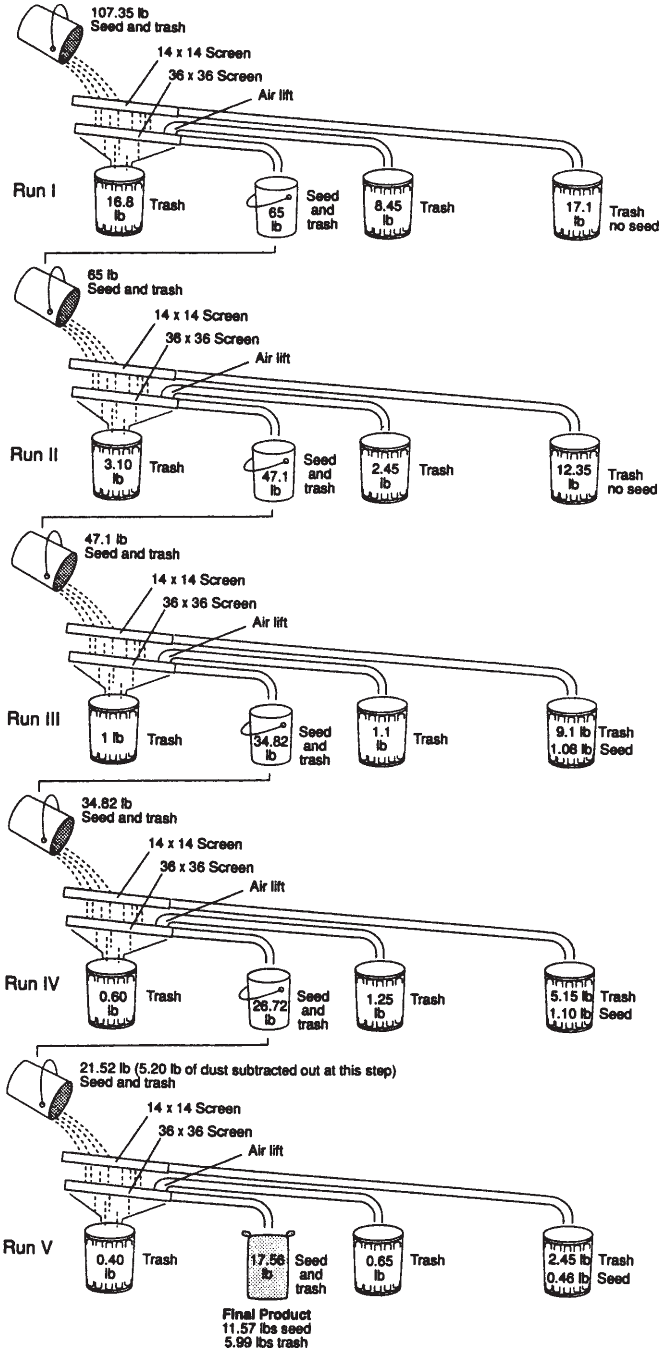

Figure 1—A flow chart outlining the movement of a big sagebrush seed lot, weighing 107.35 pounds, through an air/screen seed cleaner. Before cleaning, the seed lot was passed through a debearder. Trash was separated from seeds by being carried over the 14-by-14 mesh screen, being air lifted from the seed, passing through the 36-by-36 mesh screen, or being lost as flying dust. The final product was obtained by running the material carried off the 36-by-36 mesh screen five times through the seed cleaner. Final product had a purity of 65.9 percent and a seed viability of 93 percent.

I did not realize when conducting this experiment that the material I was using had a starting purity of 13.2 percent.

Experiment 4 was conducted to see if materials with lower percentages of purity could be cleaned to 50 percent or greater. Results were similar to those of experiment 3. After four runs through the seed cleaner, the lot that started at 6.1 percent purity was cleaned to 51.8 percent, the 7.5 percent purity lot was cleaned to 51.2 percent, and the 9.4 percent purity lot was cleaned to 58.7 percent.

Dean Swift (1993) reported that by using a combination of air/screen cleaners and a gravity table he can clean *A. frigida* seed to 98 percent purity and above. *A. frigida* seed is smaller than the seed of big sagebrush. Further, Welch and others (1986) suggested the possibility of cleaning 'Hobble Creek' mountain big sagebrush (*A. t.* ssp. *vaseyana*) to 95 percent purity with present-day technology. Shaw and Monsen (1990) reported seed dealers "cleaning sagebrush seed lots to purities of 20 to 40 percent," with some as high as 80 percent. Neither report commented on the economics of seed cleaning.

Cleaning costs are about $0.50 to $1.00 per pound of pure live seed (pls). The seed cleaner I used in the study is not a high capacity cleaner, but costs did not exceed $1.00 per pound of pure live seed (pls). Higher capacity cleaners should cut cleaning costs significantly. I believe it is reasonable for the consumer to demand a purity of at least 50 percent. Higher purities are obtainable by combining the air/screen cleaner with other cleaning machines, such as a gravity table (Swift 1993). Cost of cleaning should be offset by the savings in handling less bulk. The cost of the seed should not increase.

Savings from higher purities occur at every stage of handling. This includes sacking, transporting to buyer sites, storage, transportation to planting sites, and amount of land seeded per filling of planting hoppers. To illustrate these savings, I will compare two sales. Both sales are for 1,000 pounds pls of Gordon Creek Wyoming big sagebrush seed (Welch and others 1992). Sale number 1 seed lot has a purity of 50 percent with 80 percent viability. Sale number 2 seed lot has a purity of 12 percent with 80 percent viability.

I estimated from seed lots on hand at the Shrub Sciences Laboratory that 1 cubic foot of seed and trash from sale 1 weighs about 17 pounds, from sale 2 about 10 pounds. Sacks 25 by 36 inches provide about 4 cubic feet of space. Sale 1 sacks would weigh 68 pounds; sale 2 sacks would weigh 40 pounds. Sale 1 would be sacking 2,500 pounds total of seed and trash to obtain the 1,000 pounds pls; this would require 37 sacks. However, 260 sacks would be required for sale 2. Sale 1 would result in saving 223 sacks or $111 plus the labor it takes to fill, sew, and handle the additional 223 sacks. Sale 1 could be stored in about 148 cubic feet of space at a cost of $4.44 per month. Storage costs for sale 2's 1,040 cubic feet would be about $31.00 per month. (Storage costs are about 3 cents per cubic foot per month.) Sale 1 would save $26.56 per month on storage over sale 2. Shipping costs (from Lindon, UT to Boise, ID-freight class 100) of sale 1's 2,500 pounds (68 pounds per sack x 37 sacks) would be $489.00; sale 2's 10,417 pounds would cost $1,577.00. Again a savings of about $977.00. Total savings at the higher purity would be:

Sacks saved	$111
Labor saved by handling fewer sacks	?
Shipping cost saving	$1,078
Storage cost saving	$27+
Total savings (at least)	$1,176+

All these savings are from the producer end and should either earn the producer more money or offset the cleaning cost.

The buyer would experience savings by handling less trash. Further savings would occur in storage (6.9 times more costly for sale 2), transportation to seeding sites (3.1 times more costly for sale 2), and in the planting process. A seeding contractor estimated savings of 20 percent in seeding cost by using sale 1's seed instead of sale 2's seed (Johansen 1993). I believe the estimated savings to be low. The contractor used the figure of 12 pounds per cubic foot for 40 percent pls (50 percent purity times 80 percent viability) for his estimates. My measurement for 40 percent pls (9.3 percent moisture) was 17.2 pounds per cubic foot. If my measurements are correct, this means about a 43 percent increase in the amount of seed that can be carried per load. At any rate, significant savings can be achieved by seeding with seed lots of higher purity.

One additional benefit of cleaning big sagebrush seeds to higher percents of purity is human health. I found handling sacks of seed cleaned beyond 12 percent purity produced far less dust.

Results of experiment 5 are given below. As shown, there is no significant difference in seed viability between seeds in intact achenes and seeds outside the achenes, regardless of age of the seed.

Age of seeds	Seeds in intact achenes	Seeds outside achenes
Months	*Percent*	
52	91.0 ± 2.35	90.3 ± 1.09
76	56.0 ± 5.39	58.0 ± 6.16
88	40.0 ± 1.58	44.0 ± 3.08

The five experiments outlined in this paper conclusively indicate that the three myths examined in this study concerning sagebrush seed technology are false. Modern technology allows us to clean and sort seeds to high levels of purity quite economically, and to provide seeds of high viability whether the achene has been removed or not.

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Effects of Gravel Mulch On Emergence of Galleta Grass Seedlings

Von K. Winkel
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Abstract—A greenhouse study was implemented to determine the effects of gravel mulch on seedling emergence and soil water, and the optimal depths of gravel mulch for various native plant species. Greenhouse flats were sown with seeds and then treated with a variety of mulch treatments including no mulch, a 1-cm layer of soil over seeds, and 2- to 3-cm and 4- to 5-cm layers of 3- to 25-mm mixed gravel. Superimposed over these treatments were 3 irrigation treatments. Seedling density data were collected daily, and soil water was monitored daily with the gravimetric method. This study showed that under a variety of soil water conditions, a 2-3 cm gravel layer may aid emergence of galleta grass. Results from this study also demonstrated that a deeper layer of gravel (4-5 cm) prevents emergence, probably because it acts as a physical barrier to the seedlings.

The Department of Energy, Nevada Field Office, has identified the need to clean up several sites on the Nevada Test Site (NTS) and Tonopah Test Range (TTR) contaminated with surface plutonium. An important objective of the project is to develop technologies to stabilize and restore the disturbed sites after decontamination. Revegetation of these contaminated sites will be difficult due to their location in the arid Mojave and Great Basin Deserts. The major factors which will affect successful plant establishment and growth at these sites are limited, sporadic precipitation, limited soil water, extreme air and soil temperatures, limited topsoil, and herbivory by rabbits and wild horses.

Nearly all plutonium at the contaminated sites is limited to the top 10 cm of soil, and is associated with the <3 mm soil fraction. The >3 mm (gravel) fraction may be separated by sieving during the plutonium removal process, and then stockpiled, or reused during site restoration and stabilization activities. This material could be deposited on top of replaced soil to act as a mulch to stabilize the soil and conserve soil water.

Mulches aid plant establishment by providing microsites for seeds which enhance soil water and temperature conditions, and stabilize erosive soils (Kay 1978). Plant litter can be thought of as a natural mulch in that it can provide microsites for seeds. Evans and Young (1970, 1972) reported greater emergence of downey brome (*Bromus tectorum*), medusahead rye (*Taeniatherum asperum*), and Russian thistle (*Salsola iberica*) from seeds under plant litter than from seeds on the bare soil surface. Environmental monitoring showed that plant litter greatly moderated maximum and minimum soil temperatures, decreased the amount of light reaching the soil surface, and greatly increased relative humidity.

Rocks and gravel can also provide natural microsites for seed. Fowler (1986) observed that Texas grama (*Bouteloua rigidiseta*) and red three-awn (*Aristida longiseta*) germinated, survived, and grew better under rocks and plant litter than on the bare soil surface. In a greenhouse study, emergence of sideoats grama (*Bouteloua curtipendula*), 'A-130' blue panic (*Panicum antidotale*), and 'Cochise' Antherstone lovegrass (*Eragrostis lehmanniana* x *E. tricophera*) was highest from a gravel mulch treatment (Winkel and others 1991). Analysis of soil water content for each of the treatments in the study indicated that soil water decreased faster in a bare soil surface treatment than in a gravel mulch treatment.

Research has shown that providing microsites for seed via mulching can aid plant emergence and establishment. Since many of the soils at the sites slated for plutonium decontamination have a large percentage of gravel in the upper 10 cm of soil, the use of gravel as mulch could provide microsites for seed and stabilize soils during subsequent revegetation of the sites. In July of 1992 a greenhouse study was initiated to examine the possible benefits of gravel mulch. The specific objectives of this greenhouse study were to: 1) determine the effects of gravel mulch on seedling emergence and soil water, and 2) determine effects of irrigation rates on seedling emergence for gravel mulches and other conventional seedbed preparation techniques. A secondary objective was to determine the optimal depth of gravel mulch for seedling emergence.

Methods

The study was conducted in an evaporative-cooled greenhouse on the NTS from July 15 to August 4, 1992. Daily maximum and minimum air temperatures inside the greenhouse during the study ranged from 26.6 to 35.2 °C, and 13.8 to 19.4 °C, respectively.

A gravelly sandy loam soil from the top 15 cm was collected from an area in Plutonium Valley on the NTS,

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At the time of this study Von K. Winkel was Scientist III and Juan C. Medrano, Charles Stanley, and Matthew D. Walo were analysts, EG&G Energy Measurements, Inc., Environmental Sciences Division, Las Vegas, NV.

sieved to 3 mm and the <3-mm fraction was placed in 40x60x10-cm flats. Each flat was then seeded with 20 seeds each of the following nine species: fourwing saltbush (*Atriplex canescens*), threadleaf rubber rabbitbrush (*Chrysothamnus nauseosus consimilis*), basin big sagebrush (*Artemisia tridentata tridentata*), galleta grass (*Hilaria jamesii*), Indian ricegrass (*Oryzopsis hymenoides*), alkali sacaton (*Sporobolis airoides*), desert mallow (*Sphaeralcea ambigua*), Palmer penstemon (*Penstemon palmeri*), and spiney hopsage *(Grayia spinosa*).

The seeds of these nine species were planted in the flats several different ways to simulate conventional seedbed treatments that may be used in the field. For the "bare" treatment, seeds of all species were broadcast on the bare soil surface with no further treatment. For the "buried" treatment, seeds of all species were broadcast and then covered with a 1-cm layer of soil. The "buried" treatment was selected to simulate the placement of seeds with a seed drill, which is a standard method of placing seeds at precise depths in the seedbed. The "2-cm gravel" and "4-cm gravel" treatments consisted of broadcasting seeds on the soil surface, and then covering the seeds with a 2-3 or 4-5-cm layer of gravel. Gravel was obtained from the soil material used in the study. Three irrigation treatments were selected to simulate the wide variety of soil water conditions that may occur in the Mojave Desert of southern Nevada, and to test a range of irrigation rates. The irrigation treatments included: 1) watering on day one only, 2) watering on day one and every fifth day thereafter, and 3) watering on day one and every tenth day thereafter. Flats were watered to saturation by sprinkling on each watering day, and allowed to freely drain.

Seedling emergence data (number of emerged seedlings of each species/flat) were collected daily. Percent seed germination of each species was determined in the greenhouse with two replications of each species using the petri dish technique. For each replication, 100 seeds were placed on filter paper in a petri dish. Seeds were watered on day one and whenever necessary throughout the study to maintain optimal moisture conditions for germination. Germination counts were conducted every 24 ± 2 hours after initial watering. A seed was considered germinated when its radicle had emerged.

To determine why seeds and seedlings responded as they did to the seedbed treatments with respect to soil water, gravimetric soil water content was measured from samples obtained from additional non-seeded flats. These flats were filled with soil, treated with the seedbed treatments (without the seeds), and irrigated as above. Beginning on day one and continuing daily throughout the study (with the exception of days four and 14), approximately 10 cm^3 of soil from each of the non-seeded flats was collected. The specific depth from which soil samples were collected for each treatment was as follows: 1) bare treatment: the top 5 mm of soil; 2) buried treatment: 5 to 15 mm beneath the soil surface; 3) 2 and 4-cm gravel treatments: the top 5 mm of soil under the gravel. Soil sampling depths differed by treatment because of the need to sample soil adjacent to the seed. This allowed measurement of soil water at the soil-seed interface, which is critical to determine microsite effects. Gravimetric soil water content of the samples was determined by weighing before and after oven-drying (Hillel 1982). Soils data from several other sites on the NTS having soils similar in texture to that used in this study were used to estimate percent water content at –0.03 and –1.50 MPa matric potentials.

The experimental design was a split plot with two blocks (replications). Whole plot variables were irrigation and gravel treatments, and species; days was the split plot variable. Each irrigation treatment/gravel treatment/ species combination was randomized within blocks. The study included 24 seeded and non-seeded flats (n=2), with each block containing 12 each of seeded and non-seeded flats (4 gravel treatments x 3 irrigation treatments).

Analysis of variance was performed on seedling emergence data, and on the arcsin square root of percentage data (Sokal and Rohlf 1981) for soil water content data using the SAS GLM procedure (SAS 1989). Significant means were separated with Fisher's Least Significant Difference test.

Results and Discussion

Seedling Emergence

Seedling germination tests in petri dishes were implemented at the same time as seedbed/irrigation treatments in order to expose the germination tests to the same environmental conditions as that of the seedbed/irrigation treatments. Only galleta grass had high germination in the petri dishes and sufficient response in the seedbed/ irrigation treatments. Germination of the other eight species was below 50%, which was considered to be the minimum percent germination to allow statistical comparisons in the seedbed/irrigation treatments. Because of the lack of germination exhibited by these eight species, they will not be included in the discussion of seedbed/irrigation treatment effects.

Because only galleta grass had sufficient germination to allow statistical comparisons of seedbed/irrigation treatments, the statistical design was modified. Whole plot variables were irrigation and gravel treatments; and day was the split plot variable. Species was dropped as a whole plot factor. Analysis of variance of seedling density data showed significant ($p<0.05$) two- and three-factor interactions involving irrigation treatments, gravel treatments, and days.

When watering occurred on day one only, similar numbers of galleta grass seedlings emerged from the buried and 2-cm gravel treatments (Figure 1). In contrast, few seedlings emerged from the bare treatment, and no seedlings emerged from the 4-cm gravel treatment. The few seedlings that did emerge from the bare treatment succumbed to desiccation by day 16. A portion of seedlings that emerged from the buried treatment died from desiccation on day 15, and over one-half had died by day 20. In comparison, all seedlings emerging from 2-cm gravel survived to the end of the study.

When watering occurred every ten days, seedlings emerged from and survived in the 2-cm gravel and buried treatments equally well (Figure 2). Again, few seedlings emerged from the bare treatment. A small number of

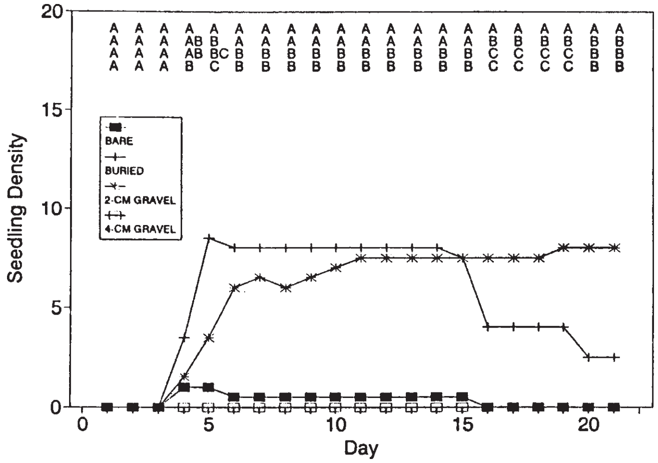

Figure 1—Mean number of emerged seedlings of galleta grass (n=2) in various seedbed treatments with watering on day one of the study only. Means for seedbed treatments having the same letter for a given day are not significantly different (p<0.05).

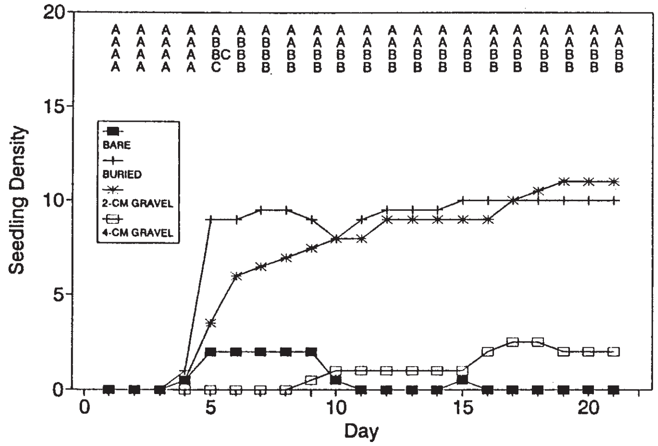

Figure 2—Mean number of emerged seedlings of galleta grass (n=2) in various seedbed treatments with watering every ten days. Means for seedbed treatments having the same letter for a given day are not significantly different (p<0.05).

seedlings emerged from the 4-cm gravel but these were not statistically different from the bare treatment.

When watering occurred every five days, galleta grass seedlings emerged and survived best from the 2-cm gravel treatment (Figure 3). Although the buried treatment produced nearly as many seedlings as did the 2-cm gravel treatment, some of the seedlings died after 15 days. No seedlings emerged from the 4-cm gravel treatment. Seeds from the bare treatment responded well to watering every five days and survived until the end of the study.

Soil Water

The analysis of variance for soil water data showed significant (p<0.05) two- and three-factor interactions involving irrigation treatments, gravel treatments, and days. When irrigation occurred on day one only, soil water content remained above a corresponding matric potential of –1.50 MPa until day five in the buried and bare treatments, and until day 10 and 22 in the 2-cm gravel and 4-cm gravel treatments, respectively (Figure 4). Again, this may help to explain why seedlings responded

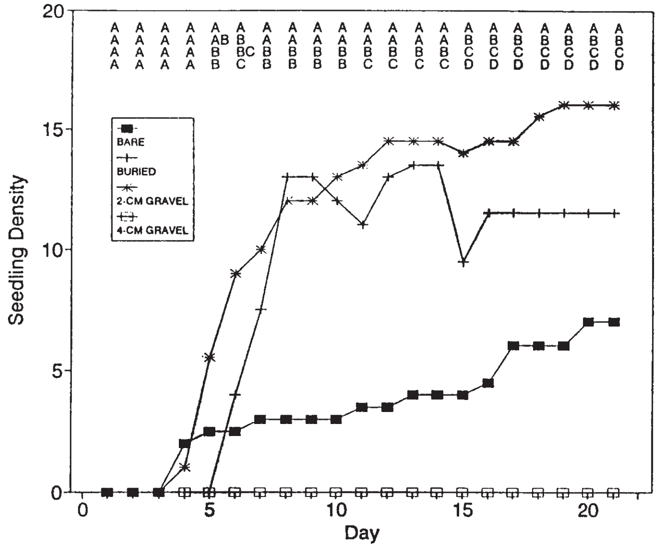

Figure 3—Mean number of emerged seedlings of galleta grass (n=2) in various seedbed treatments with watering every five days. Means for seedbed treatments having the same letter for a given day are not significantly different (p<0.05).

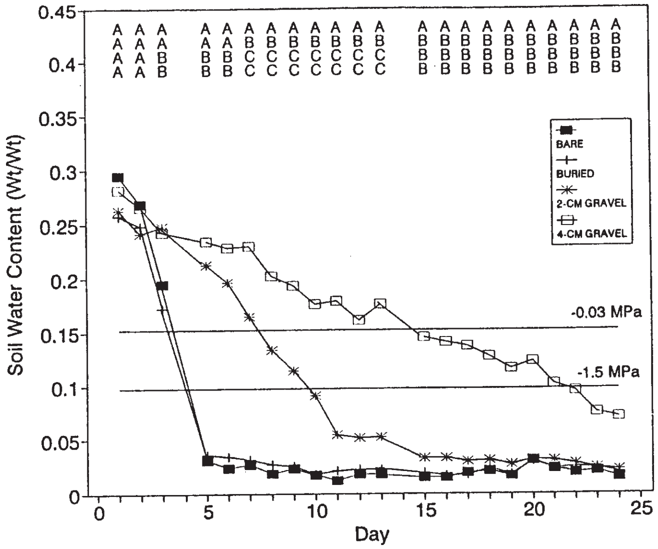

Figure 4—Soil water content of soils watered only on the first day of the study in relation to seedbed treatments across time (days). Lines indicating soil water content at soil matric potential of –0.03 MPa and –1.5 MPa have been added for reference. Points having the same letter for a given day are not significantly different (p<0.05).

better to the 2-cm gravel. The 4-cm gravel treatment conserved soil water twice as well as the 2-cm gravel, and four times as well as the bare and buried treatments. Few seedlings, however, emerged from the 4-cm gravel treatment. The thickness of the gravel layer may have been prohibitive to the emergence of seedlings. Seedlings under the 4-cm gravel layer were inspected at the end of the study. Although many seeds germinated, most of the seedlings were etiolated and growing horizontally. Some had been infested by fungi, which may indicate that conditions under the 4- to 5-cm gravel layer may have been too wet for optimal plant growth, particularly when watering occurred every five days.

When irrigation occurred every ten days, water content of soil under either 2- or 4-cm of gravel stayed above a corresponding matric potential of –1.50 MPa throughout the study (Figure 5). Water content of soil from the bare and buried treatments, however, dropped below a corresponding matric potential of –1.50 MPa after 3-4 days and remained below that level for up to seven days. When irrigation occurred every five days, the water content of soil under the two gravel treatments remained above a corresponding matric potential of –0.03 MPa throughout the study (Figure 6). In contrast, soils without gravel mulch dried to a corresponding matric potential below –1.50 MPa within 3 days after every irrigation. This may help explain why seedlings responded so favorably to the 2-cm gravel treatment, and why seedlings from the other treatments either failed to emerge, or failed to survive to the end of the study.

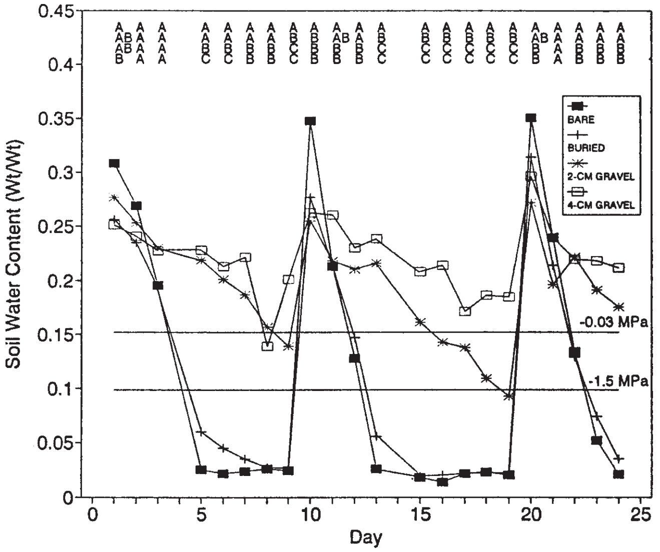

Figure 5—Soil water content of soils watered every 10 days in relation to seedbed treatments across time (days). Lines indicating soil water content at soil matric potential of –0.03 MPa and –1.5 MPa have been added for reference. Points having the same letter for a given day are not significantly different (p<0.05).

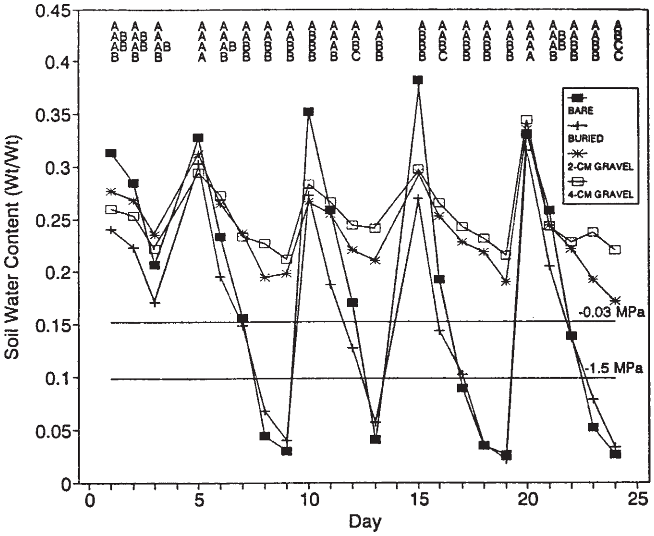

Figure 6—Soil water content of soils watered every 5 days in relation to seedbed treatments across time (days). Lines indicating soil water content at soil matric potential of –0.03 MPa and –1.5 MPa have been added for reference. Points having the same letter for a given day are not significantly different (p<0.05).

Seedlings emerged from the bare treatment that was watered every five days. Apparently this irrigation treatment kept the soil moist long enough for germination to occur. This treatment shows that frequent moisture replenishment is critical for germination of broadcast seed.

Conclusions

This study showed that under a variety of soil water conditions in a greenhouse, a 2-3 cm gravel layer may aid emergence of galleta grass. This study also demonstrated that a deeper layer of gravel (4-5 cm) prohibits emergence, probably because it acts as a physical barrier to the seedlings. Galleta grass emergence can be used as a model for how other species might respond to these seedbed and irrigation treatments, provided seeds germinate and are exposed to similar environmental conditions.

This study was conducted with native soils in a greenhouse at temperatures similar to those found during the summer in the Mojave desert. Care should be taken when attempting to extrapolate the results to actual field conditions. Further studies should beconducted in the field under natural conditions before a gravel mulch treatment is selected for implementation in a revegetation program.

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Effects of Seedbed Preparation, Irrigation and Water Harvesting on Seedling Emergence at the Nevada Test Site

Von K. Winkel
W. Kent Ostler
Warren D. Gabbert
Glen E. Lyon

Abstract—A study was conducted on the Nevada Test Site in southern Nevada to determine adaptable plant species, methods to prepare seedbeds for direct seeding and water harvesting, and proper irrigation rates. Plots were prepared with various seedbed/water harvesting treatments including, pitting, land imprinting, and straw mulching. Other plots were treated with large water harvesting structures. Three irrigation treatments were superimposed over the seedbed/water harvesting treatments. Seedling emergence data were collected, and the treatment combinations compared. Supporting meteorological and soil data were collected with an automatic data-logger. With the exception of increased shrub seedling densities in desert strips, there were no strong seedbed preparation/water harvesting treatment effects. In a year of above-average precipitation, irrigation did not generally aid germination and emergence of seeded species and only slightly increased densities of species from the native seedbank.

During the 1950's and 1960's, a series of safety tests were conducted on and adjacent to the Nevada Test Site (NTS) to determine the consequences of accidental detonation or destruction of a nuclear device. This led to the contamination of approximately 800 hectares with plutonium. The U.S. Department of Energy Nevada Operations Office has developed a feasibility study to examine methods for cleaning up these contaminated lands. The objectives of the study are to evaluate technologies to: 1) selectively excavate the contaminated soil, 2) remove the plutonium from the soil, and 3) respread the clean soil on the site, and stabilize and revegetate the site.

Revegetating these disturbed areas will be difficult for the following reasons: 1) approximately 5-10 cm of topsoil will be removed and may not be replaced, 2) the structure and biological viability of the soil will be significantly altered, and 3) these areas are in harsh environments with high temperatures and limited, erratic precipitation.

Precipitation is the dominant factor controlling revegetation success in arid lands. While 250 mm of annual precipitation is generally considered the minimum necessary for revegetation by seeding (Plummer and others 1968, Vallentine 1989), much of the Mojave Desert and portions of the Great Basin Desert receive less than 150 mm of precipitation annually. For this reason, few attempts have been made to revegetate disturbed areas in these deserts by seeding. However, various revegetation efforts in arid and semiarid regions of the Southwest have shown that reseeding is practical and cost effective, provided proper techniques such as mulching, seedbed modification, and water harvesting are applied (Graves and others 1978, Kay 1979, Anderson 1987, and Clary 1983).

Several techniques that modify soil microtopography to concentrate precipitation have been developed and used successfully in the arid Southwest. The land imprinter has been shown to successfully harvest limited precipitation (Dixon and Simanton 1980), cover broadcast seeds (Winkel and others 1991), increase seedling emergence, firm seedbeds, reduce wind erosion, and increase seed-soil contact (Haferkamp 1987, Clary 1989, Winkel and Roundy 1991).

Pits have been used since the 1930's on the Great Plains and in the Southwest to prepare seedbeds, control competing plants, and concentrate limited precipitation (Vallentine 1989). Intensive water harvesting techniques such as catchment basins, desert stripping, and runoff farming have been used for centuries in the Middle East (National Academy of Sciences 1974, Boers and Ben-Asher 1982, Evernari and others 1982), and more recently in the southwestern United States (Morin and Matlock 1975, Fink and others 1980), and Mexico (Mendina and Garza 1987); they show promise to accelerate revegetation in the Mojave Desert. Various mulches have been shown to greatly reduce evaporation, stabilize soils and increase seedling establishment (Kay 1978, Fraser and Wolfe 1982, Brammer 1982). A variety of irrigation methods have been shown to aid emergence and establishment of native plants. The objective of this study was to determine effects of seedbed preparation, irrigation, and water harvesting on emergence of native grass, forb, and shrub species in the Mojave/Great Basin Transition Desert.

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Von K. Winkel, Warren D. Gabbert and Glen E. Lyon are Scientists, and W. Kent Ostler is Director, EG&G Energy Measurements, Inc., Environmental Sciences Division, Las Vegas, NV.

Methods

The study was conducted on the NTS in southern Nevada, approximately 113 km northwest of Las Vegas (Figure 1). The study site is situated on an alluvial fan of the northern slope of French Peak mountain at an elevation of 1271 m. The soil is a gravelly sandy loam. The slope at the site is 3-5 percent and the aspect is northwest. The site is in a transition zone between the Mojave and Great Basin deserts with major plant species consisting of shadscale (*Atriplex confertifolia*), winterfat (*Ceratoides lanata*), wolfberry (*Lycium andersonii*), and Indian ricegrass (*Oryzopsis hymenoides*). The climate is characterized by hot summers and cool winters. Average annual precipitation for the past 30 years, obtained 5 km from the site, is 168 mm, falling sporadically throughout the year.

The experimental design was a split split plot. Whole plots were irrigation treatments, split plots were seedbed/water harvesting treatments, and split split plots were species. A seed mix of eight seeded species was applied to six seedbed/water harvesting treatments within three irrigation treatments. The experiment included eighteen 7.5x20-m plots in each of three blocks. Irrigation treatments were randomized within blocks and seedbed/water harvesting treatments were randomized within irrigation treatments.

During September 1992, the plots were lightly brushed with a road-grader to remove existing vegetation. Plots were harrowed in December 1992 to scarify the soil. Due to the loose structure of the soil, no further tilling was needed. Following this initial seedbed preparation, each plot (except control plots), was seeded between December 11-14 at a rate of 20 kg/ha pure live seed (PLS) with a seed mixture of the following shrubs, forbs and grasses (percentage of mix in parentheses): fourwing saltbush (*Atriplex canescens*) (10%), shadscale (*Atriplex confertifolia*) (11%), threadleaf rubber rabbitbrush (*Chrysothamnus nauseosus consimilis*) (40%), galleta grass (*Hilaria jamesii*) (10%), Indian ricegrass (*Oryzopsis hymenoides*) (9%), alkali sacaton (*Sporobolis airoides*) (5%), globemallow (*Sphaeralcea ambigua*) (4%), and spiney hopsage (*Grayia spinosa*) (11%). Seed was obtained commercially, and all species are native to the NTS. All seeds were drilled into moist soil to a depth of 1 cm. The moisture was a result of rain and snow that fell several days prior to, and intermittently during the period of seeding. Following seeding, plots were treated with one of six seedbed preparation/water harvesting treatments including: 1) control, 2) drill, 3) mulch/drill, 4) mulch/Imprint, 5) mulch/pit, and 6) desert strip.

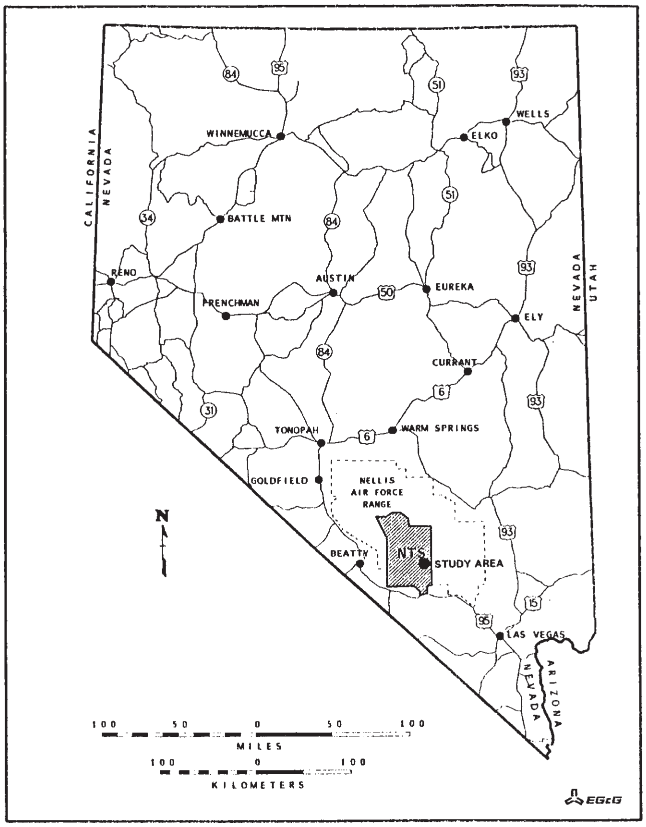

Figure 1—Location of study area on the Nevada Test Site in southern Nevada.

"Control" plots were not seeded, and received no treatment beyond brushing with a road-grader. "Drill" plots were drill-seeded with no further treatment. "Mulch/drill" plots were drill-seeded, mulched with 4500 kg/ha wheat straw, and then crimped with a disk-type crimper.

"Mulch/Imprint" plots were drill seeded, mulched with 4500 kg/ha wheat straw, and then imprinted with a Dixon-type land imprinter. The imprinter is composed of 10-cm geometric angle-iron forms welded on two separate 1x1-m cylinder capsules. The capsules are linked together with a common axle and filled with water. Total weight of the imprinter is approximately 5 metric tons. The imprinter produced imprints approximately 5-10 cm deep.

"Mulch/pit" plots were drill-seeded, mulched with 4500 kg/ha wheat straw, and then pitted with the Lee Pocket-Seeder. The Pocket-Seeder is a paddle-wheel type pitter that utilizes a hydraulic braking system to slow the speed of the paddle wheel to regulate the size of the pit it excavates.

The final treatment, referred to as a "desert strip" is a structure that includes a rainwater catchment or runoff-producing area and a plant-growing or runoff collection area. Catchments with 10% slopes were constructed with a road grader, and then sprayed with a water-shedding treatment (3% sodium methylsilanolate in water solution) at a rate of 1.25 l/m^2. The bottom 1.5 m of the plot (bottom of the slope) was drill seeded, mulched with 4500 kg/ha wheat straw and crimped with a disk-type crimper. Due to frozen soils, mulching, imprinting, pitting, and crimping were delayed until January 19-20, 1993, one month following seeding. Desert strips were formed in September 1992, and the water-shedding treatment was applied on March 12, 1993.

All plots were treated with one of three irrigation treatments: 1) control, 2) germination irrigation, and 3) maintenance irrigation. "Control" plots received no supplemental irrigation. "Germination irrigation" plots received 80 mm of supplemental irrigation between March 26 and April 19, 1993. Plots receiving "maintenance irrigation", were watered at the same frequency and rate as plots receiving "germination irrigation", until May 12-14, 1993 when they received an additional 37 mm of water. Additionally, these plots received 26 mm on June 15, 1993, and then approximately 30 mm twice monthly until the first week of September 1993.

Seedling densities of all seeded species and the six major species present in the seedbank prior to seeding (seedbank species), were counted in 20 and five 1-m^2 quadrats per plot, respectively. Data collection of both seeded and seedbank species occurred between May 11 and May 20, 1993. Due to the abundance of seedbank species in the study plots, six major species were selected by collecting seedling density of all seedbank species from fourteen 1-m^2 quadrats and selecting the six with the highest density. These species included: *Amsinkia tessellata*, *Bromus rubens*, *Descurainia sophia*, *Mentzelia obscura*, *Phacelia fremontii*, and *Phlox stansburyi*.

Significant interactions and differences among treatment means were determined with analysis of variance (SAS 1989) and significant differences were identified with Duncans New Multiple Range Test (Lentner and Bishop 1986).

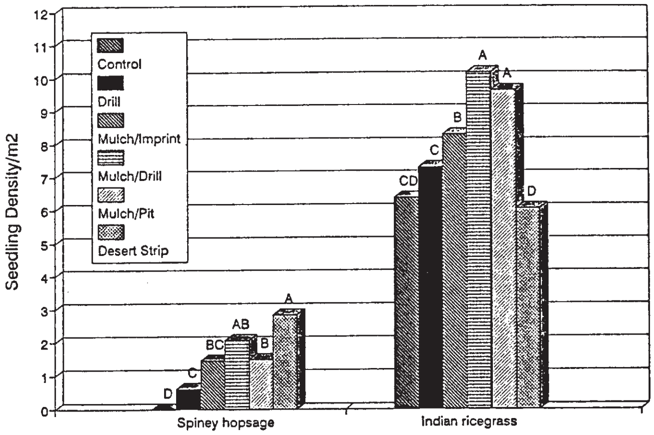

Figure 3—Seedling density of spiney hopsage and Indian ricegrass in relation to seedbed treatments with no supplemental irrigation. Seedbed treatment means for a species with the same letter are not significantly different ($p<0.05$).

Results and Discussion

Consistent precipitation began in mid-December 1992 and continued through March 1993 (Figure 2). Total precipitation from December 1, 1992 to April 5, 1993 was 270 mm, more than one and one half times the 30-year annual average. Soils were near field capacity at the surface from the first of January through February (although frozen for much of the time), and for several days during March. The top 1-3 cm of surface soils were observed to dry out for several days during mid-March. Emergence of seedbank species was first observed during the third week of January, but most did not emerge until air temperatures increased in early March (Figure 2). Seedlings of seeded species, (notably Indian ricegrass), were first observed during mid-March.

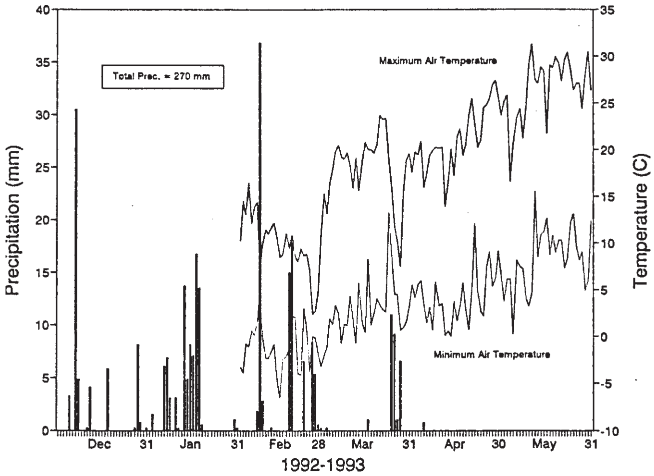

Figure 2—Daily precipitation from December 1, 1992 to May 31, 1993, and air temperature from February 1 to May 31, 1993, in Plutonium Valley on the Nevada Test Site in southern Nevada.

Analyses of variance of seedling density data for both seeded and seedbank species showed highly significant ($p<0.0001$) 2 and 3-factor interactions, involving species, irrigation treatments, and seedbed/water harvesting treatments.

No Supplemental Irrigation

Seeded Species Emergence—Only Indian ricegrass and spiney hopsage had emergence greater than 1 seedling/m^2 when no supplemental irrigation was applied (Figure 3, Table 1). With the exception of the desert strip treatment, Indian ricegrass emergence was significantly greater ($p<0.05$) from treatments with mulch, than from unmulched treatments. Indian ricegrass emergence was least from desert strips. In contrast, emergence of spiney hopsage was greatest from desert strips, moderate from the other mulch treatments, and least from unmulched treatments. Emergence of fourwing saltbush and rubber rabbitbrush from desert strips was double that from the other treatments, although this difference was not significant.

Seedbank Species Emergence—*B. rubens* and *A. tessellata* had the greatest seedling densities with no supplemental irrigation (Figure 4, Table 2). All other seedbank species produced less than 5 plants/m^2. There were significantly more ($p<0.05$) *B. rubens* plants in control plots than in all other treatments, with the exception of imprinted plots. Seedling densities of all other species (except *P. stansburyi*) were greatest in control plots, although these differences were not significant. Seedling densities of *B. rubens* and *A. tessellata* were significantly lower ($p<0.05$) in desert strip plots than in plots treated with all other seedbed treatments. Densities of *M. obscura*, *P. fremontii*, and *P. stansburyi* were also least in desert strip plots, although these differences were not

Table 1—Seedling density of seeded species in relation to seedbed and irrigation treatments. These species exhibited no significant differences (p<0.05) among seedbed treatment means.

Irrigation and seedbed treatment	Species					
	Fourwing saltbush	**Shadscale**	**Rubber rabbitbrush**	**Galleta grass**	**Alkali sacaton**	**Globemallow**
	- - - - - - - -	- - - - - - - -	- - - - - - - -	*Density (m^2)*	- - - - - - - -	- - - - - - - -
No irrigation						
Control	0	0.12	0.05	0.65	0.20	0.05
Drill	0.17	0.03	0.03	0.33	0.15	0.07
Mulch/imprint	0.23	0.12	0.07	0.18	0.73	0
Mulch/drill	0.27	0.15	0.10	0.47	0.22	0.03
Mulch/pit	0.07	0	0.02	0.30	0.72	0.03
Desert strip	0.77	0	0.32	0.20	0.12	0
Germination irrigation						
Control	0.03	0.02	0.12	0.95	0.65	0.07
Drill	0.05	0.05	0.23	0.22	0.77	0.12
Mulch/imprint	0.12	0.02	0.10	0.43	0.78	0.12
Mulch/drill	0.12	0.07	0.12	0.65	0.67	0.10
Mulch/pit	0.05	0.03	0.10	0.63	0.55	0.03
Desert strip	0.53	0	0.23	0.36	0.10	0.03
Maintenance irrigation						
Control	0	0.48	0.05	*[1]	0.55	0.05
Drill	0.27	0.85	0.13	*	1.32	0.05
Mulch/imprint	0.13	0.03	0.13	*	0.32	0.07
Mulch/drill	0.07	0.08	0.08	*	0.05	0.05
Mulch/pit	0.23	0.18	0.07	*	0.80	0.05
Desert strip	0.90	0.07	0.33	*	0.20	0.08

[1] Seedling density means for Galleta grass were significant (p<0.05) and are shown in Figure 7.

significant. Densities of seedbank species were probably lowest from desert strip plots due to the lack of seed in the seedbank as a result of removing topsoil to form the desert strips. The fact that seedbank species emergence was least from desert strip plots, and therefore provided less competition for seeded species may explain why the density of spiney hopsage, fourwing saltbush and rubber rabbitbrush was highest from these plots.

Germination Irrigation

Seeded Species Emergence—Emergence of nearly all species in plots receiving 80 mm of supplemental irrigation during March and April was similar to those plots not receiving supplemental irrigation (Figure 5, Table 1). Again, only Indian ricegrass and spiney hopsage had densities greater than one seedling/m^2. Indian ricegrass densities were highest from mulch/imprint plots, followed by drilled and mulch/drill plots, control plots, mulch/pit plots, and then desert strips. Seedling densities of spiney hopsage were greatest from desert strips and pitted plots, moderate from drill, mulch/imprint, and mulch/drill plots, and least from control plots.

Seedbank Species Emergence—Although variable among species, densities of seedbank species was generally higher with 80 mm of supplemental irrigation than with no irrigation (Figure 6, Table 2). *B. rubens* had the highest plant densities, followed by *D. sophia*, and *A. tessellata*. Densities for all other species were lower than 5 plants/m^2. Densities of *B. rubens* among seedbed treatments with supplemental irrigation was similar to that among seedbed treatments without irrigation, with the exception that drill and mulch/drill plots had greater densities in irrigated plots. *A. tessellata* densities were highest (p<0.05) from control and drill plots (both unmulched), and least from mulched plots. *D. sophia* densities in irrigated plots were more than four times higher in control, drill, and mulch/drill plots than in the same unirrigated plots.

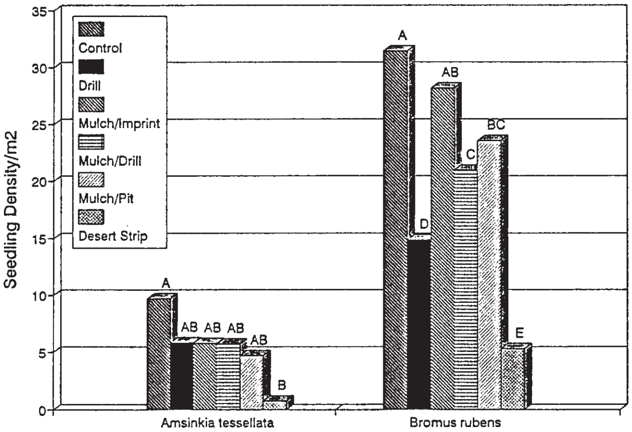

Figure 4—Seedling density of *Amsinkia tessellata* and *Bromus rubens* in relation to seedbed treatments with no supplemental irrigation. Seedbed treatment means for a species with the same letter are not significantly different (p<0.05).

Table 2—Seedling density of seedbank species in relation to seedbed and irrigation treatments. These species exhibited no significant differences ($p<0.05$) among seedbed treatment means.

Irrigation and seedbed treatment	*Amsinkia tessellata*	*Descurainia sophia*	*Mentzelia obscura*	*Phacelia fremontii*	*Phlox stansburyi*
	Density (m^2)				
No irrigation					
Control	*[1]	3.98	1.63	3.27	2.95
Drill	*	1.27	0.73	2.53	2.78
Mulch/imprint	*	0.77	0.82	2.87	1.43
Mulch/drill	*	0.57	1.02	2.70	2.97
Mulch/pit	*	0.47	1.02	2.17	3.52
Desert strip	*	2.61	0.52	0.47	0.53
Germination irrigation					
Control	*	*	1.47	3.40	4.97
Drill	*	*	1.93	2.67	2.98
Mulch/imprint	*	*	1.53	2.93	3.57
Mulch/drill	*	*	4.95	3.18	4.12
Mulch/pit	*	*	1.72	2.30	3.87
Desert strip	*	*	0.57	1.17	0.72
Maintenance irrigation					
Control	5.47	*	5.40	*	4.22
Drill	4.35	*	2.03	*	4.07
Mulch/imprint	2.63	*	2.43	*	2.63
Mulch/drill	3.97	*	2.00	*	3.45
Mulch/pit	2.95	*	1.95	*	4.53
Desert strip	0.80	*	0.82	*	1.07

[1] Seedling density means not shown were significant ($p<0.05$) and are shown in Figures 4, 6, and 8.

Maintenance Irrigation

Seeded Species Emergence—Due to the fact that irrigation rates and frequencies were the same for both irrigation treatments prior to seedling density data collection, densities of both seeded and seedbank species in plots receiving the two treatments should be similar. In general, this premise held true (Figure 7, Table 1). Again Indian ricegrass, and spiney hopsage emergence were greatest for most seedbed treatments, with densities of greater than 2 seedlings/m^2. Densities of all other seeded species, with the exception of Galleta grass and alkali sacaton, were below 1 seedling/m^2. Again, spiney hopsage densities in desert strip plots were significantly greater ($p<0.05$) than in any other treatment. Densities of

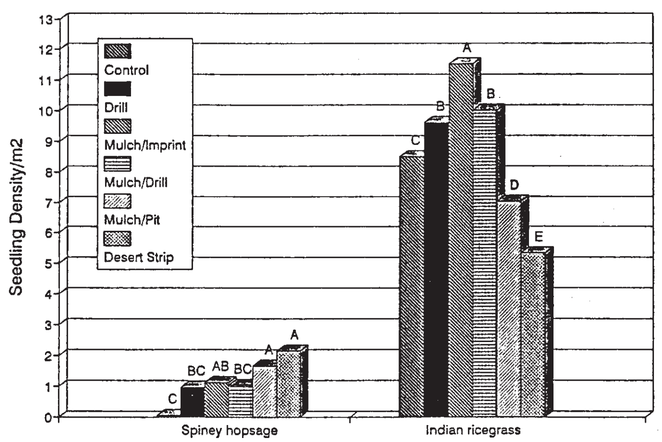

Figure 5—Seedling density of spiney hopsage and Indian ricegrass in relation to seedbed treatments with 80 mm of supplemental irrigation. Seedbed treatment means for a species with the same letter are not significantly different ($p<0.05$).

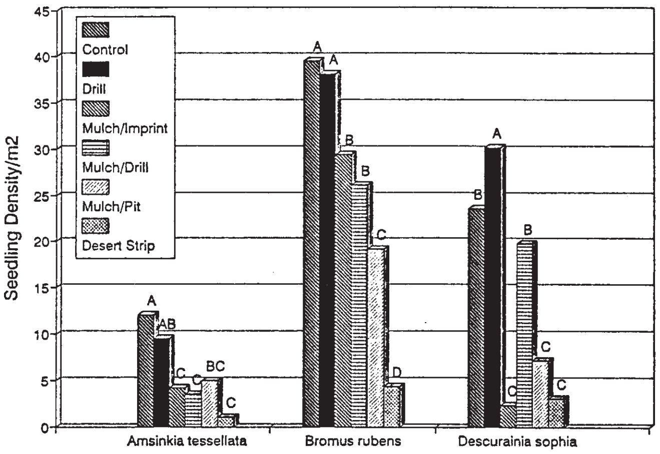

Figure 6—Seedling density of *Amsinkia tessellata*, *Bromus rubens* and *Descurainia sophia* in relation to seedbed treatments with 80 mm of supplemental irrigation. Seedbed treatment means for a species with the same letter are not significantly different ($p<0.05$).

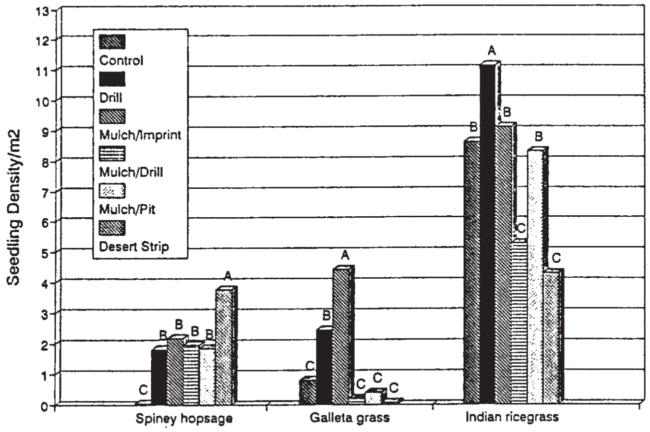

Figure 7—Seedling density of spiney hopsage, Galleta grass and Indian ricegrass in relation to seedbed treatments with approximately 230 mm of supplemental irrigation. Seedbed treatment means for a species with the same letter are not significantly different ($p<0.05$).

Galleta grass were greatest ($p<0.05$) in mulch/imprint plots, moderate in drill plots, and least in all other plots.

Seedbank Species Emergence—Densities of seedbank species were generally slightly higher in maintenance irrigation plots when compared to plots receiving the other irrigation treatments, although densities among seedbed treatments were variable (Figure 8, Table 2). *B. rubens* densities were greatest ($p<0.05$) in mulch/imprint plots, followed by control plots, drill and mulch/pit plots, and then mulch/drill. *B. rubens* densities were lowest in desert strip plots. Densities of *D. sophia* were similar in maintenance irrigation and no irrigation plots, and both were much lower than densities in germination irrigation plots for most seedbed treatments. Densities of both *M. obscura* and *P. fremontii* were highest in control plots, least in desert strip plots, and moderate for all other seedbed treatments.

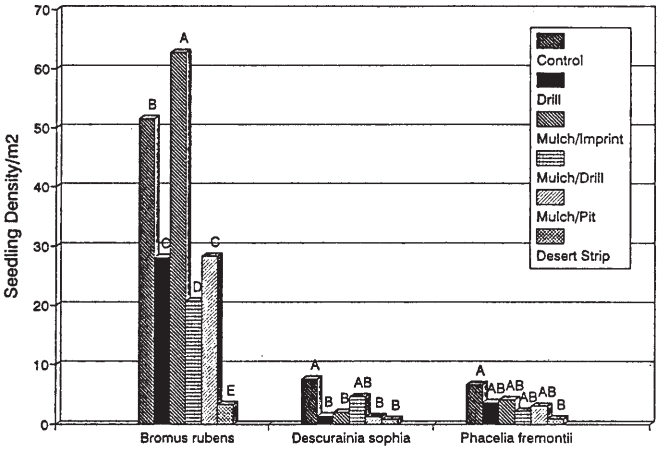

Figure 8—Seedling density of *Bromus rubens*, *Descurainia sophia* and *Phacelia fremontii* in relation to seedbed treatments with approximately 230 mm of supplemental irrigation. Seedbed treatment means for a species with the same letter are not significantly different ($p<0.05$).

Conclusions

In a year of above average precipitation, supplemental irrigation did not generally increase germination and emergence of seeded species, and only slightly increased densities of species from the native seedbank. If soil water was sufficient for germination, then other factors must have caused the limited emergence of most seeded species. These factors may have included one or more of the following factors. Fragile imbibed seeds may have been damaged by the application of the mulching, imprinting, pitting and crimping treatments that were delayed because of frozen soil. The germinability of the seed may have been lower than expected. Some of the seed may have been harvested by the rodent population at the site. Conditions such as proper light regimes, alternating temperatures, etc. may not have been adequate for the release of seed dormancy. Densities of some seeded shrubs were highest in desert strip plots, probably as a result of less competition in those plots due to decreased densities of seedbank species.

With the exception of increased shrub densities in desert strips, there were no strong seedbed preparation/ water harvesting treatment effects. Mulch treatments did not generally increase seedling densities. Seedling densities in imprinted and pitted plots were not generally any greater than those in plots applied with the other treatments. Land imprinting, pitting, and other water harvesting treatments function by concentrating rainwater from runoff. In a year of above average rainfall, extra water from water harvesting was probably not necessary to promote germination and emergence.

This study has shown that in a year of above-average rainfall, mulching and water harvesting treatments, and irrigation may not be necessary to insure adequate germination and emergence of adapted perennial grasses, forbs, and shrubs. Future collection of survival data will determine whether a maintenance irrigation program is necessary to ensure establishment of native plants in the Mojave/Great Basin Transition Desert.

Acknowledgment

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Results of Four Revegetation Treatments on Barren Farmland in the Owens Valley, California

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Sara J. Manning

Abstract—In 1991, 400 containerized fourwing saltbush (*Atriplex canescens*) shrubs were transplanted in the Owens Valley, Calif., under selected density, irrigation, fertilizer, and weed control treatments. Soil at the site, disturbed by previous agriculture, consisted of fine sand and cobbles with low electrical conductivity. Precipitation was below average the first growing season and above average the second. Results from two years demonstrated that irrigation was the most significant factor affecting survival. Planting density had little effect on survival and growth. Fertilizer had little to no effect on survival and growth the first year but increased growth the second year. Weed control increased survival and growth especially when shrubs were unirrigated and/or unfertilized or spaced close together.

The Owens Valley, in eastern California, constitutes the western edge of the Great Basin. The valley lies in the rain shadow of the Sierra Nevada mountains on the west and thus has an arid climate with low and erratic precipitation. Although precipitation is limited, snowmelt fills surface streams and recharges groundwater aquifers beneath the valley floor. Vegetation in the valley consists of a transition between Great Basin and Mojave floras; the valley floor is dominated by halophytic phreatophytes.

In the Owens Valley, the Los Angeles Department of Water and Power (LADWP) diverts these streams and pumps the aquifers to provide water to Los Angeles. Increases in pumping for export and the resulting adverse effects on the Owens Valley environment led to litigation between Inyo County and the City of Los Angeles. As partial resolution to the conflict, LADWP proposed to revegetate land that became barren due to increased water export. Thus, Inyo County and Los Angeles have begun preliminary studies to increase their knowledge of effective native plant revegetation techniques.

One revegetation study was initiated in 1991 to utilize fourwing saltbush (*Atriplex canescens*) seedlings left over from previous studies and to test various revegetation methodologies. Four treatments—irrigation, fertilization, planting density, and weed control—were selected to examine their effects on survival and growth of 400 shrubs transplanted on barren agricultural land. Available information on these treatments was either scarce or controversial, as discussed below.

Irrigation of transplants and seeds is commonly reported as essential for arid land revegetation (Packer and Aldon 1978), although Tyson (1984) claimed it would adversely affect long-term native plant survival. Knowing the advantages of irrigation is important for planning future revegetation projects because irrigation can be labor intensive, expensive, and impossible in remote areas. Overcoming these drawbacks however, has been the topic of recent investigations (Bainbridge 1991).

Two planting densities and weed control were also used as treatments. These were intended to provide insight into whether close spacing would ameliorate the microenvironment or be detrimental due to competition for resources. To improve the microenvironment by providing shade, mulch, and erosion control, one revegetation technique involves simultaneously planting a "nurse crop" to assist plant establishment (Ostler and Allred 1978). And to decrease competition, removing weeds has been reported as essential (Kay and Graves 1983) but labor intensive. Pendleton and others (1992) reported that density does not affect survival, but close spacing has been found to decrease growth (Aldon 1981).

Half of the shrubs received fertilizer as another treatment. Fertilizer has been hypothesized to decrease a plant's drought tolerance by increasing the shoot to root ratio (Virginia and Bainbridge 1987), but a greenhouse study found that fertilizer actually increased the root to shoot ratio (Holechek 1982). Fertilizer can also increase soil salts in alkaline soils; however, Romney and others (1989) reported that small amounts of slow release fertilizer enhance plant establishment and negative results occur when researchers apply fertilizer at recommended crop rates that are too high for native shrubs.

By combining the above treatments and tracking results for five years we hope to gain a better understanding of the most effective revegetation techniques for the Owens Valley. Results from this study will be used to plan subsequent revegetation efforts and to better direct future research.

Site Description

The project site is located in the northern Owens Valley. The site was cultivated until the 1920's when it was purchased by the City of Los Angeles and taken out of production. The site was again plowed in 1969 following a

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In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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winter of high runoff (D. Babb, LADWP, pers. comm.). Between crop production years, the land remained fallow and was used for grazing livestock. Currently the site has less than five percent vegetation cover consisting mainly of non-native weeds (LADWP unpublished).

The site has revegetation difficulties typical of abandoned agricultural lands. Cultivation created a leveled landscape with disrupted soil horizons. After abandonment, native species did not recolonize, topsoil was lost due to wind erosion, weedy species invaded, and groundwater pumping lowered the water table beneath the site.

The closest long-term weather recording station is located at the Bishop Airport, 4 km (2.5 mi.) SW of the site. Median annual precipitation recorded at this station for 48 years is 11.1 cm (4.4 in.) with 76% falling between November and March. The extreme fluctuations of precipitation result in a higher annual mean value of 13.7 cm (5.4 in.). Average winter minimum temperatures are below freezing and summer maximum temperatures are typically above 32.2 °C (90 °F) with low relative humidity.

The site is located near the toe of an alluvial fan. Due in part to the history of human disturbances in the Owens Valley, the pre-disturbance plant community is not known. Currently, rabbitbrush (*Chrysothamnus nauseosus*) is encroaching on the edges, and the site is dominated by a sparse cover of Russian thistle (*Salsola* sp.). Other species include poverty weed (*Iva axillaris*) and saltgrass (*Distichlis spicata*).

Soil at the site has been preliminarily mapped as Yellowrock-Seaman complex (Typic Torriorthents) (SCS unpublished). This soil type has developed from alluvial fan material consisting of mixed rock sources. The soil is mainly a loamy fine sand and is characterized as calcareous, well-drained and deep. Surface and 1.0 m deep electrical conductivity measurements ranged between 0.3 to 1.51 mScm^{-1}. Erosion from wind is listed as a severe potential hazard with this soil.

Groundwater pumping for irrigation occurs near the site. Although no piezometer is located on site, water levels in three nearby wells originally measured at 10.4 m-20.1 m (34.1-65.9 ft.) when installed in 1928 (from driller's well logs). They now measure 30.5 m-61 m (100.1-200.1 ft.) during the irrigation season.

Methods

Planting

The shrubs used in this study were started by Native Plants, Inc. (Utah) from seed not local to the Owens Valley. They were given to us in 1989 by Dr. Romney of the Nevada Test Site in Mercury, Nevada. In June 1990, the seedlings were transplanted from their original supercell containers and maintained for an additional one and a half years in 7.6 x 30.5 cm (3 x 12 in.) temporary tarpaper pots with open bottoms.

The study began in December 1991, when the fourwing saltbush plants were transplanted into a 46.5 x 62 m (153 x 203 ft.) livestock and rodent exclosure provided by LADWP. Planting holes were dug with a hydraulic drill mounted on a pickup truck. Holes measured 10.2 cm (4 in.) wide and were drilled 1 m (3.3 ft.) deep to facilitate planting and rooting.

Planting consisted of removing the temporary pot from the rootball, planting in the augered hole, and then immediately watering each shrub with approximately 2 l (2.1 qt.) of water. Plants were 3 to 4 years old at the time of planting. In late January, 11 plants that had died were replaced.

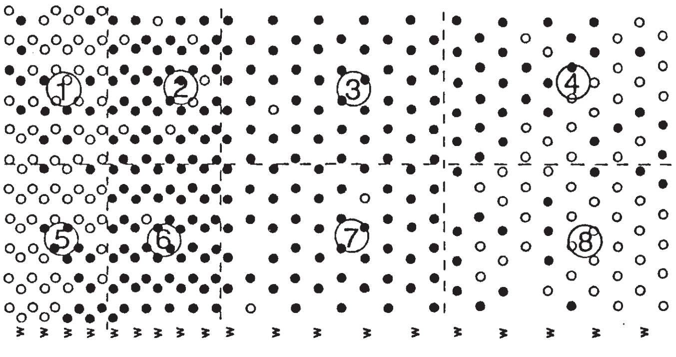
Treatments

Restrictions imposed by the high- and low-density treatments and the original intention to install a drip irrigation system made it difficult to randomize treatments; thus, plants were placed in a block design and shrubs were planted in rows to simplify monitoring (Figure 1).

Shrubs receiving supplemental water were planted with a vertically placed, perforated 2.5 x 38.1 cm (1 x 15 in.) PVC pipe. These tubes were used to ensure that irrigation water would reach the roots with minimal loss to surface evaporation and to discourage weed growth. Irrigated shrubs received 2 l of water once a month from April through September in both 1992 and 1993. All irrigation pipes were covered to reduce potential water loss in the subsurface soil and to keep out wildlife.

The density treatment consisted of spacing rows either 2 m (6.6 ft.) apart for low density planting or 1 m (3.3 ft.) apart for the high density treatment. Within rows, plants were spaced 2 m apart.

Shrubs in the fertilizer treatment received 10 g (0.4 oz.) of Osmocote 18-6-12 in a 9 month release form. This rate was approximately one-third of the recommended rate for horticultural plants. The fertilizer was placed near the bottom of the augered hole to reduce access to weedy species. Unfortunately, because the soil often collapsed into the holes after augering, the fertilizer was not consistently placed at the same depth in each hole.



Treatments
1. High density, unirrigated, unfertilized
2. High density, irrigated, unfertilized
3. Low density, irrigated, unfertilized.
4. Low density, unirrigated, unfertilized.
5. High density, unirrigated, fertilized
6. High density, irrigated, fertilized
7. Low density, irrigated, fertilized
8. Low density, unirrigated, fertilized

Figure 1—Planting scheme of study site showing shrub location, treatments, and live and dead shrubs after two growing seasons. Alternating rows were weeded as indicated by "w". Open circles are dead shrubs.

Weeds, primarily Russian thistle, within 0.5 m from the shrub were hand removed in April of both years. Removal was only necessary once a year because there was little to no regrowth following initial treatment.

Soil and Precipitation Data

To characterize the soil water content, samples were collected from the site prior to planting and when planting holes were augered.

Soil water content was measured to determine whether there were preexisting differences in the site subplots. Soil water content was derived by comparing the sample's field weight with its oven-dried weight. After June 1992 a neutron soil moisture gauge was used to expedite collection of water content data. Five access tubes for the gauge were installed, one in a control site and one in each irrigation/density treatment, approximately 0.5 m (1.6 ft.) from a shrub center. Measurements were taken in April and June 1992, and March, April, July, and November 1993. In July, readings were collected weekly to track water use before and after irrigation.

A rain gauge was installed 0.6 km (0.4 mi.) NW of the study plot in December 1991 and was used to measure precipitation at the site. Precipitation records from the Bishop Airport are used to compare long range patterns to current site precipitation.

Monitoring

Survival analyses only considered those plants that were alive in March 1992. Because shrubs were planted during the winter, death after three months was attributed to transplant damage or their initial poor vigor rather than to treatment effects. Due to the length of time these plants were held, their size and quality were variable. During planting we attempted to avoid lumping any one quality within a treatment.

Growth and survival were measured in January (for size at planting), March, June, and September in 1992 and in September 1993. Growth measurements consisted of recording each shrub's greatest height and width. These were then added together to derive an index of plant size. Differences in indices were used to track growth increases. All negative differences in growth were changed to zero because these plants were either not growing significantly or branches had broken but the shrubs were still alive. The difference in growth indices between years was examined in an analysis of variance for the individual treatments and the effects of interactions between treatments. The periods between January to September 1992 (first year), September 1992 to September 1993 (second year), and between January 1992 to September 1993 (overall growth) were used to analyze changes in growth.

Results

Precipitation Results

Annual precipitation the first and second year were very different (Figure 2). Prior to the study, precipitation in the Owens Valley had been below average for five years. Precipitation remained low, 78% of the mean, for the first year of the study. In contrast, the second year received unusually high precipitation, 142% of the mean.

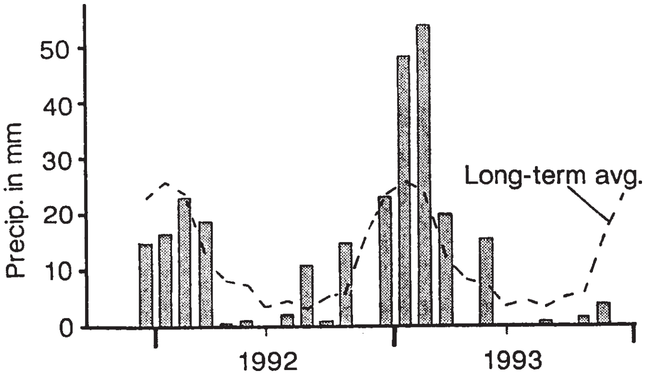


Figure 2—Monthly precipitation recorded at the study site compared to long-term trends.

Overall Survival

Of the 395 shrubs used for survival analysis, 75% survived the first growing season. The second season, an additional 36 shrubs died resulting in an 88% survival rate for that year. Overall survival of the original shrubs at the end of two years was 66%.

Single Treatment Results

Results of the four treatments appear in Table 1. Note that these "single treatment" results include combinations of the other treatments rather than representing an isolated treatment. For example, analysis of irrigated shrubs includes shrubs which did and did not receive fertilizer and weed control and that were planted in both high and low densities. It excluded all unirrigated shrubs regardless of other treatments.

Irrigation

Providing supplemental water greatly increased survival during the first dry year, 96% versus 54% (Table 1). During the second wetter year, survival rates in both the irrigated and unirrigated treatments were 98% and 70%, respectively. Overall, after two growing seasons, survival of irrigated plants was 57% higher than unirrigated plants.

Similar to survival rates, irrigation significantly increased growth the first year (p = 0.000). The following year there were no growth differences between the two treatments.

Density

Yearly survival differences tended to slightly favor the low density treatment. Overall, the low density treatment had an 11% greater survival rate than the high density treatment.

Table 1—Percent survival and growth index (GI) of fourwing saltbush transplants, categorized by single treatment effects. Standard error (SE) of growth index is also noted.

				Growth index					
	% Survival			1992		1993		Total	
Treatments	**Yr 1**	**Yr 2**	**All**	**GI**	**SE**	**GI**	**SE**	**GI**	**SE**
unirrigated	54	70	37	5	0.9	72	3.9	76	4.4
irrigated	96	98	94	12	0.6	72	1.6	84	1.9
lo density	78	92	72	8	0.7	72	2.3	79	2.6
hi density	72	83	61	9	0.8	73	3.5	81	4.0
unfertilized	78	87	68	8	0.7	62	3.3	68	3.8
fertilized	73	89	65	9	0.8	82	2.6	92	2.9
weeded	84	91	76	10	0.7	75	2.0	85	2.3
unweeded	67	84	57	8	0.8	69	3.7	75	4.2

High and low planting densities had negligible effects on shrub growth for all years. However, it is important to note that mortality, especially for the unirrigated shrubs in both density treatments, was high; thus density declined over the two year period.

Fertilizer

Fertilizer had a slightly negative effect on survival the first year, which disappeared the second growing season.

Fertilized and unfertilized shrubs exhibited similar growth rates the first year. The second year there was a significantly higher growth index for fertilized shrubs, ($p = 0.000$).

Weed Control

The first year, shrubs with weeds removed had a higher survival rate, 84% versus 67%. The second year, survival differences between the two treatments was less obvious. Overall, 76% of the shrubs with weed control survived compared to 57% of unweeded shrubs.

First year growth was significantly greater ($p = 0.043$) for shrubs with weed control than for unweeded shrubs, with growth indices of 10 and 7, respectively. The following year, although not statistically significant, growth differences still favored shrubs with weeds removed (growth index of 75 versus 69).

Multiple Treatment Results

Treatments were analyzed in all possible combinations of one to four treatments. The following are some of the more interesting findings.

Highest overall survival rates were found in all treatment combinations which included irrigation (Table 2). In fact, survival in all but one irrigation treatment exceeded 90%. The exception, 80%, occurred when irrigation was also combined with high density, no fertilizer,

Table 2—Percent survival and growth index (GI) of fourwing saltbush transplants, categorized by multiple treatments. Applied treatments—irrigation (I), low density (LD), fertilizer (F), and weed control (WC)—are indicated by the "x".

							Growth index					
				% Survival			1992		1993		Total	
I	**LD**	**F**	**WC**	**Yr 1**	**Yr 2**	**All**	**GI**	**SE**	**GI**	**SE**	**GI**	**SE**
	x		x	76	95	72	4	1.9	62	5.3	66	6.1
	x			56	86	48	2	2.2	56	6.5	55	7.4
x	x		x	100	96	96	16	1.7	67	4.6	83	5.3
x	x			100	100	100	13	1.7	54	4.5	68	5.2
	x	x	x	67	69	46	4	2.1	93	9.8	97	7.8
	x	x		30	57	17	2	3.2	72	11.3	74	12.9
x	x	x	x	96	100	96	14	1.7	94	4.6	108	5.3
x	x	x		96	100	96	11	1.8	76	4.7	87	5.4
			x	75	87	65	5	2.2	54	6.3	58	7.1
				41	8	3	5	2.4	60	22.6	57	25.8
x			x	96	96	92	11	1.7	78	4.7	89	5.4
x				88	91	80	6	1.8	67	5.1	72	5.8
		x	x	58	64	38	9	2.2	79	7.6	90	8.6
		x		32	62	20	9	3.0	103	10.1	113	11.5
x		x	x	100	100	100	13	1.6	76	4.4	88	5.1
x		x		100	96	96	12	1.8	66	4.6	77	5.3

and no weed removal. That same combination when unirrigated, resulted in the poorest survival of all groups, 3.4%.

Fertilizer did not necessarily improve survival. In the low density treatment, fertilizer had no effect on irrigated shrubs, but decreased survival of unirrigated shrubs. Fertilizer increased survival rates for irrigated high density plants. Effects of fertilizer on unirrigated high density shrubs was unclear.

Fertilizer increased growth for all treatment combinations during the second growing season except for high density, irrigated shrubs. That treatment combination resulted in average growth indices similar to those of the unfertilized shrubs.

Weed control was generally most beneficial when water stress was greatest, such as for unirrigated shrubs the first (dry) year. Thus, regardless of density or fertilizer treatment, unirrigated shrubs benefited from weed removal.

Although high density viewed as a single treatment resulted in only slightly lower survival rates than the low density treatment (Table 1), high plant density when combined with other "stresses"—such as no weed control or no irrigation—resulted in decreased survival (Table 2). For example, averaging survival rates for high density with no weed control revealed 50% survival, whereas those at a low density with no weed control had 65% survival. Also, high density unirrigated shrubs had 32% survival while low density unirrigated shrubs had 46% survival.

Soil Moisture

No correlation between density treatments and soil water content was apparent either before or after the study began. In April 1992, gravimetric soil moisture samples from the study plot ranged from 1.34% at the surface to 3.48% at 0.5 m in depth. Weekly neutron probe readings did not detect changes in soil moisture from irrigation treatments, possibly due to the small degree of change or because the irrigation water did not spread out as far as the access tube.

Discussion

Analysis of the applied treatments, combined with differences in precipitation during the first two growing seasons not only demonstrate that many variables interact in their effect on plant growth and survival, but also suggest reasons for conflicting results reported in the literature.

Irrigation was the most important factor contributing to fourwing saltbush survival; however, the degree to which irrigation affected survival was influenced by pre-growing season precipitation. Differences in survival rates and growth indices between irrigated and unirrigated shrubs were large after the first, dry year, but the difference narrowed after the second, wet year. This suggests that site precipitation plays an important role in survival results between irrigated and unirrigated treatments, especially when regional average precipitation is already very low. For management of revegetation sites, this finding illustrates the necessity for evaluating weather conditions after planting so that supplemental irrigation can be provided to avoid high transplant losses. Monitoring of these shrubs will continue for several years to evaluate the long-term consequences of providing supplemental irrigation on shrub survival.

The results of the fertilizer treatment in this study were complex. Conflicting results reported in the literature may be due to differences in plant density and available water. An increase in growth was measured in all but one treatment group with fertilizer, but it is unknown if growth translates into long-term survival, especially because some treatment combinations with fertilizer resulted in slightly lower survival rates.

Results indicated that fertilizer does not decrease transplant survival if there is enough available water. Survival differences between unfertilized irrigated shrubs was the same as fertilized irrigated shrubs. It is important to note that some of the fertilizer effects may have been delayed the first growing season because either the shrubs were unable to utilize it without adequate available water or the roots did not reach the fertilizer until the second growing season. Although the fertilizer was applied at one-third of the recommended rate, a lower rate may have had less of a negative effect on survival.

Weed removal was second to irrigation in terms of its effect on survival both years, and it was second to fertilizer in its effect on growth during the second year. The importance of weed control may be correlated with water availability; it was most effective when combined with unirrigated shrubs and during the first dry year. Thus for dry sites, weed control may be a simple means of improving transplant survival and growth.

An expected trend in the data was that plants subjected to the minimal number of "stresses" during the first two years experienced higher survival rates and growth. For example, irrigated, fertilized, unweeded plants spaced far apart had 96% survival after two seasons and an average growth index of 108. In contrast, unirrigated, unfertilized unweeded plants spaced close together had an extremely low survival rate after two seasons, 3%, and a low average growth index.

Our results showed that high transplant survival could be achieved by applying treatments that minimized plant stress. But survival and vigorous growth due to applied treatments may not lead to self sustaining plant populations. After two seasons, our results show that irrigation, low density, weed control, and to a limited extent, fertilization tend to enhance transplant survival and growth, but we do not yet know the consequences of suspending the treatments. We will continue to monitor the site for long-term survival and productivity of these shrubs and for recruitment of new native plant seedlings.

Methodological Notes

The irrigation tubes were successful at delivering water beneath the surface at the immediate base of the plant but a larger tube would have been preferable because infiltration rates were low.

Placing the fertilizer at depth appeared to keep it unavailable to weeds. Fertilized shrubs did not have more or larger weeds present. Using a slow release form allowed shrubs the opportunity to utilize it during the second year. It may have been more beneficial for the shrubs to use a smaller amount.

Weed control was relatively simple; young Russian thistle was easily removed and did not require a second treatment within the same growing season.

The open-bottom tarpaper pots worked well to keep the shrubs from becoming rootbound. But during planting, the pots should have been cut vertically several times and planted with the shrub. This would have greatly minimized root disturbance since shrub roots had grown through the tarpaper by the time they were planted.

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Ecology

Growth Factors for Woody Perennials at Western Sonoran Desert Wash Revegetation

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Roger D. Harris

Abstract—Growth factors were investigated on an experimental revegetation site in the western Sonoran Desert, located west of Blythe, Riverside County, California. Burro-weed (*Ambrosia dumosa*), creosote bush (*Larrea tridentata*), honey mesquite (*Prosopis glandulosa*), ironwood (*Olneya tesota*), and palo verde (*Cercidium floridum*) were planted in 11 desert washes over an area of 3.9 acres. Plant growth was positively associated with elevated soil electroconductivity (an indicator of salts and nutrients) and denser soils (clay rather than sand), as well as with higher irrigation rates. The association of the factors of higher electroconductivity and denser soil with plant growth was unexpected. This association represents an intercorrelation of these two soil factors, where the water retaining capacity of clay is greater when water is being regularly applied.

Five species of woody perennials were planted in an experimental revegetation effort in the western Sonoran Desert: burro-weed, creosote bush, honey mesquite, ironwood, and palo verde (LSA Associates 1992). Although some investigative work has previously been done for honey mesquite and palo verde (Anderson and Miller 1991; Anderson and Ohmart 1982, 1985), little is known about the autecological factors affecting growth of these species. The revegetation project allowed for an evaluation of some of these factors. We report on the first two years of this experiment.

Methods

Study Area

The revegetation site, located west of Blythe in western Riverside County, California, parallels the 100-foot-wide construction corridor of the Southern California Gas Company's natural gas pipeline 5000, which was installed in fall 1990. Revegetation was prescribed as partial mitigation for temporary disturbance of habitat of the threatened desert tortoise (*Gopherus agassizii*). The habitat is characterized by gently rolling bajadas at elevations of around 500 feet. Dominant vegetation is creosote bush scrub, intersected with desert wash scrub. The general area is dry; precipitation rarely exceeds 4 inches a year, with less than 1 inch in some years.

The revegetation effort, concentrated in 11 desert washes distributed along a 13-mile stretch of the former pipeline construction corridor, is oriented east and west. The construction corridor had been cleared of vegetation, but after construction the corridor was returned to its original contours. The top layer of soil had been reserved, and this was spread to conserve the naturally occurring seed bank.

Planting Plan

The choice of revegetation species reflected the dominant woody perennials on the site prior to construction. The plan was designed to allow separate analysis of shrubs and trees. Each revegetation area consisted of a central area planted in desert wash trees: palo verde, mesquite, and ironwood. Where a naturally barren low-flow channel existed through the wash system, that area was left bare and the peripheries to the east and west were planted. The tree plantings were buffered to the east and the west by a strip of desert shrubs: creosote bush and burro-weed.

Sampling Design

A subset of the total planting was intensively sampled and monitored. Parallel grids were established prior to planting. Sample points at planting locations along the grid were randomly selected for soil analysis and subsequent growth monitoring. Sample points were distributed at 63 burro-weed, 59 creosote bush, 65 palo verde, 65 honey mesquite, and 62 ironwood planting locations. Thus a quarter—13% of the shrubs and 70% of the trees—were intensively monitored.

Each sample point was staked and flagged; other planting points were just staked. Prior to planting, a soil sample was taken at each of the 314 sample points. A 16-inch-diameter hole was drilled with a tractor-mounted auger. Soil samples were taken from the first foot of soil and from near the bottom. Holes were designed to be 8 feet deep, but in some cases rocks or dry, dense clay prevented the auger from reaching the intended depth. In each case, the depth was recorded.

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Plant Installation

Since 1991 was a drought year with low prospects for revegetation success, the project was delayed until 1992. Seed was locally collected, placed in containers, and propagated in a green house during early spring of 1992. Before installation, container-grown plants were hardened outdoors near the revegetation site.

Container-grown stock was installed in April and May 1992 at densities of 100 trees or 400 shrubs per acre. Plantings of the three tree species were alternated on 15-foot centers over 1.4 acres, for a total of 92 palo verde, 91 ironwood, and 92 honey mesquites. Plantings of the two shrub species were alternated on 10-foot centers over 2.5 acres, for a total of 484 creosote bushes and 484 burro-weeds. A total of 3.9 acres was planted on parallel grids.

Soil Analysis

Soil samples were graded from –3 for sand to +3 for clay (Anderson and Ohmart 1982). Soil electroconductivity (EC) was determined from distilled water extracted from saturated soil. EC is a measure of dissolved solids, a reflection of soil salt content, and is expressed as millimhos of solute per cm of soil (mmhos/cm).

Irrigation

Irrigation systems consisted of a polyethylene 2-inch diameter mainline with 1/2 inch lateral lines placed every 10-15 feet along the main. Water was delivered to each plant through a 2-gallon per hour pressure compensating emitter. Water was brought to each site in a water truck five days per week during the growing season. Irrigation was not done during the dormant season. In year 2, as plant size increased, more water was required to sustain growth. To learn more about relationships between irrigation levels and growth, we subdivided samples of each tree species into those receiving 5, 9, 12 and 18 GPW beginning in July of the second growing season. Shrubs were divided into two groups: those receiving 5 GPW and those receiving 8 GPW.

Monitoring

Individuals planted at soil sample points were monitored each week from May through October. Monitoring consisted of measuring plant height from trunk base to the tip the tallest upstretched leaf. Growth during any period equals height at the start of the period subtracted from height at the end of the period. This, a simple measure of plant vigor, is predictably related to crown diameter (Anderson and Ohmart 1982).

Data Analysis

Multiple linear regression (MLR) was used to show relationships between growth over both seasons (SUMGR) and after additional irrigation was supplied in the second year (GR3). Because relationships between plant growth and variables affecting growth might not be simple linear relationships, the raw data were transformed in one or two ways. First, if distributions did not approximate normal, they were transformed using log10 of the value. Secondly, because curvilinear relationships could be associated with growth, we transformed all data to z-scores, where the mean equals 0 and the standard deviation equals 1. Horseshoe shaped relationships, those where growth increases as the variable increases to a certain level then decreases precipitously as more of the variable is added, are revealed by using the square of the standardized scores in the MLR. Another simple curvilinear relationship is where, for example, growth increases as the variable increases to a point at which growth levels off as more of the variable is added over a considerable range of the variable, then, increases sharply again as the variable becomes more abundant. This can be determined by using the cube of the standardized values in the MLR involving growth. These descriptions are of positive relationships; the reverse represents negative relationships (Anderson and Ohmart 1984; Meents and others 1982).

For a clearer understanding of how the MLR results actually relate to growth, for each species we divided the sample into three groups on the basis of the variables contributing to the MLR result. For example, if two variables were involved, group 1 included all individuals greater than the mean for both variables; group 2 included all individuals where the values for these variables were less than the mean for the entire sample, and group 3 included individuals above the mean for one variable and below the mean for the other. Differences among groups for variables or growth were tested with a t-test. The form of the t-test was determined by whether or not variances in compared groups were equal at P>.05.

Results

Growth of Shrubs and Environmental Variables

Significant MLR equations were obtained for both shrub species but the variables involved were different (Table 1). For burro-weed the level of irrigation was significant, but not for creosote bush. Burro-weed showed an association with soil containing more clay (+soil values) at shallow levels; creosote bush was associated with clay at deeper levels. Burro-weed was complexly associated with soil EC. If surface EC levels were high, growth was stunted, but growth was better where EC at deeper levels was higher. These relationships accounted for 16% of the variance in total growth. Creosote bush, too, was stunted where surface EC levels were higher, but at deeper levels, EC apparently did not affect growth after two seasons. The environmental variables explained 11-16% of the variance associated with GR3.

Burro-weed

For the purposes of analysis we divided the burro-weed plants into three groups: (1) included those irrigated >5 GPW and with deep soil EC values >0.7 mmhos/cm (N=22); (2) irrigated levels <5 GPW and with deep soil EC values <0.7 mmhos/cm (N=18); and, (3), with these two factors

Table 1—Factors entering significant regression equations of correlations between growth and environmental variables. SS, SD=soil type near the surface and at deep levels, respectively, ZS4CB=z-score of soil from deep levels cubed, LEC1=log10 of the EC of near surface soil, ZEC1SQ=z-score of the near surface soil EC squared, LEC4CB=z-score of the deep soil EC cubed, EC4=log10 of the EC at deeper soil levels, IRR=irrigation level in gallons per week.

Species	Percent total variance acc't for	Variables entering MLR and associated probability levels								
		P	SS	SD	ZS4CB	LEC1	ZEC1SQ	LEC4CB	LEC4	IRR
Burro-weed	16	.04	.052			–.110			.030	.044
Creosote bush	11	.03		–.019		–.019				
Palo verde	18	.01		.010	–.011		–.021			
Honey mesquite	19	.01			.002					.279
Ironwood	21	.01						–.067	.190	.029

mixed (N=21). Those in group 1 grew about 10 inches more (60%) than those in group 3 (Fig. 1). Group 1 received more water during the second growing season and soil EC was significantly greater relative to plants which grew least. Assuming equal variances (P=.1), t=2.54, P=.015. Differences in soil type or DAH were not significant. The middle category had intermediate values for environmental variables and for growth over both seasons (SUMGR).

Creosote Bush

For purposes of analysis, the creosote bush cohort was also divided into three groups: (1) including those where SD was >–.25 and LEC1 was >.05 (N=14); (2) those where both of these variables were < the values in group 1 (N=29); and (3) those where the variables were mixed (N=15). The results (Fig. 1) indicate that group 1 individuals did not

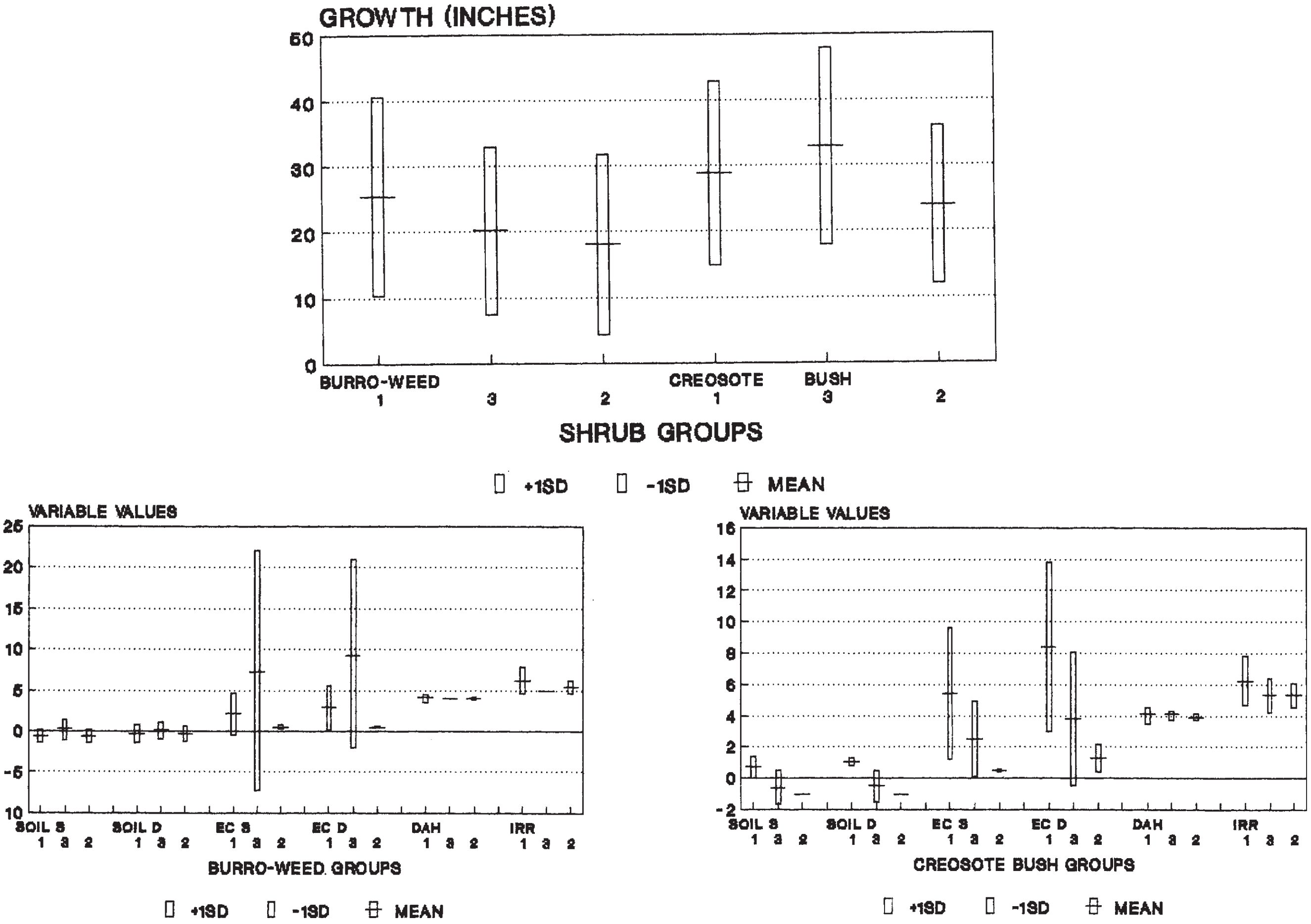

Figure 1—Growth of burro-weed and creosote bush and environmental conditions associated with each of three groups of plants. The rectangles include one standard deviation above and below the mean. Means are represented by the horizontal lines. See text for explanation of groups for each species. Soil S=soil from the surface, Soil D=a deep soil sample, EC S and EC D=soil electroconductivity near the surface and at a deep level, respectively, DAH=depth of augered hole, Irr=irrigation rate in gallons per week.

have significantly better growth than those in the group with lower irrigation and lower soil EC. However, group 3 did grow about 9 inches more (39%) than the group with lower irrigation and lower soil EC levels. This difference is statistically significant (P of equal variances =.7, T=2.2, 2-tailed P=.03). This group also had significantly higher soil salinity levels and averaged less sand in the soil, such that, when all soil samples are combined, the difference is significant (P<.05).

Growth of Trees and Environmental Variables

The MLR analysis revealed a significant correlation between GR3 and environmental variables for all three tree species (Table 1); four of these were curvilinear relationships. Palo verde growth related to soil type and EC levels in complex ways involving curvilinear soil and EC relationships (Table 1). These relationships explained 18% of the variance in GR3 for palo verde.

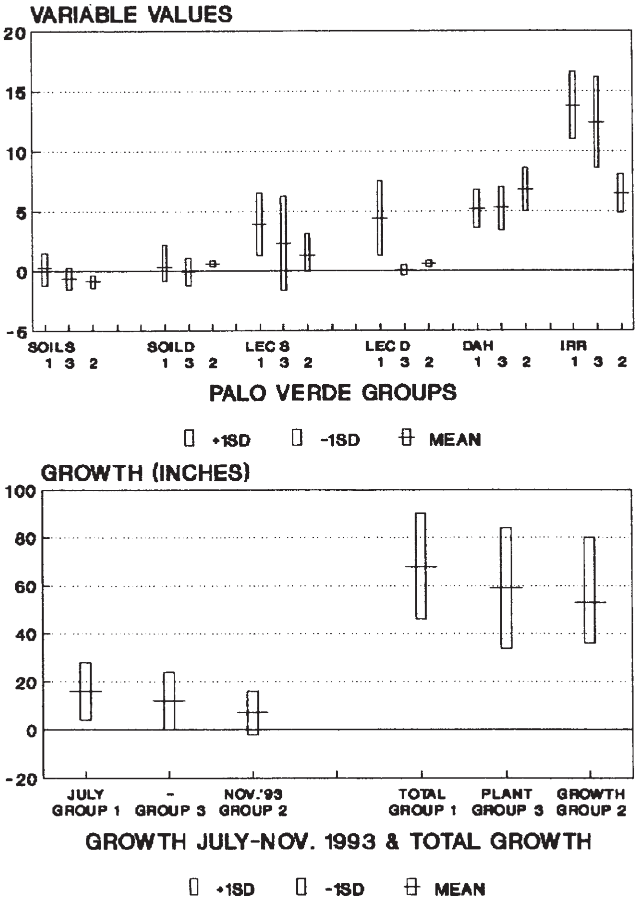

Figure 2—Growth of palo verde across two growing seasons and from July to the end of the second growing season after additional irrigation water was supplied. The top graph shows values for environmental variables associated with palo verde. Abbreviations as in Fig. 1.

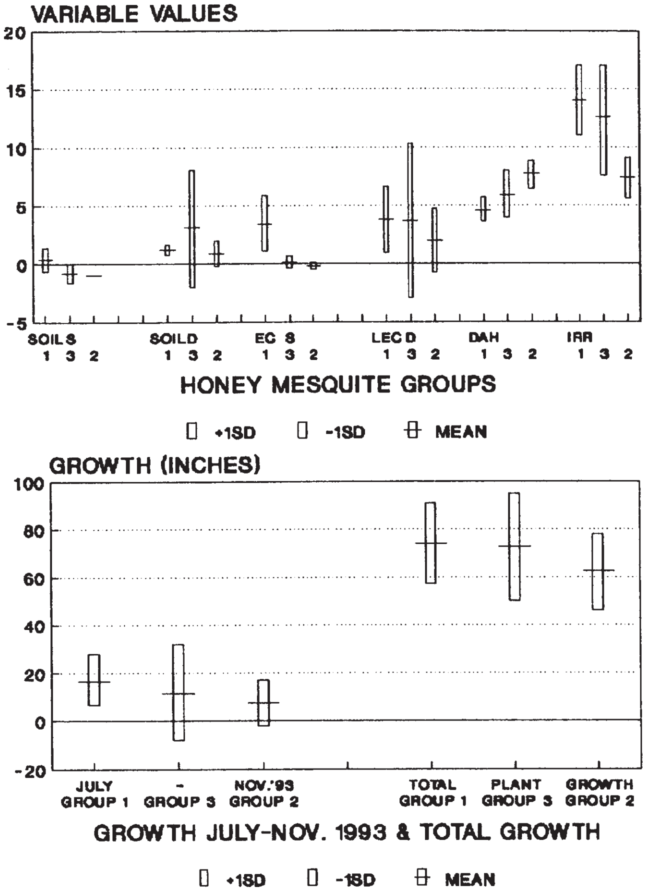

Figure 3—Growth of honey mesquite across two growing seasons and from July to the end of the second growing season after additional irrigation water was supplied. The top graph shows values for environmental variables associated with honey mesquite. Abbreviations as in Fig. 1.

Palo verde—Palo verde trees were placed into three groups: (1) irrigated >11 GPW and with surface EC levels >1.47 mmhos/cm (N=24), (2) irrigated <12 GPW and with soil EC levels <1.5 mmhos/cm (N=12), and (3) mixed conditions (N=29). Trees in group 1 grew about 15 inches more (28%) than those for group 2 (SUMGR). Assuming equal variances (P=.3), t=2.3, P=.09. Growth after additional irrigation was supplied the second year (GR3) in group 1 was about 9 inches more (118%) than in group 2. Again assuming equal variances (P=.4), t=2.3, P=.03. Group 1 had significantly more clay in the soil (+ soil type values), significantly higher soil EC levels, shallower augered holes, and was irrigated more (Fig. 2).

Honey mesquite—Honey mesquite trees were divided into three groups: (1) individuals irrigated >11 GPW and with deep soil samples averaging >–.1 (N=21), (2) both of these variables had values less than values for group 1 trees (N=12), and (3) those individuals with mixed values (N=31, Fig. 3). SUMGR was about 11 inches (18%) greater for trees in group 1 than group 2. Assuming equal variances (P=>.9), t=1.94 and P=.063. For GR3 growth was 9 inches greater (120%) for trees in group 1 relative to

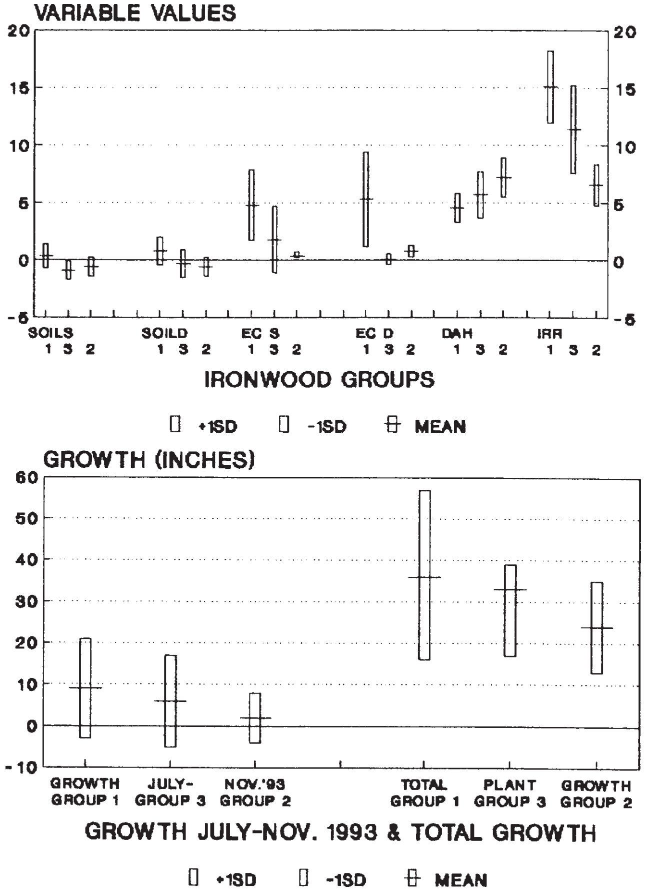

Figure 4—Growth of ironwood across two growing seasons and from July to the end of the second growing season after additional irrigation water was supplied. The top graph shows values for environmental variables associated with ironwood. Abbreviations as in Fig. 1.

group 2. Again assuming equal variances (P=.5), t=2.5 and P=.019. At points where group 1 trees were planted, the soil had significantly (P<.05) more clay and higher soil EC (Fig. 3). Depth of tillage (DAH) was significantly less and irrigation was significantly more for trees in group 2 (Fig. 3).

Ironwood—Ironwood trees were placed into three groups: (1) irrigation >11 GPW and deep soil EC values > 2.19 mmhos/cm (N=23), (2) smaller values than stated for group 1 (N=10), (3) mixed values (N=29., Fig. 4). SUMGR for the group 1 was 13 inches more (53%) than for group 2. Assuming equal variances (P=.06), t=1.9, P=.07. For GR3, trees in group 1 grew 7 inches (351%) more than trees in group 2 (Fig. 4). Assuming equal variances P=.46), t=2.5, P=.019.

Discussion

It is not surprising to find growth of trees and shrubs to be related significantly to soil variables. Beyond that generality, however, the nature of these relationships is not as expected in a majority of cases. The greatest growth was associated with greater soil clay content for all three tree species, although for neither shrub species. This is not expected because the clay was unusually dense in some of the soil. Ordinarily, roots struggle to penetrate dense soil and growth is often retarded. Even more surprising was the association of high growth with increasing EC. If the soil were depauperate of nutrients, this might be expected. Anderson and Vasquez (1993) for example, found stunted growth in nutrient poor soil for cottonwood (*Populus fremontii*). But the EC levels in the current situation are relatively high, higher than might be expected for normal growth of honey mesquite. Soil EC tolerances for palo verde and ironwood are unknown. Burro-weed also grew best in the more saline, albeit somewhat sandier, soils. Salinity levels, especially above 8 mmhos/cm, are generally found to stunt growth (Anderson 1989). High growth was consistently associated with soil EC in excess of 8 mmhos/cm (Figs. 1, 2).

Deep tillage promotes growth (Anderson 1988a, 1989; Anderson and Ohmart 1982). But in this study, deep tillage was associated with poor growth. Not surprisingly, the best growth for all five species was significantly associated with larger irrigation amounts at P=.05 for four of them. In the fifth case, creosote bush, the best growth was associated with above average irrigation rates. The averages attained only a marginal level of statistical significance (.1>P>.05), but this may be biologically significant. The association of growth and water allows for the unraveling of these unexpected associations.

The correlation between soil type and soil EC was significantly positive such that the variance of one accounted for roughly 25% of the variance in the other. This means that as the amount of clay in the soil increased, soil EC also tended to increase. We have found this to be generally true in the entire lower Colorado River Valley (Anderson 1988b). This is reasonable—solutes are leached from coarse soil more readily than from dense soil, the result is lowered EC levels. Because plants tended to grow most where salinity was higher it is not surprising that soil type was also higher; more clay and higher EC tended to correspond.

The positive correlation between clay soil and high EC also explains the relationship between tillage depth and plant growth. Our auger drills to 8 feet deep in 30 seconds or less in sand. In this study area we could not drill a hole to 8 feet even in 5 minutes because the soil was so hard and dense. Areas with more clay had shallower holes and that's why growth tended to be greatest where tillage was shallowest. Before answering the question of why growth was associated with dense, saline soils, we discuss growth in relation to irrigation level.

Growth was positively associated with irrigation; that is, more water led to more growth. However, even 16 GPW, the largest amount supplied in this study, is really not very much water, and it did not lead to optimal growth. At the same time that honey mesquite receiving 16 GPW on this project grew 16-17 inches, individuals of this species on another project supplied 40-45 GPW grew 45-50 inches (Anderson, unpublished data). In context of this study, it is clay soil that retains water best. Even when water is supplied on a daily basis, sandy soils may lose water quickly through a combination of plant use and drainage. Clay soil in desert areas may actually lose water more quickly by capillary action than, say, fine sand when water is not being frequently applied. Loss by capillary action is accelerated by the hot mid-summer desert temperatures.

Another point bears emphasizing. Laboratory analysis of soil EC is done on water pulled by a vacuum pump from soil saturated with water. When a soil with a saturated soil EC of 3 mmhos/cm is at the fringe of field capacity, the water available to a plant contains salts at a higher concentration than at saturation—perhaps as high as 9 mmhos/cm. This means that low EC levels for coarser soils are in effect often higher than soil paste extracts indicate because of water drainage from the soil. Water retention properties of dense soil dilute the salts; EC is closer to the values obtained from saturated soil. Since we do not plan to continue irrigating these plants indefinitely, what does this mean in terms of future survival?

When we stop irrigating, coarse soils will become even drier. Dense soils will lose water quickly through capillary action and salts will concentrate. Roots in these places are likely to be rather shallow, constrained by the packing action of the auger on the sides of the hole and by the density of the soil itself. Unless they find a crack through which to escape and follow a trickle of water to some point protected from dissection, these plants are likely to perish. Plants may prosper if located in washes at points where the soil is coarse enough to allow deep root penetration (facilitated by a deep augured hole) but dense enough to retain water long enough to allow the plant to remain alive between the infrequent occasions when the soil is recharged with water. The more drought tolerant species (creosote bush) have a better chance of survival than the least drought tolerant (honey mesquite). Copious research on several species, including honey mesquite and palo verde, indicates that after irrigation ceases, inadequate tillage, high soil clay content, or high EC levels, acting individually or in concert, take their toll (Anderson 1988a, 1989; Anderson and Miller 1991; Anderson and Ohmart 1982, 1985).

Acknowledgments

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Spatial and Temporal Variability of Microbes in Selected Soils at the Nevada Test Site

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W. K. Ostler
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Abstract—Large land areas encompassing almost 700 hectares on the U.S. Department of Energy Nevada Test Site, Nellis Air Force Range and the Tonopah Test Range are contaminated with plutonium. Plutonium decontamination of these sites may involve removal of plants and almost 370,000 cubic meters of soil from the sites. The soil may be subjected to a series of plutonium removal processes. After decontamination, the soils may be returned to the site and revegetated. Because a paucity of information exists on the microbial components of the Mojave and Great Basin Deserts, especially how the components vary spatially and temporally, this study was initiated to determine baseline microbial activity and biomass in soils prior to decontamination. Information from this study will aid in determining the effects of plutonium decontamination on soil microorganisms, and what measures, if any, will be required to restore microbial populations upon subsequent revegetation of these sites. Soils were collected to a depth of 10 cm along each of five randomly located 30-m transects at each of four sites. In order to ascertain spatial differences, soils were collected from beneath major shrubs and from associated interspaces. Soils were collected at 3 to 4 month intervals to determine temporal (seasonal) differences in microbial parameters. Analysis showed that soils from beneath shrubs generally had greater active fungi and bacteria, and greater non-amended respiration than soils from interspaces. Temporal variability in the microbial components were found, with total and active fungi, and non-amended respiration being highly correlated to soil moisture at the time of sampling.

Large land areas on the Nevada Test Site, Tonopah Test Range (TTR), and the Nellis Air Force Range (NAFR) were contaminated with plutonium (Pu) during safety tests conducted in the late 1950's and early 1960's. The Resource Conservation and Recovery Act (RCRA), and the Comprehensive Environmental Response, Compensation and Liability Act (CERCLA) may require that these sites be decontaminated. Plutonium decontamination of these areas will potentially involve the removal of the upper 5-10 cm of topsoil. Because of the large soil volume involved, an examination of alternatives for separating Pu from the soil prior to disposal is required to minimize the quantity of disposed soil. Many of the Pu separation processes will require destruction of soil structure and washing of the soil particles. The impact of these processes on the viability of soil organisms such as bacteria, fungi, algae, protozoa, and nematodes is not known. In order to ascertain how plutonium decontamination will affect the microbial population, an assessment of the spatial and temporal variability of microbes must be conducted to provide baseline information on how the decontamination processes will affect the soil microbial components. The baseline information will also provide guidelines for re-establishment of the microbial population during subsequent reclamation after decontamination of these sites.

In deserts, the topsoil is a valuable ecosystem component serving as a source of nutrients and water (Ostler and Allred 1987; Wallace 1980). The upper 5-10 cm of soil contains the majority of the seed bank and a large percentage of the living organisms associated with nutrient cycling (Foth and Turk 1972). The soil microbial population (bacteria, fungi, algae, etc.) plays an important role in ecosystem stability. Microbial processes essential to ecosystem stability include soil structure development, the synthesis of various plant nutrients through biogeochemical cycling, and the improvement of unfavorable physical and chemical conditions (Tate 1985). The productivity of any ecosystem, whether undisturbed or disturbed, is dependent on the resident microbial community. The availability of organic matter and soil water can have a great influence on microorganisms in desert soils (Dommergues and others 1978; Focht and Martin 1979). Microbial numbers are closely associated with the amount of organic material available for breakdown and uptake (Fuller 1974). Generally, microbial species diversity and biomass varies more in deserts than in other ecosystems (Kieft 1991).

A paucity of information exists on the microbial components of the Mojave and Great Basin Deserts, especially how the components vary spatially and temporally. In other arid and semi-arid ecosystems, spatial and temporal variability in soil microbial populations has been documented. Spatial variability exists within a site, with soils from beneath plants generally having greater microbial

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numbers and diversity than soils associated with bare areas (Fuller 1974). Litter accumulation, windblown soil and plant material, and greater root biomass beneath perennial plants leads to the creation of "fertile islands" (Garcia-Moya and McKell 1970), which tend to have greater microbial activity. In the Chihuahuan desert, microbial biomass was 3.6 times higher, and organic carbon was 2.6 times higher underneath canopies of *Larrea tridentata* when compared to associated bare areas (Kieft 1991). Bacterial numbers were greater in soil beneath *Prosopis glandulosa* than in soil in interspaces (Baker and Wright 1988). Spatial and temporal variability can be the result of variable soil moisture conditions (Skujins 1984), litter inputs, and physical stress (Kieft 1991). In the Chihuahuan desert, bacterial and fungal numbers did not fluctuate during repeated wetting and drying of the soil; in contrast, protozoan numbers fluctuated with the wetting and drying cycles (Parker and others 1984). The spatial and temporal variability in soil microbial components brought about by varying moisture, temperature, litter inputs and plant cover poses problems for a single point in time sampling of the microbial population. Therefore, sampling of microbial populations should be continued over a significant period of time to properly address microbial population variations (Parkinson 1978).

Objectives and Hypotheses

The principal objectives of this study were to: 1) determine the spatial variability in soil microbial components (bacteria, fungi, and respiring biomass) within and between selected sites and 2) determine the temporal (or seasonal) variation in soil microbial components within selected sites. The hypotheses of this study were: 1) soil microbial components would vary spatially within sites, with soils from beneath perennial shrub canopies having greater microbial activity and biomass than soils in associated interspaces (bare areas); 2) soil microbial components would vary over time because of seasonal differences in soil moisture; 3) soil microbial components would vary between sites due to differing soils and climatic patterns.

Study Area and Methods

Soil microbial samples were collected from soils adjacent to Pu-contaminated areas in Area 5 and Area 11 of the Nevada Test Site, Area 13 of the Nellis Air Force Range and Clean Slate 1 of the Tonopah Test Range (Figure 1). These sites follow a general south to north elevation and temperature gradient with Area 5 having the highest temperatures and lowest elevation and Clean Slate 1 having the lowest temperatures and highest elevation (Table 1). Average annual precipitation collected at nearby sites indicated that precipitation is lowest in Area 5 and highest in Area 13. Soils in Area 5 are gravelly, sandy loams and vegetation is typical of the lower Mojave Desert (Table 1). Area 11 has gravelly loam soil and is the most ecologically diverse, containing elements of both the Mojave and Great Basin Deserts. Area 13 and Clean Slate 1 have gravelly sandy loam soils and have vegetation that is typical of the Great Basin Desert.

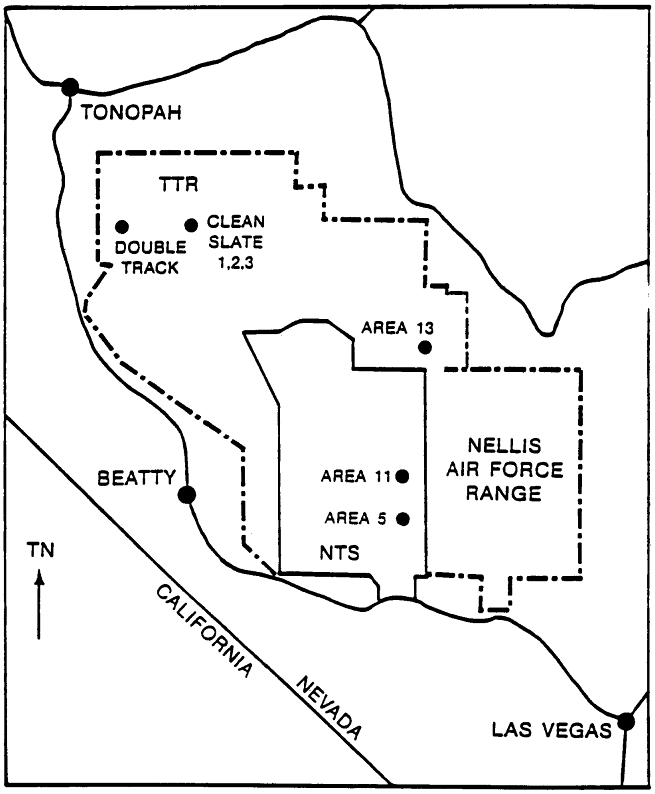

Figure 1—Location of plutonium contaminated sites where baseline microbial samples were collected. Tonopah Test Range = TTR. Nevada Test Site = NTS.

Five random 30-m transects (replication) were established in uncontaminated areas at each site. In order to ascertain spatial variability, stratified sub-samples were collected at 20 locations along each transect; 10 beneath the canopy of the dominant shrub species (Table 1) and 10 in adjacent interspaces. Samples were collected with a 6-cm-diameter metal cylinder that was inserted into the soil to a depth of 10 cm. Each of the ten sub-samples from each zone were combined into one bulk sample. Samples were analyzed within 48 hours for microbial numbers and biomass. The bulk sample was treated as the experimental unit for each corresponding location, transect and site. Soil microbial samples were collected on three occasions: August 1992, December 1992, and April 1993.

The experimental design for this study was a split plot with five replications. The whole plot variables were site and date of collection, and the split plot variable was zone (beneath shrub or interspace). General linear model procedures (analysis of variance) (SAS 1984) were conducted on means for the variables being measured to test for the significance of variables and their associated interactions. Fischer's Least Significant Difference mean separation procedure was used to determine significant differences among means. T-tests were used to separate means for zone effects. Appropriate error terms (those used to test significance of the variable or interaction in the analysis of variance) were used as the variance in the mean separation procedures.

Table 1—Comparison of sites contaminated with plutonium at the Nevada Test Site, Nellis Air Force Range, and Tonopah Test Range used for determination of baseline spatial and temporal variability of soil microbial components.

Site	Elevation	Soil type	Major perennial species	Latitude	Longitude	Annual rainfall	January max - min temperature	August max - min temperature
	(m)					*(mm)*	*(°C)*	*(°C)*
Area 5	997	Gravelly, sandy loam	*Larrea tridentata* *Ambrosia dumosa* *Acamptopappus schockleyi*	36° 50' 38"	115° 56' 07"	124[1]	12, –3	34, 17
Area 11	1257	Very gravelly loam	*Menodora spinescens* *Atriplex confertifolia* *Chrysothamnus viscidiflorus*	36° 58' 32"	115° 57' 24"	170[2]	11, –6	34, 15
Area 13	1390	Gravelly, sandy loam	*Atriplex confertifolia* *Ceratoides lanata* *Kochia americana*	37° 19' 09"	115° 54' 20"	185[3]	8, –1	31, 19
Clean Slate 1	1644	Gravelly, sandy loam	*Hilaria jamesii* *Atriplex confertifolia* *Artemisia spinescens*	37° 42' 30"	116° 39' 25"	135[4]	3, –4	28, 16

[1] Precipitation and temperature data are from long-term averages of the Area 5 - B National Weather Service weather collector (approx. 2 miles west of the site).

[2] Precipitation and temperature data are from long-term averages of the Yucca Lake National Weather Service weather collector (approx. 5 miles west of the site).

[3] Precipitation and temperature data are from long-term averages of the P-H Farm National Weather Service weather collector (approx. 14 miles southwest of the site).

[4] Precipitation and temperature data are from long-term averages of the Tonopah Airport National Weather Service weather collector (approx. 16 miles northwest of the site).

Microbial analyses were conducted by Microbial Biomass Services at Oregon State University in Corvallis, OR. Samples were analyzed to determine active and total fungal biomass, and active bacterial numbers and biomass by counting FDA (fluorescein diacetate) stained bacteria in agar-film soil suspensions (Lodge and Ingham 1991). The active component is important in determining the activity levels of the fungi or bacteria at different times of the year and how these relate to environmental conditions.

Non-amended soil respiration (Page 1982) and glucose-amended respiration were determined for samples. Determination of non-amended soil respiration is a useful tool in assessing the total respiring biomass of microbes in the soil. Increases in soil respiration over time indicates greater respiring microbial biomass. At times, respiration rates may be low due to limited degradable carbon sources. Glucose-amended respiration is a useful tool in determining if a soil is carbon-substrate limited. A comparison of the respiration rate of a non-amended soil to the respiration rate of the same soil that has had a glucose mixture (a readily degradable carbon substrate) added to it, can give an indication of the amounts of readily degradable substrates that are available to the respiring biomass (Parkinson and Coleman 1991). Increases in the respiration rate from the glucose-amended soil over that of the non-amended soil may indicate that the non-amended soil is carbon-substrate limited. Also, the amount of time it takes for a soil to reach maximum respiration after substrate addition can be indicative of the physical and chemical stresses to the soil, with stressed soils requiring more time to reach peak respiration (Visser et al. 1984; Visser and Parkinson 1989).

Soil moisture was measured gravimetrically at the time of respiration determination. Determination of soil moisture at the time of sampling allowed assessments of moisture stress, if any, during that sampling period. Because soil moisture varies temporally, it can be used as a correlation variable to assess temporal differences in microbial components.

Results and Discussion

Active and Total Fungal Biomass

Analysis of variance for active fungal biomass indicated a significant site-date of collection-zone interaction (Table 2). Site and zone were not significant main effects. Date of collection was highly significant, indicating that this variable had the greatest influence on the three-way interaction. Active fungal biomass means ranged from 0.0 to 4.6 µg/g soil dry weight with an overall average of 1.2 µg/g. The analysis of variance for total fungal biomass indicated a significant interaction between site, date of collection and zone (Table 2). In contrast to active fungal biomass, the main effects of date of collection and zone were reversed, with zone being a significant main effect and date of collection not significant. This may be an indication that total fungal biomass does not vary widely over time across sites, but the activity levels may vary widely.

Zone Influences—Mean active fungal biomass (µg/g soil dry weight) beneath perennial shrubs and in interspaces was not significantly different for each site and sampling date except for Area 5 during the December sampling (Figure 2). Total fungal biomass varied significantly between zones in Area 11 and 5 during the August 1992 sampling, Area 11 during the December 1992 sampling, and Area 13 during the April 1993 sampling. Area 5 had significantly greater active and total fungal biomass beneath shrubs. Area 11 exhibited significantly greater total fungal biomass beneath shrub canopies during August, but exhibited

Table 2—Analysis of variance levels of significance (p-values) for site, date of collection, zone (interspace or under canopy) and interactions of these variables for determining sources of variation in active fungal biomass, total fungal biomass, active bacterial numbers, non-amended respiration, glucose amended respiration and gravimetric soil moisture. Main effects and interactions were considered significant if the p-value was less than 0.05.

Variable	Active fungal biomass	Total fungal biomass	Active bacterial numbers	Non-amended respiration	Glucose amended respiration	Soil moisture
Site	0.8113	0.1490	0.3955	0.0753	0.0743	0.5146
Date (of collection)	0.0004	0.2747	0.0548	0.0002	0.0929	0.0004
Zone	0.8940	0.0065	0.0001	0.0001	0.0001	0.0004
Site*Date	0.3238	0.0134	0.0001	0.0091	0.0001	0.0001
Site*Zone	0.0034	0.1439	0.8863	0.0305	0.0001	0.3750
Date*Zone	0.3885	0.0233	0.0017	0.0001	0.0001	0.1633
Site*Date*Zone	0.0001	0.0002	0.1517	0.0006	0.0107	0.0002

greater active and total fungal biomass in the interspaces during the December sampling. Area 13 had greater total fungal biomass beneath shrub canopies during the April sampling.

Date of Collection Influences—Variability in active fungal biomass on a temporal scale was apparent and appeared to be related to soil moisture conditions. The December sampling period generally had significantly higher fungal biomass followed by the April sampling date (Figure 2). The differences in biomass for these dates closely resembled the pattern of soil moisture (Figure 3) for these sites. Soil moisture was positively correlated to active fungal biomass (r = 0.53; Table 3) for all sites regardless of zone. However, correlation analysis on the means for each zone over time indicated that interspace active fungal biomass was strongly correlated to soil moisture (r = 0.71), whereas under canopy active fungal biomass had a low correlation (r = 0.33; Table 3). This may indicate that the activity of fungi under plant canopies is less dependent on soil moisture.

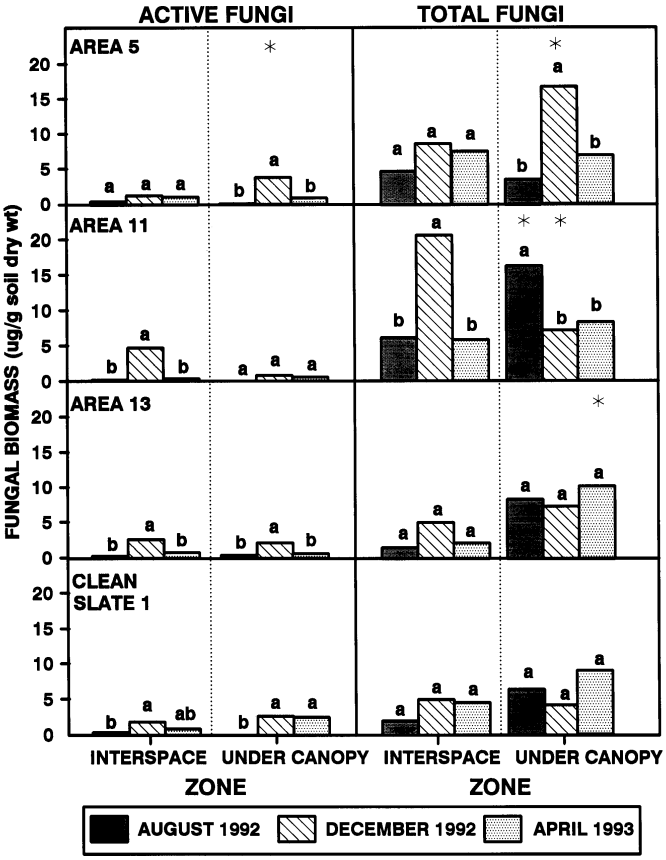

Figure 2—Mean active and total fungal biomass for soil beneath plant canopies and interspace zones for selected sites on three dates. Date mean values having the same letter within zones and sites were not significantly different. Means having a "*" indicate a significant difference in the interspace and under canopy means for that date and zone.

Total fungal biomass varied significantly over time within zones in Areas 5 and 11. Area 5 had significantly greater total fungal biomass beneath plant canopies during December (Figure 2). Area 11 had greater fungal biomass in interspaces during December and significantly higher total fungal biomass beneath shrubs during August. For Area 13 and Clean Slate 1, total fungal biomass apparently did not fluctuate greatly over time. There was a general tendency for total fungal biomass in interspaces (Figure 2) to follow soil moisture patterns (Figure 3). This trend was positively correlated with a significant r-value of 0.60 (Table 3). However, this trend was not apparent for under canopy total fungal biomass, which had low a low correlation with soil moisture (r = 0.17; Table 3).

Site Influences—Active and total fungi in interspace soils did not differ significantly between sites for each date of collection except for the Area 11 interspace soil during December, which had significantly greater active and total fungal biomass (Figure 2). Soil moisture at this site was significantly greater than at the other sites (Figure 3) and may have influenced this difference. Active and total fungal biomass under shrub canopies had significant differences between sites for the dates of collection. However, no consistent pattern was detected, with significant differences varying with each site and date of collection.

Numbers of Active Bacteria

Analysis of variance for numbers of active bacteria indicated a non-significant, site-date of collection-zone interaction (Table 2). Site and zone were not significant main

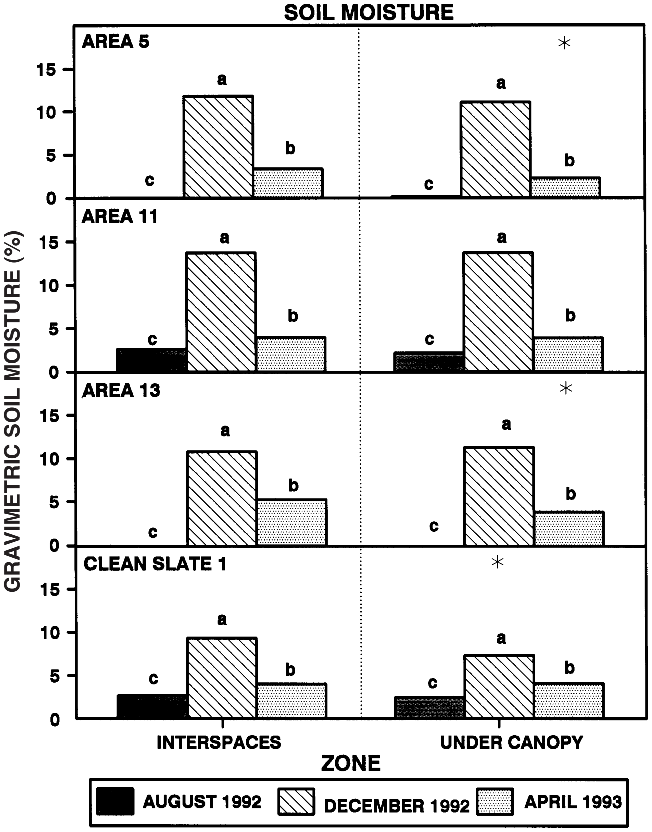

Figure 3—Mean gravimetric soil moisture for soil beneath plant canopies and interspace zones for selected sites on three dates. Date mean values having the same letter within zones and sites were not significantly different. Means having a "*" indicate a significant difference in the interspace and under canopy means for that date.

Table 3—Pearson's correlation coefficients and associated p-values for correlation of mean values of active and total fungal biomass, active bacterial numbers, soil respiration, and glucose amended respiration to that of soil moisture at the time of sampling. Correlations were conducted by zone (interspace or under canopy) regardless of site, and for all sites and zones combined.

	Soil moisture	
Variable	Pearson's correlation coefficient	p-value
Interspaces (n = 12)		
Active fungal biomass	0.71	0.0093
Total fungal biomass	0.60	0.0412
Active bacterial numbers	–0.44	0.1562
Respiration	0.76	0.0042
Glucose amended respiration	–0.11	0.7273
Under Canopy (n = 12)		
Active fungal biomass	0.33	0.2876
Total fungal biomass	0.17	0.5805
Active bacterial numbers	–0.28	0.3739
Respiration	0.92	0.0001
Glucose amended respiration	–0.48	0.1135
Zones and Sites Combined (n = 24)		
Active fungal biomass	0.53	0.0083
Total fungal biomass	0.37	0.0716
Active bacterial numbers	–0.36	0.0807
Respiration	0.73	0.0001
Glucose amended respiration	–0.28	0.1817

effects. However, date of collection was highly significant. Although the three-way interaction was not significant, mean separation procedures were conducted to determine if any consistent patterns in active bacterial numbers could be seen for the variables.

Active bacterial numbers ranged from 4.5 to 21.9 x 10^6 propagules/g dry soil. This range for active bacteria exceeded that found previously for total bacterial propagules of Mojave Desert soils in Nevada (Vollmer and others 1977). They reported total bacterial numbers ranging from 3 to 16 x 10^6 propagules per gram of soil. Their data represented total bacterial propagules, whereas the data reported in this study were for active bacterial propagules only. Total bacterial numbers for this study, although incomplete, indicate ranges of 11.9 to 73.0 total bacterial propagules per gram of dry soil for Area 5 and 11 which represent Mojave Desert habitats. Active bacterial numbers for Clean Slate 1 and Area 13, which have vegetation components like that of Great Basin Desert, were greater than total bacterial numbers reported for other Great Basin Deserts. Skujins (1984) reported that Great Basin soils had approximately 0.9 x 10^6 total bacterial propagules per gram of soil. As before, the reported data for this Great Basin site was for total bacterial propagules only. Active bacterial propagules for Great Basin-type areas in this study ranged from 6.2 to 21.9 propagules x 10^6 and total bacterial numbers, although incomplete, ranged from 13.8 to 27.6 propagules x 10^6.

Zone Influences—Numbers of active bacteria beneath shrubs were not significantly different from interspaces during the August sampling period (Figure 4). There was a general trend of greater numbers of active bacteria beneath shrubs during December and April. These differences were statistically significant for Areas 11 and 13 during December, and Areas 5 and 13 during April. Active bacteria numbers beneath shrubs and in interspaces had statistically insignificant correlations with soil moisture (r = –0.44 and –0.28, respectively; Table 3).

Date of Collection Influences—Temporal variability in numbers of active bacteria was apparent for both collection zones in Areas 5, 11, and 13 with the August sampling date having significantly greater bacterial numbers (Figure 4). Soil moisture at all four of these sites was lowest during this collection date (Figure 3). Active bacterial numbers at Clean Slate 1 did not differ significantly over time for both interspaces and beneath shrub canopies.

Site Influences—Significant differences in active bacterial numbers for sites were variable across dates of collection and zones. There was a general trend for Area 13 to have greater active bacterial numbers, but this was generally not significant.

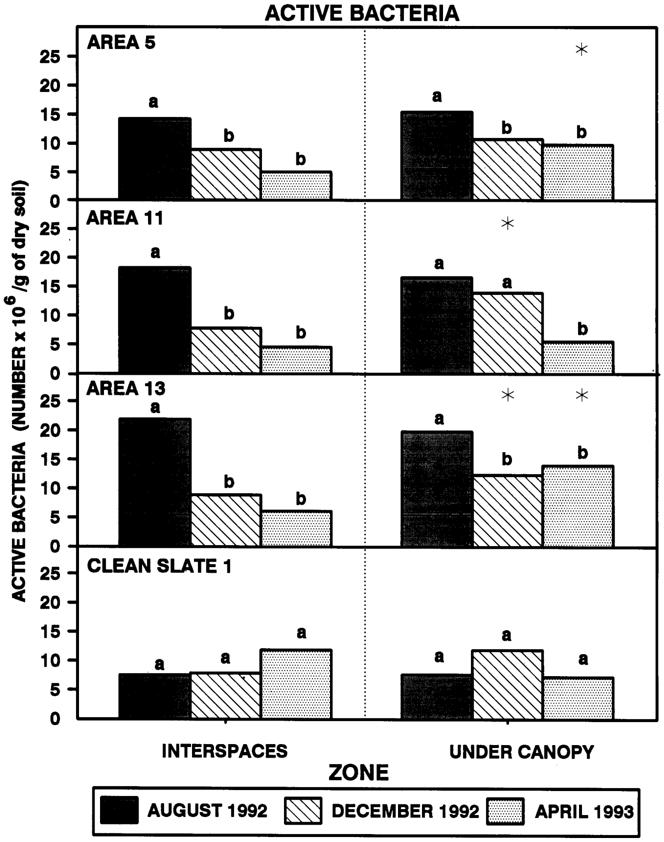

Figure 4—Mean active bacterial numbers for soil beneath plant canopies and interspace zones for selected sites on three dates. Date mean values having the same letter within zones and sites were not significantly different. Means having a "*" indicate a significant difference in the interspace and under canopy means for that date.

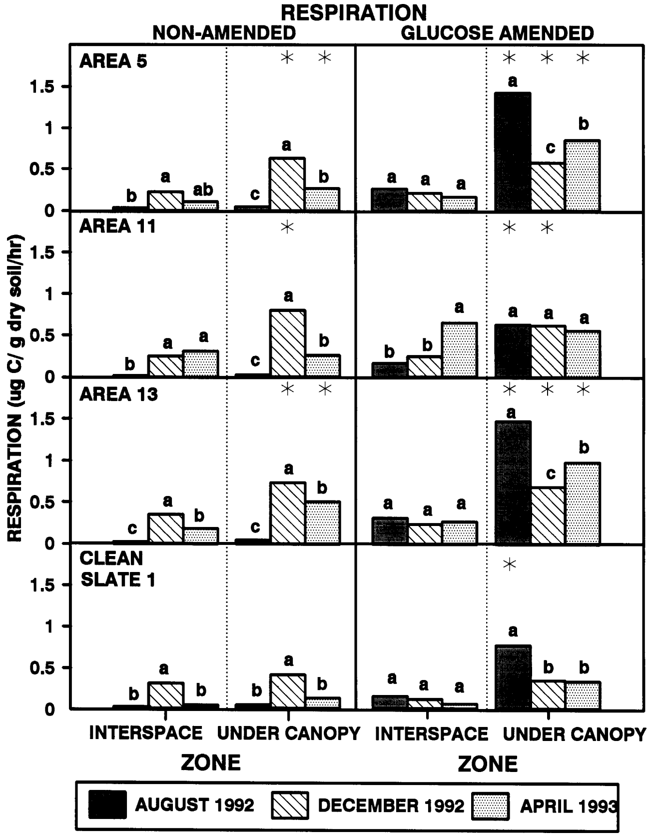

Figure 5—Mean non-amended and glucose amended respiration for soils beneath plant canopies and interspace zones for selected sites on three dates. Date mean values having the same letter within zones and sites were not significantly different. Means having a "*" indicate a significant difference in the interspace and under canopy means for that date.

Soil Respiration

Analysis of variance for non-amended soil respiration indicated a significant site-date of collection-zone interaction (Table 2). Date of collection and zone were significant main effects whereas site was not significant (Table 2). Non-amended soil respiration means ranged from 0.0139 to 0.798 with an overall mean of 0.241 µg C/g of dry soil/hr. In contrast to non-amended respiration, date of collection and site main effects for glucose-amended respiration were not significant; however, as with the non-amended respiration, the zone main effect and the three way interaction between site, date of collection and zone was significant. Glucose-amended respiration means ranged from 0.057 to 1.474 with an overall mean of 0.505 µg C/g dry soil/hr.

Zone Influences—Differences in non-amended soil respiration between interspaces and shrub canopies (Figure 5) existed on several dates with soil from beneath shrub canopies in Areas 5 and 13 exhibiting greater non-amended respiration during both December and April, and soils from beneath shrubs in Area 11 having greater non-amended respiration in December (Figure 5). Clean Slate 1 exhibited no significant differences in interspace and under canopy non-amended respiration for any of the dates sampled.

Glucose-amended soils from beneath plant canopies generally had greater respiration rates than that of interspace soils (Figure 5). Glucose-amended soil respiration averaged across sites and dates indicated that respiration beneath shrub canopies was 4 times greater than that in interspaces. This may be an indication that the respiring microbial biomass was greater in soils beneath shrub canopies.

Date of Collection Influences—Temporal variability in non-amended respiration was apparent among sites and zones with December generally having greater non-amended respiration than other collection dates (Figure 5). The pattern of non-amended respiration over time closely resembled that of soil moisture during sampling (Figure 3). Non-amended respiration rates of soils from interspaces and beneath shrub canopies were highly correlated to soil moisture (r = 0.76 and 0.92, respectively; Table 3). This may be an indication that the activity levels of the microbial population as a whole are closely tied to soil moisture levels. The high correlation of non-amended respiration to soil moisture status is consistent with that reported in other desert climates. Knight and Skujins (1981) reported an exponential decrease in non-amended respiration with decreasing water potentials for two desert soils. Generally, respiration rates are greatest when soils are at field capacity (Sommers and others 1981).

Glucose-amended respiration exhibited temporal patterns. The August 1992 sampling period exhibited significantly greater respiration than that of other collection dates (Figure 5) and did not appear to be related to soil moisture conditions at the time of sampling (Figure 3). Glucose-amended respiration from interspace soils had a low correlation with soil moisture (r = –0.11; Table 3). Glucose-amended respiration from under shrub canopy soils had a slightly higher correlation value and was negative (r = –0.48; Table 3). The negative correlation coefficient may indicate that there is a slight tendency for an increased moisture status beneath shrubs which leads to a decrease in the response of the microbial biomass to glucose substrate addition. Therefore, during periods of low soil moisture beneath shrubs, the microbial biomass may be carbon-substrate limited rather than water limited.

The increased respiration response after glucose addition of both interspace and under canopy soils over that of non-amended soils may partially be due to the fact that water was used to solubilize the glucose amendment. Non-amended soil respiration rates were highly correlated to soil water, especially for soils from under shrub canopies. The addition of water during the glucose amendment does not fully explain why the glucose amendment had a much greater response from under canopy soils as compared to interspace soils, when the non-amended respiration rates for each of these zones were not significantly different across sites. A partial explanation for this may be the influence of active bacteria. Glucose-amended respiration from soils beneath shrubs was positively correlated to active bacterial numbers (r = 0.62, p = 0.03), but was not correlated to active bacteria from interspaces (r = –0.10, p = .76). However, active bacterial numbers did not vary significantly between interspace and under canopy soil during the August sampling period (Figure 4). This may indicate that active bacteria and other microbial components beneath shrubs were water and carbon substrate limited whereas the components in interspaces were only water limited.

Site Influences—Significant differences in non-amended respiration rates were not consistent between sites when compared across sampling dates and zones of collection. However, when respiration from glucose-amended soils was compared between sites, Area 13 exhibited a general trend of having greater respiration than that of the other sites (overall mean of 0.66 for Area 13 as compared to 0.58, 0.47, and 0.29 for Area 5, Area 11 and Clean Slate 1, respectively). Although this greater respiration was not always significantly different across sampling dates and zones, it may indicate that Area 13 has a greater microbial biomass than the other sites.

Conclusions

Zone Influences

The differences in interspace and under canopy microbial components measured in this study (active and total fungi, active bacteria and soil respiration) were statistically inconsistent among sites and dates of sampling. However, when significant differences between interspace and under canopy microbial components were observed, there was a general tendency for under canopy soils to have higher values for the microbial components.

Date of Collection Influences

Temporal variability existed for total and active fungi in interspace soils and appeared to be related to soil moisture. Soil moisture was positively correlated to interspace active and total fungal biomass indicating the dependence of these components on soil moisture in this zone. Active and total fungal biomass for soils from beneath shrub canopies was not correlated to moisture status, and therefore may be carbon substrate dependent rather than moisture dependent. Active bacterial numbers varied with dates of collection but were generally not correlated to soil moisture. The negative correlation of active bacteria with soil moisture may indicate that bacterial numbers are uncoupled from soil moisture conditions and may be coupled to amount of available carbon substrates. The greater number of bacteria during the summer months may allow a competitive advantage over the more moisture dependent fungi.

The temporal variability in non-amended respiration is an indication that the activity levels of the total microbial population varies over time. The high correlation of non-amended respiration for soils beneath shrubs and interspaces indicates that soil moisture plays an important role in maintaining soil microbial activity and biomass. The greater respiration after glucose amendment exhibited by soils underneath plant canopies indicates that these soils may be carbon substrate limited at certain times of the year.

Site Influences

The dominance of a microbial component varied across sites, dates of collection and zones. No consistent pattern was detected among sites for each of the microbial parameters measured. Apparently, the soils, elevation and temperatures at these sites do not greatly influence the soil microbial parameters as much as the temporal variability in soil moisture.

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Effects of Afterripening on Cheatgrass (*Bromus tectorum*) and Squirreltail (*Elymus elymoides*) Germination

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Susan E. Meyer
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Abstract—Cheatgrass or downy brome (*Bromus tectorum*), an exotic facultatively fall-germinating annual, is displacing native plant communities throughout the Intermountain West. Squirreltail (*Elymus elymoides*), a native facultatively fall-germinating perennial, can reestablish naturally in rangelands infested by cheatgrass. This study was conducted to determine whether cheatgrass and squirreltail afterripen during dry storage in preparation for possible fall-germination and to compare between-population differences in response to afterripening. Seeds of four populations of each species were stored at 0, 10, 20, 30, and 40 °C over a period of four months and then incubated at four temperature regimes. Afterripening in dry storage resulted in complete loss of dormancy and faster germination. In general, afterripened squirreltail collections never germinated as rapidly as cheatgrass. Between-population differences in afterripening patterns were habitat-correlated and ecologically relevant. Artificial seed bank experiments showed that both species fall emerge, although cheatgrass consistently germinated earlier than squirreltail. Our results indicate that both species afterripen in dry storage; this can permit fall-germination when it is advantageous for survival. Early fall seeding of squirreltail into cheatgrass-infested rangelands could be effective in future restoration projects.

Cheatgrass or downy brome (*Bromus tectorum*; Poaceae) was introduced into the Intermountain West through contaminated grain from Eurasia in the late 1800's. Deteriorating range conditions in the early 1900's fostered the initial invasion and widespread establishment of this exotic weed (Mack 1981). Cheatgrass is an effective competitor for soil water resources, enabling it to infest the more arid regions of Washington, Idaho, Oregon, Nevada, Utah, and British Columbia. Currently it is displacing various native plant communities. Billings (1990) reports that millions of acres of sagebrush and pinyon-juniper are now dominated by cheatgrass. Other habitat types invaded by cheatgrass include salt desert shrub, mountain brush, and some mountain meadows. Studies also show that cheatgrass invasion has increased frequency and intensity of fires in the Intermountain West, disrupting the entire natural ecosystem (Whisenant 1990). Overall, invasion by cheatgrass and associated fires affect at least 40 million hectares, making this perhaps the most significant plant invasion in North America (D'Antonio and Vitousek 1992). Thus, restoration of lands dominated by cheatgrass has become an important issue in the Intermountain West.

Squirreltail (*Elymus elymoides*; Poaceae; previously *Sitanion hystrix*) is a perennial bunchgrass native to the Intermountain West. It is a natural invader of disturbed areas in deserts, valleys, foothills, and mountain meadows. Squirreltail can reestablish naturally in rangelands infested by cheatgrass and medusahead (Hironaka and Sindelar 1973). Therefore, squirreltail is a logical native species to examine for possible restoration of degraded rangelands. To understand the successful long-term persistence of cheatgrass and the ability of squirreltail to reestablish in cheatgrass-infested rangelands, the germination strategies of both species must be considered.

Cheatgrass is an exotic winter annual that facultatively fall-germinates; squirreltail is a perennial bunchgrass that is also known to facultatively fall-germinate (Hironaka and Sindelar 1973). Squirreltail, like cheatgrass, flowers in spring or early summer. Seeds of both species from lower elevation populations mature in early June, while seeds from high montane populations do not ripen until late July. Dispersal occurs a few weeks after seed maturation. While cheatgrass seeds are dispersed over long distances by becoming attached to animals or over short distances by wind, squirreltail seeds are dispersed primarily by wind. As an annual, cheatgrass relies entirely on seeds for population replacement and invasion of new habitats. As a nonclonal perennial, squirreltail relies on seeds for population expansion as well as for invasion of new habitats.

Cheatgrass and squirreltail, like many summer-ripening and facultatively fall-emerging species, have safeguards against early summer germination (seed dormancy and/or slow germination), losing these protective mechanisms through afterripening. A variety of definitions of afterripening are used in the literature (Vegis 1964; Taylorson and Brown 1977; Baskin and Baskin 1986). For the purpose of this paper, afterripening will be defined as a process that takes place in dry seeds and results in a reduction of dormancy and/or decrease in mean germination time (days to 50% germination). In other words, afterripening is the mechanism by which fall germination becomes possible.

There are conflicting reports concerning the afterripening of cheatgrass and squirreltail. Most studies involved

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investigations of only one plant population per species. Young and Evans (1977) suggested that cheatgrass and squirreltail seeds do not have afterripening requirements dependent on temperature. Other researchers, however, have shown that afterripening is often a characteristic of fall-germinating grass species (Laude 1956; Taylorson and Brown 1977; Thill and others 1980; Baskin and Baskin 1986). Afterripening at high storage temperatures has occurred in cheatgrass, reducing the initial level of dormancy (Laude 1956; Thill and others 1980) and decreasing the mean germination time (Milby and Johnson 1987). A variety of grass seeds showed increased germination percentage when stored at 50 °C for 14 days (Taylorson and Brown 1977). Afterripening not only increased seed germination percentage, but also the temperature range over which seeds could germinate (Thill and others 1980; Baskin and Baskin 1989). Currently published research is not in agreement as to whether cheatgrass and squirreltail seeds afterripen.

The objectives of this study were to: (1) determine whether cheatgrass and squirreltail seeds afterripen during dry storage; (2) investigate the effects of storage and incubation temperatures on germination percentage and mean germination time (days to 50% germination); (3) relate changes in the mean germination time to species and habitat; and (4) evaluate fall germination of cheatgrass and squirreltail through artificial field seed bank experiments.

Materials and Methods

Afterripening Storage Treatments

Mature fully ripened seeds (caryopses with associated lemma and palea) were hand stripped from four populations each of cheatgrass and squirreltail in the summer of 1992. Collections were cleaned using a rubber seed cleaning board and a small fanning mill. Seeds were hand-selected to improve fill. Collection sites represented four distinct habitats: two low-elevation sites, one cold desert and the other salt desert; and two high-elevation sites, one mountain brush and the other mountain meadow (Table 1). Elevation was determined from topographic maps for each collection site.

Storage

Within 2 weeks of harvest, seeds (7-8% moisture content) were placed in controlled dry storage treatments. Squirreltail and cheatgrass seeds were stored at 0, 10, 20, 30, and 40 °C for 16 weeks, except for cheatgrass seeds from mountain brush and mountain meadow collections, which were stored at 0, 20, and 40 °C only.

Incubation

Germination experiments were conducted when storage treatments began (recently harvested seeds) and at 4-week intervals afterward. For each species collection and storage temperature treatment, four replications of 25 seeds were placed in 100- x 10-mm plastic petri dishes on two germination blotters (Anchor Paper, St. Paul, MN) saturated with tap water. Petri dishes were grouped and randomly stacked in plastic bags closed with rubber bands to retard water loss. Dishes were rewetted as needed. A blank dish was placed on each stack to ensure that all dishes received equal light. Dishes were incubated in controlled-environment chambers under cool-white fluorescent lights with a 12-hour photoperiod. Temperatures corresponded to possible field temperatures for germination: 5/15, 10/20, 15/25, and 20/30 °C (5 °C during darkness, 15 °C during light, for instance). Seeds were classified as germinated when the radicle had elongated to 1 mm. Dishes were inspected for germination on days 2, 4, 7, 11, 14, 21, and 28 after incubation began. Dormant seeds were defined as seeds that did not germinate within 28 days, but were viable. At the end of the 4-week incubation period, the viability of ungerminated seeds in each dish was determined using a cut test to examine the tissue of the seeds. Fully developed, firm tissue with the normal coloring was considered viable while shriveled, decayed, and discolored tissue, or seed lacking an embryo, were considered nonviable (Association of Official Seed Analysts 1988).

Germination percentage (viable seed basis) and mean germination time (calculated as days to 50% of total germination) were determined for each replication. Analysis of variance (ANOVA) was used to test for the effects of species, habitat type, storage temperature, storage duration, and incubation temperature. Linear regression was used to examine progressive changes in mean germination time as a function of storage duration for each collection by storage temperature by incubation temperature combination.

General weather information for each seed collection site was examined to evaluate conditions seeds naturally undergo during ripening and after dispersal. Mean monthly temperature and monthly precipitation were obtained for each collection by interpolating on isotherm maps, supplemented with information from nearby weather stations when available (Water Information Center 1974; Stevens and others 1983).

Table 1—Species and habitat information for seed collection sites.

Species	Location	Elevation (m)	Habitat type
Cheatgrass	Whiterocks, UT	1,450	Cold Desert
Cheatgrass	East of Green River, UT	1,280	Salt Desert
Cheatgrass	East of Salina, UT	2,040	Mountain Brush
Cheatgrass	North of Helper, UT	2,070	Mountain Meadow
Squirreltail	Whiterocks, UT	1,450	Cold Desert
Squirreltail	South of Price, UT	1,340	Salt Desert
Squirreltail	East of Salina, UT	2,040	Mountain Brush
Squirreltail	Strawberry, UT	2,400	Mountain Meadow

Table 2—Location and habitat information for field sites used in artificial seed bank experiments with cheatgrass and squirreltail collections.

Location	Elevation (m)	Habitat type	Annual precipitation (cm)
Whiterocks	1,450	Cold Desert	18
Point of the Mountain	1,480	Mountain Brush	43
Strawberry	2,400	Mountain Meadow	65

Artificial Seed Bank Experiment

Artificial field seed bank experiments were carried out with two of the four cheatgrass collections and three of the four squirreltail collections. Before being placed in the field experiment, seeds were stored at 20 °C. Groups of about 100 seeds (determined by weight) were placed in flat nylon mesh packets. In mid-August, the packets were buried at a depth of 0.5 cm, with the exception of the squirreltail collection from Strawberry, which was buried in mid-September. Each group of packets was protected with a hardware cloth cone. Cones were arranged in three blocks at each of three field sites: a cold desert site (Whiterocks), a mountain brush site (Point of the Mountain), and a high-elevation mountain meadow site (Strawberry) (Table 2). At monthly intervals through mid-November, mid-March (mid-May at Strawberry), and mid-June, three sets of packets were retrieved from each site and transported to the laboratory in an insulated chest. Within 6 hours, germinated seeds in each packet were counted, and remaining seeds were placed in petri dishes, incubated at 10/20 °C for 4 weeks, and scored at least weekly for germination as described previously. Seeds that germinated during post-field incubation were classified as ungerminated but laboratory-germinable, while any viable seeds remaining at the end of 4 weeks were classified as dormant.

Results

Afterripening Storage Treatments

Storage temperature and duration had a dramatic effect on both germination percentage and mean germination time. Recently harvested seeds (before afterripening storage treatments) showed some dormancy and germinated slowly. Fully afterripened seeds came out of dormancy and germinated much faster than recently harvested seeds (Table 3).

Although recently harvested cheatgrass and squirreltail collections showed dormancy, squirreltail was less dormant than cheatgrass. Following the dry afterripening treatment, cheatgrass and squirreltail seeds for all collections reached 100% germination. Recently harvested cheatgrass and squirreltail collections showed a relatively long mean germination time, contrasting with a shorter mean germination time for fully afterripened seeds. Squirreltail collections never germinated as rapidly as cheatgrass.

Recently harvested desert collections had higher levels of dormancy than did mountain collections. Fully afterripened seeds from all habitats came out of dormancy. Seeds from all habitats germinated faster when fully afterripened, although seeds from the mountain meadow population had the slowest germination.

Table 3—Mean germination percentage and mean germination time (days to 50% total germination) for recently harvested and fully afterripened seeds. Main effects and interactions are averaged across different treatments (species, habitat, incubation temperature). All main effects and interactions were highly significant ($p < 0.0001$) for both response variables.

	Recently harvested seeds		Fully afterripened seeds	
Effects and interactions	Mean germination Percent	Mean germination Time (Days)	Mean germination Percent	Mean germination Time (Days)
Afterripening Main Effect (Averaged Across Species-Habitat-Incubation Temperature)	63	13.4	100	4.4
Averaged Across Habitat-Incubation Temperature				
Cheatgrass	50	15.7	100	3.0
Squirreltail	77	11.3	100	5.9
Averaged Across Species-Incubation Temperature				
Cold Desert Habitat	44	15.4	100	4.2
Salt Desert Habitat	52	13.9	100	4.1
Mountain Brush Habitat	77	11.3	99	4.0
Mountain Meadow Habitat	78	13.2	100	5.5
Averaged Across Species-Habitat				
5/15 °C Incubation Temperature	59	13.2	99	7.4
10/20 °C Incubation Temperature	83	10.9	100	4.1
15/25 °C Incubation Temperature	70	12.8	100	3.2
20/30 °C Incubation Temperature	40	17.2	100	3.1

Incubation Temperature Effects

The optimum incubation temperature for recently harvested seeds for both germination percentage and time was 10/20 °C (Table 3). The least favorable incubation temperature was 20/30 °C. However, when seeds were fully afterripened, the optimum incubation temperature for mean germination time occurred at 20/30 °C. All fully afterripened collections came out of dormancy across the tested range of incubation temperatures.

Recently harvested cold desert and salt desert cheatgrass populations were quite dormant and germination was reduced at some incubation temperatures (Figure 1). Furthermore, salt desert cheatgrass germination was extremely restricted at both 15/25 and 20/30 °C. In contrast, the recently harvested cold desert and salt desert squirreltail populations showed less restriction in germination, although dormancy was greatest at 20/30 °C for the cold desert squirreltail and at both 5/15 and 20/30 °C for the salt desert squirreltail. Recently harvested mountain cheatgrass and squirreltail populations showed less dormancy than the desert populations. Mountain squirreltail collections were less dormant than mountain cheatgrass collections at high incubation temperatures. Mountain cheatgrass dormancy was most pronounced at 20/30 °C; mountain squirreltail dormancy was most pronounced at 5/15 °C.

Mean germination time of fully afterripened seeds was shorter than that of recently harvested seeds for all incubation temperatures for both species (Figure 2). The optimal incubation temperature for fast germination was reversed as a result of afterripening for cheatgrass collections. While recently harvested cheatgrass seeds germinated fastest at 5/15 °C, fully afterripened seeds germinated fastest at 20/30 °C. Squirreltail populations did not reverse optimal incubation temperature following storage. Afterripened squirreltail populations germinated more quickly, but not to the degree that the cheatgrass populations did. Recently harvested squirreltail seeds did show a higher initial germination time across the incubation temperatures.

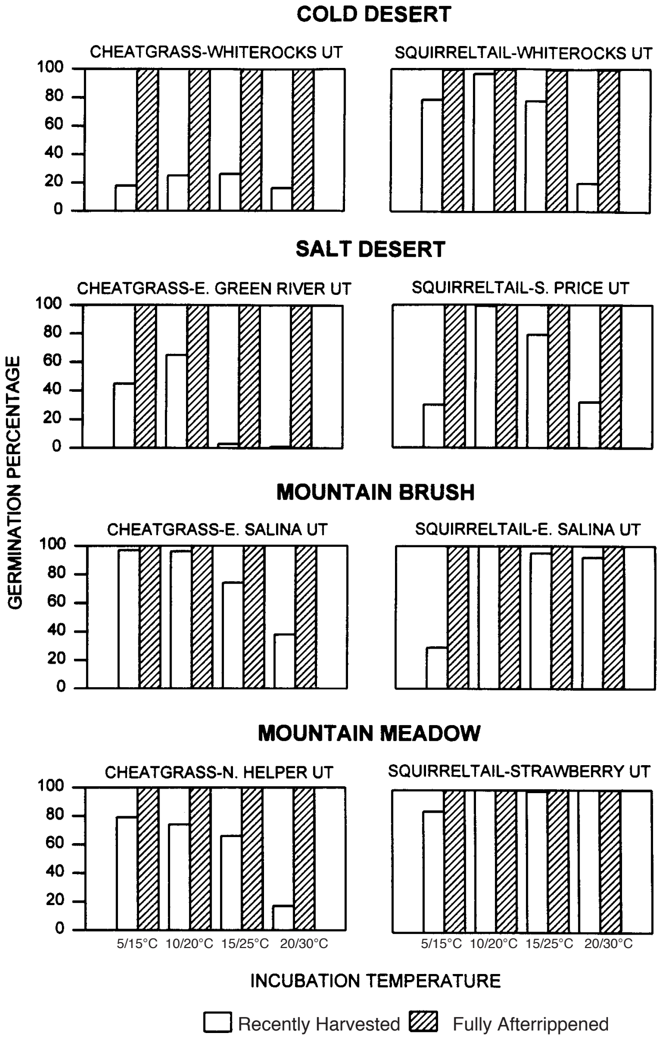

Figure 1—Germination percentages at four incubation temperatures for recently harvested and fully afterripened cheatgrass and squirreltail seeds from four habitats.

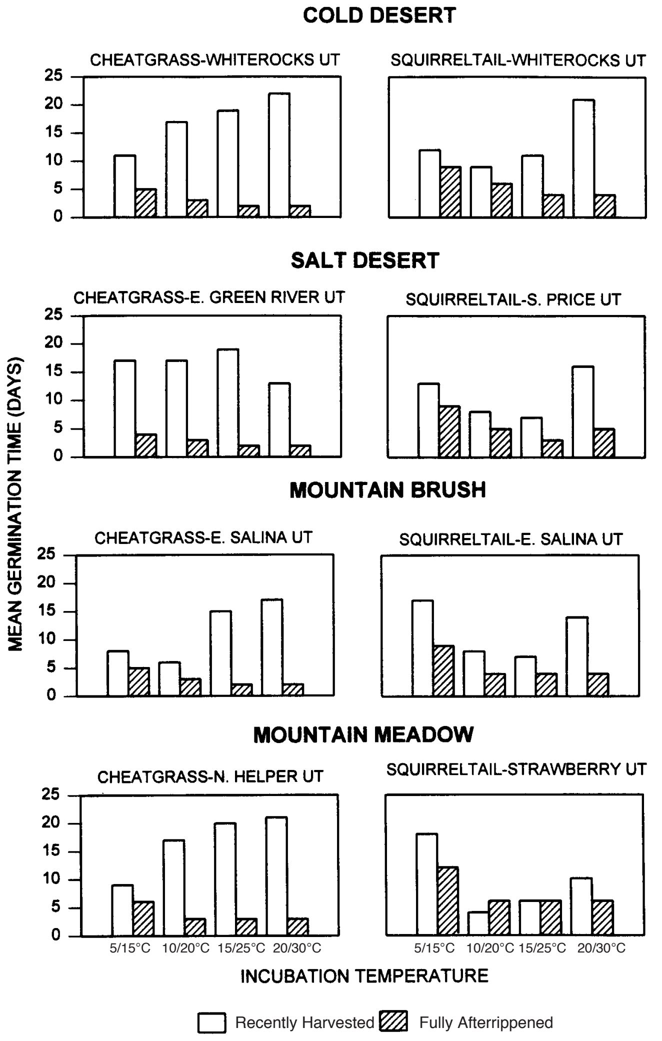

Figure 2—Mean germination time (days to 50% total germination) at four incubation temperatures for recently harvested and fully afterripened cheatgrass and squirreltail seeds from four habitats.

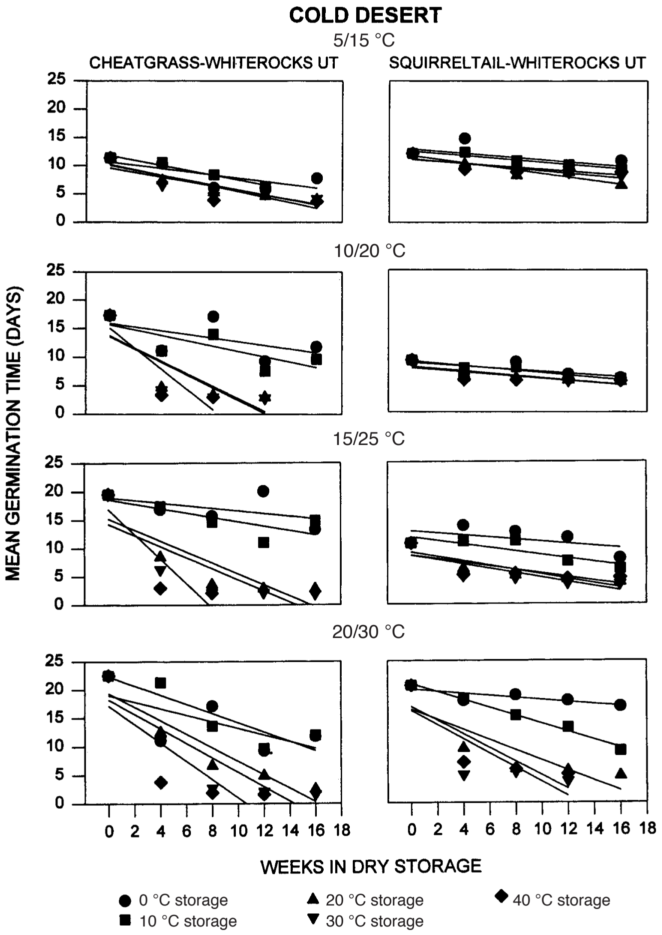

Figure 3—The effect of storage duration and temperature on mean germination time (days to 50% total germination) at four incubation temperatures for cold desert cheatgrass and squirreltail collections.

Storage Temperature Effects

Comparing changes in mean germination time across weeks in dry storage revealed clear patterns for both species. Cold desert (Figure 3) and mountain meadow populations (Figure 4) represented the two extreme habitat types. The mean germination time changed less at incubation temperatures of 5/15 and 10/20 °C than the mean germination times at 15/25 and 20/30 °C for both habitat types. In general, the negative relationship between mean germination time and weeks in dry storage for each collection was significant ($p < 0.05$) at 10, 20, 30, and 40 °C storage temperatures. Changes during storage at 0 °C usually were minimal; changes in mean germination time became greater at higher storage temperatures. The mountain cheatgrass and squirreltail populations are an exception to this pattern; 40 °C storage resulted in minimal or increased germination time. This effect was possibly due to loss of vigor resulting from extended storage at high temperature, unlikely conditions for mountain populations. Comparing habitat types, mountain populations showed less change in mean germination time following afterripening than desert populations. Change was most pronounced in cheatgrass populations, although squirreltail cold desert populations also showed a slight change in mean germination time.

Artificial Seed Bank Experiment

Results from the artificial seed bank experiments showed that both species do facultatively fall germinate (Figure 5). At the cold desert Whiterocks site, both cheatgrass collections reached 100% germination by mid-November, but only the south of Price squirreltail collection germinated (60%) by this time. The other two squirreltail collections postponed germination until late winter. When packets were excavated from beneath the snow in mid-March, squirreltail germination percentages ranged from 80% for the Strawberry collection to 98% for the south of Price collection.

At the mountain brush Point of the Mountain site, both cheatgrass collections had reached between 70% (east of Green River) to 90% (Whiterocks) germination by mid-September. By mid-November, cheatgrass collections reached 100% germination. All three squirreltail collections reached 100% germination by mid-November, although there was no field germination before seed packets were retrieved in mid-November.

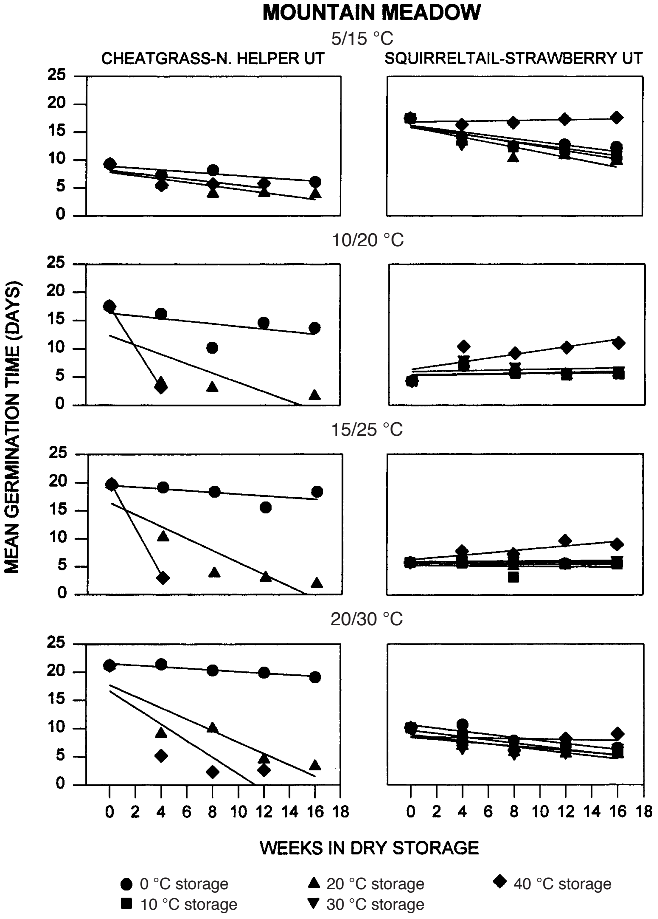

Figure 4—The effect of storage duration and temperature on mean germination time (days to 50% total germination) at four incubation temperatures for mountain meadow cheatgrass and squirreltail collections.

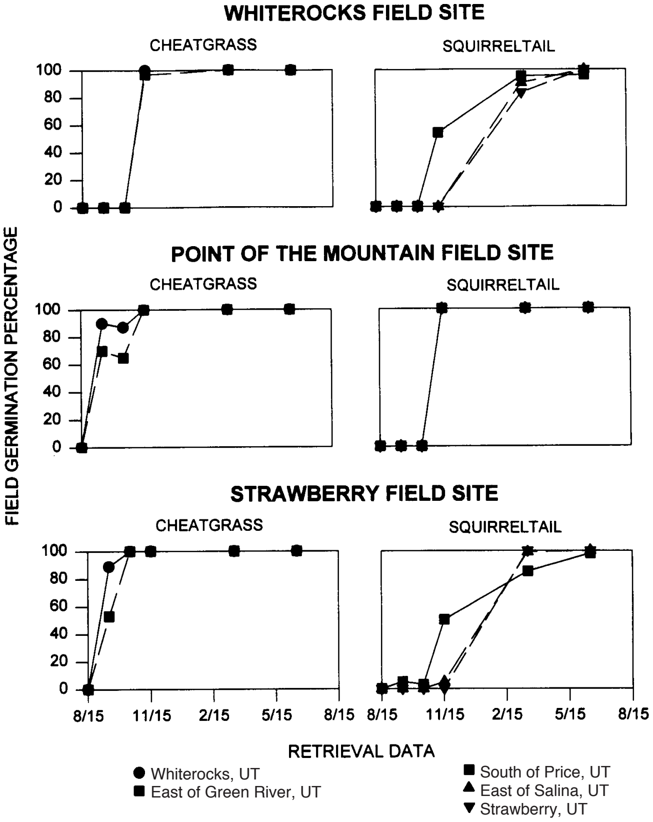

Figure 5—Field germination percentages for cheatgrass and squirreltail collections retrieved from artificial seed bank at Whiterocks, Point of the Mountain, and Strawberry field sites in late summer.

At the high-elevation Strawberry site the east of Green River collection had reached 50% germination and the Whiterocks collection reached 90% germination by mid-September. By mid-November both cheatgrass collections reached 100% germination. Only one squirreltail collection had germinated by mid-November (south of Price, 50%). All the other squirreltail collections postponed germination until late winter. When packets were excavated from beneath the snow in mid-May, squirreltail germination percentages ranged from 80% for the south of Price collection to 100% for both the east Salina and Strawberry collections.

Discussion

Completion of afterripening can be marked by reduction in dormancy and faster germination (Thill and others 1980; Milby and Johnson 1987). Populations of cheatgrass and squirreltail are at least conditionally dormant when recently harvested and respond to the afterripening treatments by reaching 100% germination, indicating that both species afterripen in dry storage. However, a reduction in dormancy is not the only factor influencing the probability of fall germination; a change in mean germination time is also necessary. Our results show that mean germination time decreased for both cheatgrass and squirreltail from 13.4 to 4.4 days following afterripening. The afterripening mechanism protects seeds from early summer germination but allows for fall germination (Milby and Johnson 1987). The results of afterripening are clearly indicated by a reduction in dormancy and a decrease in mean germination time; however, mechanisms controlling afterripening are still not fully understood.

Germination of recently harvested squirreltail seeds occurs primarily at moderate incubation temperatures (10/20 and 15/25 °C), while higher incubation temperatures (20/30 °C) inhibit germination. An examination of desert weather patterns (Figure 6) shows that in June and July, when field dispersal occurs, it is unlikely that seeds will experience temperatures of 10/20 and 15/25 °C in combination with adequate moisture. In contrast, mountain sites may experience these temperatures in July. However, seeds collected in the mountains ripen much later than those of desert populations. The critical point is that the recently harvested seeds were dormant at 20/30 °C incubation temperature, which represents conditions seeds will likely experience during June and July. Furthermore, recently harvested squirreltail seeds show a long mean germination time (11.3 days). Therefore, it is unlikely that squirreltail seeds would germinate in early to midsummer.

The annual species, cheatgrass, germinates faster than squirreltail, a perennial. From an ecological standpoint, this implies that cheatgrass benefits more from early fall germination than does squirreltail. This may be due to the total plant reproductive output, which is directly affected by fall germination and subsequent spring seed production for the annual species (Mack and Pyke 1983). The lifetime reproductive output of squirreltail, a perennial, is probably not as dependent on the time of emergence, because plants will have more than one season to produce seed.

Recently harvested seeds from desert populations of both cheatgrass and squirreltail show more dormancy than mountain populations. This difference can partly be explained by the weather data, which show that the earlier ripening desert populations experience a longer period of warm and relatively dry weather before conditions are suitable for fall germination (Figure 6). Mountain populations, which ripen later, have a relatively shorter period to wait for fall germination.

Precipitation, a limiting resource in the desert, is received principally in the winter. It provides seedlings with adequate moisture for growth, increasing their probability of survival. Seedlings in a desert environment face a lower risk of winter mortality if they emerge in the fall. The fact that desert populations show a greater change in the mean germination time in comparison to the mountain populations suggests that fall germination is more important to desert populations.

Low incubation temperatures were optimal for germination of recently harvested cheatgrass and squirreltail seeds; high incubation temperatures were optimal for fully afterripened seed. This study supports others (Thill and others 1980; Baskin and Baskin 1989) in demonstrating that afterripening broadens the range of incubation temperatures at which germination occurs. In addition, the change in the mean germination time across weeks of storage was greater at higher incubation temperatures (20/30 °C).

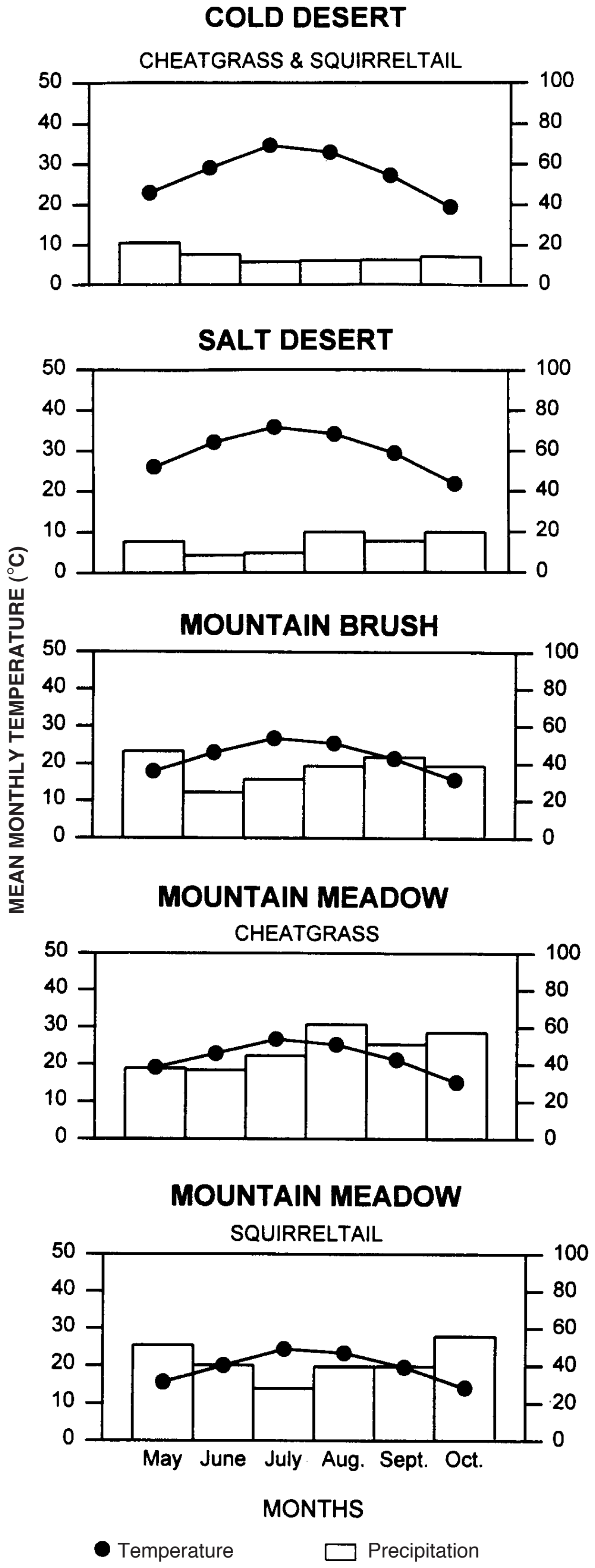

Figure 6—Climate diagrams for squirreltail seed collection sites: cold desert, salt desert, mountain brush, and mountain meadow.

The artificial seed bank experiment indicates that both species can fall emerge in years of above-average autumn precipitation (such as occurred in 1992). All cheatgrass populations germinated completely by mid-November at all three field sites. Squirreltail populations fall-germinated completely at the mountain brush site, and partially at the other two sites. Cheatgrass consistently germinated earlier than squirreltail.

Results from the artificial seed bank experiments support conclusions from the afterripening laboratory experiments, which showed that afterripened cheatgrass germinates more rapidly than afterripened squirreltail. The germination of squirreltail populations may be too slow to facilitate fall emergence in some habitats. For example, mountain population seeds that fall-emerge face a higher risk of winter mortality; therefore, germination may be postponed to avoid death. These adaptive mechanisms for cheatgrass and squirreltail permit fall emergence when it is advantageous for survival. However, our data suggest that early fall seeding of squirreltail into cheatgrass-infested rangelands could be effective in future restoration projects. Further studies are needed to examine seedling establishment and competition between the two species.

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The Soil Beneath Shrubs Before and After Wildfire: Implications for Revegetation

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J. A. Young
F. L. Allen

Abstract—Physical and chemical attributes of the soil seedbed influence the success of seed germination and plant establishment. In big sagebrush (*Artemisia tridentata*)/bunchgrass plant communities, soil seedbed attributes are spatially and temporally heterogeneous. Wildfires can alter the seedbed beneath shrubs, thereby, affecting both natural and artificial post-wildfire revegetation. Soil physical and chemical attributes and the soil fabric were characterized in the seedbed beneath shrubs, pre- and post-wildfire. Compared with unburned controls, significant ($P \le 0.05$) decreases in water-soluble nitrate and significant increases in water-soluble sulfate and several organic acids occurred immediately post-wildfire in the surface 5 cm of the soil. In addition, post-wildfire hydrophobicity reduced water infiltration into shrub subcanopy soil. Wildfires considerably altered the fabric of the soil seedbed. As compared to the pre-wildfire soil fabric, wildfires: (1) caused the compaction of mineral grains through loss of organic detritus, (2) carbonized plant litter to a depth of approximately 5 cm, (3) caused the loss of fluorescent compounds in sagebrush litter, (4) coated mineral particles with organic compounds, and (5) cleaved micaceous minerals. The synergism of fire effects undoubtedly influences post-wildfire revegetation. Field studies are underway to elucidate these effects.

The physical, chemical, and biological attributes of the soil seedbed influence seed germination and seedling establishment. Within the sagebrush-steppe of the intermountain west, the location of favorable sites for seedling emergence [safesites, Harper and others (1965)] are heterogeneously distributed. Eckert and others (1986) categorized the soil surface morphology in northern Nevada into: (1) coppice-eolian dust and litter accumulating beneath shrubs and bunchgrasses; (2) coppice bench-flat zone around coppice; (3) intercoppice microplain-gently sloping area from coppice bench to playette; and (4) playette-flat to slightly depressed areas among shrubs. These micropositions vary considerably in nutrient status, texture, moisture status, and the number of safesites. In general, the proportion of safesites increases as range condition increases and from playette to coppice positions.

Wildfires occur at regular intervals in the sagebrush-steppe, becoming more frequent with the invasion of cheatgrass (*Bromus tectorum*). Wildfires represent a major ecological disturbance which considerably alters the soil seedbed via: (1) changing fertility (Raison 1979); (2) influencing seed viability and seed germination potential (Went and others 1951; Komarova 1985); (3) production of hydrophobic compounds (DeBano and others 1976); and (4) production of compounds stimulating germination of some seeds (Keeley and others 1985).

Few studies have examined fire-induced chemical changes, by microsite, in the heterogeneous sagebrush-steppe of North America. Moreover, we are unaware of research characterizing the fabric of the soil seedbed pre- and post-wildfire in the sagebrush-steppe. Our purpose, therefore, was: (a) quantify pre- and post-wildfire soil physical and chemical properties, by microsite, and; (b) characterize the soil fabric pre- and post-wildfire. In this paper, we will only report on fire-induced changes occurring in the soil beneath the shrubs big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and antelope bitterbrush (*Purshia tridentata*). Due to high fuel amounts, shrub subcanopies attain higher temperatures than other positions and, as a consequence, are the focus of heat-induced changes in soil properties during and after wildfires (Blank and others 1994).

Materials and Methods

The Study Area

Research was conducted approximately 50 km north of Reno, NV, on coarse-textured granitic soils that occur on alluvial fans along the eastern Sierra Nevada front. Vegetation is dominated by sagebrush, bitterbrush, and cheatgrass. Other native species include desert peach (*Prunus andersonii*), needle-and-thread (*Stipa comata*), and Indian ricegrass (*Oryzopsis hymenoides*). The study area receives 250 mm of precipitation a year with considerable spatial and temporal variability.

In August of 1986, the Clark Incident fire burned over 16,000 hectares in the Plumas National Forest. We studied this wildfire at the Bird Flat ranch. The soils are sandy, mixed, mesic Torripsammentic Haploxerolls and loamy, mixed, mesic Xerollic Haplargids. In September 1987, the Hallelujah Junction fire burned about 300 hectares. The soils here are loamy-skeletal, mixed, frigid Lithic Haploxerolls. Field studies were initiated immediately post-fire, before any precipitation or soil-blowing events.

In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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Laboratory

All field-collected soils were air dried, sieved through a 2-mm sieve, and stored before analysis. Samples were analyzed as soon as possible. Soluble anions in the soil were extracted with 0.15 percent KCl solution and quantified by ion chromatography (Blank and others 1994). Cation exchange capacity was determined by the neutral ammonium acetate procedure (Soil Survey Staff 1984). Soil pH was determined in $CaCl_2$ (McLean 1982). Hydrophobicity was quantified using the water drop penetration time (WDPT) method (DeBano 1981). Organic carbon determination used the Walkley-Black method (Nelson and Sommers 1982). Soil N was quantified by the Kjeldahl method (Bremner and Mulvaney 1982) with NH_4^+ quantitation by membrane flow injection. Plant available Fe, Mn, Zn, and Cu was gauged by DTPA extraction (Lindsay and Norvell 1978). Phosphorus availability was determined by bicarbonate extraction (Olsen and Sommers 1982). Intake rate was measured with a single ring cylinder infiltrometer (Bouwer 1986).

To examine the soil fabric, replicate intact samples of burned and unburned sagebrush subcanopy soil were collected for manufacture into thin sections. Thin sections are made by grinding a block of material until it is thin enough to pass light—it can then be microscopically examined. Field samples were collected by carefully excavating material away to leave a mound the shape and size of a small paper cup. A paper cup was inserted over the mound until the soil surface contacted the bottom of the cup. The cup was carefully inverted so as to not disturb the soil, returned to the laboratory and impregnated with a commercial resin. The impregnated samples were sent to a commercial lab where they were cut into thin sections. Thin sections were examined with a polarizing microscope and by reflected light microscopy using blue-violet excitation and a barrier filter which attenuates wavelengths less than 500 nm.

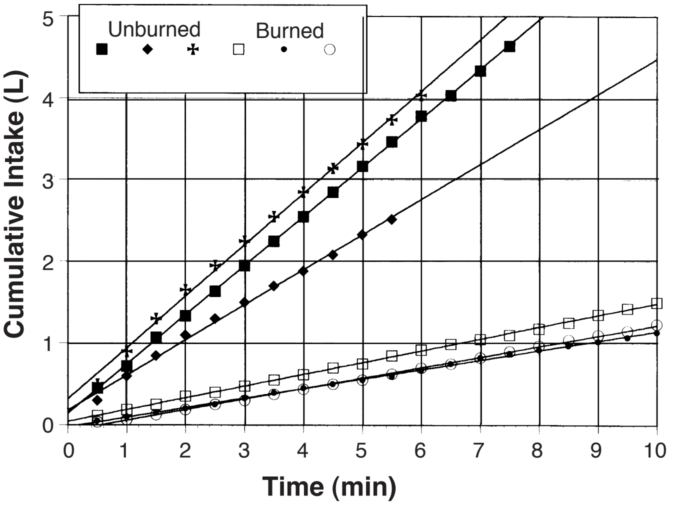

Figure 1—Cumulative constant head soil infiltration (three replicates) beneath burned and unburned sagebrush canopies. Basal area of infiltrometer 180 cm^2.

Table 1—Chemical attributes of soil collected beneath shrub subcanopies in post-wildfire and a similar unburned control at the Bird Flat study site

	Treatment	
Attribute	**Unburned**	**Burned**
CEC (cmol kg^{-1})	18.0a[3]	8.0b
Bicarb-P (mg kg^{-1})	635a	462a
Khejdahl N (%)	0.32a	0.16b
pH	6.34a	6.41a
Organic C (%)	4.59a	2.02b
DTPA Fe (mg kg^{-1})	7.4a	16.9b
DTPA Mn (mg kg^{-1})	14.7a	18.4a
DTPA Cu (mg kg^{-1})	1.5a	0.8b
DTPA Zn (mg kg^{-1})	3.2a	1.1b
KCl-nitrate (mg kg^{-1})	43.5a	10.1b
KCl-ortho-P (mg kg^{-1})	25.4a	9.8b
KCl-sulfate (mg kg^{-1})	9.7a	38.8b
KCl-acetate (mg kg^{-1})	2.4a	139.4b
KCl-formate (mg kg^{-1})	0.5a	16.9b
WDPT[2] (0-5 cm) (sec)	517a	1,224a
WDPT (5-10 cm) (sec)	1.3a	165b

[1] Unless otherwise noted, data are for soil collected from 0-5 cm.

[2] WDPT is the water drop penetration time, the time it takes for one drop of water to penetrate the soil.

[3] Means followed by the same letter are not significantly different at the $P \leq 0.05$ level.

Results and Discussion

Physical and Chemical Effects of Wildfire

Hydrophobic compounds, created by the wildfire, considerably reduce water intake rate of soil beneath sagebrush plants (fig. 1). Excavation of soil after the infiltration experiments showed preferential water flow paths through the upper 10 cm of the soil—much of the soil remained dry. Fire-induced hydrophobicity extends greater that 5 cm in the soil (table 1). A possible ramification of preferential water flow is that a portion of viable seeds remaining after the wildfire may not receive water for germination until the hydrophobic compounds are broken down. In the case of the Bird Flat wildfire, field measurements the following summer showed that elevated hydrophobicity had decreased to pre-wildfire levels.

A fire-induced chemical change that may impact seed germination and seedling establishment is the high levels of certain organic acids (table 1). We have measured elevated post-wildfire levels of acids such as acetic, glycolic, formic, oxalic, and succinic acid in shrub subcanopy soils which have been shown to retard or increase the germination of seeds (Mayer and Evenari 1953; Cohn and others 1987). Some of the organic acids are phytotoxic (Harper and Lynch 1982). Levels of organic acids in the seedbeds of shrub subcanopies can increase significantly in the months following the wildfires, but return to prefire levels by the following summer (Blank and others 1994). The compounds are leached downward by winter precipitation or lost via microbial utilization.

The heat from wildfires volatilize considerable nitrate in the soil (table 1; Raison 1979). Moreover, levels of ammonium increase following wildfires (Raison 1979). Such changes may impact seed germination and plant successional trajectories (Gigon and Rorison 1972; Hendricks and Taylorson 1974).

Other chemical changes, as a consequence of wildfire, may impact revegetation success and vigor of new plants (table 1). These changes include reduced cation exchange capacity, lower total soil N and C, and decreased levels of DTPA-extractable Cu and Zn.

Influence of Fire on the Soil Fabric

The surface fabric of sagebrush subcanopies consists of 0.5-2.0 cm of largely undecomposed litter which creates an open framework with high porosity (fig. 2A). The litter is mostly undecomposed and fluoresces strongly in greenish-yellow, under blue-violet excitation, around the margins of leaf material. The fluorescence appears to emanate from spheroidal oil-rich bodies in sagebrush leaves. Beneath this litter layer is a region 2 to 15 cm thick consisting of a mixture of plant litter and eolian mineral particles (fig. 2B). The plant litter serves to form a more open structure than would occur if the eolian particles, themselves, packed together. Sagebrush litter is in various stages of decomposition, with increasing decomposition deeper in the soil; however, even in an advanced stage of decomposition, much of the leaf litter fluoresces strongly, suggesting the compounds are long-lived. Mineral grains in unburned soil are often coated with an alteration rim of clay minerals (figs. 2B, C). When decomposed, the spheroidal oil-rich bodies in sagebrush leaves are melanized (fig. 2C). Throughout sagebrush subcanopy soils, spheroidal to oblate fecal pellets are evident (fig. 2D). One pathway of sagebrush decomposition is via ingestion by soil invertebrates. Even though the litter has passed through the gut tract, the fluorescent compounds are still active.

The upper 3-5 cm of a burned sagebrush subcanopy soil is completely charred (fig. 2E). As compared to the surface of unburned sagebrush subcanopies, the formerly open fabric has collapsed due to destruction of plant litter. Moreover, in this charred region, no fluorescence of

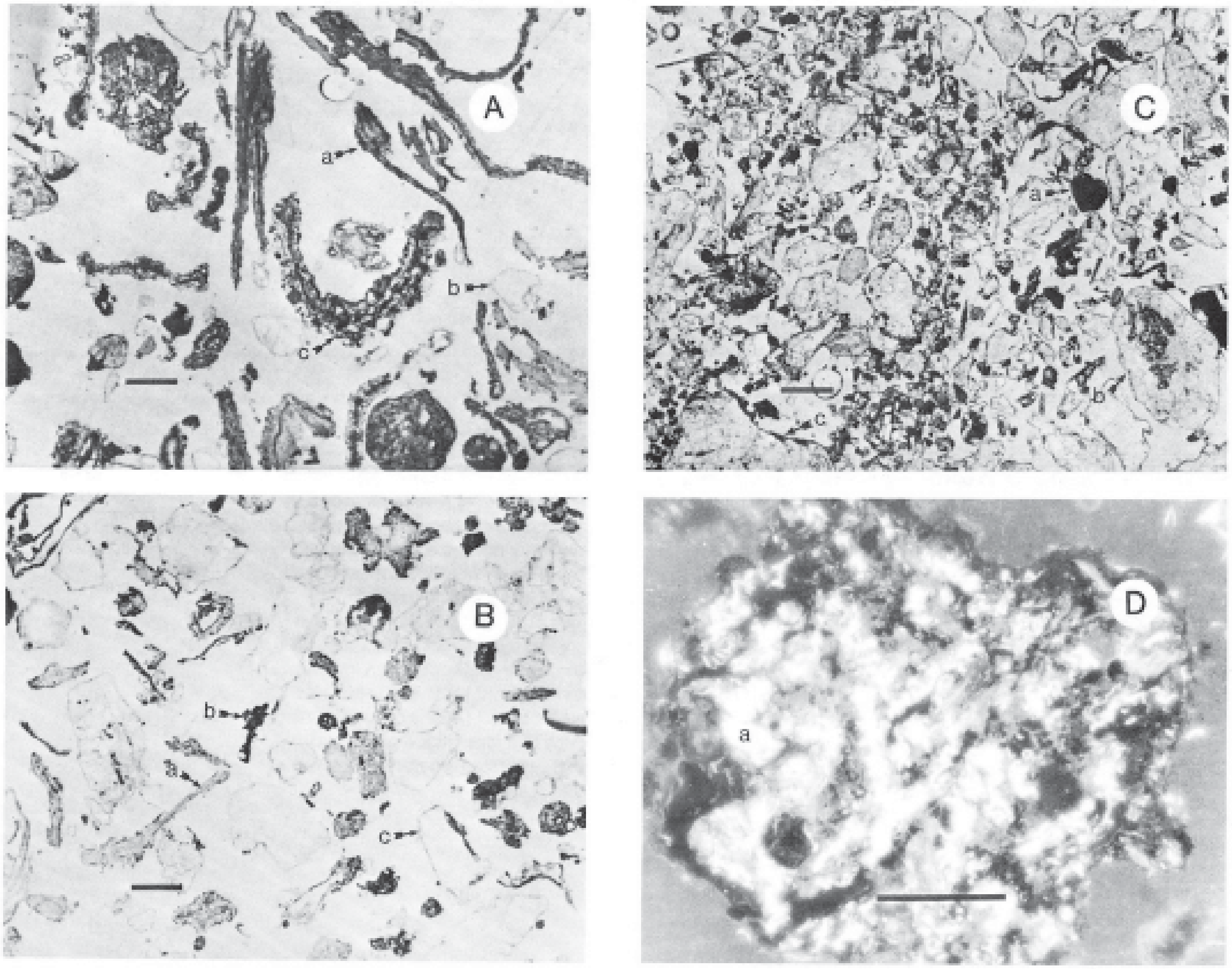

Figure 2 continued

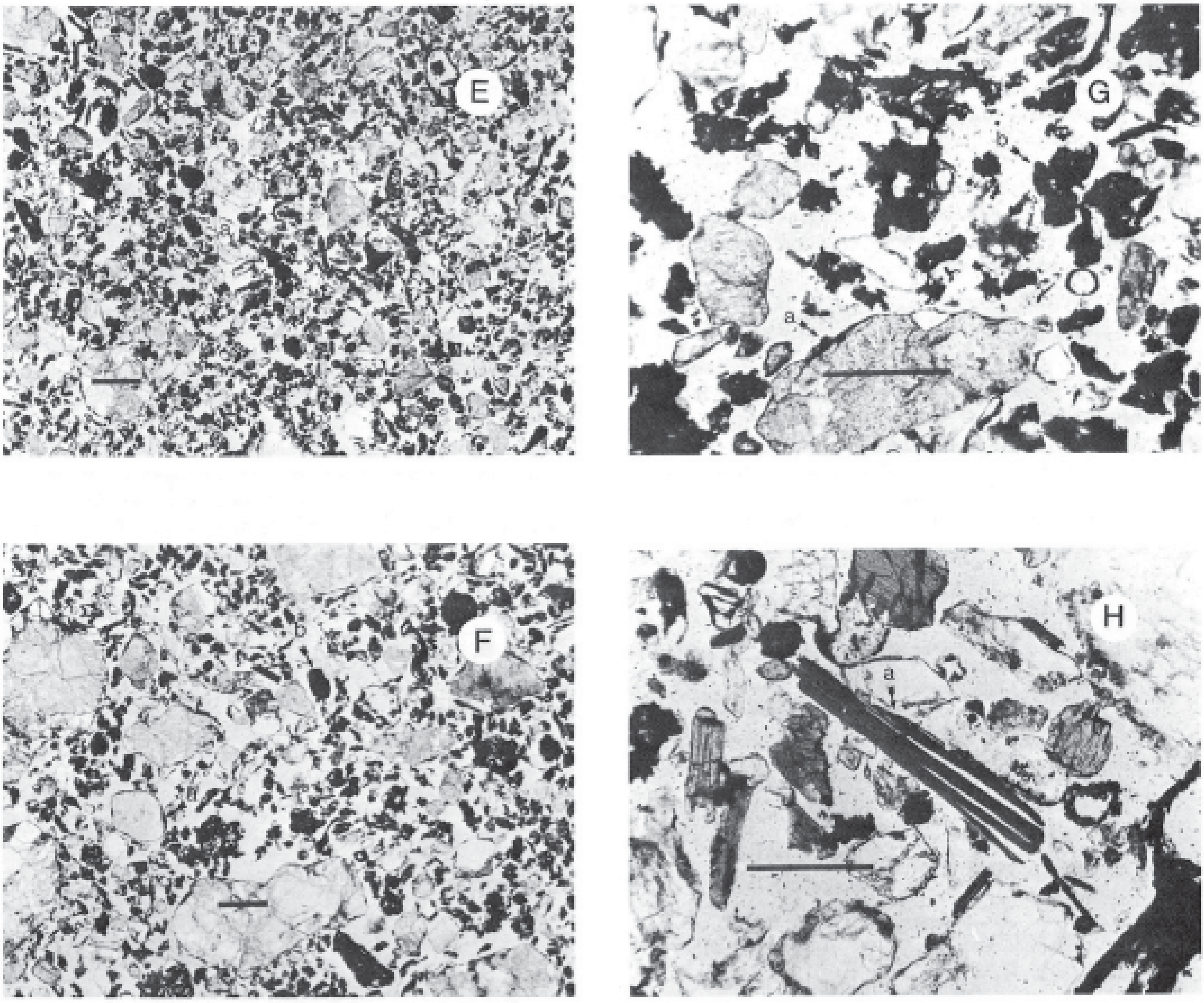

Figure 2—Thin section photomicrographs. (A) The fabric of the surface litter layer of an unburned sagebrush subcanopy soil consists of an open framework of slightly decomposed sagebrush leaves and stems (a) in which mineral grains (b) are rare. Unburned sagebrush leaves have numerous dark-colored oil-rich spheroidal bodies (c). Line scale = 1 mm. (B) Below the surface plant litter zone is a region 2 to 15 cm thick consisting of a mixture of plant litter in various stages of decomposition from slightly decomposed (a) to very melanized (b). Many mineral particles have thin alteration rims of clay (c). Line scale = 1 mm. (C) Deeper in the seedbed beneath unburned sagebrush, the fabric is more compact due to litter decomposition (a). Mineral particles have clay alteration rims (b) but also dark coatings (c) similar to those that occur in burned soil; are these a remnant of a previous wildfire? Line scale = 1 mm. (D) Numerous fecal pellets occur in unburned sagebrush subcanopy soils. Under blue-violet excitation, the fecal pellets strongly fluoresce, even after passing the gut tracts of an invertebrate (a). Line scale = 0.2 mm. (E) In burned sagebrush subcanopy soil, litter is charred (a) to a considerable depth. Line scale = 1 mm. (F) Magnified view of charred zone showing charred material (a) and organic coatings on mineral grains (b). Line scale = 1 mm. (G) Close-up view of mineral coatings that form after a wildfire (a). Line scale = 0.2 mm. (H) As a consequence of heat, biotite particles have been separated along cleavage faces (a). Line scale = 0.2 mm.

sagebrush leaves is left. Immediately below the charred zone, some mineral grains have become thickly coated by dark material and plant litter has become darkened (figs. 2F, G). We suspect that these coatings are formed by condensation of organic vapors on the cooler soil mineral particles at depth; these are the hydrophobic compounds so often found after wildfires (DeBano and others 1976). Another consequence of wildfires is the cleavage of biotite flakes (fig. 2H). Nearly all biotite in the surface 2 cm has been cleaved in this manner, which enhances post-wildfire potassium fertility.

Implications

Viable seeds attempting to germinate in the seedbed beneath unburned sagebrush are faced with several obstacles. Sagebrush litter may allelopathically reduce seed germination and plant growth (Groves and Anderson 1981). We suspect the fluorescence in sagebrush leaves is related to the compounds which are responsible for its allelopathy. If this is so, allelopathic compounds are long-lived in the soil. The open framework in unburned sagebrush subcanopies would also be an impediment for seed germination because the hydraulic gradient to the imbibing seed is reduced (Collis-George and Hector 1966). Seedbed conditions following wildfires would appear to mitigate these obstacles. Heat, generated from wildfires, destroys fluorescent compounds, which reduces allelopathic effects of litter. In addition, by compacting the soil seedbed, wildfires increase hydraulic conductivity to the seed. These positive influences of wildfires may be minimized by the negative effects of phytotoxic organic acid production, loss of nitrogen, and loss of carbon. It is exceedingly difficult to predict the synergism of these effects in real field situations. Moreover, these effects would undoubtedly differ depending on the degree of seedbed disturbance following artificial revegetation. We are presently undertaking field experiments to deduce how post-wildfire factors interact to influence natural and artificial revegetation.

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Dryland Degradation: Symptoms, Stages, and Hypothetical Cures

W. R. J. Dean
Suzanne J. Milton
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Abstract—We studied shifts in the relative abundance and species richness of native plants and animals in dwarf shrubland in the Karoo, South Africa. With heavy grazing, there is a shift in the ratio of perennial to annual plants, both in abundance and species, and an increase in seeds on the soil surface. Along with this, there is a shift in the abundance of seed-harvesting ants, because there is more available seed in the heavily grazed rangeland. There are also changes in the abundance of certain root-feeding insects, such as cicadas. The relative abundance of members of bird foraging guilds changes, with increases in the numbers of nomadic granivores. We conclude that, as rangelands degrade, changes in the ratio of ephemeral to perennial plants and concomitant changes in seed abundance cause a cascade that runs through the granivore community, increasing variability in populations and making rangelands more difficult to restore.

Although ecologists have expressed some concern about the apparent progressive loss of secondary productivity and diversity of arid and semi-arid rangelands over the past century (see review in Milton and others 1994), shifts in the abundance of plant species other than those palatable to domestic livestock or losses of native animals have received less attention. Although no specific study has demonstrated that heavy grazing by domestic livestock has led to the extinction of species and the loss of species richness from an area, several studies have shown that changes in habitat diversity caused by grazing can affect some animal species (see review in Milton and others 1994).

Karoo rangelands lack stability but are apparently strongly resistant (see Pimm 1986). We have suggested elsewhere that degradation in Karoo rangelands proceeds in measurable stages, with changes in the relative abundance of plants (Milton and others 1994). Severely degraded rangelands in general may not return to their original state even when rested for decades (Westoby and others 1989; O'Connor 1991). Conservation problems in the arid parts of South Africa have recently received some attention (Siegfried 1989) and it is of interest to examine which species, other than palatable plants, are affected by changes in rangeland status. Our preliminary findings suggest that initial changes involve subtle differences in plant and animal populations and guild structures as rangelands degrade. The reduction in the relative abundance of some species may lead to cascading effects and the disruption of seed dispersal and other mutualistic relationships. As part of a study aimed at quantifying the status of semi-arid and arid rangelands, we present preliminary data on the changes in vegetation and seed abundance, and in insect and avian assemblages in heavily grazed Karoo rangeland.

Methods and Study Sites

We censused seeds and birds once a month for 36 months at 40 randomly selected sites in dwarf shrubland on sheep and Angora goat ranches in the southern Karoo. Of these 40 sites, we classified three as lightly grazed, 19 as moderately grazed, and 18 as heavily grazed. All sites were situated between Tierberg Karoo Research Centre (33°10' S, 22°17' E) and Rietbron (32°54' S, 23°10' E), South Africa. Rainfall for the general area averages about 160 mm per year, with a coefficient-of-variation of about 22%. There is a slight seasonal difference in the pattern of rainfall between the two places with Tierberg receiving about 10% more of its rain in winter.

Seeds were censused by sweeping the soil surface with a mini-vacuum cleaner for two 30-s periods at each site. The first sweep was over bare soil and the second sweep under the cover of vegetation. Samples were bagged and sorted later in the laboratory, when all seeds were counted. Birds were censused for 5 min at each site, and all birds seen within 100 m were counted.

In addition, we intensively sampled three sites at Tierberg Karoo Research Centre. Tierberg KRC has been fully described by Milton and others (1992). Our study sites at this locality were:

- A fenced exclosure 1 km square from which all domestic livestock have been excluded for the last 7 years (the Tierberg study site).
- Rangeland immediately adjacent to the Tierberg site on which Merino sheep have been stocked at 1 sheep per 6 ha for the past 40 years.
- Adjacent rangeland that has a history of overstocking and heavy grazing by ostriches and wool and mutton sheep until about 1960, and that subsequently has been less heavily stocked.

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Richard Dean, Sue Milton, and Morné du Plessis are Senior Research Officers, and Prof. Roy Siegfried is Director of the Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Rondebosch 7700, South Africa.

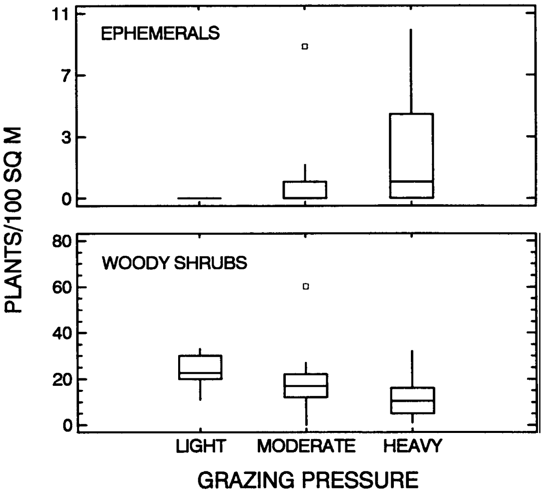

Figure 1—The effect of grazing pressure on the abundance of ephemerals and woody shrubs at 40 sites in the southern Karoo. Lightly grazed, $n = 3$, moderately grazed, $n = 19$, heavily grazed, $n = 18$.

On all three Tierberg sites, we pit-trapped insects once a month for 24 months (methods given in Dean and Griffin 1993), censused cicada (*Quintillia* sp.) emergence holes in random 10-m^2 plots, counted harvester ant (*Messor capensis*) nest-mounds on 1-km x 10-m transects and counted Tractrac Chats (*Cercomela tractrac*) and Karoo Chats (*C. schlegelii*) on transects 1 km long once a week for 100 weeks. All birds seen within 50 m on either side of the transect line were counted, so we effectively sampled an area of 10 ha.

Results

Vegetation

Plants showed a general trend towards more ephemerals and fewer perennials with increasing grazing pressure (Fig. 1). Total plant cover (of all species) decreased with increasing grazing pressure (Fig. 2).

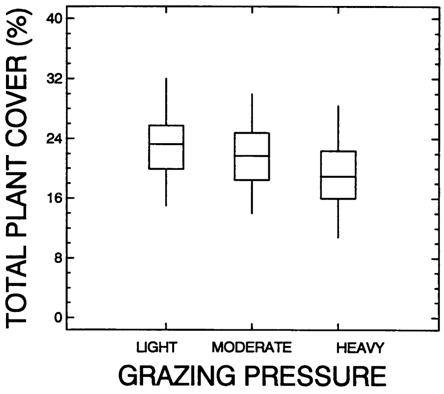

Figure 2—Changes in relative plant cover with increasing grazing pressure. Sites as Figure 1.

The number of seeds on the soil surface is shown in Figure 3. Although there is little difference in mean numbers, the data show a trend towards increasing numbers of seeds on the soil surface as grazing pressure increased. Surface seed assemblages in lightly grazed sites were dominated by perennial shrubs, whereas seed assemblages in heavily grazed sites were dominated by annual forbs and annual grasses.

Insects

Numbers of ants caught in pit-traps at Tierberg showed trends towards an increase in numbers of granivorous ants with increased grazing pressure (Fig. 4), but there were no clear trends in insectivorous ants. Figure 5 shows numbers of harvester ant nest-mounds at Tierberg, supporting the trend shown by the pit-trap data. Counts of cicada

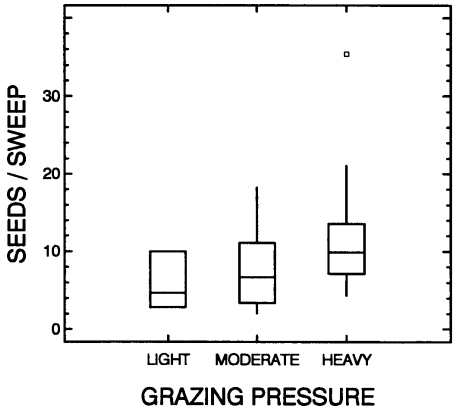

Figure 3—The number of seeds on the soil surface in relation to grazing pressure. Sites as Figure 1.

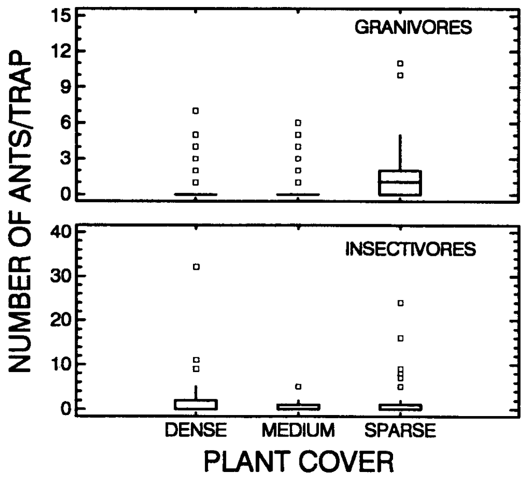

Figure 4—The number of granivorous and insectivorous ants pit-trapped at Tierberg. For lightly grazed areas, $n = 40$ traps, and for moderately and heavily grazed areas, $n = 20$ traps.

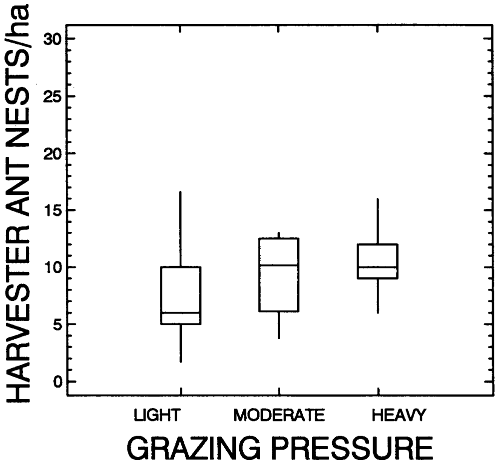

Figure 5—The number of harvester ant (*Messor capensis*) nest-mounds counted in 1-km x 10-m transects at Tierberg. For each site, *n* = 10.

emergence holes (Fig. 6) show decreasing numbers of holes with increasing grazing pressure.

Birds

Numbers of birds followed similar patterns to ants, with granivorous species increasing with increasing grazing pressure (Fig. 7A), and similar inconclusive results in insectivores (Fig. 7B). Numbers of resident species of birds did not show clear trends (Fig. 8A), but numbers of nomadic birds increased with increasing grazing pressure (Fig. 8B). Resident Tractrac Chats and Karoo Chats censused at Tierberg showed diametrically opposed trends, with the Tractrac Chat decreasing with increasing grazing pressure (totally absent from the heavily grazed site), and the Karoo Chat increasing in numbers with increasing grazing pressure (Fig. 9).

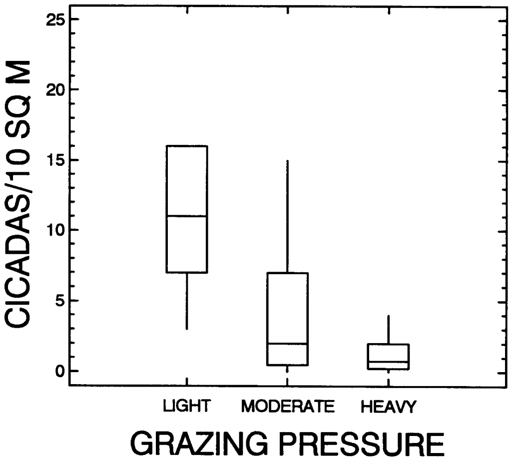

Figure 6—The number of cicada (*Quintillia* sp.) emergence holes in 10-m^2 plots at Tierberg. For each site, *n* = 10.

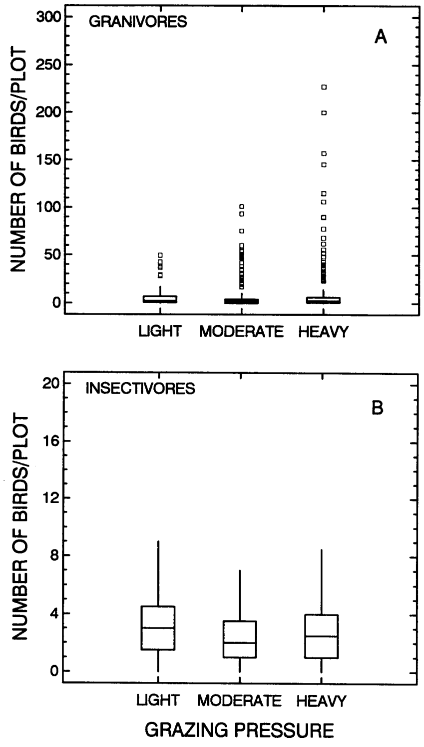

Figure 7—The number of granivorous (A) and insectivorous (B) birds counted in 10-ha plots. Sites as Figure 1.

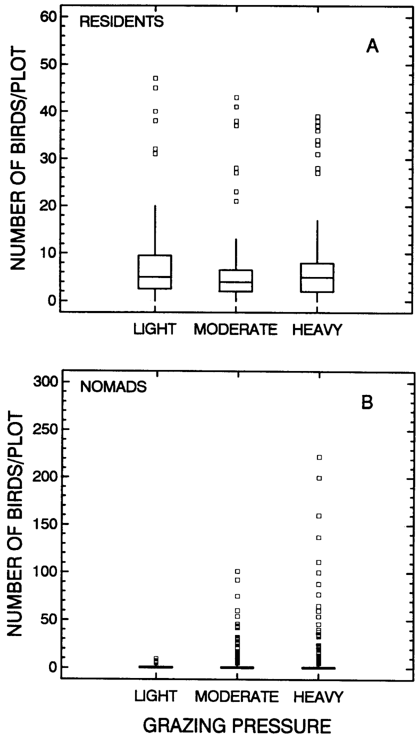

Figure 8—The number of resident (A) and nomadic (B) birds counted in 10-ha plots. Sites as Figure 1.

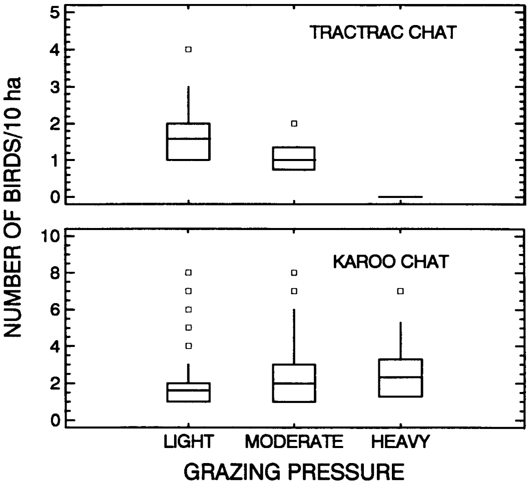

Figure 9—The numbers of Tractrac Chats (*Cercomela tractrac*) and Karoo Chats (*Cercomela schlegelii*) counted on 1-km transects at Tierberg.

Discussion

Vegetation

The total canopy cover of perennial plants was generally lower in sites with a history of heavy grazing. In the hot summer months, many shrubs were leafless and the inter-shrub gaps were bare. After autumn rains, the inter-shrub gaps on over-grazed range were colonized by annual grasses (*Enneapogon, Aristida* and *Karoochloa* spp.) and forbs (*Galenia, Leysera, Trianthema, Tribulus* and *Gazania* spp.). The densities and compositions of these ephemeral assemblages differed greatly from year to year. A decrease in perennial biomass or cover and an increase in ephemeral biomass has been observed elsewhere in arid rangelands that have been overgrazed (Andrew and Lange 1986). Temporal fluctuations in ephemeral cover influence both forage flow for domestic livestock and the availability of resources for granivores.

Certain insects benefit from the resources provided by both ephemeral and perennial plants of heavily grazed sites. Seed-harvesting ants apparently take the most abundant, most available seed, and are not constrained by the toxicity of the plant (Milton and Dean 1993). For example, the harvester ant appears to increase in abundance in karroid shrublands with grazing regimes that favor medium- to large-seeded plants (Milton and Dean 1993). However, in semi-arid grassland, Vorster and others (1992) found that the number of harvester ant nests was correlated with grazing pressure, and that the lowest nest density was found on "continually overgrazed" sites.

Cicadas appear to be dependent on a stable food resource in the form of roots of perennial shrubs, because the nymphs are subterranean feeders on root xylem sap. Cicada density was positively correlated with woody shrubs, and decreased as ephemerals and grazing pressure increased (Milton and Dean 1992). Changes in the abundance of certain root-feeding insects, such as cicadas, can affect the amount of water in the soil because infiltration is significantly improved in patches where there are cicada emergence holes (Dean 1992).

The relative abundance of members of bird foraging guilds changes with grazing pressure. Granivorous birds apparently increase in numbers with increasing grazing pressure, a pattern also found by Baker and Guthery (1992) in south Texas. Tidemann (1990), however, found that granivorous birds (grass-finches) were negatively affected by cattle grazing in northern Australia. On heavily grazed rangelands in the southern Karoo, there are also increases in the numbers of such nomadic species as sandgrouse, granivorous larks and buntings that feed on the seeds of ephemerals (Maclean 1993). This increase in the number of nomads indicates a lack of stability in seed resources, supported to some extent by the high variance of the samples obtained in the seed sweeps (Fig. 3).

These preliminary data suggest that, as rangelands degrade, changes in the ratio of ephemeral to perennial plants and concomitant changes in seed abundance cause a cascade that runs through the granivore community, resulting in increased variability in populations (see Pimm 1986). This will influence both the value of the area as a rangeland and its potential for conservation and restoration. In natural, lightly grazed rangelands, the biomass and composition of vegetation varies with random variations in rainfall. The avifauna is largely resident, with fluctuations in the proportion and abundance of nomadic species depending on particular rainfall events. At the next stage, reductions in the recruitment of palatable plants allows populations of unpalatables to increase (Milton and others 1994) and produce abundant seed. This allows harvester ants to increase in abundance, increasing the number of nutrient patches (Dean and Yeaton 1994) and providing germination sites for seedlings (Dean and Yeaton 1992) that further increase the number of unpalatable plants. Plant species that fail to recruit are lost or drastically reduced in numbers, together with mutualistic relationships with animals and other plants (for example, nurse and nursed plants). As the rangelands degrade further, the biomass and productivity begins to fluctuate as ephemeral plants benefit from the loss of perennial cover, and the number of nomadic seed-eating animals increases disproportionately. Rangelands finally reach a stage where vegetation is largely absent, seed numbers have been markedly reduced and few animals of any species are evident.

Restoration of animal communities, particularly invertebrates and birds, can be achieved only through the restoration of habitats and the recolonization of the area by animals from adjacent areas. The use of mixed species patches of plants, particularly including species that produce juicy fruits, and the creation of other microhabitats will encourage the colonization of the area by animals. We have no data on the time needed for the restoration of severely degraded rangelands, but observations suggest that recovery and restoration time is in the order of decades, and that the more extensive a degraded patch, the more time it will require to restore.

Acknowledgments

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Plant Succession on Disturbed Sites in Four Plant Associations in the Northern Mojave Desert

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J. P. Angerer
W. K. Ostler

Abstract—The U. S. Department of Energy (DOE) is studying Yucca Mountain, Nevada, to determine the mountain's suitability for the long-term storage of high-level nuclear waste. DOE has made a commitment to reclaim all lands disturbed by the project, and to return disturbed sites to a stable ecological state, with a vegetation composition and productivity similar to predisturbance conditions. During 1991 and 1992 EG&G Energy Measurements implemented a study to determine which plant species naturally invade disturbed sites in the Yucca Mountain Project area. Fifty-seven study plots were established on disturbances in four primary vegetation associations. Measurements of absolute perennial plant density occurred in three to six belt transects in each study plot. Mean density was calculated and density values from the disturbed sites were compared with those of undisturbed sites. Across all four vegetation associations, needle-leaf rabbitbrush (*Chrysothamnus teretifolius*) had the highest relative density in disturbed sites, but was not a major component in undisturbed sites. Bursage (*Ambrosia dumosa*) had the highest density in undisturbed sites, but also had high densities in disturbed areas. Total species density was higher in undisturbed sites, compared to disturbed sites. The results of this study will aid in the development of reclamation plans for site-specific disturbances at Yucca Mountain.

In 1979, the Department of Energy identified Yucca Mountain in Nye County, Nevada as a potential site for the long-term storage of high-level nuclear waste. Initial geologic exploration to determine the suitability of Yucca Mountain for waste storage commenced shortly thereafter. Road construction, drill pad construction, trenching activities, drilling geologic exploration wells, and other construction activities created disturbances at many locations. Site characterization activities will ultimately disturb approximately 180 ha (445 ac), which the DOE, Yucca Mountain Project, has made a commitment to reclaim. The ability to conduct successful reclamation in the Mojave Desert may require an understanding of which plant species are best adapted to environmentally harsh sites. In order to aid in the development of a program for reclaiming areas disturbed by site characterization activities, a study was initiated to determine characteristics of natural plant succession that has occurred on various disturbances since the commencement of activities in 1979.

Natural succession in the Mojave Desert appears to be a slow process. Carpenter and others (1986) reported that disturbed areas in the eastern Mojave Desert require approximately 65 to 100 years for plant cover to be comparable to that of undisturbed areas. Vasek and others (1975) stated that natural revegetation of disturbed areas in the Mojave Desert is a process that may require centuries.

Secondary succession studies conducted in the Mojave Desert have indicated that in the early seral stages, disturbed sites are dominated by short-lived and intermediate-lived plant species. Vasek (1980) reported that a severely disturbed borrow pit was dominated by short-lived shrubs such as brittlebush (*Encilia frutescens*), wire-lettuce (*Stephanomeria pauciflora*), and bursage, whereas undisturbed areas surrounding the borrow pit were dominated by long-lived perennials such as creosote bush (*Larrea tridentata*) and prickley-pear cactus (*Opuntia bigelovii)*. The author concluded that the long-lived perennials were removed during disturbance and approximately 9 years was required for long-lived perennial seedlings to appear in the disturbed area. Succession studies conducted at the Wahmonie ghost town (located on the Nevada Test Site and is within 20 kilometers of Yucca Mountain) have shown similar results. Wells (1961) reported that after 31 years since disturbance at the Wahmonie site that the disturbed areas had greater numbers of desert needlegrass (*Stipa speciosa*), burrobrush (*Hymenoclea salsola*), and Nevada Mormon tea (*Ephedra nevadensis*). Creosote bush and hopsage (*Grayia spinosa*) were absent in the disturbance, but were dominants in the undisturbed areas adjacent to the site. Webb and Wilshire (1979) visited the Wahmonie sites 24 years after the study conducted by Wells 1961. These researchers noted that after 55 years, the disturbed areas were lacking in density of long-lived perennials such as creosote bush, hopsage, box thorn (*Lycium andersonii*), and Nevada Mormon tea found in the adjacent undisturbed areas. They suggested that the rate of revegetation at the disturbance was related to the soil compaction levels.

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Objectives

This study was designed to inventory past disturbances and describe the plant succession that has occurred since the initial disturbance. Specific objectives were to: 1) identify the species present in disturbed sites, and categorize these by the four vegetation associations present at Yucca Mountain; 2) determine the differences in species density and composition in disturbed and undisturbed sites; 3) determine if species occurred in the same proportion in both disturbed and undisturbed sites.

Study Area and Methods

Yucca Mountain occurs in the Northern Mojave Desert (Figure 1). Four primary vegetation associations, Creosotebush-Bursage (CB), Creosotebush-Boxthorn-Hopsage (CBH), Blackbrush (B), and Boxthorn-Hopsage (BH), characterize the area (Beatley 1976). Elevation in the study area ranges from 994 to 1,789 m above sea level, and the average annual precipitation varies from about 115 to 170 mm (4.5 to 7.0 in), depending upon elevation. Most precipitation occurs between November and March; however, intense localized thunderstorms may occur during the summer months.

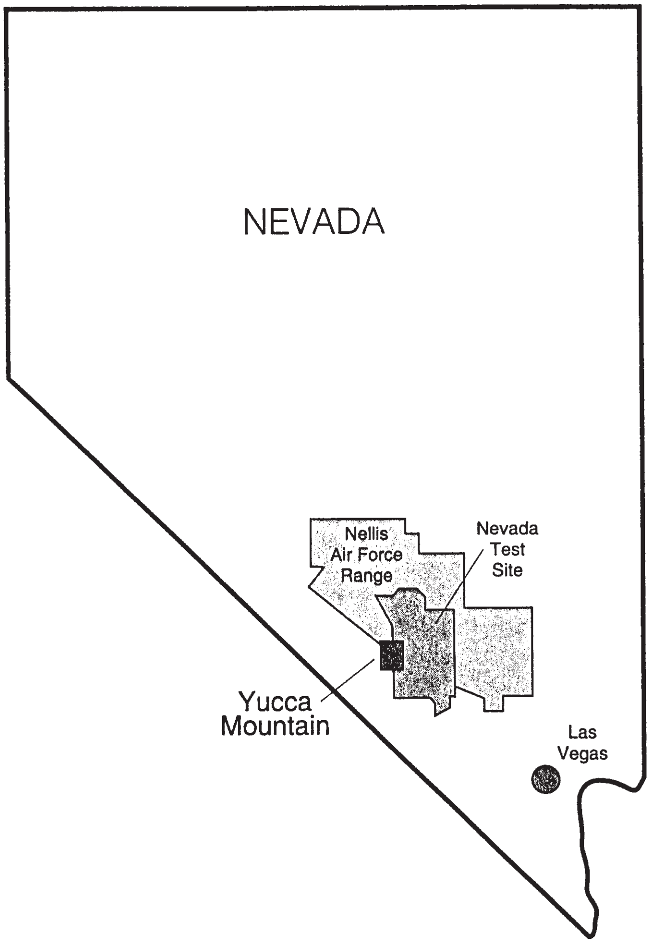

Figure 1—General location of Yucca Mountain, Nevada (not to scale).

During 1991 and 1992, 57 disturbed sites were identified which were large enough to establish belt transects for vegetation studies. Disturbance ages range from six to twelve years since heavy equipment operations ceased; however, some of the disturbance sites have had light vehicle disturbance after the initial activities. The disturbance type (e.g., cut slope, drill pad, etc.) and the initial vegetation association present at each site was recorded. Three to six, 2 x 20-m belt transects were randomly located and established on each disturbed site. Absolute density was measured for each perennial species present in each belt transect. Mean density (plants/100m^2) of each species was calculated.

Twelve study plots were established in undisturbed areas in each of the four vegetation associations (48 total study plots). Absolute density measurements occurred in 1992, in eight to ten randomly located 2 x 50-m belt transects in each study plot. Species absolute density was converted to mean density values for each vegetation association. Mean density values between disturbed and undisturbed areas within vegetation associations were compared.

Results

Disturbed vs. Undisturbed

Average density on disturbed sites across all vegetation associations was 72.3 plants/100 m^2 which was over 70% that in undisturbed areas (101.7 plants/100 m^2) (Table 1). Within the disturbed areas, needle-leaf rabbitbrush had the highest density, followed by matchweed (*Gutierrezia sarothrae*), bursage, wire-lettuce, desert trumpet (*Eriogonum inflatum*), shadscale (*Atriplex confertifolia*) and rubber rabbitbrush (*Chrysothamnus nauseousus*) (Figure 2). With the exception of bursage, these species were minor components in the undisturbed areas as indicated by their low densities (<3 plants/100 m^2). Within the undisturbed areas, bursage had the highest plant densities (26.9 plants/100 m^2), followed by Nevada Mormon tea, ratany (*Krameria parvifolia*), blackbrush (*Coleogyne ramosissima*), menodora (*Menodora spinescens*), and goldenhead (*Acamptopappus shockleyi*) (Figure 2; Table 1). Nevada Mormon tea, ratany, blackbrush, menodora and goldenhead were minor components in the disturbed areas, with each species comprising less than 1% of the total density.

Vegetation Association Characteristics

Differences in densities of species were apparent within vegetation associations. Generally, many of the species that were dominant in the disturbed areas, were minor components in the undisturbed areas and vice-versa.

Creosotebush-Bursage Association—Density in the undisturbed Creosotebush-Bursage vegetation association was four times greater than that in the disturbed areas. Bursage had the highest density in both disturbed and undisturbed sites (Figures 3); however, density of bursage was over three times as high in the undisturbed as that in

Table 1—Mean density (plants/100 m^2) of perennial plant species present in disturbed (DIS) and undisturbed (UND) communities in Creosotebush-Bursage (CB), Blackbrush (B), Boxthorn-Hopsage (BH), and Creosotebush-Boxthorn-Hopsage (CBH) vegetation associations at Yucca Mountain, Nevada. Nomenclature follows Munz, 1974.

			B		CB		BH		CBH	
Species	**Common Name**	**Code**	**DIS (n=37)**	**UND (n=108)**	**DIS (n=34)**	**UND (n=108)**	**DIS (n=116)**	**UND (n=108)**	**DIS (n=88)**	**UND (n=108)**
Acamptopappus shockleyi	Goldenhead	ACSH	0.0	0.0	0.2	18.3	0.0	0.2	0.0	0.3
Ambrosia dumosa	Bursage	AMDU	0.5	17.9	20.3	70.0	1.8	7.8	6.4	11.7
Aristida longiseta	Sandwort	ARFE	0.1	0.0	0.0	0.0	0.4	0.5	0.0	0.0
Aristida purpurea	Purple threeawn	ARPU	0.0	0.0	0.0	0.0	1.7	0.0	0.3	0.0
Artemesia spinescens	Budsage	ARSP	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Artemesia tridentata	Big sagebrush	ARTR	0.3	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Atriplex canescens	Fourwing saltbush	ATCA	3.7	0.2	0.0	0.0	2.1	0.4	0.1	0.1
Atriplex confertifolia	Shadscale	ATCO	0.5	5.8	0.0	1.7	8.2	5.0	0.0	0.2
Brickellia watsonii	Brickellbush	BRWA	0.0	0.0	0.0	0.0	3.3	0.3	0.9	0.0
Ceratoides lanata	Winterfat	CELA	0.0	0.1	0.0	3.4	0.1	4.9	0.0	1.0
Chrysothamnus nauseosus	Rubber rabbitbrush	CHNA	5.1	0.0	0.0	0.0	6.0	0.3	0.9	0.0
Chrysothamnus paniculatus	Black-stem rabbitbrush	CHPA	0.0	0.0	0.3	0.0	0.1	0.0	0.0	0.0
Chrysothamnus teretifolia	Needle leaf rabbitbrush	CHTE	19.3	1.4	0.1	0.0	33.5	3.4	15.4	0.0
Chrysothamnus viscidiflorus	Yellow rabbitbrush	CHVI	0.5	0.2	0.0	0.0	3.7	1.6	0.0	0.0
Coleogyne ramosissima	Blackbrush	CORA	3.2	17.9	0.0	1.4	0.1	0.0	0.0	0.5
Descurainia sophia	Tansy-mustard	DESO	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.1
Echinocereus engelmanii	Hedgehog cactus	ECEN	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Echinocactus polycephalus	Cottontop barrelcactus	ECPO	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Encelia virginensis	Brittlebush	ENVI	1.6	1.8	0.0	0.1	3.1	0.8	0.3	0.9
Ephedra nevadensis	Nevada Mormon tea	EPNE	0.1	7.1	0.4	5.6	0.6	14.5	1.0	8.3
Ephedra viridis	Green Ephedra	EPVI	0.0	0.2	0.0	0.0	0.0	1.0	0.0	0.0
Eriogonum fasciculatum	California buckwheat	ERFA	0.1	0.6	0.4	0.0	1.0	10.8	1.1	0.7
Eriogonum inflatum	Desert trumpet	ERIN	0.0	0.0	1.2	0.0	3.2	0.3	12.0	0.0
Eriogonum microthecum	Buckwheat	ERMI	0.0	0.0	0.0	0.0	0.1	0.8	0.0	0.0
Erioneuron pulchellum	Fluff grass	ERPU	0.0	0.4	0.1	0.3	2.7	10.7	5.8	0.8
Euphorbia albomarginata	Rattlesnake weed	EUAL	0.0	0.1	1.5	0.0	0.0	0.0	0.4	0.1
Grayia spinosa	Spiny hopsage	GRSP	0.0	1.2	0.0	1.6	0.0	8.1	0.1	0.6
Gutierrezia sarothrae	Matchweed	GUSA	0.3	0.0	0.0	0.0	12.4	4.1	0.0	0.0
Haplopappus cooperi	Goldenbush	HACO	0.3	0.8	0.0	1.2	0.6	10.7	1.0	2.1
Haplopappus linearifolius	Interior goldenbush	HALI	1.1	0.0	0.1	0.0	0.8	1.1	0.0	0.0
Hilaria jamesii	Galleta	HIJA	2.4	2.3	0.0	0.0	0.3	8.1	0.0	0.0
Hymenoclea salsola	Burrobrush	HYSA	1.6	0.9	0.1	0.0	1.3	5.5	2.4	2.8
Krameria parvifolia	Ratany	KRPA	0.0	9.0	0.2	5.6	0.0	0.0	0.0	10.1
Larrea tridentata	Creosote bush	LATR	0.0	0.7	1.3	6.0	0.1	0.2	1.1	5.5
Lepidium fremontii	Desert pepperweed	LEFR	0.3	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Leptodactylon pungens	Prickly gilia	LEPU	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0
Lycium andersonii	Box thorn	LYAN	1.3	2.5	0.3	0.8	0.5	7.0	0.3	3.8
Lycium pallidum	Wolfberry	LYPA	0.1	2.3	1.0	5.3	0.0	0.6	0.2	0.9
Machaeranthera tortifolia	Desert-aster	MATO	0.0	0.5	0.0	0.6	0.4	0.1	0.0	0.0
Menodora spinescens	Menodora	MESP	0.3	1.3	0.0	14.6	0.3	1.3	0.2	2.4
Mirabilis bigelovii	Desert wishbone bush	MIBI	0.0	0.0	0.0	0.1	0.1	0.1	0.0	0.1
Muhlenbergia porteri	Bush muhly	MUPO	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.0
Opuntia basilaris	Beavertail pricklypear	OPBA	0.0	0.1	0.0	0.0	0.0	0.4	0.0	0.1
Opuntia echinocarpa	Strawtop pricklypear	OPEC	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Oryzopsis hymenoides	Indian ricegrass	ORHY	1.0	0.0	0.0	1.3	0.3	0.1	0.1	0.1
Psorothamnus fremontii	Indigo bush	PSFR	0.0	0.0	0.0	0.2	0.0	0.0	0.1	0.0
Salazaria mexicana	Bladdersage	SAME	0.0	0.4	0.0	0.1	0.0	0.7	0.0	1.1
Sitanion hystrix	Squirreltail	SIHY	0.0	0.0	0.0	0.0	0.1	0.0	0.0	0.0
Sitanion jubatum	Foxtail barley	SIJU	1.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sphaeralcea ambigua	Globemallow	SPAM	6.2	0.0	0.0	0.1	2.3	12.2	1.0	0.1
Sporobolus cryptandrus	Sand dropseed	SPCR	0.0	0.0	0.0	0.0	0.4	0.1	0.0	0.0
Stephanomeria pauciflora	Wire-lettuce	STPA	1.5	0.1	3.5	0.0	5.3	0.3	8.2	0.2
Stipa speciosa	Desert needlegrass	STSP	0.6	0.4	0.0	0.1	2.5	12.1	0.6	1.0
Tetradymia axillaris	Longspine horsebush	TEAX	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0
Tetradymia glabrata	Littleleaf horsebush	TEGL	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Yucca brevifolia	Joshua tree	YUBR	0.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Total Forbs			8.0	0.2	6.3	0.1	10.9	12.9	21.7	0.5
Total Grasses			5.7	3.0	0.1	1.6	8.2	31.7	6.7	1.9
Total Shrubs			40.1	73.3	24.9	136.5	80.4	92.9	31.7	53.2
Total Mean Density			53.7	76.4	31.3	138.3	99.6	137.4	60.1	55.6

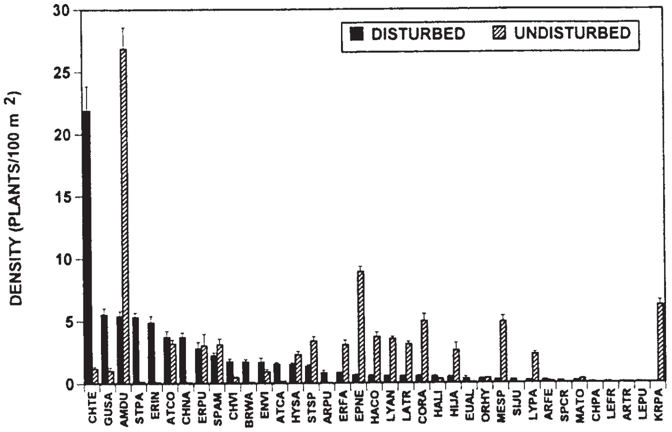

Figure 2—Average density (±SE) of perennial plants found in 57 disturbed sites and 48 undisturbed sites at Yucca Mountain, Nevada. Minor species, found in both disturbed and undisturbed areas, are not shown. See Table 1 for species codes.

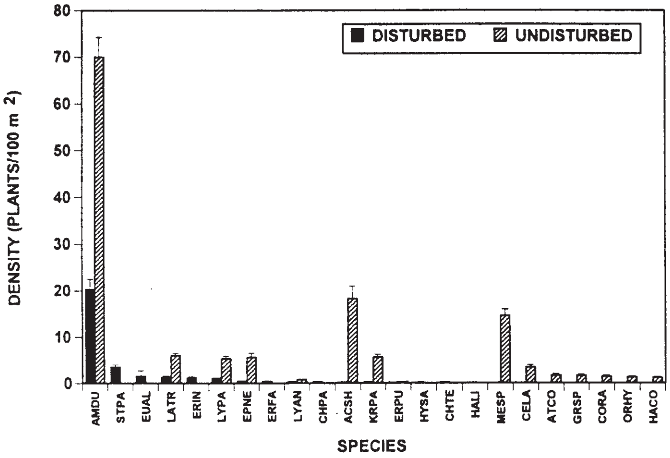

Figure 3—Average density (±SE) of perennial plants found on disturbed and undisturbed sites in the Creosotebush-Bursage vegetation association at Yucca Mountain, Nevada. Minor species are not shown. See Table 1 for species codes.

the disturbed sites (70.0 and 20.3 plants/100 m respectively; Table 1). Wire-lettuce and desert trumpet had substantially greater densities (95 and 64 times greater) within disturbed sites when compared to undisturbed sites (Table 1). Creosotebush densities in disturbed and undisturbed areas were substantially different (Table 1). Menodora, wolfberry (*Lycium pallidum*), and winterfat (*Ceratoides lanata*), subdominants in the undisturbed sites were not encountered in the disturbed sites.

Creosotebush-Boxthorn-Hopsage Association—Density in the disturbed areas was similar to that of the undisturbed areas (Table 1). Generally species occurring in this association that had high densities in disturbed sites had low densities in undisturbed sites (Figure 4; Table 1). The converse was apparent for the undisturbed sites (Figure 4; Table 1). Needle-leaf rabbitbrush, desert trumpet, and wire-lettuce had the highest density of all species occurring in the disturbed sites. These same species were either absent or virtually absent from undisturbed sites. Disturbances in Creosotebush-Boxthorn-Hopsage sites apparently has altered the environmental conditions so that these three species, which do not normally occur in this vegetation association, not only became established, but dominated the new plant assemblage. Disturbance virtually eliminated ratany, the second most abundant species in undisturbed sites.

Blackbrush Association—Species density in undisturbed area in this association was 22.9 plants/100 m^2 greater than that in the disturbed sites (Table 1). Again many of the species that were the most common in disturbed sites were not among the common species in undisturbed sites (Figure 5; Table 1). Needle-leaf rabbitbrush was the dominant species in the disturbances and its density was nearly 14 times greater than in the undisturbed (Table 1). Nine additional species, Globemallow (*Sphaeralcea ambigua*), rubber rabbitbrush, fourwing saltbush (*Atriplex canescens*), Squirreltail (*Sitanion jubatum*), wire-lettuce, interior goldenbush, and Indian ricegrass (*Oryzopsis hymenoides*) occurred in disturbed sites, but were essentially absent in the undisturbed sites (Figure 5; Table 1). Five species, blackbrush, bursage, shadscale, ratany, and Nevada Mormon tea had substantially greater densities in undisturbed sites. The latter four species were almost absent in the disturbed sites.

Boxthorn-Hopsage Association—Density in the disturbed areas was less than that of the undisturbed sites within this vegetation association. As seen in the Blackbrush and the Creosotebush-Boxthorn-Hopsage

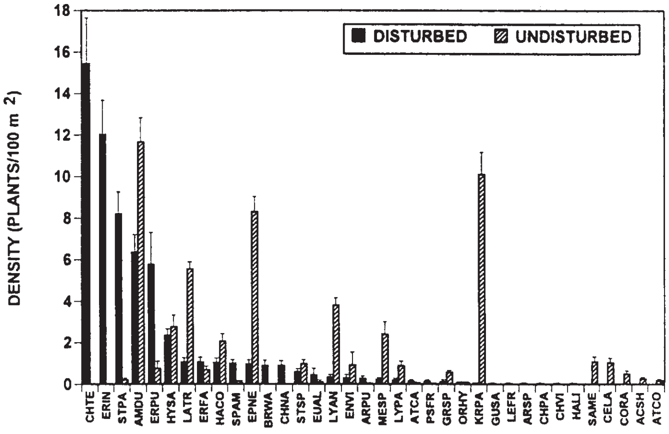

Figure 4—Average density (±SE) of perennial plants found on disturbed and undisturbed sites in the Creosotebush-Boxthorn-Hopsage vegetation association at Yucca Mountain, Nevada. Minor species are not shown. See Table 1 for species codes.

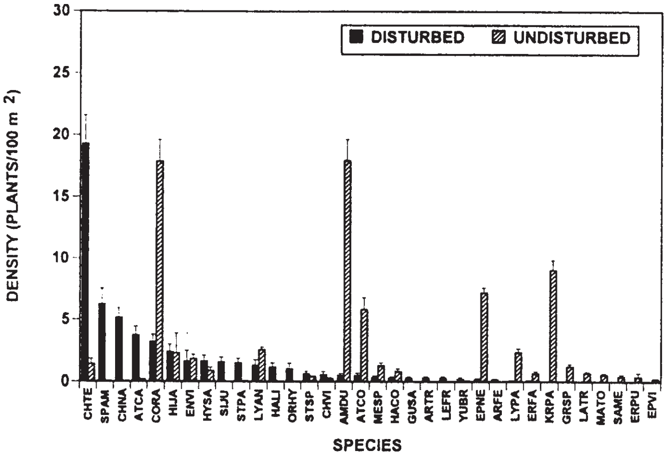

Figure 5—Average density (±SE) of perennial plants found on disturbed and undisturbed sites in the Blackbrush vegetation association at Yucca Mountain, Nevada. Minor species not shown. See Table 1 for species codes.

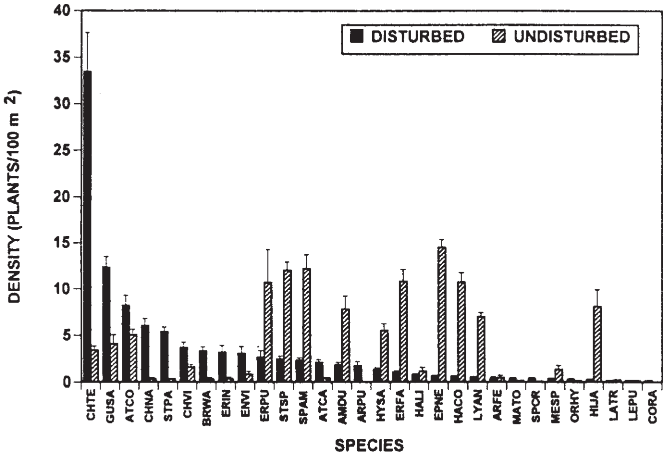

Figure 6—Average density (±SE) of perennial plants found on disturbed and undisturbed site in the Boxthorn-Hopsage vegetation association at Yucca Mountain, Nevada. Minor species not shown. See Table 1 for species codes.

associations, species that had high relative densities in disturbed sites generally did not have high relative densities in undisturbed sites (Table 1) Three species, needle-leaf rabbitbrush, matchweed, and shadscale had the highest densities in disturbed sites. These same species accounted for less than 10% of the plants present in undisturbed sites (Figure 6). Eight additional species had densities that were higher in disturbed sites, compared to undisturbed sites. Ten species had substantially higher densities in undisturbed sites when compared to disturbed sites. Mormon tea, the most abundant species in undisturbed sites, was among the least abundant species in disturbed sites (Table 1).

Discussion and Conclusions

Generally species that had high densities in disturbed vegetation associations in the Northern Mojave Desert did not have similar density values in undisturbed vegetation associations. Bursage in the Creosotebush-Bursage vegetation association was the lone exception. Although the absolute density between disturbed and undisturbed sites for bursage was markedly different (Table 1), this species was the dominant in both disturbed and undisturbed as indicated by the proportions of the total density (Figure 3). Bursage germinates and grows well in slightly disturbed soils and lightly shifting sands (Vasek, 1979). These conditions probably prevail in both the undisturbed and disturbed sites of the Creosote-Bursage vegetation association at Yucca Mountain which have soils that generally have >90% sand content.

Needle-leaf rabbitbrush dominates secondary succession in the Blackbrush, Boxthorn-Hopsage, and Creosotebush-Boxthorn-Hopsage vegetation associations. The high abundance of needle-leaf rabbitbrush on disturbed sites in three different vegetation associations suggests that this species may be a good choice for use in reclaiming disturbed sites. Even though this species is lacking in the undisturbed areas it may be important in ameliorating the disturbance, thus enhancing the germination and establishment of the more desirable species in the adjacent undisturbed areas. Other species having high densities in disturbed sites may also be good candidates for use during site-specific reclamation for this same reason.

Densities of species in this study when compared to that of the studies conducted at the Wahmonie ghost town (located approximately 20 km east of Yucca Mountain) (Wells, 1961; Webb and Wilshire, 1980) are somewhat different. Vegetation at the Wahmonie site is a Boxthorn-Hopsage/Blackbrush transition similar to those described in this study. Wells (1961) reported that desert needlegrass, boxthorn and Nevada Mormon tea were the most abundant species in the disturbed areas after 33 years since disturbance. Webb and Wilshire (1980) revisited the site and reported that desert needlegrass, Nevada Mormon tea and burrobrush were the most abundant species 51 years after disturbance. In this study, these species were found in the disturbance areas, but they were generally minor components of the total density. The differences in the species composition between the Wahmonie studies and this study may be age related; all disturbances in this study were less than 15 years old. Carpenter and others (1986) noted that disturbed sites in early successional stages in the eastern portion of the Mojave Desert are dominated by short-lived species that include globemallow, rayless goldenhead (*Acamptopappus spaerocephalus*), burrobrush, and matchweed. The disturbed sites in this study appear to be dominated by short-lived species, some of which are similar in growth form and reproductive strategy to those described above. The dominance of needle-leaf rabbitbrush in most of the disturbed areas in this study and the lack of it in the undisturbed areas may be indicative that this species is short-lived.

Disturbances at Yucca Mountain appear to have altered the micro-environment to such an extent that plant species which do not normally occur, or rarely occur in a plant community now dominate the new plant assemblage. After six to twelve years of succession, vegetation density in disturbed sites is still substantially less than in undisturbed sites (except in the Creosote-Boxthorn-Hopsage association). The dominant species of undisturbed areas are in low proportion or are generally lacking in the disturbed sites indicating that after 15 years that the disturbed sites are in early successional stages. Secondary succession appears to be a very slow process on these disturbed sites.

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A Bitterbrush Dieback in the Upper Gunnison River Basin, Colorado

J. Arthur Hayes

Abstract—During a significant drought period (1988-1993), an extensive dieback of antelope bitterbrush (*Purshia tridentata* [Pursh] DC.) occurred in the Upper Gunnison River Basin of Colorado. The area affected by the dieback includes at least 500 square miles. The dieback symptom was a necrosis of leaves and stems. Fifty-four sites were examined. The amount of dieback at a site ranged from 88% to 1% with an average of 41%. A canker fungus, tentatively identified as *Coniochaeta ligniaria* (Grev.) Cook, was found on stems of affected bitterbrush. Prolonged drought stress could be the factor that predisposed shrubs to fungus-caused disease development.

A period of significant drought began in October 1987 and continued through 1993. The Palmer Drought Severity Index, which is compiled by the Colorado Climate Center of Colorado State University, uses precipitation and temperature records to model soil moisture (Palmer 1965). The model is a simple soil moisture budget which describes drought severity in four categories: mild, moderate, severe and extreme. Data from six cooperative stations in the Upper Gunnison Basin is used to model soil moisture to determine drought severity. During the 72 months between October 1987 and September 1993, 24 months were in the mild drought category, 18 were in the moderate category, 18 were in the severe category and 12 months were in the extreme category. The Palmer Index indicates that this drought period was the most severe in terms of duration and depth or severity of drought since 1950 (Figure 1). Comparison over a longer period indicates this drought probably equals or exceeds the most severe in the last 100 years (Nolan Doesken, pers. comm.).

The first occurrence of bitterbrush dieback was observed in 1990 in the Willow Creek area west of the city of Gunnison, north of Blue Mesa Reservoir and in the Wood Gulch Area, approximately 15 miles east of Gunnison. Plants in both areas were observed to be dry and brittle and appeared to have an unusual amount of dead branches. Soil moisture monitoring in 1990 and 1991 revealed two areas in the Gunnison Basin that were among the most drought affected in terms of soil moisture; the Chance Gulch Area, 3 miles southeast of Gunnison, and the lower Antelope Creek Valley, 3 miles northwest of Gunnison. In May of 1991, an area of at least five hundred acres of big sagebrush (*Artemisia tridentata* Nutt.) in the Chance Gulch area was observed to be defoliated, with plants partially or completely dead. In July of 1991, observations in the Antelope Creek Valley revealed several hundred acres where bitterbrush was affected, with the majority of plants having more than 50% dead stems. The appearance of the plants (the bark appearing to have recently separated from the stems and the presence of small, dead stems of a size which would be removed by weathering in two or three years) suggest that the stems had recently died. This study was undertaken to determine the extent of the bitterbrush dieback, the areas affected and to describe the sites where bitterbrush occurs in the Upper Gunnison River Basin.

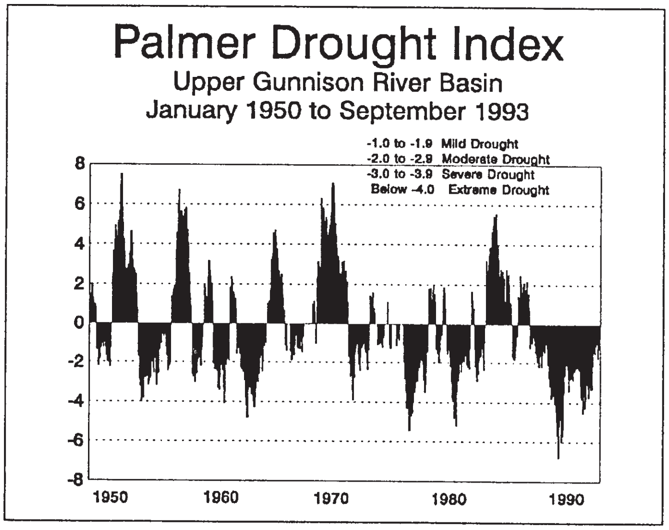

Figure 1—Palmer Drought Severity Index for the Upper Gunnison River Basin, Colorado for the period January 1950 to September 1993. Source: Colorado Climate Center, Ft. Collins, Colorado.

Study Area

The upper Gunnison Basin ranges in elevation from about 7,500 feet to over 13,000 feet. The average annual precipitation at Gunnison (7,700 ft. elevation) is 9.7 inches. Annual precipitation at 10,000 feet elevation could be expected to be in the 20 to 25 inch range. Table 1 shows the monthly precipitation and temperature averages for Gunnison.

In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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Table 1—Monthly averages for precipitation and temperature for Gunnison, Colorado.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Precipitation (inches)	0.74	0.62	0.64	0.54	0.64	0.56	1.37	1.54	1.03	0.80	0.56	0.77
Temperature (°F)	8.9	14.8	27.0	38.2	47.4	55.6	61.6	59.0	51.8	41.3	28.3	14.4

Source: Colorado Climate Center, Dept. of Atmospheric Science, Colorado State University (25 years of record).

Methods

A large portion of the Upper Gunnison Basin was surveyed to locate areas where bitterbrush was a significant component of the plant community. Within each area, a representative site was selected by ocular estimate and sampled to determine canopy cover of bitterbrush and the percentage of dead bitterbrush. A total of 54 sites were selected for sampling in 1993. One 200 foot long transect was run at each site to measure the canopy cover of bitterbrush. The percent of dead branches (branches that had the appearance of having died within the last 3 or 4 years) on each bitterbrush plant along the transect was estimated. Aspect, elevation and a description of the plant community were noted at each site. Sample bitterbrush branches were sent to the Forest Service, U.S. Department of Agriculture, Shrub Sciences Laboratory in Provo, Utah for the identification of possible causal fungus.

Results

The elevational range of bitterbrush in the Gunnison Basin was found to be from 7,800 feet to 9,600 feet. Bitterbrush was found most commonly associated with plant communities dominated by big sagebrush, and forest types dominated by ponderosa pine (*Pinus ponderosa* Lawson) and Douglas-fir (*Pseudotsuga menziesii* [Mirbel] Franco). While bitterbrush was found on all aspects, it is more commonly found on southeast, south and southwest aspects. Bitterbrush was also found on a wide variety of soil types, indicating it could be a component of many ecological types. The canopy cover of bitterbrush on the 54 sites examined ranged from 2.2% to 33%, with an average for all sites of 13%, indicating that bitterbrush is often a significant component of plant production on the sites where it occurs.

A possible canker fungus, the characteristics of which place the fungus "near the genus *Coniochaeta*, perhaps *C. ligniaria*" (Nelson 1993) was found on live and dead stems and was restricted to the vicinity of cankers. Many cankers on live stems appeared to have originated from cicada (Fam. Cicadidae) ovipositing wounds (Nelson 1993). The variation in the amount of dieback among sites was high. The most severely affected area was found to have an average of 88% of each plant defoliated with many whole branches dead. Two sites that burned about 10 years ago had the least dieback (1% and 2%). Excluding the burned sites, the range of average individual plant dieback for the 52 remaining sites was 13% to 88%. Eighty-three percent (45/54) of the sites examined had an average plant dieback of at least 25%. Fifty percent (27/54) of the sites had an average plant dieback of at least 40%. A total of 812 bitterbrush plants were examined with 1.7% (14/812) of all plants completely dead.

Although a multivariate analysis was not done, it appears that there was little correlation between elevation or aspect and the amount of dieback at a site. The apparent lack of correlation between elevation or aspect and dieback was likely because of the variability in precipitation and micro-climates within the basin.

The age of the dead stems ranged from one to 45-years old. The age of a 1/4 inch diameter stem was generally between 5 and 10 years. Stems 1/2 inch in diameter were between 8 and 15 years old.

The amount of hedging of bitterbrush by big game animals between sites ranged from none to severe. There appeared to be little correlation in the degree of hedging and the amount of dieback at a site.

Short leader growth and dead stems on big sagebrush, serviceberry and aspen suggests that these species had also been affected by the drought.

Discussion

The prolonged deficiency in soil moisture and the occurrence of the dieback in bitterbrush strongly suggest that moisture stress could have been a factor in the dieback. Ordinarily weak or secondarily pathogenic fungi may become active when plants are predisposed or weakened by environmental stress (Nelson et al. 1990). The model proposed by Houston (1992) describes dieback-decline diseases in forest systems as a "Host-Stress-Saprogen" relationship where environmental stress initiates disease. Drought initiated declines of oak (*Quercus* sp.) and ash (*Fraxinus* sp.) are discussed by Houston (1992). It is likely that the drought and subsequent moisture stress predisposed bitterbrush to a secondarily pathogenic fungus such as *Coniochaeta*.

While identification of the cause of plant disease often requires intensive investigation, climate monitoring using indices such as the Palmer Drought Severity Index is comparatively simple and can be useful in predicting and identifying areas where environmental stress of plants can be expected. The ability to predict possible environmental stress to wildland plant communities would be useful for land managers for wildlife habitat and livestock forage management.

Acknowledgments

The initial study to evaluate the dieback of bitterbrush was funded by the Gunnison Basin Habitat Partnership Program. I would like to thank Shawn Miller for his efforts in the data collection and Sandy Hayes, Barry Johnston and Scott Sherwood for their help in the design of this study, identifying areas of shrub dieback and in reviewing this report. I would also like to thank Pete Angwin and David L. Nelson for their efforts in the identification of the canker fungus and for reviewing this report.

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Composition and Distribution of Blackbrush (*Coleogyne ramosissima*) Communities in Southern Nevada

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Lawrence R. Walker

Abstract—The distribution of blackbrush (*Coleogyne ramosissima* Torr.) communities was surveyed on 15 elevational transects in the Spring and Sheep Mountain Ranges adjacent to Las Vegas Valley in southern Nevada. Species richness, density, and abundance were compared among the 15 transects and within subsets of the data delineated by geographical and elevational distribution. Three communities were classified into five vegetation zones: below blackbrush, where the plant community was dominated by creosote bush-bursage (*Larrea tridentata-Ambrosia dumosa*), at the lower and upper ecotones and in the center of the blackbrush community, and above blackbrush where the community is dominated by pinyon-juniper-sagebrush (*Pinus monophylla-Juniperus osteosperma-Artemisia tridentata*). Blackbrush communities shared relatively broad upper and lower ecotones with pinyon-juniper-sagebrush and creosote bush-bursage, respectively. Blackbrush communities were more frequently found on level topography than on steep slopes or in washes. Lower blackbrush ecotones generally contained the highest species richness, whereas pinyon-juniper-sagebrush stands normally contained the lowest. Blackbrush was less dense at lower blackbrush ecotones than at upper ecotones, primarily due to the presence of other shrub species. Soil moisture generally increased with elevation along the lower blackbrush boundary in Lucky Strike Canyon of the Spring Mountains.

Blackbrush communities are one of the major plant communities in southern Nevada and the Mojave Desert. They are distributed at a particular elevation between creosote bush-bursage and pinyon-juniper-sagebrush communities and are distributed on terraces and slopes of gravelly soils (Bowns 1973). Their current distributions probably developed since the last pluvial period (20,000-10,000 B.P.; Bradley 1964). West (1983) states that blackbrush communities establish primarily in sandstone and limestone-derived soils and have a low tolerance of excessive salinity and low soil moisture. Blackbrush growth begins in March but ceases when soil moisture is depleted in June; a low growth rate of blackbrush may be caused by shallow soils and a caliche layer, approximately 30 to 50 cm below the surface that impedes root growth and soil moisture (West 1983). Bowns (1973) proposed that cold air temperature limits the upper elevational boundary and that low soil moisture limits the lower elevational boundary of blackbrush communities in the state of Utah. However, no one has examined the factors limiting blackbrush distribution in southern Nevada. In this paper, we assess the composition and distributional patterns of 15 blackbrush communities on the Spring and Sheep Mountain Ranges, both located just north of Las Vegas in southern Nevada and compare those distributions to various physical factors.

Methods

We calculated species richness, density, and proportional abundance of all perennial woody species on 15 transects that spanned the elevational distribution of blackbrush in the Spring Range (12 transects) and the Sheep Range (three transects) near Las Vegas, Nevada. The transects in the Spring Range were subdivided into three geographical areas based on aspect of the mountain. Five vegetation zones were represented in our study and identified by their dominant species: creosote bush-bursage, blackbrush, pinyon-juniper-sagebrush and the upper and lower blackbrush ecotones. Mean elevations of the five vegetation zones among the 15 transects were recorded. Each of the 15 transects ran from the upper portion of creosote bush-bursage through the blackbrush belt, and terminated at the lower portion of the pinyon-juniper-sagebrush plant community. Circular plots with a 5.65-m radius (100 m^2) were placed at a fixed altitudinal interval of 65 m. Transects generally contained 9 to 16 plots depending on the range of the upper and lower boundaries of the blackbrush community; a total of 181 plots were sampled. Habitats included in the transects were classified as slopes, flat surfaces, and dry washes. Cliffs and stream beds were excluded, but substitute plots were measured at the identical elevation. All plots were greater than 50 m from existing roads to eliminate possible road effects. Rank abundance curves were plotted based on the proportional abundance (Pi) for each species in 15 transects and in each vegetation zone. The value of Pi was calculated by dividing the total number of individual species by the total number of all species present at each plot. We measured water content in soils across the lower elevational boundaries of blackbrush in Lucky Strike Canyon on the east side of the Spring Mountain Range in order to determine if a positive relationship existed between elevation,

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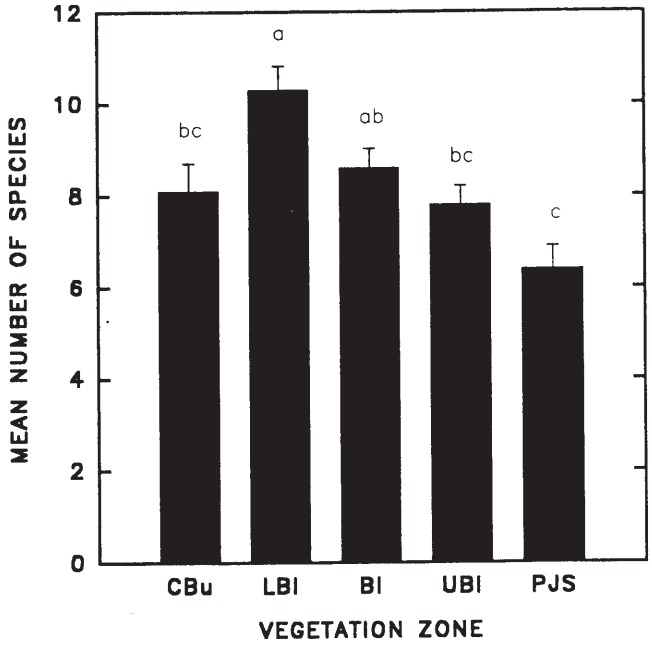

Figure 1—Mean species richness with standard errors among 15 elevational transects divided into five vegetation zones in the Spring and Sheep Mountain Ranges. Symbols: Creosote bush-bursage (CBu); lower blackbrush ecotone (LBl); blackbrush (Bl); upper blackbrush ecotone (UBl); and Pinyon-juniper-sagebrush (PJS). Columns with the same letter are not significantly different ($p < 0.05$).

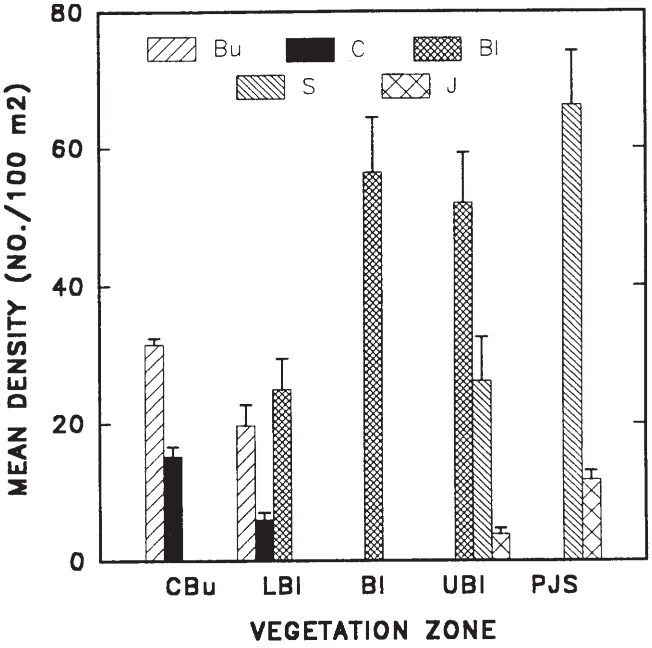

Figure 2—Mean densities with standard errors of dominant woody plant species in 15 transects within five major vegetation zones in the Spring and Sheep Mountain Ranges. Symbols are explained in Figure 1.

soil moisture content, and blackbrush density. Soil samples (0-15 cm) were collected from 36 plots, sifted through a 2-mm sieve in the field, then weighed, dried for 72 hours at 110 °C, and reweighed to determine gravimetric moisture content.

Results and Discussion

With all 15 transects combined, species richness declined significantly (p = 0.0001) from the lower blackbrush ecotone to the pinyon-juniper-sagebrush plant community (Fig. 1). The only deviation from this pattern was among the transects on the south side of the Spring Mountain Range, where greater species richness occurred at higher elevation, mainly due to the presence of riparian vegetation in Red Rock Canyon. Plants in riparian areas were generally more diverse, perhaps due to less water stress during droughts. Creosote bush and bursage both had highest mean densities at plots below the lower limits of blackbrush and lower densities in the lower blackbrush ecotone (Fig. 2). They were completely absent from the central portion of the blackbrush communities. Sagebrush first appeared at the upper blackbrush ecotone with less than 10% cover and replaced blackbrush at higher elevation with greater than 60% cover (Fig. 2). In southern Nevada, blackbrush stands rarely established above 2,000 m unless they were situated on south-facing slopes. Blackbrush sometimes established below 1,350 m in elevation on north-facing slopes. Mean elevations of the five vegetation zones on the 15 transects were: 1,155 m in the creosote bush-bursage stand; 1,335 m in the lower blackbrush ecotone; 1,560 m in the blackbrush stand;

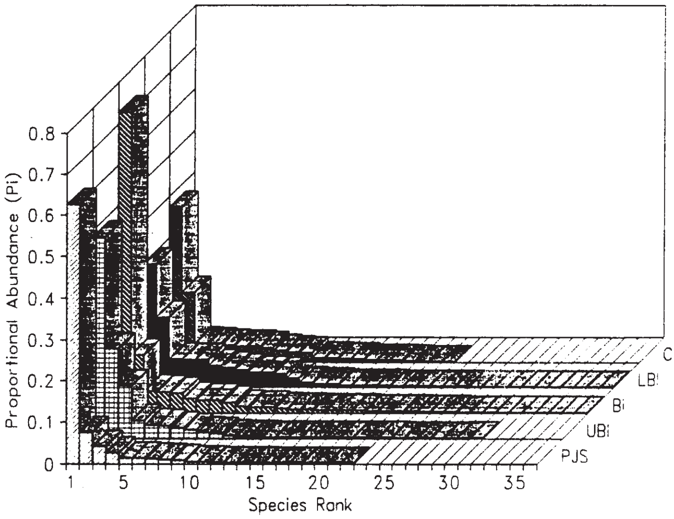

Figure 3—Rank-abundance curves of woody plants in five vegetation zones in the Spring and Sheep Mountain Ranges. Symbols are explained in Figure 1.

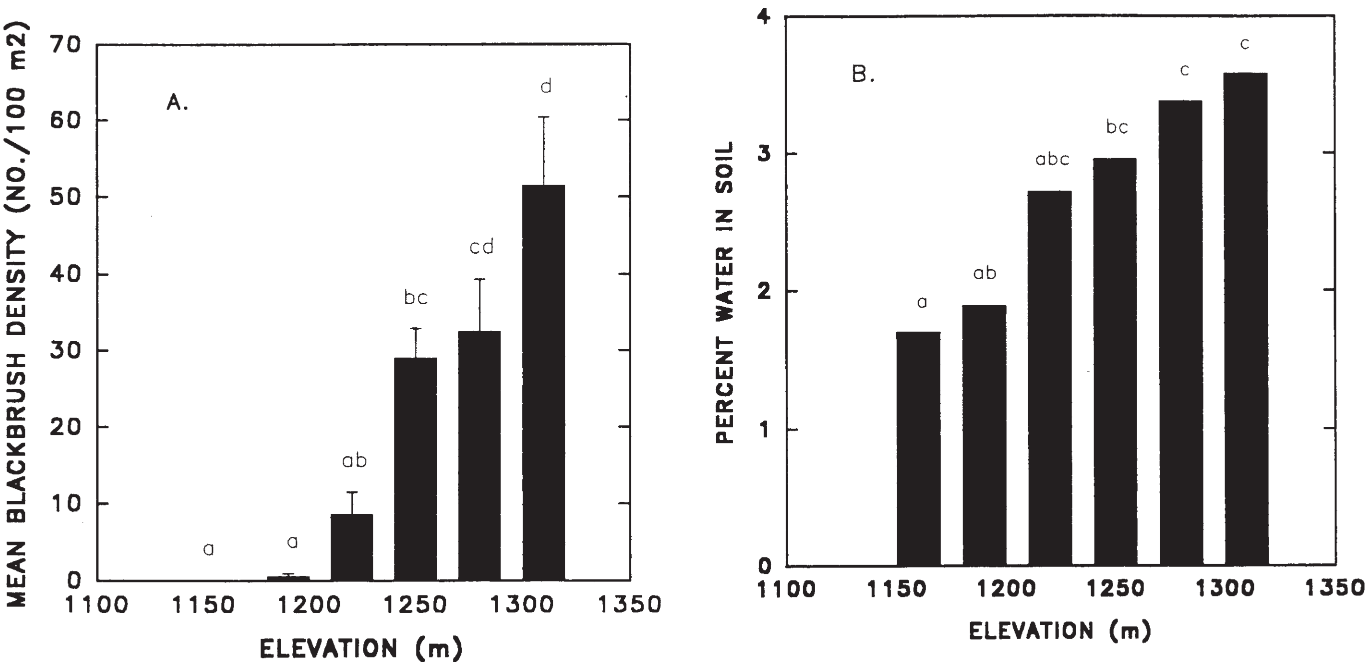

Figure 4—A. Mean density of blackbrush in Lucky Strike Canyon on the east side of the Spring Mountain Range. B. Soil moisture content measured at Lucky Strike Canyon in the month of August. Columns with the same letter are not significantly different ($p < 0.05$).

1,770 m in the upper blackbrush ecotone; 1,870 m in the pinyon-juniper-sagebrush stand. Blackbrush communities generally have relatively broad upper and lower ecotones. The zone of vegetation dominated by blackbrush overlapped with creosote bush-bursage and pinyon-juniper-sagebrush communities by as much as 100 m in elevation.

Creosote bush-bursage, blackbrush, and big sagebrush dominated their respective plant communities (Fig. 3). The blackbrush and lower blackbrush ecotones had the greatest species richness with 36 species in each community. The creosote bush-busrage stand had the highest species evenness (E = 0.24) as noted by the flat abundance curve, indicating similar abundance of most shrub species. However, the blackbrush community had the lowest evenness (E = 0.05) due to the dominance of blackbrush shrubs. Relatively mature and stable blackbrush stands tend to form monospecific communities. Pinyon-juniper-sagebrush stands also had a low species evenness (E = 0.09 and a relatively steep rank-abundance curve because of the domination of big sagebrush. Pinyon and juniper trees, although visually a dominant component of the vegetation at the upper elevation, were not abundant in our study plots. The upper blackbrush ecotone had a higher evenness (E = 0.11) than the pinyon-juniper-sagebrush community. Blackbrush stands are more commonly established on level topography (39%) or gentle slopes (50%) than on steep slopes (>45°; 5%) or in active washes (6%).

Bowns and West (1976) suggested that low soil moisture is a factor limiting the distribution of blackbrush at its lower elevational boundaries. Our data support their suggestion. The mean density of blackbrush differed significantly along the lower blackbrush limits (Fig. 4A) and was positively correlated with elevation ($r = 0.98$; $p < 0.0000$) and soil moisture (Fig. 4B; $r = 0.84$; $p = 0.0434$) in Lucky Strike Canyon on the east side of the Spring Mountain Range. Correlations between blackbrush density and soil moisture increased as the summer season progressed.

Conclusions

The blackbrush community is one of the dominant vegetation types in southern Nevada. Blackbrush stands range from approximately 1,350 m elevation on north-facing slopes to over 2,000 m on south-facing slopes. The lower blackbrush boundary had the greatest species richness; pinyon-juniper-sagebrush stands had the lowest richness. However, this pattern was only significant when all 15 elevational transects were combined, presumably due to elevational and topographical variations among transects. Despite broad ecotones, blackbrush communities were nearly monospecific. All five vegetation zones were dominated by one or two species that accounted for greater than 16% of all vegetation cover of the dominant species. Species evenness generally decreased with elevation, but was lowest for the blackbrush community. Only sagebrush had higher densities than blackbrush. A positive correlation between abundance of blackbrush and soil moisture across the lower elevational limits of blackbrush in Lucky Strike Canyon suggested that moisture may be a factor that limits the distribution of blackbrush at its lower elevational boundary.

Acknowledgments

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Responses of Big Sagebrush and Spiny Hopsage to Increasing Water Stress

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Abstract—Ecophysiological observations were taken on big sagebrush (*Artemisia tridentata* ssp. *tridentata*) and spiny hopsage (*Grayia spinosa*) to assess their response to increasing seasonal water stress. Non-destructive whole plant leaf area measurements indicated that big sagebrush produced more leaf area than spiny hopsage. Stem diameter dynamics revealed similar patterns for both species with diameter increases in the spring and shrinkage in the summer. The final stem diameter increase was greater for big sagebrush than spiny hopsage. Xylem pressure potential values were much lower by summer for spiny hopsage than for big sagebrush. Net photosynthesis, stomatal conductance and transpiration were maximal in the spring and declined thereafter for both species.

Desert plants are usually grouped by the manner in which they cope with water stress. One coping mechanism has to do with the maintenance of foliage. Most desert shrubs are drought deciduous or evergreen. Many evergreens will drop portions of their canopy in response to drought, but because they retain some active foliage they are considered evergreen (Smith and Nobel 1986). Drought deciduous shrubs drop foliage as xylem pressure potential (Ψ) falls until all foliage is gone (Smith and others 1990). Drought deciduous species exhibit a wide range of Ψ at which they can maintain turgor, and Ψ values can be lower than those found in evergreen species (Smith and Nobel 1986). We compared the responses of spiny hopsage (*Grayia spinosa*), a drought deciduous shrub, to the evergreen shrub, big sagebrush (*Artemisia tridentata* ssp. *tridentata*), under increasing seasonal water stress.

Spiny hopsage is a chenopod endemic to the western United States. It is distributed east of the Cascades and Sierra Nevada from central Washington to southern California and eastward to southwestern Montana and western Colorado (Shaw and Haferkamp 1990). Rickard (1965) observed that spiny hopsage accumulated high levels of K and Mg in leaves, suggesting it has a high potential for osmotic adjustment. Branson and others (1976) found that spiny hopsage dropped its leaves earlier in the summer than five other deciduous shrubs, had a relatively shallow rooting depth of only 60 cm, and had a minimal Ψ of –8.0 MPa. This value was lower than that of big sagebrush (–6.5 MPa), but was only mid-range among the other species (–4.0 to –10.5 MPa). Smith and others (1990) found that spiny hopsage had a minimum predawn Ψ of –7.6 MPa and dropped foliage through the season as Ψ values dropped.

Big sagebrush is a member of the Compositae family and is distributed throughout the Great Basin, the Columbia Basin, and the Colorado Plateau regions of the Intermountain West (West 1979; Hironaka 1979). Big sagebrush can potentially gain carbon all year because it is evergreen, but highest photosynthetic rates occur in late spring, declining to minimal values in late summer with increasing water stress (DePuit and Caldwell 1973). Minimal values of Ψ have been recorded between –6.0 and –7.0 MPa with physiological activity (Branson and others 1976; DeLucia and Schlesinger 1990; Evans and others 1992). Caldwell (1979), in reviewing the physiology of big sagebrush, concluded that although it is geographically successful, it is not physiologically superior to other coexisting species. It has relatively low rates of photosynthesis, rates are reduced at moderate plant water stress and high temperature, and its roots are costly to maintain. Its success may be related to photosynthetic activity at low temperatures, maintenance of active foliage, sensitive stomatal control, and the ability to withdraw water from dry soils (Caldwell 1979).

The objective of this study was to compare changes in leaf area, stem diameter dynamics, water relations, and gas exchange responses of spiny hopsage and big sagebrush as seasonal water stress increased in a summer-dry climate.

Materials and Methods

The study site (46°35'N, 119°44'W, 244 m elevation) is on the United States Department of Energy's Hanford Site in southeastern Washington. The area is semiarid with warm, dry summers and cool, wet winters. Average yearly precipitation at the study area is about 160 mm,

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falling mostly in the fall and winter (Rickard 1988a). The area is dominated by spiny hopsage and big sagebrush.

Precipitation and other meteorological variables were collected at the site and are summarized in Link and others (1990).

Non-destructive measurements of leaf area dynamics were made with an automated point frame (Caldwell and others 1983). Observations were taken in March and May on the same three individuals of each species, yielding whole plant leaf area values. These values were then converted to a percentage increase.

Stem diameter changes were measured with sensitive (± 0.1 µm) strain gauges attached to stems (Beedlow and others 1986). Data from the strain gauges were collected hourly with a Campbell Scientific CR7-X data acquisition system from March through July on three individuals of each species. Initial values were set to zero for all sensors so that all subsequent values represented a change from initial conditions.

Plant water status was determined with a pressure chamber (Soil Water Equipment Co.) and with a psychrometer (Decagon Devices). Water potential data were collected at midday in March, April, May and July in conjunction with gas exchange observations on six individuals of each species. Xylem pressure potential data were obtained by placing cut stems (about 10 cm in length) in the pressure chamber and slowly pressurizing with nitrogen gas until the tip of the stem first showed evidence of a color change due to expressed water. A wet paper towel was placed in the chamber to maintain a humid atmosphere around the stem and leaf material during pressurization. Leaves were then stripped from the stems, placed in Tygon tubing, capped and placed on dry ice for determination of osmotic potential (Ψ_π) with the psychrometer (Evans and others 1990).

Net photosynthesis (P_n) and stomatal conductance (*g*) data were gathered with a null-balance gas exchange system (Data Design Group Co.) in March, April, May and July on three individuals of each species. The same individuals were observed in each month. Standard conditions of light (full sun), leaf temperature (30°C), and vapor pressure gradient (3.2 kPa) were maintained in the exposure chamber for all observations. Rates were expressed on a single-sided leaf area basis with leaf area values obtained with a Licor-3100 leaf area meter (Licor, Inc.).

Data are presented as means with one standard-error bar. Comparisons were made with Student's t-test. Species effects for water relations and gas exchange variables were tested using second order polynomial regression relationships in time. Regression relationships were compared using a general linear test (Neter and Wasserman 1974). Hypotheses were tested using an F test. Hypotheses were tested at the $\alpha = 0.05$ level.

Results

Non-destructive leaf area estimates indicated an increase from March to June of 319 ± 72% for big sagebrush and 197 ± 54% for spiny hopsage.

Stem diameter dynamics were observed for both species between days 67 and 203 (Fig. 1). After an initial stem shrinkage, big sagebrush stems increased in size until day 137 with shrinkage thereafter (Fig. 1a). Final stem diameter increases ranged from 0.04 to 0.37 mm. Observations on spiny hopsage also indicated initial stem shrinkage with a maximal value on day 129 and shrinkage thereafter (Fig. 1b). Final stem diameter increases were 0.08 and 0.13 mm for two individuals, while the stem of the third apparently died. Maximal stem diameter increases occurred later for big sagebrush than for spiny hopsage, and the average final stem diameter increase was greater for big sagebrush (0.23 mm) than for spiny hopsage (0.11 mm). The periodic spikes on the stem diameter graphs occur with precipitation events (Fig. 1c). Precipitation occurred during three periods: days 80 to 93, 108 to 120 and 146 to 158. The greatest amount of precipitation (8.5 mm) fell on day 108. Other daily totals were less than 4 mm.

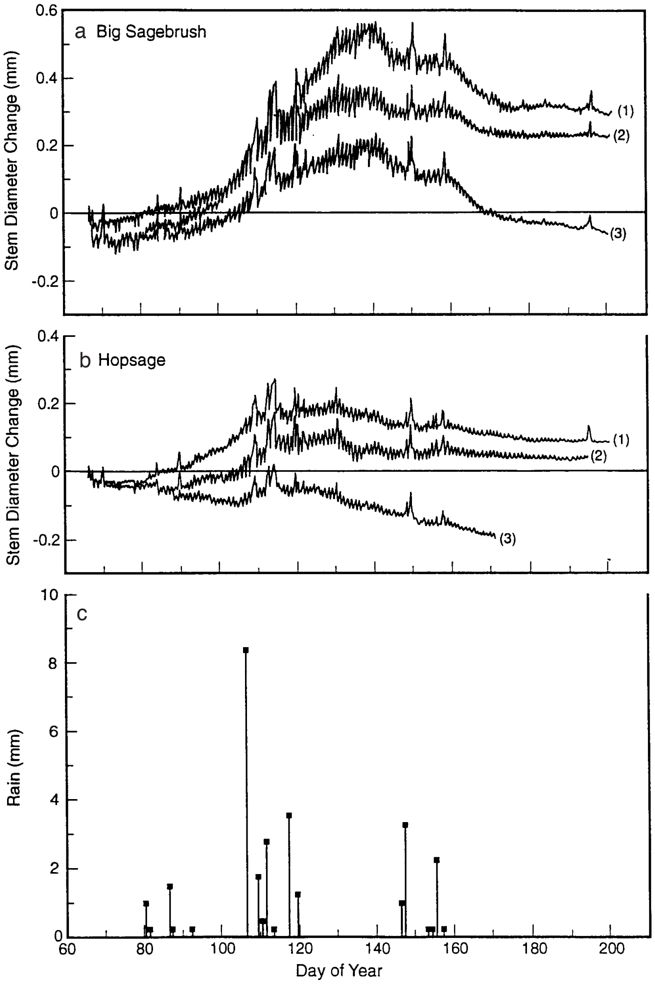

Figure 1—Change in stem diameter of (a) big sagebrush and (b) spiny hopsage and (c) total daily precipitation at McGee Ranch for days 70 to 194.

Water relations varied with time and species. Xylem pressure potential (Fig. 2a) decreased from values near –2.0 MPa for both species in March to –6.2 MPa for spiny hopsage and –3.3 MPa for big sagebrush in July. Regression relationships were significantly different for the two species ($F^* = 55.75 > 2.76$) with values for spiny hopsage

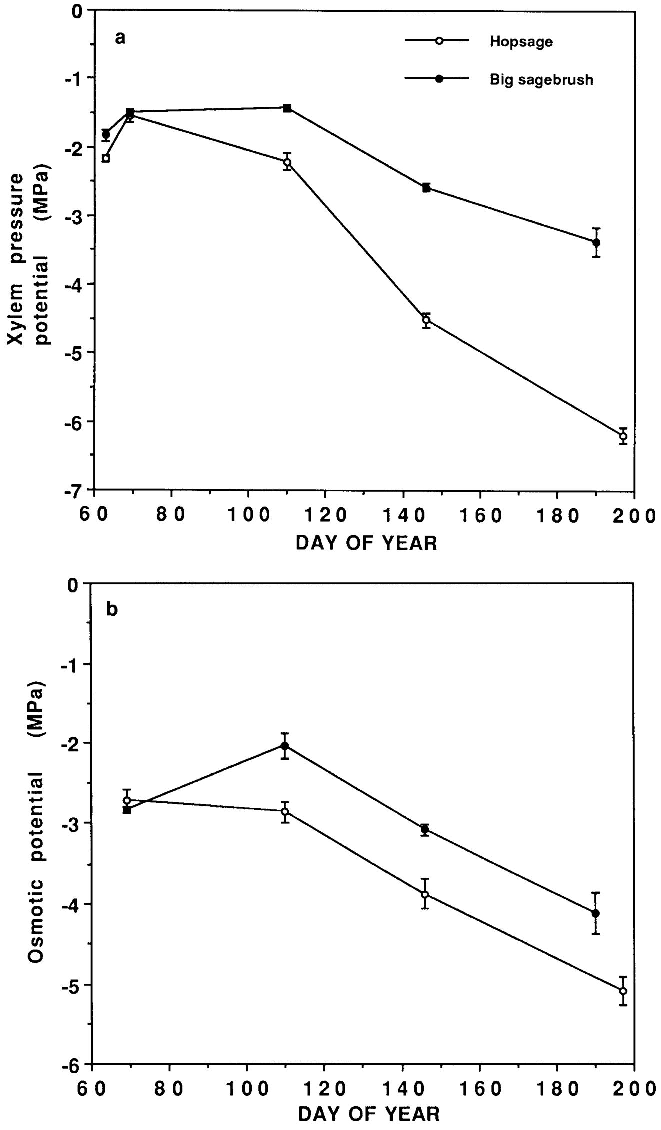

Figure 2—Average xylem pressure potential (a) and osmotic potential (b), for big sagebrush and spiny hopsage at midday from March to July. Error bars are one standard error of the mean (*n* = 6).

lower than those of big sagebrush. Osmotic potential was near –2.7 MPa for both species in March, did not change for spiny hopsage and increased to –2.1 MPa for big sagebrush in April (Fig. 2b). Values decreased for both species after April, to –5.1 MPa for spiny hopsage and –4.2 MPa for big sagebrush. Regression relationships were significantly different (F* = 8.48 > 2.87) for the two species with values for spiny hopsage lower than those of big sagebrush.

Gas exchange characteristics changed with time and were similar for the two species. Net photosynthesis decreased from near 18 µmol $m^{-2}s^{-1}$ and 16 µmol $m^{-2}s^{-1}$ in March to –2 µmol $m^{-2}s^{-1}$ and 0.5 µmol $m^{-2}s^{-1}$ in July for big sagebrush and spiny hopsage, respectively (Fig. 3a). Regression relationships were not significantly different (F* = 0.70 < 3.51) for the two species. Stomatal conductance was maximal in April and decreased thereafter for both species (Fig. 3b). Maximal values were near 200 mmol $m^{-2}s^{-1}$ and 150 mmol $m^{-2}s^{-1}$, falling to 15 mmol $m^{-2}s^{-1}$ and 25 mmol $m^{-2}s^{-1}$ in July for big sagebrush and spiny hopsage, respectively. Regression relationships were not significantly different (F* = 1.17 < 3.23) for the two species. Transpiration showed the same patterns as *g* because observations were obtained with constant values of the vapor pressure gradient. Maximal values were near 6 mmol $m^{-2}s^{-1}$ and 5 mmol $m^{-2}s^{-1}$, falling to 0.5 mmol $m^{-2}s^{-1}$ and 1 mmol $m^{-2}s^{-1}$ in July for big sagebrush and spiny hopsage, respectively.

Discussion

Our data on the responses of big sagebrush and spiny hopsage to increasing seasonal water stress indicate that big sagebrush grew more than spiny hopsage, spiny hopsage had lower values of Ψ than big sagebrush as the season progressed, and there were no differences in gas exchange rates between the two species.

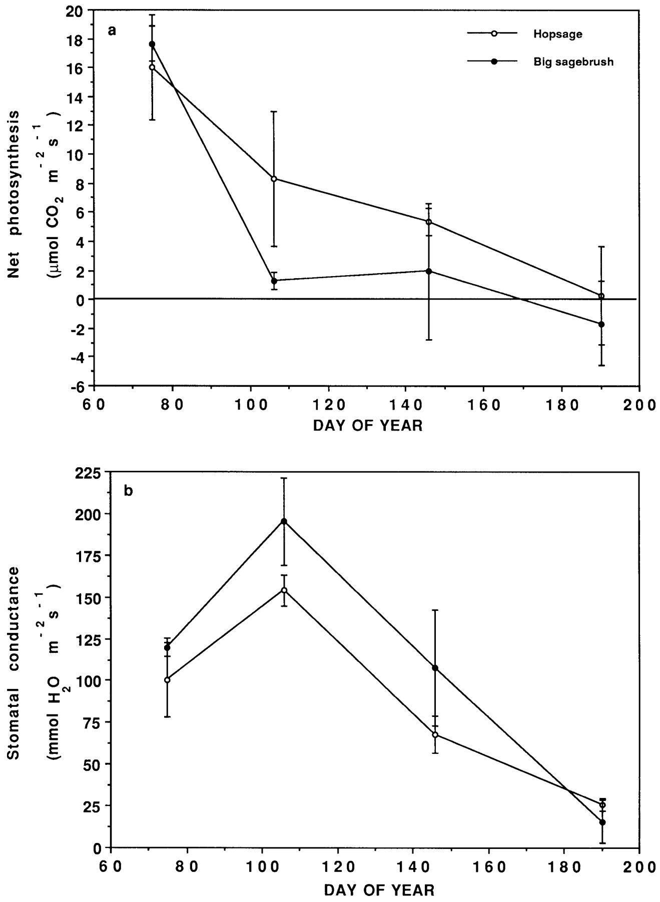

Figure 3—Average net photosynthesis (a) and stomatal conductance (b), for big sagebrush and spiny hopsage at midday from March to July. Error bars are one standard error of the mean (*n* = 3).

Growth

Big sagebrush grew more than spiny hopsage as assessed by percentage increase in leaf area. Spiny hopsage is deciduous and displays only one type of leaf during the growth period. Big sagebrush, in contrast, has a more complex phenology, having deciduous and evergreen leaves (Caldwell 1979). Initial leaf area measurements were made in March. At this time spiny hopsage leaves were new and very small in comparison to evergreen leaves of big sagebrush. Big sagebrush had considerably more leaf area than was present on spiny hopsage in March. The deciduous leaves of big sagebrush arise in the early spring, but fall in the early summer when water stress increases. The increase in big sagebrush leaf area was greater than that for spiny hopsage; in addition the initial leaf area of big sagebrush was greater; thus, the final leaf area of big sagebrush was proportionately much higher than that of spiny hopsage.

Stem diameter increases were greater in big sagebrush than in spiny hopsage. A change in stem diameter is a result of growth processes and changes in hydration (Klepper and others 1973; Lassoie 1979). The extension of stem diameter increases for big sagebrush beyond that of spiny hopsage suggests that each of these species reaches a plant water status that critically influences the allocation of carbon to the measured stems. The ending measurements reflect the net amount of wood added to the stems over the growth period. Big sagebrush had greater stem diameter increases than spiny hopsage, indicative of greater growth. We conclude that big sagebrush grows more than spiny hopsage on the basis of leaf area and stem diameter changes over the time observed.

The relationship between stem diameter dynamics and plant water status was recognized in studies with *Gossypium hirsutum* (Klepper and others 1971), *Quercus alba* (Hinckley and Bruckerhoff 1975), *Pseudotsuga menziesii* (Lassoie 1979), and cacao trees (Alvim 1975). Three observations will help us interpret the relationship between plant water status and stem dynamics: the relationship between precipitation and stem dynamics, the size of diurnal fluctuations and long-term effects.

Precipitation events and spikes in stem diameters occurred at the same time (Fig. 1). This indicates that stems are rehydrated when it rains. Similar results were observed by Hinckley and Bruckerhoff (1975) and Alvim (1975). Hinckley and Bruckerhoff (1975) observed increases in stem circumference after a rain, and concluded that *Q. alba* takes up rain water from shallow depths in addition to water at deeper depths. We conclude that big sagebrush and spiny hopsage are able to take up water after light rains of 2 mm during a 24-hr period. These shrubs must have active roots near the surface, because such light rains do not infiltrate deeply. Big sagebrush also responds to infrequent summer rains (Romo and Haferkamp 1988; Evans and others 1992). Another explanation for the observed patterns is that during a rainy period the weather is usually cloudy and cool, reducing the transpiration. It is possible that the plants were still rehydrating from deeper soil water reservoirs faster than the losses because of transpiration; thus, stem diameters would increase.

The second observation that relates stem diameter to plant water status is the size of diurnal stem dynamics over the entire observation period. Diurnal dynamics were smaller in late winter (up to day 90) and in summer (after day 160), with larger values between days 90 and 160. Minimal values occurred after day 180. This pattern is similar to the pattern of g. Minimal *g* occurred around day 190, when stem diameter dynamics were also at a minimum, and so it is likely that diurnal stem diameter dynamics are positively correlated with diurnal transpiration rates. Lassoie (1979) found that diurnal stem shrinkage was closely related to daily water loss in *P. menziesii*. Hinckley and Bruckerhoff (1975) found a similar result for *Q. alba*, but concluded that a large component of daily transpiration was water stored in the trunk of the tree. Water is stored in the trunk during rehydration at night and makes up a substantial amount of transpiration before noon. They conclude that daily transpired water is made up of stem water and soil water, with that from the stem becoming appreciable when the soil reservoir becomes depleted. Water stored in stems is significant for large trees (Hinckley and Bruckerhoff 1975; Lassoie 1979), and may also be significant in these shrubs. The large increase in stem diameter after precipitation events suggests that stems can store relatively large amounts of water. This stored water may make up a significant amount of the transpiration stream, as in trees. However, there has been little work on the significance of stored water in stems for arid land shrubs.

The last observation that relates stem diameter to plant water status was long-term shrinkage of stems as the summer progressed. If carbon allocation to stems decreases as photosynthetic rates decline, then the decrease in stem size in big sagebrush must be caused by increasing dehydration. Stems must have a large potential to store water given the large increase in stem diameter after rains and the large decrease with increasing water stress and decreasing Ψ over time. Similar decreases with time with increasing water stress have been observed in *G. hirsutum* (Klepper and others 1973; Gensler and Diaz-Munoz 1983), *Q. alba* (Hinckley and Bruckerhoff 1975) and in *P. menziesii* (Lassoie 1979). These investigators concluded that the decrease was a result of continuing dehydration over time. Plants experiencing significant water stress can not rehydrate stems completely at night before transpiration and loss of water from living cells reduces stem diameters further (Lassoie 1979).

Plant Water Relations

Plant water relations, narrowly defined, refer to Ψ and Ψ_π and how the plant responds to them. Arid land shrubs are able to tolerate low soil water potentials by actively or passively adjusting cellular osmotic concentrations so that water can be withdrawn from the soil while maintaining cellular turgor (Turner and Jones 1980). We found that the Ψ of spiny hopsage fell to much lower values than for big sagebrush by July; yet, both species maintained turgor and physiological activity. We hypothesized that Ψ_π values would be similarly different for the two species to maintain turgor. Although the Ψ_π of spiny hopsage was lower than that of big sagebrush after March, values did not exhibit the same pattern as for Ψ. We feel that when leaves were ground for Ψ_π measurement, apoplastic water diluted the symplastic osmotica yielding artificially high values. This may be the case for spiny hopsage and not for big sagebrush. Spiny hopsage, a halophyte, has higher levels of K, Cl and Na than big sagebrush, which supports the hypothesis that spiny hopsage can actively adjust Ψ_π to maintain turgor (Rickard 1988b). If turgor pressure is the difference between Ψ and Ψ_π, and if the true turgor pressure of spiny hopsage is 0.5 to 1.0 MPa, we can hypothesize that its true Ψ_π was closer to –6.7 to –7.2 MPa at the end of the season. Big sagebrush, in contrast, passively adjusts Ψ_π by decreasing leaf water volumes to maintain turgor (Evans and other 1992). Dilution bias in Ψ_π is probably small in big sagebrush.

The lower values of Ψ for spiny hopsage (–6.2 MPa) compared to big sagebrush (–3.3 MPa) in July may be related to differences in soil moisture profiles. Spiny hopsage must have extracted more water from the profile than big sagebrush. We have observed differences in soil water profiles for these shrubs at the same study site (Link and others 1994). Soil water down to 125 cm was extracted more rapidly by spiny hopsage than by big sagebrush from February to May. After May, little water was extracted by spiny hopsage, while big sagebrush continued to extract significant amounts of water until July. This pattern of soil water extraction is correlated with the differences observed in Ψ even though these observations were taken in different years. Volumetric soil water content at the 45 cm depth on August 3 was 3% beneath spiny hopsage and 6% beneath big sagebrush. There were no significant differences at deeper depths beneath these two species (both were 7%). Roots were observed down to 200 cm under both species. Root biomass was an order of magnitude greater under spiny hopsage than under big sagebrush down to 75 cm, which could account for the dryer profile under spiny hopsage at shallow depths. The consequence of this is that spiny hopsage can remove water from the soil at lower soil water potentials than can big sagebrush.

Gas Exchange

Net photosynthesis and *g* were similar for both species with P_n decreasing over time. Because temperature, relative humidity, CO_2 and light were constant during these measurements, other factors must account for the observed pattern in P_n. A strong determinant of P_n is *g*. Stomatal conductance decreased from April to July, accounting for some of the decrease in P_n over that period. The decrease in *g* from April to July is associated with decreases in Ψ. Reductions in *g* with increasing water stress are a common response for plants (Larcher 1980) and have been observed in big sagebrush (DePuit and Caldwell 1973; Evans and Black 1993). Reductions in *g* cannot account for all the variation in P_n, however, because P_n decreased from March to April while *g* increased. This observation may be due to high respiration rates associated with young tissue (Larcher 1980). Big sagebrush leaves grow rapidly in April at this site and have high respiration rates (Evans and Black 1993). Leaves of spiny hopsage have expanded by April and most likely have lower respiration rates that could account for the higher rates of P_n at this time, compared with big sagebrush. The low rates of P_n observed in big sagebrush can also be due to the temperature at which data were collected (30°C). DePuit and Caldwell (1973) observed that big sagebrush has an optimum temperature of 20°C with high respiration and low P_n rates at 30°C.

Conclusions

Ecophysiological observations taken on big sagebrush and spiny hopsage to assess their response to increasing seasonal water stress indicated that big sagebrush grew more than spiny hopsage, and spiny hopsage experienced more water stress than did big sagebrush. One possible reason for lower growth rates in spiny hopsage than big sagebrush is that spiny hopsage expends energy to maintaining turgor, while big sagebrush does not. This possibility is a topic of current research.

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Association of Native Grasses and Overstory Species in Southern Arizona

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Abstract—This research considered whether three native grasses, Arizona cottontop [*Digitaria californica* (Benth.) Chase], plains lovegrass (*Eragrostis intermedia* Hitchc.), bush muhly (*Muhlenbergia porteri* Scribn.), and other herbaceous understory species have greater density and cover under overstory species compared to open areas. Arizona cottontop had either significantly ($P \leq 0.05$) greater, less, or similar density under canopies compared to open areas. Arizona cottontop had significantly greater or similar cover among canopied and open areas. Plains lovegrass had significantly lower density and cover under velvet mesquite (*Prosopis velutina* Wooton.) than in open areas at one site, while no significant differences were observed among canopied and open areas at a higher elevation site. Bush muhly had greater density and cover under canopies for all sites.

Much research has shown that soil water availability generally controls plant growth in desert environments (Franco and Nobel 1988; Jordan and Nobel 1979). Germination of warm-season species may occur following summer rainstorms, but soil drying after germination is often fatal for young seedlings. High solar irradiance and dry periods during the summer months also create high soil surface temperatures that may kill seedlings (Turner and others 1966). These factors may be ameliorated by overstory species, sometimes termed nurse plants (an existing adult plant growing adjacent to a seedling) (Nobel 1989; Parker 1987; Turner and others 1966; Welsh and Beck 1976). While offering protection during dry periods, nurse plants can also compete for soil water with the associated species (Wright and Mooney 1965). Nobel (1989) calculated reduced water uptake of an agave seedling (*Agave deserti* Engelm.) in the presence of big galleta (*Hilaria rigida* Thurb.). Franco and Nobel (1988) also noted that competition for water and light from nurse plants greatly reduces the growth of associated seedlings compared with seedlings in open areas.

Other studies have demonstrated the moderating effect that nurse plants may have on soil surface temperatures (Despain 1974; Holland 1973; Nobel 1980; Parker and Muller 1982). Soil temperatures on an open desert surface can exceed 65 °C—temperatures that may be fatal to young seedlings regardless of soil moisture status (Jordan and Nobel 1979; Nobel 1989; Turner and others 1966). Nobel (1989) compared soil temperatures of open areas to that beneath big galleta, which serves as a nurse plant for *Agave deserti* Engelm. and *Ferocactus acanthodes* (Lemaire) Britt. & Rose in the northwestern Sonoran Desert. Shade from big galleta reduced the maximum surface temperatures by over 10 °C. Franco and Nobel (1988) showed that soil temperatures were 14 °C lower adjacent to the crown and 23 °C lower on the north side of big galleta compared to an exposed site, and that seedlings were generally located near the crown or on the north side of big galleta. Jordan and Nobel (1979) stated that although water uptake by the nurse plants must be considered, lower temperatures in shaded microhabitats likely lead to an extension of the growing season, and modulation of the effects of competition.

The structure of overstory plants may also promote seedling establishment by trapping seeds, reducing wind and water erosion, and modifying litter and soil nutrients (Barkman 1988; Callaway and others 1991; Ebersohn and Lucas 1965; Frost and Edinger 1991; Holland 1968 & 1973; Vallentine 1989; Wood and del Moral 1986). Phosphorus and nitrogen may be more concentrated under nurse plant canopies than surrounding bare soil because canopies may capture and accumulate organic debris (Charley and West 1975; Garcia-Moya and McKell 1970; Tiedemann and Klemmendson 1973; Muller 1953). Franco and Nobel (1988) found that soil nitrogen under the canopy of big galleta was 60% higher than in exposed locations and stated that increased soil nitrogen may offset competition for soil water induced by nurse plants in desert ecosystems. Nobel (1989) believed that the high levels of nitrogen under nurse plants reflected uptake of nitrogen by roots over a wide soil area followed by nutrient deposition under the canopy from litter fall. Accumulation of debris near nurse plants was also due to reduced wind speed and localization of fecal deposition of nitrogen.

While nitrogen may be greatly increased under some canopies, it is also possible to have increased levels of potentially toxic elements near overstory plants (Charley and West 1975; Glendening and Pase 1964). Muller (1953) noted that brittlebush (*Encelia farinosa* Gray.), which produces allelopathic compounds, did not serve as an effective nurse plant, whereas *Franseria dumosa* Gray. growing in the same community was a nurse plant for several species. Researchers studying litter under Pringle manzanita (*Arctostaphylos pringlei* Parry) shrubs found increased germination when litter was removed from the soil surface under the plant canopy (Glendening and Pase 1964). Fowler (1988) also

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noted negative effects of litter on two native grasses in Texas. This may have been due to pathogens favored during conditions of high soil moisture and soil surface humidity in litter. These explanations may not be applicable in more arid climates where increased germination has been associated with litter (Evans and Young 1970).

Under certain conditions, the benefits overstory plants provide small seedlings apparently outweigh any negative effects of competition between the nurse plant and seedlings for soil moisture (Jordan and Nobel 1979; Nobel 1989; Wood and del Moral 1986). Past research indicates the effects of nurse plants on seedling establishment vary among species and site conditions. In areas where soil moisture is generally higher, tree canopies may be lusher and understory herbaceous growth is reduced due to shade or pathogens present in moist litter under canopies (Fowler 1988; Frost and McDougald 1989). Open grasslands generally have higher herbaceous cover in these moist sites than canopied areas. However, Callaway and others (1991) noted that blue oak (*Quercus douglasii* H. and A.) trees on the same site can have a positive or negative influence on understory production. They found that belowground competition from shallow roots of blue oak led to lower production, whereas elevated nutrients under some deeper-rooted trees led to increased production compared to adjacent open areas.

In arid regions, some species are found almost exclusively under canopies. In general, it appears that in these regions establishment is more critical than maximum growth (Franco and Nobel 1988). However, some species protected by canopies appear to become more aggressive after establishment, and growth of the nurse plant may decline. Almeida and Donart (1980) suggested that a symbiotic relationship may exist between bush muhly and the nurse plant creosotebush (*Larrea tridentata* Coville), while others have observed loss of lower leaves and eventual death of creosotebush branches as bush muhly matures (Welsh and Beck 1976).

Some researchers have identified nurse plants by recording understory species that consistently associate with particular overstory species (Almeida and Donart 1980; Haque and others 1991; Turner and others 1966; Welsh and Beck 1976). Identifying overstory species that are associated with desirable understory forage species may aid land managers and researchers in recognizing potential microsites for less aggressive species that may not accept a wide range of conditions or sites for establishment. With this in mind, the objective of this work was to determine whether three native grasses, Arizona cottontop, plains lovegrass, and bush muhly, and other herbaceous understory species have greater association with the dominant overstory species than open areas of various sites in southern Arizona.

Materials and Methods

Data were collected at seven sites in southern Arizona previously selected for seed collection of Arizona cottontop, bush muhly, and plains lovegrass (as advised by Dan Robinette, District Range Conservationist, Soil Conservation Service, Tucson, Arizona). Each site has a relatively abundant stand of at least one of these native grasses. An area of approximately 1 ha represented the experimental plot at each site.

Site Description

Two sites with natural stands of Arizona cottontop were included in this study. The first was Diamond Bell Ranch between Sasabe and Tucson, Arizona (31°75'N, 110°20'W), and the second was an area on the Santa Rita Experimental Range near Green Valley, Arizona (31°48'N, 110°50'W) (Table 1). Buenos Aires National Wildlife Refuge near Sasabe (31°35'N, 111°32'W) and Fort Huachuca Military Reservation in southeastern Arizona (31°34'N, 110°20'W) were the two sites selected for plains lovegrass (Table 1). North of Organ Pipe National Monument near Ajo, Arizona (32°12'N, 112°53'W), adjacent to San Xavier Indian Reservation southwest of Tucson (32°05'N 111°13'W), and Falcon Valley Ranch north of Tucson (32°42'N, 110°57'W) were the three bush muhly sites (Table 1).

Data Collection

Percent cover was measured for each site to determine dominant species. The line-intercept method (Canfield 1941) was used with 5 randomly-chosen, parallel 100 m-long

Table 1—Site descriptions for seven sites where natural stands of either Arizona cottontop, plains lovegrass, or bush muhly occur in Arizona.

Location	Elevation (m)	Precipitation zone (cm)	Range site	Vegetation type	Soil series & family
Diamond Bell	945	28-36	Sandy loam upland	Upper Sonoran desert shrub/ Chihuahuan semidesert grassland	Sonoita (coarse-loamy, mixed, thermic, Typic Haplargids)
Santa Rita	1150	30-40	Deep sandy loam	Chihuahuan semidesert grassland	Tanque (coarse-loamy, mixed, thermic, Typic Torrifluvent)
Buenos Aires	1050	30-40	Loamy upland, sandy loamy upland	Chihuahuan semidesert grassland	Whitehouse (fine, mixed, thermic, Ustollic Haplargids) / Caralampi (loamy-skeletal, mixed, thermic, Ustollic Haplargids)
Fort Huachuca	1520	30-40	Loamy upland	Chihuahuan semidesert grassland	Whitehouse and Bernadino (fine, mixed, thermic, Ustollic Haplargids)
Organ Pipe	511	18-25	Sandy bottom	Lower Sonoran desert shrub	Carrizo (sandy-skeletal, mixed, hyperthermic, Typic Torriorthents)
San Xavier	1020	28-36	Deep sandy loam	Upper Sonoran desert shrub	Hayhook (fine-loamy, mixed, thermic, Typic Haplargids)
Falcon Valley	1200	33-43	Loamy upland limy slopes	Chihuahuan semidesert grassland	Nolan and Hathaway (loamy-skeletal, mixed, thermic, Aridic Calciustolls)

transects. Means were calculated for each species using data from the 5 line intercepts to determine percent cover and dominant overstory species of each site.

Plants of dominant overstory species were randomly selected for understory sampling using randomly generated coordinates at each site. Density was measured and percent foliar cover estimated in 0.25 m^2 quadrats placed under the two dominant overstory species except at Santa Rita and Buenos Aires, which had only one dominant overstory species, and in an open area adjacent (approximately 6 m from) but not under overstory canopies. Quadrats were placed approximately one-third crown-width from the center of overstory species and 4 sub-samples were taken in the cardinal directions. The four sub-samples were averaged for each individual. Twenty individual overstory plants and open areas were sampled at each site, except for locations where the total number of individuals per treatment (overstory or open) was less than 20. In this situation, all individuals of the dominant overstory were sampled. Fort Huachuca had 15 replicates/treatment due to low number of overstory individuals.

Cover and density data were tested for normality (Shapiro and Wilk 1965) and ranked data were used in analyses of variance due to non-normality. Means were separated with the Tukey Studentized range test. Canopied and open areas were compared among sites by calculating a ratio of total density and cover in open areas/total value under canopies. A ratio of 1.0 indicates an equal density or cover in open and understory areas. Analysis of variance was performed on ratios and mean separations were done using the Tukey Studentized range test. Throughout, $P \leq 0.05$ was used to define statistical significance. Measured species with a mean density greater than 1/0.25 m^2 or with significant differences among treatments were included in results.

Results and Discussion

Arizona Cottontop Sites

Density of Arizona cottontop was less under canopies compared to open areas, whereas cover was similar for all areas at Diamond Bell (Table 2). Many small seedlings were observed in open areas, which may explain the greater density, but not cover, in these areas. Arizona cottontop was the dominant herbaceous species at this site with only threeawns (*Aristida* spp.) having a density greater than one plant/0.25-m^2 quadrat. The range of mean density of Arizona cottontop under dominant overstory canopies was nearly five times greater, 5-11 plants/quadrat, at Diamond Bell compared to Santa Rita, which had 1-2 plants per quadrat. Diamond Bell is an excellent site for Arizona cottontop (personal communication: Phil Ogden, University of Arizona, and Dan Robinette, SCS, Tucson, Arizona). Deep sandy loam soils and lack of grazing for more than 20 years at Diamond Bell may partially explain the high density of this species at this site. It appears that both open and canopied areas are suitable for establishment of Arizona cottontop even though microsite factors in each of these areas may differ greatly.

Table 3—Density (no./0.25 m^2) and cover (%) of understory species*, Santa Rita Experimental Range.

Species*	Treatment			
	Velvet mesquite		Open	
	Density (no.)	*Cover (%)*	*Density (no.)*	*Cover (%)*
Arizona cottontop	1.6a	8.7a[+]	0.5b	2.6b
Burroweed	0.2a	4.0a	0.1a	0.3b
Bush muhly	0.6a	6.1a	0b	0b
Black grama	0.7b	2.9a	2.1a	4.3a
Plains bristlegrass	0.7a	2.9a	0b	0b
Total species**	5.4a	31.2a	4.6a	12.5b

*Understory species with significant ($P \leq 0.05$) differences between treatments or mean density > one plant/quadrat included in table.

**Mean based on all understory species present at site.

[+] Values followed by different letters within a row are significantly ($P \leq 0.05$) different by Tukey Studentized range test.

Arizona cottontop had greater density and cover under canopies compared to open areas at the higher elevation Santa Rita site (Table 3). Cover for all species was also greater under velvet mesquite canopies than in open areas at this site. Researchers have suggested that increased litter and nitrogen under leguminous species such as mesquite may encourage understory establishment (Haque and others 1991).

Santa Rita had similar density for canopied areas for all herbaceous species whereas Diamond Bell had greater density in open areas (Tables 2 and 3). Cover for all species was greater under mesquite than in open areas at Santa Rita. Overall, Santa Rita had significantly lower density and cover ratios than Diamond Bell (Table 4).

Table 2—Density (no./0.25 m^2) and cover (%) of understory species*, west of Diamond Bell Ranch in southern Arizona.

Species*	Treatment					
	Blue paloverde		Velvet mesquite		Open	
	Density (no.)	*Cover (%)*	*Density (no.)*	*Cover (%)*	*Density (no.)*	*Cover (%)*
Arizona cottontop	4.2b	24.6a[+]	5.2b	15.3a	11.0a	18.1a
Threeawn species	1.3a	3.1a	0.3ab	0.3b	0.2b	0.5b
Total species**	6.6b	38.1a	6.4b	24.2b	11.9a	22.0b

*Understory species with significant ($P \leq 0.05$) differences between treatments or mean density > one plant/quadrat included in table.

**Mean based on all understory species present at site.

[+] Values followed by different letters within a row are significantly ($P \leq 0.05$) different by Tukey Studentized range test.

Table 4—Ratios of density (no. in open areas/no. under canopied areas) and cover (% in open areas / % under canopied areas) at seven sites in southern Arizona.

Location	Density ratio	Cover ratio
Buenos Aires	2.34a$^+$	2.78a
Fort Huachuca	2.33a	2.60a
Diamond Bell	1.99ab	0.74b
Falcon Valley	1.42bc	0.50c
Santa Rita	0.89c	0.41c
San Xavier	0.87c	0.54bc
Organ Pipe	0.09d	0.08d

$^+$Values followed by different letters within a column are significantly ($P \leq 0.05$) different by Tukey Studentized range test.

Table 5—Density (no./0.25 m^2) and cover (%) of understory species*, Buenos Aires Wildlife Refuge in southern Arizona.

Species*	Treatment			
	Velvet mesquite		Open	
	Density (no.)	Cover (%)	Density (no.)	Cover (%)
Plains lovegrass	0.4b	2.5b$^+$	1.5a	10.8a
Lehmann lovegrass	0.9a	4.8a	1.1a	7.5a
Arizona cottontop	0.9a	4.7a	0.1a	0.8b
Grama species	0.1b	0.4b	1.3a	5.9a
Total species**	2.3b	12.4b	4.3a	26.5a

*Understory species with significant ($P \leq 0.05$) differences between treatments or mean density > one plant/quadrat included in table.

**Mean based on all understory species present at site.

$^+$Values followed by different letters within a row are significantly ($P \leq 0.05$) different by Tukey Studentized range test.

Plains Lovegrass Sites

Results for Buenos Aires, the low-elevation plains lovegrass site, showed greater density and cover of plains lovegrass in open areas compared to areas under the dominant overstory, velvet mesquite (Table 5). Besides plains lovegrass, only grama species (*Bouteloua* spp.) exhibited less density under a canopy at Buenos Aires. These results corroborate research by Tiedemann and others (1971) showing low tolerance of black grama (*Bouteloua eriopoda* Torr.) to canopy shade. Lehmann lovegrass (*Eragrostis lehmanniana* Nees.), and Arizona cottontop had similar density for open and canopied areas at Buenos Aires (Table 5). However, Arizona cottontop had greater cover under velvet mesquite than in open areas.

Plains lovegrass and sideoats grama [*Bouteloua curtipendula* (Michx.) Torr.] had similar density and cover in open and canopied areas at the higher elevation study site, Fort Huachuca (Table 6). Curly mesquite [*Hilaria berlangeri* (Steud.) Nash] occurred only in open areas at this site. Total density and cover was less under canopies compared to open areas for both of these mesic, higher elevation sites in southern Arizona (Tables 5 and 6). These results supported findings by Haworth (1992) indicating greater biomass was found in open areas than under canopies in another site sampled in the Fort Huachuca area. Cover ratios were also significantly greater than the other five sites, suggesting larger plants are found in exposed open areas (Table 4). Density ratios for Fort Huachuca and Buenos Aires were greater than for all sites except Diamond Bell.

Bush Muhly Sites

Organ Pipe, the low-elevation study site for this species, had higher bush muhly density, 2.5 and 2.7 plants/0.25 m^2 quadrat, under the two dominant overstory species, velvet mesquite and creosotebush, compared to a density of 0.1 plant/0.25 m^2, in open areas (Table 7). Globemallow (*Sphaeralcea ambigua* Gray.), wolfberry (*Lycium pallidum* Miers.), and creosotebush also exhibited greater density under mesquite canopies compared to open areas, but they did not occur under creosotebush canopies at Organ Pipe. Bush muhly had 42% cover under creosotebush. Its dominance under creosotebush may have interfered with establishment of other species. Total density and cover of all herbaceous species were greater under canopies than in open areas. In addition, the density and cover ratios, 0.09 and 0.08, were significantly lower than the six other sites (Table 4). Such low occurrence of species in open areas may be due to the low rainfall and high temperatures experienced at this site. Other work suggests that understory plants have higher establishment under canopies in environments where soil moisture may be greater and temperatures may be lower than adjacent open areas (Nobel 1989, Parker 1987).

Bush muhly had 16 and 25% cover under velvet mesquite and blue paloverde (*Cercidium floridum* Benth.),

Table 6—Density (no./0.25 m^2) and cover (%) of understory species*, Fort Huachuca in southeastern Arizona.

Species*	Treatment					
	Emory oak		Mexican blue oak		Open	
	Density (no.)	Cover (%)	Density (no.)	Cover (%)	Density (no.)	Cover (%)
Plains lovegrass	1.5a	5.2a$^+$	1.0a	3.4a	1.5a	5.3a
Sideoats grama	0.7a	2.5a	1.3a	4.9a	1.3a	5.7a
Curly mesquite	0b	0b	0b	0b	1.7a	2.7a
Total species**	3.2b	15.6b	3.7b	14.0b	6.7a	30.8a

*Understory species with significant ($P \leq 0.05$) differences between treatments or mean density > one plant/quadrat included in table.

**Mean based on all understory species present at site.

$^+$Values followed by different letters within a row are significantly ($P \leq 0.05$) different by Tukey Studentized range test.

Table 7—Density (no./0.25 m^2) and cover (%) of understory species*, north of Organ Pipe National Monument in southwestern Arizona.

Species*	Velvet mesquite	Creosotebush	Open
	Density (no.) | Cover (%)		
Bush muhly	2.5a | 29.1a$^+$	2.7a | 42.4a	0.1b | 5.0b
Velvet mesquite	0.1a | 0.5a	0a | 0a	0.3a | 1.2a
Globemallow	0.1a | 1.2a	0b | 0b	0b | 0b
Wolfberry	0.1a | 6.5a	0b | 0b	0b | 0b
Creosotebush	0.2a | 13.5a	0b | 0b	0b | 0b
Total species**	3.0a | 51.5a	2.7b | 42.4a	0.3b | 6.2b

*Understory species with significant ($P \leq 0.05$) differences between treatments or mean density > one plant/quadrat included in table.

**Mean based on all understory species present at site.

$^+$Values followed by different letters within a row are significantly ($P \leq 0.05$) different by Tukey Studentized range test.

respectively, and was not located in any quadrats in open areas at San Xavier, the mid-elevation study site for this species (Table 8). Arizona cottontop and plains bristlegrass (*Setaria macrostachya* H.B.K) had similar establishment under velvet mesquite and in open areas, but had greater density and cover under blue paloverde than in open areas. Density for all species was similar under canopies and in open areas, whereas cover was significantly greater under canopies than in open areas (Table 8). It appears that plants may establish in both areas, but tend to flourish more in canopied areas. However, McPherson and Wright (1990) showed that understory plants were etiolated and single-layered, indicating that greater cover does not always imply greater biomass under canopies. Density ratio (0.87) was similar to Falcon Valley and Santa Rita (Table 4). Cover ratio was similar to Santa Rita, Falcon Valley, and Diamond Bell. All of these sites had cover ratios less than 1, indicating greater relative cover under canopies.

Bush muhly had 17 and 12% cover under velvet mesquite and cholla (*Opuntia acanthocarpa* Lag.), respectively, at the high elevation study site, Falcon Valley (Table 9). Cane beardgrass (*Bothriochloa barbinodis* Lag.) had higher density and cover in open areas than in areas under mesquite. Cane beardgrass density and cover under cholla, the other dominant overstory species, was similar to open areas. The open canopy structure of cholla may result in similar environmental conditions under and between canopies. Desert holly (*Perezia nana* Gray.) was also more abundant under canopies for this site. Similar to San Xavier, total density was similar under canopies and in open areas, but cover was significantly greater under canopies (Table 9). This site had a high density ratio, largely due to the high number of cane beardgrass seedlings present in open areas and under cholla (Table 4). Cover ratio was less than 1, suggesting bigger plants under canopies than in open areas.

Bush muhly had greater density and cover under canopies for all three sites where this species dominated (Tables 6-8). This corroborates research demonstrating the high occurrence of this species under shrub canopies compared to open areas (Welsh & Beck 1976; Haque and others 1991). The high-elevation bush muhly site, Falcon Valley, had the highest density ratio, 1.42, whereas Organ Pipe, the lowest elevation of the bush muhly study sites, had the lowest ratios (Table 4). Cover ratios were significantly greater for the mid- and high-elevation bush muhly sites than for the Organ Pipe site.

Table 8—Density (no./0.25 m^2) and cover (%) of understory species*, west of San Xavier Indian Reservation in southern Arizona.

Species*	Velvet mesquite	Blue paloverde	Open
	Density (no.) | Cover (%)		
Bush muhly	1.8a | 25.4a$^+$	1.3a | 15.6a	0b | 0b
Arizona cottontop	0.2ab | 1.8ab	0.4a | 3.7a	0b | 0b
Cholla	0.1a | 1.3a	0b | 0b	0b | 0b
Plains bristlegrass	0.2ab | 2.0ab	0.3a | 3.3a	0b | 0b
Dyssodia	0.2b | 1.2b	0.2b | 1.6b	2.3a | 13.5a
Total species**	3.3a | 36.8a	2.8a | 33.2a	2.6a | 16.8b

*Understory species with significant ($P \leq 0.05$) differences between treatments or mean density > one plant/quadrat included in table.

**Mean based on all understory species present at site.

$^+$Values followed by different letters within a row are significantly ($P \leq 0.05$) different by Tukey Studentized range test.

Table 9—Density (no./0.25 m^2) and cover (%) of understory species*, Falcon Valley Ranch in southern Arizona.

Species*	Treatment					
	Velvet mesquite		Cholla		Open	
	Density (no.)	Cover (%)	Density (no.)	Cover (%)	Density (no.)	Cover (%)
Bush muhly	2.0a	17.2a+	1.2a	12.3a	0b	0b
Desert holly	3.1a	5.6a	2.9a	6.0a	0.8b	1.0b
Ragweed	2.2a	4.5a	1.0a	3.4a	0.9a	2.8a
Cholla	0b	0b	0.3a	1.7a	0b	0b
Cane beardgrass	1.4b	1.9b	2.0ab	4.3ab	8.8a	5.7a
Total species**	9.3a	38.7a	8.5a	40.8a	12.4a	18.7b

*Understory species with significant ($P \leq 0.05$) differences between treatments or mean density > one plant/quadrat included in table.

**Mean based on all understory species present at site.

+Values followed by different letters within a row are significantly ($P \leq 0.05$) different by Tukey Studentized range test.

Conclusions

Data presented here demonstrate that certain understory species are associated more with canopied than open areas in southern Arizona. For example, bush muhly had consistently greater density and cover under canopies than in open areas, corroborating previous research (Haque and others 1991; Welsh and Beck 1976). This species was most frequently associated with velvet mesquite. Furthermore, bush muhly was not found in open areas for three of four sites. It is not certain whether greater occurrence of bush muhly under canopies is due to greater establishment, or persistence, or both compared to open areas. In situations where bush muhly is a desired revegetation species, it may be advantageous to re-seed under mesquite, blue paloverde, and creosotebush canopies or under a layer of litter to simulate microsites where this species occurs naturally.

Arizona cottontop and plains lovegrass microsites varied among locations. For example, plains lovegrass had either lower density and cover under canopies or showed no differences among canopies and open areas, whereas Arizona cottontop had either greater, less or no differences in density under canopied versus open areas. Cover was either greater under canopies or similar among canopied and open areas for Arizona cottontop.

Greater fertility and more mesic conditions under canopies might increase the ability of understory plants to tolerate grazing (Tiedemann and Klemmendson 1973). Seeding of native grasses under existing, and in particular leguminous, overstory plants on currently grazed or recently ungrazed lands may encourage seedling establishment of less aggressive, shade tolerant species. In time, these species may move into open areas as management practices change.

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Desert Rodents in Disturbed Shrub Communities and Their Effects on Plant Recruitment

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Abstract—Nocturnal, seed-eating rodents of the family Heteromyidae are the most widespread and abundant mammals in North American deserts. In contrast to other desert rodent taxa, heteromyid densities and species diversity are generally maintained or increased when shrub cover is reduced or removed by disturbance; this pattern is particularly true of the kangaroo rats, a diverse group of bipedal heteromyid species, but quadrupedal heteromyids (pocket mice) may also maintain relatively high densities in disturbed habitats. I illustrate these patterns with rodent population data from a desert shrub habitat following disturbance by wildfire. Based on observational and experimental studies of heteromyid interactions with Indian ricegrass (*Oryzopsis hymenoides*), I also present several lines of evidence indicating that heteromyid activities can have profound effects on the distribution and abundance of particular plant species during successional recovery of disturbed sites. The apparent importance of these animals' interactions with many native plant species suggests close coevolutionary ties between heteromyids and desert plants, and further suggests that these animals may act as natural "engineers" for restoration of disturbed desert environments.

In North American desert environments a diverse array of animals, including various taxa of rodents, birds, and ants, have diets consisting largely of seeds. Seed-eating (or "granivory") is common among these desert herbivores because, compared with the ephemeral availability of plant foliage in deserts, seeds are relatively non-perishable. Thus, they remain available year-round in soil seedbanks and they retain their nutritional properties when properly stored. Because of this latter attribute two groups of desert granivores, rodents and ants, cache large quantities of seeds for later consumption.

The family Heteromyidae is a New World family of nocturnal, granivorous rodents. The vast majority of species representing four of six extant heteromyid genera (*Dipodomys*—kangaroo rats, *Microdipodops*—kangaroo mice, and *Chaetodipus* and *Perognathus*—pocket mice) are restricted to deserts where they often coexist in remarkably diverse assemblages of four to six species (Brown and Harney 1993). It is well known that heteromyids, especially bipedal kangaroo rats and kangaroo mice, often utilize very open desert habitats rather devoid of vegetation, such as exposed, unstable sand dunes. Even in shrub-dominated habitats, bipedal heteromyids tend to concentrate their activities in the open spaces between shrub canopies (Price and Brown 1983, Reichman and Price 1993). Thus, bipedal heteromyids often increase in abundance and/or species diversity when disturbances such as wildfire remove the shrub component of desert habitats (Price and Waser 1984, Simons 1991, Stangl et al. 1992, Whitford and Steinberger 1989). Populations of quadrupedal pocket mice, which tend to prefer more structurally complex habitats than bipeds, may also persist or increase following disturbance if sufficient vegetation or rock cover is available (Bock and Bock 1978, Quinn 1979). By contrast, non-heteromyid rodents are generally absent from disturbed desert environments until substantial vegetation cover is re-established (Simons 1991).

These taxonomic differences in responses of desert rodent populations to disturbance can be explained on the basis of habitat- and taxon-specific risk of predation. Desert rodents in general are more vulnerable to capture by a primary predator—owls— in open habitats than in vegetated ones. However, heteromyid species, being superior to other desert rodents at detecting and evading attacking predators, are less constrained by this risk differential, and within the heteromyids, bipeds are superior to quadrupeds at avoiding predators (Longland and Price 1991, Webster and Webster 1984). Thus, the tendency of these different desert rodent taxa to utilize disturbed, open habitats is inversely correlated with their relative vulnerability to predators. Although numerous studies have documented the above response patterns of desert rodents to disturbance, potentially profound impacts of early-colonizing desert heteromyids on post-disturbance successional patterns are much less appreciated.

With one notable exception (the Great Basin kangaroo rat—*Dipodomys microps*—which eats the foliage of *Atriplex confertifolia*), desert heteromyid species are obligate granivores. Heteromyids locate seeds, even in small quantities buried greater than 10 cm in soil (Johnson and Jorgensen 1981, Lockard and Lockard 1971), using olfaction. These rodents are also very efficient at harvesting seeds after they are located (Nikolai and Bramble 1983, Price and Podolsky 1989); seeds are rapidly separated from the soil matrix with the forepaws and placed in external cheek pouches outside the mouth, which can hold hundreds to thousands of seeds depending on sizes of particular rodent species and seed types. I have measured rates at which desert kangaroo rats (*D. deserti*) harvest and "pouch" Indian ricegrass (*Oryzopsis hymenoides*) seeds at greater than 40 seeds per second using pure piles of seed and greater than 5 seeds per second when seeds were thoroughly mixed with fine sand.

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Harvested seeds are transported in the cheek pouches either to the rodent's burrow, where seeds are either consumed or cached in an underground granary, or they are cached in scattered shallow holes dug by the rodent around its home range and covered by soil to conceal evidence of cache locations. Seeds cached in the latter manner ("scatterhoards") that are not later recovered and consumed by rodents may germinate and establish, but seeds cached in burrows ("larderhoards") are generally too deep to permit seedling emergence. A single kangaroo rat may have hundreds of scatterhoards each containing tens to hundreds of seeds around its home range (Hawbecker 1940, Reynolds 1958, Shaw 1934), and its larder may contain several kilograms of seed (Shaw 1934, Vorhies and Taylor 1922).

The above discussion of the large quantities of seeds which are harvested, transported, consumed, and cached by a single heteromyid rodent serves to illustrate the potentially tremendous impact that dense heteromyid populations and diverse heteromyid species assemblages may have on desert plant communities. Indeed, in several studies heteromyids and other arid-land rodents have been found to harvest a large majority of the annual seed production of a particular plant species (Table 1). Numerous plant species' seeds have also been found to germinate from heteromyid scatterhoards (Table 2). Because heteromyids cache multiple seeds in scatterhoards, their locations are revealed by clumps of germinating seedlings, although solitary seedlings may also result from scatterhoarded seeds that remain after a rodent partially recovers a cache. If seed harvest by rodents limits recruitment for certain plant species, or if rodents selectively scatterhoard particular seeds and this has a significant effect on plant recruitment, then the activities of these rodents could be said to "cascade" to community-level effects at the producer trophic level.

While the studies listed in Tables 1 and 2 elucidate mechanisms such as seed predation, seed caching, and germination from seed caches by which heteromyids may affect plant populations, an experimental field study by Brown and Heske (1990; see also Heske and others 1993) directly demonstrates dramatic community-level effects of heteromyid activities on desert plant assemblages. Using long-term exclosures in the Chihuahuan Desert that are selectively permeable to specific taxa of desert rodents, Brown and Heske (1990) found that exclusion of medium-sized kangaroo rat species (*D. merriami* and *D. ordii*) resulted in a shift from a shrub- to a grass-dominated desert plant community. Although this study indicates a keystone effect of kangaroo rats in maintaining Chihuahuan Desert shrub environments, some evidence suggests that these animals may also play a keystone role in maintaining the grass component of salt desert plant assemblages in the Great Basin Desert. Here, I illustrate with empirical data the responses of heteromyid communities to the large-scale removal of a desert shrub community and present initial data from a study of mechanisms by which these rodents affect plant successional patterns during recovery from the disturbance.

Table 1—Studies documenting percentages of plant seed production harvested by rodents

Plant type (Site)	Seeds harvested (%)	Source
Annual grasses (California Central Valley)	93	Pearson 1964
Annual grasses (Southern California)	30-65	Borchert & Jain 1978
Erodium cicutarium (Mojave Desert)	95	Soholt 1973
Larrea tridentata (Chihuahuan Desert)	87	Chew & Chew 1970
Oryzopsis hymenoides (Great Basin Desert)	46	McAdoo & others 1983
Desert plants (Mojave Desert, NV)	30-80	Nelson & Chew 1977

Table 2—Studies documenting germination of desert plant seeds from rodent scatterhoards

Plant species	Location	Source
Velvet mesquite	Arizona	Reynolds & Glendening 1949
Indian ricegrass	Nevada	McAdoo and others 1983
Antelope bitterbrush	California	Hormay 1943
	Oregon	West 1968
	Nevada	Vander Wall 1990
Paloverde	Arizona	McAuliffe 1990
Cheatgrass	Nevada	La Tourrette and others 1971

Methods

Field studies were initiated near Flanigan, NV (Washoe Co., Flanigan Quad. T27N.R18E.S2) three years after a 1985 wildfire removed shrubs from one side of a road bisecting the site. The study area has a fine sand (xeric Torripsament) substrate. Unburned vegetation is dominated by desert shrub species, especially big sagebrush (*Artemisia tridentata tridentata*), which comprises more than 80% of the plant community. The burned area is dominated by Indian ricegrass (*Oryzopsis hymenoides*) and the introduced annual barbwire Russian thistle (*Salsola paulsenii*). In late April 1991, after Indian ricegrass seed germination had occurred, I estimated densities of seedlings and mature clumps of ricegrass in the burned and unburned habitat types using 80 randomly placed 1.0-m^2 sampling frames per habitat.

Rodent populations in the burned and unburned habitats were censused monthly beginning in September 1988 by livetrapping with wild bird seed as bait. Captured rodents were identified by species, given a uniquely numbered metal eartag, and released immediately at the site of capture.

From April 1989 to November 1990 I conducted 27 trials of an experiment to quantify harvest rates of Indian ricegrass seeds as a function of seed density and depth in the sand substrate. Seeds were planted in 20-cm-long PVC plastic tubes with a 15-cm diameter and 2-mm mesh screening covering the bottom opening. Two replicate linear transects of 20 tubes each were placed in both the burned and unburned habitats for a total of 80 tubes during each trial of the experiment. Each transect included one tube with seeds planted at a unique combination of four densities (either 1, 2, 10, or 100 seeds) and five planting depths (either 0, 1, 2, 4, or 6 cm); the position of tubes representing different seed density and depth combinations was randomized within transects. Each tube along a transect was buried flush with the ground surface, supplied with seeds at the specified density and depth, and left out for 7 nights before being checked for seed removal by rodents.

I used Indian ricegrass seeds labeled with powdered fluorescent pigments to estimate the proportion of seeds harvested by heteromyids which are scatterhoarded. Longland and Clements (in press) provide a detailed description of this technique. Before dusk on each of nine dates between 4 August and 3 November 1989, I placed three square (9.0 x 9.0 cm) petri dishes each containing 40 g of seeds mixed with 3 g of pigment in both the burned and unburned habitats at Flanigan. Seed dishes were separated from one another by at least 30 m. Rodents had access to these seeds during the night until I began searching for seed caches with a UV lantern at 0300 h the following morning. Seed cache locations were revealed by large pigment marks on the sand surface. I marked locations of scatterhoards found in the dark and returned shortly after daylight to recover them. The number and mass of seeds within each scatterhoard was determined later.

In early June 1993, after Indian ricegrass seed germination was complete, I determined germination success for seeds within rodent scatterhoards by digging up 100 clumps of seedlings emerging from caches and counting numbers of seedlings and ungerminated seeds. It is impractical to do the same for single seedlings that are unassociated with caching, because locations of ungerminated seeds are not revealed by germinated seedlings as they are in caches. Therefore, I compared field germination of seeds within rodent caches to laboratory germination success of mature Indian ricegrass seeds collected by hand at Flanigan. I also compared the depth of emergence from the sand between single seedlings and the above-mentioned seedling clumps that were taken from rodent caches. I measured emergence depth for five randomly chosen seedlings from each of the 100 dug up scatterhoards and for the five single seedlings nearest to each scatterhoard. I calculated the mean and standard deviation of emergence depths for each group of five seedlings, and compared the grand mean and the mean standard deviation between the 100 groups of seedlings emerging singly versus the groups emerging from caches.

After above-average precipitation from January through March, the Indian ricegrass population at Flanigan exhibited exceptional seedling emergence in spring 1993. I monitored the number of living Indian ricegrass seedlings in four 5 x 5-m plots that were fenced to exclude medium and large herbivores (jackrabbits, pronghorn antelope, cattle) weekly from 20 April through 2 November 1993. I resumed monitoring in late March to early April 1994 to determine numbers of 1993 seedlings in these plots which survived through their first winter. Small gates at the bottom of each fence permitted access by desert rodents. Each week I counted clumps of seedlings representing heteromyid scatterhoards and the number of individual seedlings per clump within each 25-m^2 exclosure plot. In each exclosure I also counted single seedlings within 8 randomly located 0.25-m^2 frames and used these counts to estimate total numbers of single seedlings per 25 m^2 for comparing relative numbers of seedlings presumably unassociated with caching with numbers emerging from scatterhoards.

Table 3—Relative abundances (percent) of rodent species occurring in a burned and unburned (control) habitat at Flanigan, NV, study site based on 1988 to 1990 live trapping data. Heteromyid rodents, the primary scatterhoarding species at this site, include species in the genera *Dipodomys* and *Perognathus*

	Percentage of captures	
Rodent species	Burned habitat (Indian ricegrass)	Unburned habitat (Sagebrush)
Dipodomys merriami	54	89
Dipodomys ordii	27	2
Dipodomys panamintinus	12	1
Dipodomys deserti	3	0
Perognathus longimembris	3	1
Ammospermophilus leucurus	1	7

Results and Discussion

Five species of heteromyid rodents and one non-heteromyid (*Ammospermophilus leucurus*, white-tailed antelope ground squirrel) were found at Flanigan based on 1988 to 1990 live trapping data. The rodent community in the unburned sagebrush habitat consisted primarily of one heteromyid species (*Dipodomys merriami*, Merriam's kangaroo rat) and a few ground squirrels, while the burned habitat had a rodent community with considerably greater heteromyid diversity (four kangaroo rat species and *Perognathus longimembris*, the little pocket mouse) and ground squirrels were almost completely absent (Table 3). This is consistent with previous reports that heteromyid abundance and diversity are maintained or enhanced following major disturbances, but that other desert rodents are uncommon in disturbed areas (Bock and Bock 1978, Price and Waser 1984, Whitford and Steinberger 1989).

In 1991, nearly six years after the Flanigan fire, densities of both established clumps and seedlings of Indian ricegrass were significantly greater in the burned than in the unburned habitat; seedling densities differed by more than an order of magnitude (Table 4). The vast majority of established clumps were quite robust considering that most were no more than six years old. By uprooting several established clumps I found that most were composed of multiple individual plants of similar stature, suggesting that

Table 4—Densities of established plants and seedlings of Indian ricegrass in burned and unburned habitats at Flanigan, NV (1991)

	Density (#/m^2 ± sd)	
Habitat	Established plants	Seedlings
Burned	1.5 ± 1.3	8.8 ± 6.5
Unburned	0.3 ± 0.2	0.8 ± 1.4

these clumped individuals emerged at roughly the same times. This constitutes indirect evidence that much of the Indian ricegrass recruitment following the Flanigan fire resulted from rodent scatterhoarding.

Seed Harvest Rate

The 1989-90 seed harvest rate experiment indicated that the probability of Indian ricegrass seeds being harvested by a rodent differed significantly as a direct function of seed density and as an inverse function of planting depth (Table 5). Seeds planted 6 cm deep in small numbers (1, 2, or 10 seeds) were seldom harvested, but clumps of 100 seeds at this depth were found and at least partially removed by rodents within seven days approximately 10% of the time. By contrast, harvest rates for unburied seeds on the surface ranged from approximately 30% to more than 80% depending on seed density (Table 5). These effects also yielded a significant seed density x depth interaction in a contingency test of numbers of seed clumps harvested versus unharvested ($X^2 = 87.35$, $df = 12$, $P < 0.001$). In addition to these depth and density effects, seed harvest rates were significantly greater in the unburned than in the burned habitat ($X^2 = 38.02$, $df = 1$, $P < 0.001$), probably reflecting the lower availability of seeds in the former habitat where Indian ricegrass occurred in significantly lower densities. Indian ricegrass seed is a highly preferred food for desert heteromyids (McAdoo et al. 1983, Kelrick et al. 1986, Henderson 1990), so higher harvest rates in the unburned habitat may be due to a greater demand for a valuable, preferred resource where it is rare.

This argument may also apply to comparisons of scatterhoarding rates between the burned and unburned habitats. Specifically, one might expect rodents to consume relatively more and cache less of a valuable seed resource where that resource is less abundant. Indeed, I found that both the mean and maximum numbers of seeds per scatterhoard were greater in the burned ($\bar{x}$ = 275 seeds/cache, max. = 1,427 seeds, n = 25 caches) than in the unburned habitat ($\bar{x}$ = 240, max. = 730, n = 25) using Indian ricegrass seeds labeled with fluorescent pigments. I also located greater proportions of the initial 40 g of labeled Indian ricegrass seeds in rodent caches in the burned habitat (up to 14.1 g or 35.2%) than in the unburned habitat (up to 9.1 g or 22.7%).

Table 5—Proportion of experimental seed clumps harvested by heteromyid rodents either partially or completely over 7-day periods as a function of seed density and planting depth. Experiment was conducted in both burned and unburned habitats at Flanigan, NV during 1989-90

Habitat*	Planting depth (cm)*	Number of seeds per clump (density)* 1	2	10	100
Unburned	surface (0)	.291	.463	.727	.836
	1	.164	.200	.400	.436
	2	.200	.127	.291	.600
	4	.055	.036	.164	.255
	6	.018	.019	0	.109
Burned	surface (0)	.352	.352	.556	.778
	1	.111	.130	.111	.241
	2	.204	.111	.074	.222
	4	.037	.019	.037	.130
	6	.019	0	0	.074

*Effect of variable on seed harvest rate significant ($P < 0.001$) based on contingency analysis of numbers of seed clumps harvested versus unharvested by heteromyid rodents.

The latter figures represent maximum proportions of experimental seeds recovered, and are probably more reflective of true scatterhoarding rates than mean proportions among all seed caching trials, because it is unlikely that I often located the majority of the seeds which were cached (Longland and Clements, in press). These maximum caching rates also compare favorably with rates at which heteromyids scatterhoard harvested Indian ricegrass seeds in laboratory experiments; about 25% of harvested seeds are cached in this manner (McAdoo et al. 1983, Longland 1994a). Because scatterhoarding is an efficient mechanism of seed burial and buried seeds of many plant species, including Indian ricegrass (Kinsinger 1962), have enhanced germination and establishment rates relative to unburied seeds, scatterhoarded seeds that are not later recovered by a granivore for consumption may often benefit from burial. In the case of Indian ricegrass, however, benefits of rodent scatterhoarding extend beyond simple seed burial, because seeds harvested by heteromyids have enhanced germinabilities relative to seeds which are not handled by these rodents (McAdoo et al. 1983).

Field Germination

Enhanced germinability due to seed handling by heteromyids may have contributed to the dramatically higher field germination rates of seeds I found in heteromyid scatterhoards ($\bar{x}$ % germination ± sd = 90.4 ± 10.8%) relative to laboratory germination of hand collected Indian ricegrass seed (less than 2.0% for all trials with native seeds from Flanigan). It is also possible that this resulted from heteromyids selectively harvesting and caching the most viable seeds available, which may also be the most nutritious. Laboratory tests have shown that these rodents avoid aborted Indian ricegrass seeds or those with low viability (McAdoo et al. 1983; Longland, unpublished data).

Another potential mechanism by which germinability may be enhanced for Indian ricegrass seeds in heteromyid scatterhoards concerns the management of caches by rodents in such a manner that germination is favored. In contrast to my initial expectations, seedlings in rodent scatterhoards at Flanigan emerged from significantly shallower depths ($\bar{x}$ = 4.2 cm) than nearest-neighbor single seedlings ($\bar{x}$ = 4.4 cm) (paired t-test: $t = 1.99$, $df = 99$, $P < 0.05$). Although greenhouse experiments have shown that Indian ricegrass seedling emergence is inversely related to planting depth, the 2 mm difference found in this study between emergence depth of rodent-cached and single Indian ricegrass seeds is probably insufficient to account for much of a difference in germination rates (Young and others 1994).

A relatively greater effect of cache management by heteromyids may be due to the significantly greater variation in depths from which single seedlings emerged (sd of emergence depth for 100 groups of 5 single seedlings = 1.4 cm) at Flanigan relative to seedlings in scatterhoards (sd = 0.3 mm) (paired t-test = 18.69, $df = 99$, $P < 0.001$). Both the greater mean and variation in emergence depth found for single seedlings in this study may be unique to areas with unstable substrates such as the sands at Flanigan; blowing sands may accumulate to varying levels over uncached seeds while they lie dormant for varying periods of time, but rodents may recache scatterhoarded seeds frequently at a relatively constant depth.

If the rather constant emergence depth of clumped seedlings represents a similarly constant scatterhoarding depth that approximates an optimum for establishment of Indian ricegrass seedlings, this could contribute to the high germination and emergence found among scatterhoarded seeds at Flanigan. Field observations by Kinsinger (1962) suggest that the mean emergence depth of scatterhoarded seeds found in this study (4.2 cm) is indeed within the optimal germination depth range for Indian ricegrass. However, because controlled greenhouse experiments imply that Indian ricegrass seedling emergence is optimized at depths of less than 4.0 cm, a more likely explanation is that the emergence depth of scatterhoarded seeds represents a tradeoff between reduced seedling emergence at greater depths and increased levels of seed detection and predation by rodents at shallower depths (Young and others 1994). The latter possibility is supported by data in Table 5 indicating greatly reduced harvest rates of Indian ricegrass seeds planted 4 cm versus 2 cm deep at all seed densities.

While it is certainly true that the above difference between field germination of rodent-cached Indian ricegrass seeds and laboratory germination of uncached seeds could be due to a variety of factors, field monitoring of the survival of single seedlings versus seedlings in scatterhoards during 1993-94 directly demonstrates a greater establishment rate for the latter seedlings. Initial seedling counts shortly after emergence in April 1993 showed that numbers of single seedlings ($\bar{x}$ = 740/exclosure) exceeded seedlings in scatterhoards ($\bar{x}$ = 274/exclosure) by a factor of approximately three. The final counts in fall 1993 showed that this discrepancy had considerably narrowed ($\bar{x}$ = 190 single seedlings and 112 scatterhoard seedlings/25-m^2 exclosure). Counts in spring 1994 were virtually identical to these fall counts indicating minimal overwinter mortality. Based on the numbers given above, survival rates of clumped seedlings in scatterhoards (40.9%) were significantly greater than those of single seedlings (25.7%) (*G*-test of independence on initial numbers of single vs. scatterhoard seedlings that were alive vs. dead at last 1993 count: $G = 21.34$, $df = 1$, $P < 0.001$). Although attrition was not negligible for seedlings within caches, the density of seedling clumps ($\bar{x}$ = 11.5 caches/25-m^2 exclosure), while small, remained constant over time because at least some seedlings survived in virtually all clumps.

Seedlings Attributed to Caches

The seedling survival data can be compared with rough estimates of expected proportions of seedlings attributable to rodent seed caches based on data from the seed harvest rate and caching rate experiments described above. Assuming that the majority of Indian ricegrass seeds harvested by heteromyids are taken from the soil surface shortly after being shattered from a seed head, the harvest rate data for surface seeds (Table 5) can be used to estimate harvest rates of native Flanigan seeds. During a foraging bout it is unlikely for a rodent to find large clumps of fallen seeds that have accumulated at a single foraging point, because seed maturation is not strongly synchronized. Therefore, the harvest rate data for clumps of 100 seeds on the soil surface (Table 5) probably overestimate natural harvest rates. Based on the remaining data, it seems reasonable to estimate that not more than 50% of shattered Indian ricegrass seeds are harvested by heteromyids. This also seems reasonable as an upper estimate of harvest rates in view of the fact that data in Table 5 represent proportions of seed clumps that were harvested either completely or partially. Many of the partially harvested clumps had substantial numbers of seeds remaining; there were no combinations of seed density and planting depth that had complete harvest rates as high as 50%.

If up to 50% of Indian ricegrass seeds are harvested by heteromyids and approximately 25% of harvested seeds are scatterhoarded (see above), then the proportion of the seedling population which is attributable to scatterhoarding should not exceed 20% ([.25(.5) X 100] / [.5 + .25(.5)]) assuming that cached and uncached seeds have similar germination and establishment rates. Actual proportions of seedlings due to scatterhoarding should be substantially less than this estimate, because heteromyids eventually recover and consume the vast majority of their caches (Jacobs 1992). The seedling count data summarized above show that actual proportions of seedlings coming from heteromyid scatterhoards at Flanigan were initially greater than this hypothetical maximum of 20%, and that this proportion increases temporally as seedling attrition progresses. Moreover, these counts probably underestimate the fraction of seedlings arising from scatterhoards, because some of the single seedlings probably resulted from caches that were partially recovered (partial harvest of seed clumps was not uncommon in the seed harvest rate experiment).

Taken together, the combination of experimental and observational data reported here supports the assertion that activities of desert heteromyid rodents enhance the germination of Indian ricegrass seeds and/or the establishment of seedlings. Table 2 indicates that potential benefits of germination from heteromyid seed caches are not limited to Indian ricegrass or even to native plants of the North American deserts. However, while some evidence suggests that scatterhoarding may benefit other native plant species (McAuliffe 1990, Reynolds and Glendening 1949), I have observed that seedlings of three introduced annual weed species (cheatgrass—*Bromus tectorum*, Russian thistle—*Salsola australis*, and barbwire Russian thistle—*Salsola paulsenii*) usually die before producing viable seeds under the clumped conditions associated with emergence from caches. Coevolutionary interactions between desert rodents and the native plant species whose seeds are commonly cached may have selected for greater tolerance for crowding in the seedling stage, but introduced plants certainly lack any coevolutionary ties with local desert granivores. Such coevolutionary rodent/seed relationships may be unique to North American deserts, since the diversity and ecological importance of granivorous rodents here is greater than in other desert regions of the world (Mares 1993). If coevolved rodent/seed interactions affect the species composition of either herbaceous plant or rodent assemblages in Great Basin Desert communities, this may explain the relative lack of seed-caching rodents in disturbed shrublands of the western Great Basin which have been dominated by introduced weeds (Longland 1994b). Additionally, if a cause-and-effect relationship could be assigned to this pattern (if rodents are absent because important plant species are absent or vice versa), then it may be possible to influence successional recovery of disturbed areas through interventive management of either rodent communities or their seed resources.

Results of this study imply that activities of desert heteromyid rodents are of utmost importance for recruitment in Indian ricegrass populations. Heteromyids have been shown to have keystone effects in maintaining the diversity of winter annuals (Samson et al. 1992) and the shrub component (Brown and Heske 1990) of Chihuahuan Desert plant assemblages. Other studies indicate that heteromyids affect recruitment of mesquite (*Prosopsis glandulosa*) (Reynolds and Glendening 1949) and paloverde (*Cercidium microphyllum*) (McAuliffe 1990) in the Arizona Sonoran Desert, of blackbrush (*Coleogyne ramosissima*) in the eastern Mojave Desert (B. Pendleton, personal communication), and of various shrub and grass species in the Great Basin Desert (Everett and Kulla 1977; J. Young, personal communication). Thus, while specific responses of vegetation communities to desert rodent activities may vary geographically, the ubiquitous distributions, seed gathering, and seed harvesting activities of heteromyid rodents within the North American deserts may generally have keystone effects on associated desert plant communities.

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Factors Influencing Recruitment of Forage Plants in Arid Karoo Shrublands, South Africa

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Abstract—We recorded mortality and natality in populations of long-lived shrubs over five years in arid rangelands of the southern Karoo, South Africa and studied natural regeneration and survival of sown seeds in cleared plots protected or exposed to grazing. Very little recruitment occurred in undisturbed shrub populations. Germination was a function of seed availability and of autumn rainfall, whereas recruitment was influenced by proximity of seedlings to established shrubs and by follow-up rainfall in spring and summer. On the basis of these observations, we propose a simple model to predict the circumstances under which rangeland forage plants may be restored by resting, reseeding, clearing or combinations of these procedures.

There is a perceived need to increase the productivity and species diversity of overgrazed arid shrublands in the Karoo region of South Africa. Experience has shown that this goal cannot be achieved simply by resting or intensive browsing of range, because overgrazed shrublands are often dominated by long-lived shrubs that are distasteful to domestic livestock. Overgrazed shrubland may remain unsuitable for ranching for many years because the component species are long-lived and do not necessarily facilitate succession to alternative states (Westoby and others 1989). Partial clearing of existing vegetation to alter water and nutrient availability (Luken 1990), or re-seeding to establish indigenous forage species, could possibly increase carrying capacity or nature conservation value of such shrublands.

This paper reports on the demography of shrub populations of the arid Karoo and on effects of weather, neighboring plants, microsites and grazing animals on the survival of seedlings. These preliminary observations provide a basis for assessing the feasibility of rehabilitating Karoo rangeland.

Study Site and Methods

The study was carried out at Tierberg Karoo Research Center (TKRC), from which domestic livestock were excluded, and on adjacent sheep ranches (33°10'S, 22°17'E, 800 m above sea level) in the arid shrublands of the southern Karoo, South Africa (Milton and others 1992). The area receives a variable rainfall (167 mm p.a., range 50-400 mm over 92 years) that peaks in autumn (March-April). Soils are fine and alkaline and the vegetation is low growing (<0.8 m) and clumped with a projected canopy cover <25% (Figs 1a & 1b).

Rangeland at TKRC was in good condition (20,900 forage plants/ha). Adjoining ranch 1 was in good condition and moderately grazed (about 6 ha/sheep). Ranch 2 was in poor condition, and although moderately stocked during the study period (7.5 ha/sheep), was still carrying too many

Figure 1—(a) Arid shrubland at Tierberg Karoo Research Centre in the southern Karoo, South Africa. (b) Mixed species clumps of dwarf shrubs surrounded by bare ground.

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sheep for the available forage (4,200 forage plants/ha). Indigenous steenbok (*Raphicerus campestris*: Bovidae) and hares (*Lepus capensis*: Leporidae) were present at all three sites at low densities (total biomass of mammalian herbivores 135 kg/km^2).

Flowering, Natality and Mortality

Three common species of dwarf shrubs (all Asteraceae) were selected for study: deciduous broad-leaved *Osteospermum sinuatum* preferred by sheep, evergreen microphyllous *Pteronia empetrifolia* palatable to sheep, and evergreen microphyllous *P. pallens* which is toxic to sheep. All individuals in 50 permanent 5 x 5 m quadrats were measured (height, canopy diameter, basal stem diameter) and labelled in November 1988. They were subsequently monitored annually until December 1991. Throughout this time the plots were subjected to one of four different grazing treatments as shown in Fig. 2. Despite the partly pseudo-replicated sampling design, inferential statistics were used to test for site and treatment effects on growth, survival and natality.

Seedling Emergence and Survival in Natural Vegetation

Emergence and survival of seedlings in natural vegetation was monitored in 100 wire hoops (160 mm diameter), two in each of 50 plots used for demographic monitoring. All seedlings in the hoops were recorded five days after each major rain event (>10 mm) and in dry periods, at 4-6 weekly intervals.

Seedling Survival in Cleared Plots

Twenty plots in TKRC, 10 in exclosures and 10 open to grazing by indigenous mammals, were cleared of all vegetation in July 1989 by cutting plants at soil level. Cut plants were removed from 5 plots in each treatment and left on the remainder of the plots. All seedlings on these plots were counted in April 1991, 1992 and 1993.

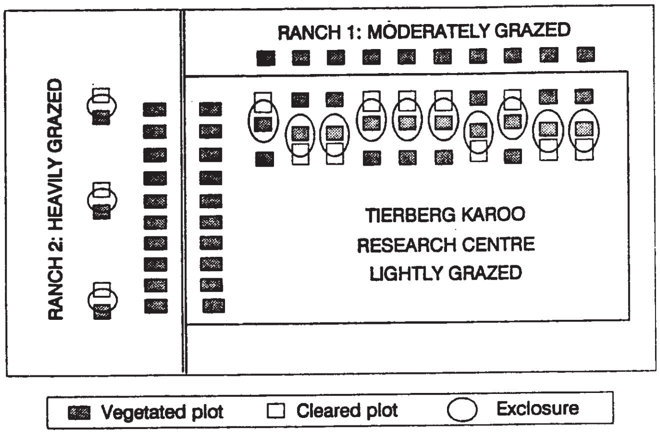

Figure 2—Layout of exclosures, grazing and clearing treatments at Tierberg Karoo Research Centre (TKRC) and on adjacent sheep ranches. Exclo–sures on Argentina ranch were used only in the second seeding trial.

Sowing Experiments

A total of 700 seeds of each of the 3 shrub species and 700 seeds of a winter annual (*Tetragonia echinata*: Aizoaceae) were sown in March 1990 in the 50 vegetated monitoring plots and in the 20 cleared plots. Treatments were replicated as shown in Fig. 2. Germination and survival of seedlings emerging from the planted seeds were made 5 days after every rain event, and once monthly in the absence of rain. It was assumed that seedlings emerging in demarcated rows originated from sown seed.

A further trial, using only *O. sinuatum* seeds, was initiated in April 1991. Approximately 100 seeds (1 g) were planted in and adjacent to each of 6 cleared plots on the heavily grazed sheep ranch. Three of these plots were in exclosures and three were in the surrounding area that was grazed by sheep.

Weather Records and Soil Moisture

Rainfall, mean daily temperature maxima and minima, relative humidity and soil moisture data were collected by a data logger at TKRC. Relative soil moisture was measured using calibrated nylon sensors buried at 50 and 150 mm below the soil surface in one vegetated and one cleared plot.

Results

Flowering, Natality and Mortality

First flowering occurred at 2-3 years (5 mm b.d.) in *O. sinuatum* and at 3-5 years (>10 mm b.d.) in *Pteronia* spp. Sheep reduced flower production by 63% in *O. sinuatum* and by 68% in *P. empetrifolia* but had no effect on toxic *P. pallens*. The numbers of seedlings of a given species that emerged in a plot were related to the numbers of flowers (or seeds) of that species in the plot (Fig. 3). There was therefore little regeneration of palatable species where sheep removed most of the flowers. Over the 3 yr period (1988-1991) the annual turnover was <6% in all three species. Grazing had no effect on the natality : mortality ratio, and 88% of the 104 recorded fatalities were among seedlings.

Background Seedling Emergence and Survival

Seedlings emerged in early winter (April-June) when relative humidity was high and temperatures were low (Figs 4a & 4b). Although the emergence density of seedlings was related to pre-emergence rain, their survival was correlated ($P < 0.001$) with post-emergence rainfall (July-October).

More seedlings emerged on the overgrazed ranch than elsewhere ($P < 0.001$) but the percentage that survived did not differ between sites or treatments (Fig. 4b). Survival averaged (mean ± SD) 3.0 ± 2.5% in 1989, 3.3 ± 2.0 in 1990 and 26.1 ± 5.2 in 1991. Most seedlings (86%) were of small (<0.5 mm) seeded Aizoaceae, the seeds of which

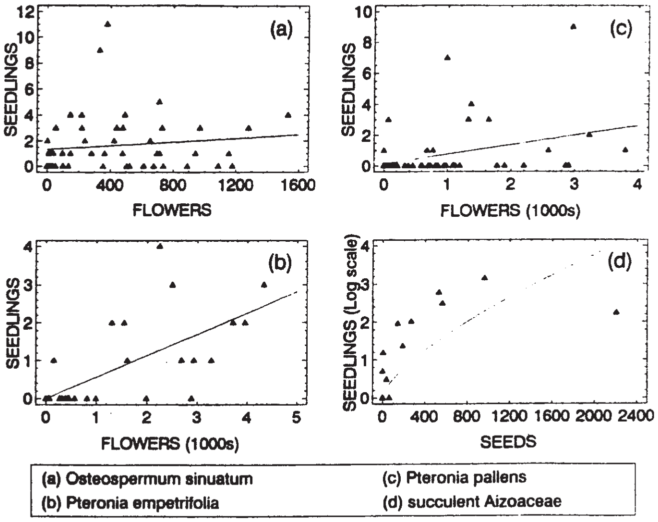

Figure 3—Relationships between densities of emerging seedlings and the number of flowers or seeds of three non-succulent shrubs and of succulent Mesembryanthema in the southern Karoo.

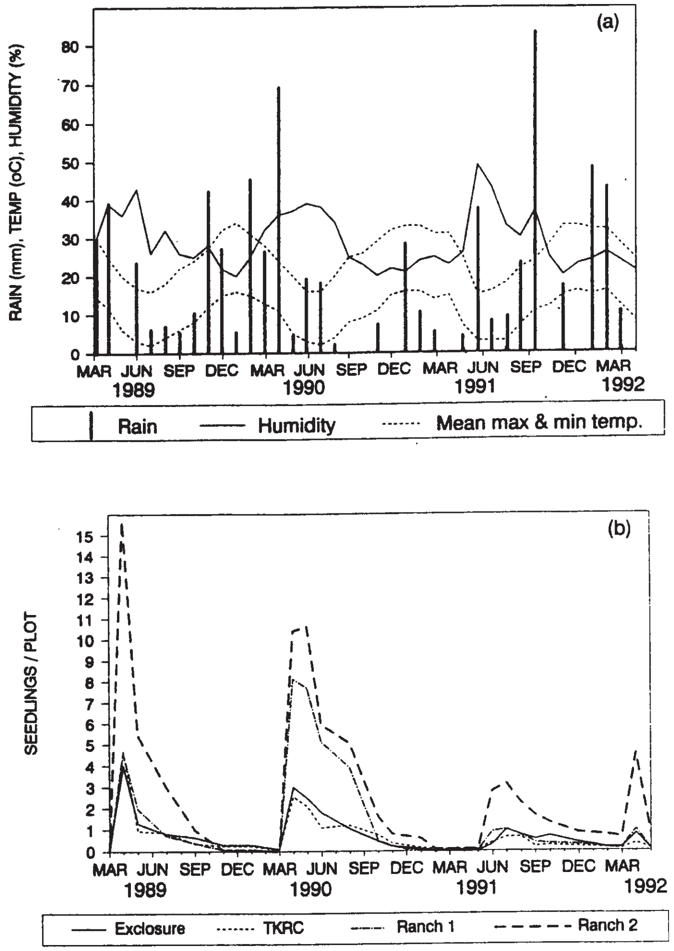

Figure 4—(a) Rainfall, temperature range and humidity at Tierberg Karoo Research Centre in the southern Karoo, and (b) seedling emergence over four years in exclosures at TKRC (no sheep) and on adjoining sheep ranches.

were dispersed from hygroscopic capsules during rain showers. However, on littered or vegetated microsites, 19% (247/1320) of emergent seedlings were species with large (>2 mm) wind dispersed seeds, compared with 7% (78/1056) of seedlings that emerged on bare soil.

Clearing Experiments

Clearing of vegetation reduced the rate at which moisture was lost from the upper 15 cm of the soil (Fig. 5).

The species composition of seedlings emerging from naturally dispersed seeds on cleared plots was correlated ($P < 0.001$) with the cover composition of the vegetation on the plots prior to clearing. The distance between a seedling and the perimeter of the cleared plot influenced its chances of survival. Seedlings emerging 2-3 m from established plants survived at higher densities ($P < 0.001$), and reproduced earlier ($P < 0.05$) than seedlings that emerged closer to neighbours (Fig. 6).

In the first sowing trial, more seedlings emerged on cleared (7.0 ± SD 9.5%) than on vegetated plots (3.9 ± SD 8.6%). Some of these shrub seedlings survived on cleared plots, but all shrub seedlings that emerged in vegetated plots died during their first summer (Fig. 7). No further shrub emergence occurred in the second autumn, but the winter annual (*T. echinata*) had many innately dormant seeds which emerged at higher densities in the second autumn (Fig. 7). The resultant plants set more seed in cleared than in vegetated plots (Table 1).

In the second sowing trial, on the overgrazed ranch, 25 *O. sinuatum* seedlings emerged in vegetated plots and 92 emerged in cleared plots. Survival, after 2 years, was similar in vegetated (24%) and cleared (23%) plots.

In the first sowing trial, emergence and survival of shrub seedlings, but not winter annuals, was greater on overgrazed Ranch 2 than elsewhere (Fig. 7). In the second sowing trial on the overgrazed ranch, 59 *O. sinuatum* seedlings emerged in grazed areas and 58 emerged in exclosures. After 2 years, survival in grazed plots (10%) was lower

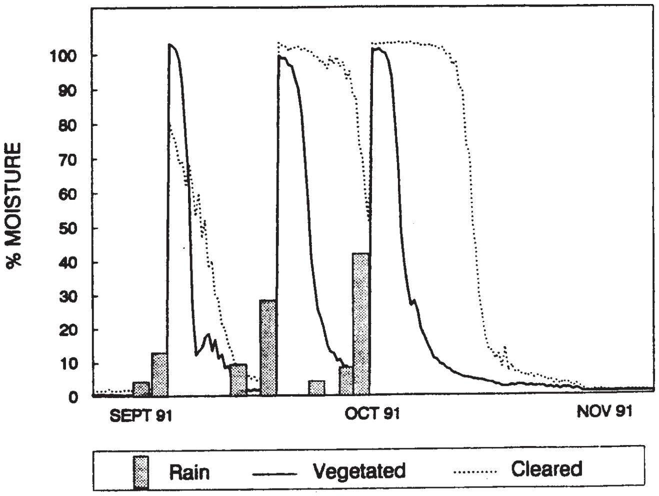

Figure 5—Soil moisture fluctuations at 150 mm below soil surface in undisturbed and cleared vegetation. Rain in millimeters per day.

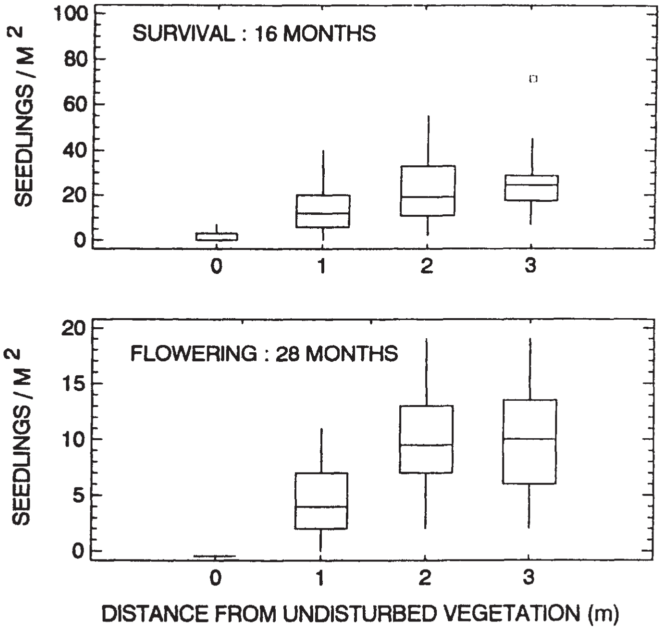

Figure 6—Box and whisker plot showing median, upper and lower quartiles and ranges of seedling densities at three years in undisturbed vegetation and in cleared plots at distances of 1, 2, and 3 m from neighboring plants.

Table 1—Numbers of seeds produced by a winter annual (*Tetragonia echinata*) grown in cleared and vegetated plots in exclosures and grazed rangeland in the southern Karoo. Means with shared superscripts do not differ significantly (ANOVA, P < 0.01).

Treatment	Number of plants	Seeds per plant	
		Mean	± SD
Exclosure cleared	11	6.36a	7.77
Rangeland cleared	24	4.00ab	6.83
Exclosure vegetated	24	0.95b	0.85
Rangeland vegetated	28	1.21b	1.19

(X^2 = 9.7, 1 df, P < 0.01) than in exclosures (36%). Seedlings in exclosures were larger (P < 0.001) than in plots grazed by sheep (Table 2).

Discussion

Implications of Low Turnover Rates for Management

Karoo shrublands, in common with those in arid parts of the United States (McAuliffe 1988) and Australia (Eldridge and others 1990), are dominated by plants that live for decades or centuries. Population turnover rates are low. For this reason, compositional losses caused by overgrazing or resting will be very slow. Restoration of productivity or diversity to over-exploited arid shrubland within a human lifetime may require re-seeding and active management of herbivory, competition and microsites.

Factors Influencing Forage Recruitment in Karoo Shrublands

Defoliation and florivory reduces seedling recruitment in many Karoo plants (Milton 1992; Milton and Dean 1988, 1990b, 1993; van Breda and Barnard 1991). Few species of Karoo succulents (Esler and others 1992) and long-lived shrubs have innately dormant seeds. Such species rely on regular seed production for population perpetuation, and are therefore lost from overgrazed rangeland (Milton 1992; O'Connor 1991). By altering the growth rates of forage

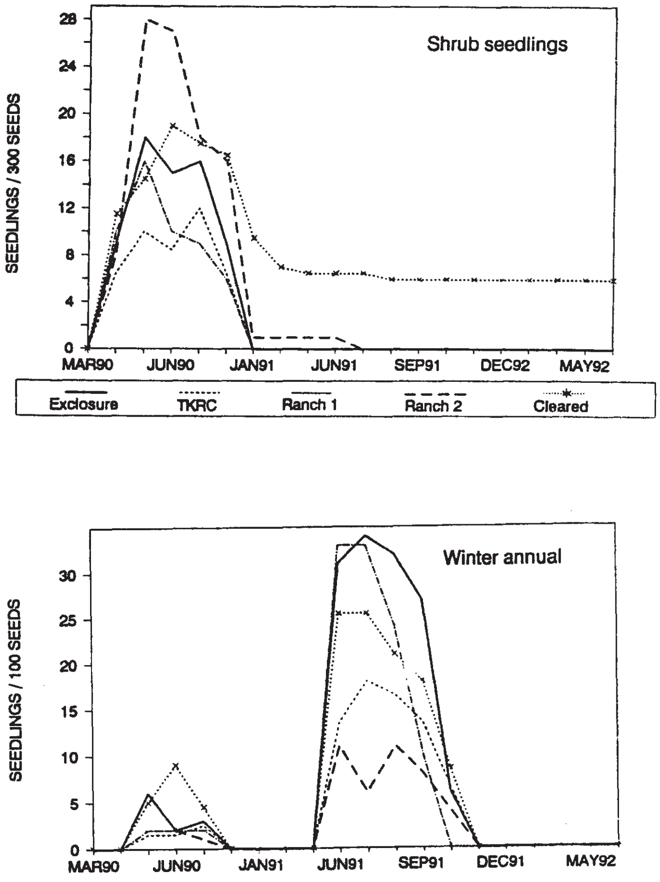

Figure 7—Emergence and survival of sown seeds in exclosures, grazed vegetation, and cleared plots.

Table 2—Heights (mean ± one standard deviation) of one- and two-year-old *Osteospermum sinuatum* seedlings from seeds sown in Trial 2 on an overgrazed Karoo shrubland. Seeds were sown in cleared or vegetated exclosures and in cleared or vegetated rangeland grazed by sheep. Means with shared superscripts do not differ significantly (ANOVA, P < 0.01).

Treatment	May 1992			August 1993		
	n	height ± SD		n	height ± SD	
Exclosure cleared	12	11.6a	3.7	15	13.0a	3.2
Exclosure vegetated	16	4.6b	1.7	6	6.7b	3.4
Rangeland cleared	13	3.2b	1.3	6	4.5b	1.5
Rangeland vegetated	3	4.0b	2.0	0	no survivors	

plant populations, herbivory can bring about changes in vegetation composition.

Most shrubs and succulents germinate in autumn in the southern Karoo (van Breda and Barnard 1991). Large germination events were related to seed availability (dependent on vegetation composition, current herbivory and rainfall). Few seedlings reach reproductive maturity in undisturbed, arid shrublands (Eldridge and others 1990; Milton 1993; Owens and Norton 1992). In the southern Karoo, seedling survival was dependent on moisture availability in the six months after emergence. Seedlings survived where competition from established plants had been reduced, prolonging water availability after rain events.

Droughts (Danckwerts and Stuart-Hill 1988), hail storms (Powrie 1993) and intensive trampling and grazing (Bosch and Gauch 1991) also reduce competition and provide opportunities for seedling establishment. Insects and mammals that uproot plants, dig pits, or excavate nests ensure continual seedlings recruitment by creating establishment sites in stable vegetation (Dean and Milton 1991; Milton and Dean 1990a; Dean and Yeaton 1992).

Seed traps influence the composition and arrangement of Karoo vegetation (Fig. 8). Small seeds (mostly produced by low-growing succulent mesembryanthemaceae) are trapped by fine soil particles so that their seedlings occur mainly in inter-shrub gaps. Winged or bristled seeds (Liliaceae, Asteraceae, Aizoaceae) are tumbled by wind until trapped in multi-stemmed plants, litter or mammal diggings (Dean and Milton 1991; Hoffman and Cowling 1987; Milton 1993).

Non-succulent shrubs establish beneath low-growing, succulent hosts which they later out-compete (Yeaton and Esler 1990). The shrubs tolerate one another for decades, forming mixed-species clumps. In this way Karoo vegetation is arranged in a mosaic of plant islands and bare ground, much like the vegetation of the Chihuahuan Desert, Mexico (Montaña 1992). Grazing, and other factors that increase the proportion of bare ground to vegetated and littered microsites, influence the composition of vegetation.

Model for Change in Southern Karoo Shrublands

On the basis of the foregoing discussion, improvement in composition of Karoo rangeland could be achieved by: a) removing herbivores, b) adding seed of forage species, c) reducing competition from established plants, and d) adding seed traps. In addition to this it may be necessary to restore ecosystem functioning (Milton and others 1994). This could involve soil amelioration (Dean 1992; Roux and Opperman 1986; Schlesinger and others 1990; Snyman and Fouché 1991), and reintroduction of animal or microbe species that move soil, facilitate nutrient uptake, pollination or dispersal, or alter competitive interactions between plant species (Bond 1993; MacMahon 1987).

The model (Fig. 9) presents hypothetical mechanisms by which an overgrazed arid shrubland (1), could be rehabilitated to a more productive and diverse shrubland (2), or further degraded to distasteful (3) or ephemeral vegetation (6).

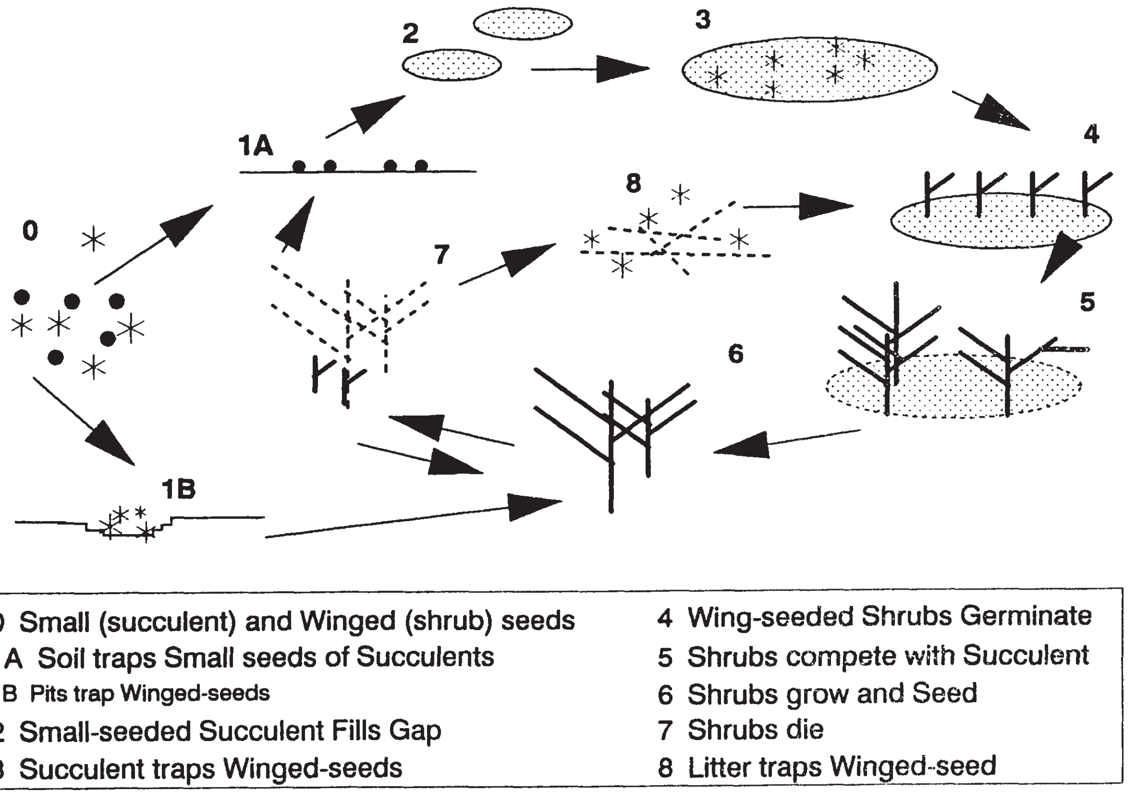

Figure 8—Recruitment opportunities for plant species with small, smooth seed and large, winged seed.

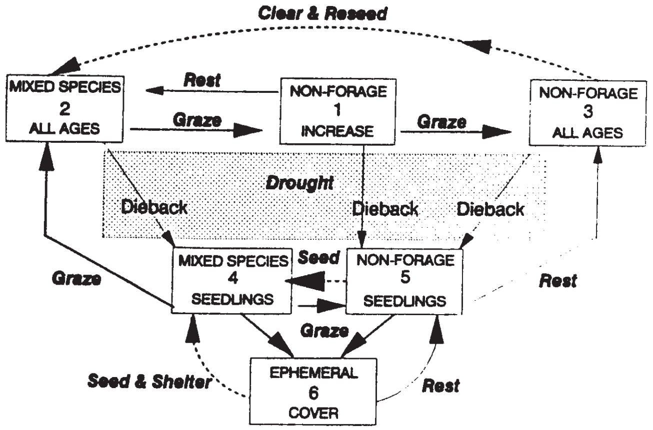

Figure 9—Rehabilitation model for Karoo shrubland.

The mechanisms for transitions between these states of the vegetation include stock withdrawal, natural disturbances (grazing, trampling, drought), and active management of either the vegetation (selective clearing, re-seeding) or of the environment. Although oversimplified, the model provides a variety of testable hypotheses. Following Savory (1991), many livestock ranchers believe that short-duration, high-intensity grazing increases both productivity and abundance of forage species. We have excluded this mechanism from our Karoo rehabilitation model because there is no evidence that it increases forage plant populations in arid Karoo shrubland (Hoffman 1988).

Hazards of Vegetation Manipulation

As indicated in Fig. 9, reversal of changes involving the replacement of one long-lived plant species by another may require active intervention by the land manager. There is no universally correct way to manage rangeland (Noy-Meir 1993): all techniques should be critically evaluated by experiment for each type of range. Reseeding, with or without partial clearing, tilling or mulching have all been attempted in arid and semi-arid southern Africa (Roux and Vorster 1983). All are costly, none is infallible, and some may exacerbate existing rangeland problems.

Seed addition could increase forage plant abundance but is unlikely to succeed without some reduction of established plants and temporary protection from grazing. Clearing should be approached with caution because it increases runoff (Snyman and Fouché 1991) and because the costs involved in vegetation manipulation are unlikely to be offset by short-term benefits in arid rangelands (Danckwerts and Marais 1989).

Droughts and hail storms that kill many established plants may provide windows of reduced competition when supplementary seeding of forage plants could lead to recruitment. Walker and others (1986); and Westoby and others (1989); suggested that opportunistic management could capitalize on just such natural disturbances. Clearing prior to re-seeding appears to be unnecessary where grazing has reduced above-ground perennial biomass below the normal range for the region.

There is little information on how transitions from ephemerals to perennials may be facilitated, but our experiments suggest that seed traps should be provided, or small-seeded species that can establish in the open should be selected for initial re-seeding.

An important aspect for future research is the effect of scale on vegetation rehabilitation. We have no information on the effects of the size of an area of transformed Karoo vegetation on its prospects for recovery, and annual dispersal distances of the component plant species are unknown.

Acknowledgments

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Blackbrush Biology: Insights After Three Years of a Long-Term Study

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Abstract—Blackbrush (*Coleogyne ramosissima*, Rosaceae) is one of the least studied of the landscape-dominant shrubs in the western United States. Previous studies have been limited to relatively small geographic areas. No studies have examined the variability of blackbrush across its range. We have begun a series of long-term studies of blackbrush biology, establishing study sites across a large portion of the shrub's range. Studies deal with: (1) reproductive biology, including factors influencing flowering and fruit set, (2) seed germination biology (laboratory and field studies), (3) seedling emergence, survival, and growth rate, (4) population size and structure, and (5) community relationships. We present data from the 1991 to 1993 growing seasons. While some of these data are preliminary, results indicate the need to reevaluate the classification of blackbrush as a paleoendemic species (ancient taxa with restricted distribution) that possesses little genetic variation. Data from these studies also provide insights into the problems of blackbrush community restoration.

Before beginning our studies on blackbrush (*Coleogyne ramosissima*, Rosaceae), we reviewed the available literature to learn what was known about the species and to identify areas of research that might prove fruitful. It quickly became apparent that there are many conspicuous gaps in the knowledge of blackbrush biology. In most definitive study of blackbrush to date, Bowns (1973) listed areas needing additional research. Many of these areas remain to be addressed. Most studies were conducted at either the Nevada Test Site (Clark County, NV) or in southwestern Utah (primarily western Washington County). No one has studied blackbrush across the whole of its range or made comparisons outside of a local area. Yet, while no such comparisons have been made, Stebbins and Major (1965) are often cited by authors categorizing blackbrush as a species of low variability. We are attempting to address the lack of data on blackbrush variability with our studies.

In defining our research goals, we took into account not only the gaps in existing knowledge, but also techniques commonly used in our laboratory when studying other species. Reproductive biology, including pollination, fruit production, seed germination, and seedling establishment, is critical to understanding the population dynamics of blackbrush. Therefore, it is the prime focus for our initial studies. The series of studies was designed to provide broad, integrated knowledge of the biology of blackbrush. We expect that this knowledge will be useful in designing protocols for the successful management and revegetation of blackbrush communities.

Research in Progress

We began our series of studies on blackbrush biology in 1991. After viewing as much of the range of blackbrush as possible, we selected representative study sites that included a variety of soil types, elevations, and as broad a geographic range as we could cover. Seeds were collected from 30 locations (from southeastern Nevada to eastern Utah) for laboratory and field germination studies. Fifteen long-term sites were established to look at flowering intensity, reproductive output, and community structure. In 1992, we tagged approximately 2,000 natural seedling caches at four locations; two in the Mojave Desert and two on the Colorado Plateau. These seedlings emerged from heteromyid rodent (primarily pocket mice and kangaroo rats) scatter hoards, seeds the rodents place in shallow depressions and cover with soil (Longland 1994). At three of the four locations, additional transects were established on adjacent pipeline corridors to examine natural recruitment on small-scale disturbances. We also followed seedling emergence and survival from artificial scatter hoards at two locations. The pollination biology of blackbrush was studied at three locations over a 2-year period beginning in 1992. A brief synopsis of these studies is given below. The complete results have been or will be published in more detail elsewhere.

Reproductive Biology

Flowering in blackbrush is induced by moderate to heavy winter precipitation (Beatley 1974). Flowering on individual plants is not synchronous, occurring over a period of 1 to 2 weeks. Flowering in the population lasts from 2 to 3 weeks (Bowns and West 1976, personal observation). Prior to our work, the pollination system had been postulated as either wind pollinated (McArthur 1989) or insect pollinated (Pendleton and others 1989).

In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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Our studies have demonstrated that blackbrush is wind pollinated (Pendleton and Pendleton 1994). Net bags that excluded insect pollinators had no significant effect on fruit set when compared with open-pollinated branches. Results were consistent among the three study sites.

Blackbrush is also highly self-incompatible (the plants do not self pollinate). The overall fruit set for selfed branches was 3.4 percent, compared with 39.9 percent for open-pollinated branches. Production of fruit within bakery bags to which outcross pollen had been added (29.2 percent fruit set) demonstrates that the lack of fruit production within the selfed bags was not due to conditions within the bag. Self-incompatibility is known in other shrubby genera of the Rosoideae (Blauer and others 1975; McArthur 1989; Pendleton and McArthur 1994).

Blackbrush exhibits several characteristics that would indicate a switch from insect to wind pollination in the recent geologic past. The large, bright yellow-green calyx would appear to be attractive to pollinators. However, we did not observe any pollinator activity during our field work. The occasional presence of yellow petals (Welsh and others 1987) lends additional support to this hypothesis.

Significant differences in fruit set also occur among populations and among individual plants (Pendleton and Pendleton 1994). The adjusted fruit set (fruit set divided by percent fill) for 15 open-pollinated populations ranged from 3 to 72 percent (Meyer and Pendleton, unpublished data). Differences in fruit set among individual plants and populations likely reflect differences in resource reserves and the degree of resource replenishment since the last major fruiting event. Even when winter precipitation is adequate for flower initiation occurs in successive years, blackbrush does not produce successive large fruit crops (Meyer and Pendleton, unpublished data). This suggests that blackbrush is a mast fruiting species, and that the size of the fruit crop is a function of available stored resources. Studies in progress are intended to clarify the respective roles of weather and resource reserves in mast fruiting cycles.

Seed Germination

Seed germination in our field studies occurred from December to February, with seedling emergence approximately 1 month later (Pendleton and Meyer 1994b). During the period between radicle emergence and cotyledon emergence, stored resources produce several inches of root growth. Bowns and West (1976) also report March emergence for populations in southwestern Utah. Seedling emergence has been reported as early as November (Graham 1994).

Blackbrush seed, when freshly collected, is largely dormant (the mean from our collections was approximately 65 percent dormant). Laboratory-stored seed maintained dormancy through the first 4 months of storage. In contrast, seeds cached in retrieval bags during the same 4 months (ending in November) were only 10 percent dormant at the Hurricane field site and only 50 percent dormant at the Arches field site. After 6 months, field-stored seed was 100 percent nondormant at both sites, and the seed never reentered dormancy. Laboratory-stored seed was only 50 percent nondormant after 10 months of storage. Our working hypothesis is that summer and fall rains reduce initial dormancy under field conditions; winter chilling removes any remaining dormancy (Pendleton and Meyer 1994a,b, unpublished data).

A significant relationship exists between collection-site elevation and seed germination response at 5 to 15 °C, with and without a short (2-week) chill (Pendleton and Meyer 1994a). Seeds collected from low-elevation sites were less dormant than seeds from high-elevation sites. Seeds from all elevations responded positively to a 2-week chill, but the response of seeds from low-elevation sites was roughly twice that of seeds collected at high-elevation sites. Data from our low-elevation (Clark County, NV, and Washington County, UT) sites are comparable to the germination characteristics and chill responses reported for similar locations by Wallace and Romney (1972) and by Bowns and West (1976). These authors did not, however, examine seeds collected from high-elevation sites, which yield quite different results.

Seed from a site near Hurricane, Washington County in southwestern Utah, and from Arches National Park, in southeastern Utah, were used in reciprocal seedling emergence trials. Multiple lots of seeds from both Hurricane and Arches were cached at both sites. Percent emergence and survivorship was highest for Arches seed at the Arches site, and for Hurricane seed at the Hurricane site (unpublished data). These data and the previously discussed correlation between dormancy status and elevation of the collection site strongly suggest that—at least for germination and establishment ecology—blackbrush has evolved ecotypes.

Establishment Ecology

Blackbrush is cached in scatter hoards by heteromyid rodents. The fate of scatter hoard seed was addressed by examining seedling survival in natural caches, as well as emergence and survival of artificial caches. Cache survival, the percentage of natural caches with at least one surviving seedling, varied from 1.4 to 90.2 percent for the period from emergence through two growing seasons (Meyer and Pendleton unpublished data). Percent seedling survival and percent cache survival were lowest on Mojave Desert sites and highest on Colorado Plateau sites. Personal observations during our field travels and community size-class data corroborate this finding; seedling survivorship and frequency of recruitment episodes are higher on the Colorado Plateau than in the Mojave Desert.

Seedling and cache survival are influenced by a number of factors. Most mortality of natural scatter hoards took place early in the first year. Early spring mortality was primarily due to animals grazing the new sprouts. Mortality due to drought occurred in late May through early June (Meyer and Pendleton, unpublished data). A majority of seedlings and caches that survived the first summer also survived through the second summer.

During our field trips, we observed recruitment on small-scale disturbances. We paired transects of natural seedling caches on pipeline rights-of-way with similar transects in established stands. Survivorship on the pipeline rights-of-way was higher, particularly for transects in the Mojave

Desert. This may indicate that mature stands tie up resources and space, excluding seedling establishment. When space becomes available, seedlings can become established.

Reestablishing blackbrush following disturbance is an increasingly important issue. Mining and fire disturb the most acreage in the blackbrush community. There are two reports of blackbrush reestablishing after fire (Bates 1984; Thatcher 1975), but these reports are the exception. As a rule, blackbrush does not reestablish after fire (Bowns and West 1976; Callison and others 1985). Possible hypotheses for the lack of natural reestablishment following burning are:

(1) Lack of seed. Blackbrush does not form long-term seedbanks, and mast events that produce short-term seedbanks are relatively rare (Meyer and Pendleton, unpublished data). If no scatter hoards are established in the year or two before a burn, reestablishment would depend upon rodents transporting seed from unburned areas out onto the burn, an unlikely possibility for large disturbances. We suggest that the reports by Thatcher (1975) and Bates (1984), in which blackbrush reestablished following fire, represent cases in which a short-term seedbank was in place.

Habitat preference by scatter hoarding rodents may also be a factor. Beatley (1976) reported that, on the Mojave, the kangaroo rat, *Dipodomys microps*, occupies blackbrush communities to the exclusion of other species of kangaroo rat. In contrast, *D. merriami* occupies open and disturbed habitats. In the event of fire in blackbrush, *D. microps* is displaced by *D. merriami* on the burn. Seed transport from the blackbrush community onto the burn would be minimal, at least in the Mojave Desert.

(2) Blackbrush is slow-growing, and is not competitive with pioneering species after a burn.

(3) Fire or the introduction of exotic annuals alters the soil microflora to the detriment of blackbrush establishment. These and other hypotheses should be tested.

The establishment of a cohort of blackbrush seedlings is the result of a set of events, some independent and some interrelated. Based on the literature and on our experiments and observations, the following sequence of events is necessary for blackbrush seedlings to become established.

(1) Precipitation in the fall and winter must be sufficient to trigger massflowering (Beatley 1974).

(2) The plant must have sufficient resource reserves to support flowering and fruit production. Blackbrush is a mast flowering and fruiting species; it doesn't produce large fruit crops in successive years even if rainfall is adequate (Meyer and Pendleton, unpublished data). Ongoing experiments will show the time between mast events under a variety of rainfall regimes.

(3) Blackbrush seeds are cached in scatter hoards by heteromyid rodents. For seedling establishment, there must be enough rodents to process the seed and enough seed so the rodents do not consume all or most of the scatter hoards (Longland 1994). Rodents excavate and consume seeds from the time the seeds are first buried until well after the seedlings have emerged (personal observations). If only a small number of seedlings survive this "rodent sieve," drought-related mortality generally eliminates the remaining seedlings. Mast fruit crops provide sufficient seed so the potential exists for a cohort to establish.

(4) Rainfall must be adequate to trigger germination (Beatley 1974).

(5) Rainfall must be adequate during the spring and early summer to support the establishment of seedlings. Moisture for seedling establishment may be an important limiting factor in the drier *Coleogyne-Larrea* ecotone, where moisture is sufficient to support adult blackbrush plants but may be insufficient to establish seedlings (Beatley 1975). In our studies, the vast majority of seedling mortality occurred between emergence and midsummer, when seedling growth ceases and dormancy occurs (Meyer and Pendleton, unpublished data).

(6) Space and resources must be sufficient to support new plants. Undisturbed mature blackbrush stands may be "closed" (with their resources locked up); young plants are often very rare. When openings occur in mature stands due to small-scale disturbances, seedling recruitment is evident in many cases (personal observations).

We hope this model will be useful as we work to develop techniques for revegetating blackbrush from seed.

Conclusions

Classification of blackbrush as a paleoendemic (Stebbins and Major 1965) is appropriate in that *Coleogyne* is a monotypic genus, has no close relatives, and its relationship to other taxa within the Rosaceae is unclear (Morgan and others 1994). However, this classification is not particularly relevant to the management of blackbrush communities. What is relevant is that *Coleogyne* is an ecotonal species. Ecotonal species under changing climatic conditions are subjected to a suite of selection pressures. Three natural outcomes of these selection regimes are: (1) the species becomes extinct, unless (2) the species possesses a wide range of tolerance or evolves new ranges of tolerance in response to the change in climate, or (3) the species migrates with the ecotonal boundary. While ectonal species are tracking the climatic conditions to which they are best adapted, they may also have to adapt to new edaphic (soil) conditions (Stebbins and Major 1965).

We have demonstrated ecotypic variation in characters that are important to the establishment of blackbrush seedling cohorts. We have also demonstrated high rates of seedling establishment and relatively frequent seedling establishment events in blackbrush communities of the Colorado Plateau. We hypothesize that blackbrush is a fairly recent arrival to at least some areas on the Colorado Plateau, and that it is migrating into areas where it is adapted to the edaphic and climatic conditions.

Examination of the paleoecological literature reveals two important points relevant to blackbrush ecotones. First, during the Quaternary (the most recent geologic period), the *Coleogyne-Larrea* ecotone has undergone frequent migrations in response to climatic shifts. Secondly, evidence from packrat middens demonstrates that blackbrush has repeatedly moved up and down elevational gradients in response to shifts in temperature and rainfall patterns (Cole and Webb 1985; Phillips and Van Devender 1974;

Tausch and others 1993; Spaulding 1990). In contrast, Wells (1983) states that, on the high deserts of the Mojave, blackbrush has persisted more or less in place, while woodland conifer species with which it formerly was associated are now found at much higher elevations.

The paleoecological evidence and the results of our research argue against labeling blackbrush as a paleoendemic species with little variation and, perhaps, on the way to extinction. A species with ecotypic variation, the gene pool necessary to evolve new ranges of tolerance in place, and that has migrated successfully along environmental gradients certainly does not fit this label.

Management of ecotonal species is a challenge, and blackbrush is no exception. Continued research is needed to acquire knowledge for successful management of blackbrush in the face of more frequent large fires, disturbances such as roadbuilding and mining that require revegetation, and changes in community composition caused by the invasion of exotic species.

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Effects of Prolonged Drought on Vegetation Associations in the Northern Mojave Desert

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Abstract—EG&G Energy Measurements initiated a study in 1991 to determine the effect a prolonged drought had on vegetation structure and composition at Yucca Mountain, Nevada. A substantial die-off apparently occurred in the low-elevation blackbrush (*Coleogyne ramosissima*) association; only 46% of the plant crowns present in 1991 were alive. The creosote/bursage (*Larrea tridentata-Ambrosia dumosa*) and creosotebush/boxthorn/hopsage (*Larrea tridentata-Lycium andersonii-Grayia spinosa*) associations, respectively, had 58% and 57%, of their plant crowns alive. The high-elevation blackbrush and the boxthorn/hopsage (*Lycium andersonii-Grayia spinosa*) associations had the most live plant crowns, 79% and 81%, respectively. Indian ricegrass (*Oryzopsis hymenoides*), desert needlegrass (*Stipa speciosa*), and shadscale (*Atriplex confertifolia*), were the species most affected by the drought; live plant crowns were 3%, 43% and 52%, respectively. Many other species had highly variable survival rates among the vegetation associations.

Desert vegetation associations contain many perennial plant species that are well adapted to arid environments; therefore, one would intuitively believe that perennial species in desert ecosystems readily survive drought conditions. Abundant research on plant-soil-water relationships in North American deserts has shown that many species can maintain water uptake and growth when soil-water potential is low (MacMahon and Schimph 1981). However, little research has focused on how both a prolonged and severe drought may affect either vegetation associations, or individual species present across vegetation associations.

From 1987 through 1991 a prolonged drought occurred in much of the western United States, including the Yucca Mountain area, in the northern Mojave Desert. The mean annual precipitation from a 25-year record (1968-1993) for a weather station near Yucca Mountain (Jackass Flats) is 137 mm (5.38 in) and the October through March mean is 90 mm (3.53 in) (Table 1). The October through March period is important because soil moisture recharge occurs during these months. During the drought the average precipitation from October through March was 58 mm (2.27 in), or 64% of the 25-year average. More important, from a vegetation perspective, were the back-to-back dry winters in 1988-1989 and 1989-1990. The respective October through March precipitation in both years was 13 and 19 mm (0.50 and 0.75 in); or less than 21% of normal. During the 25-year precipitation record in Jackass Flats, there was only one other time when the winter precipitation was less than 25.4 mm (1.0 in). Also, there were no two consecutive years when the total precipitation from October through March was less than 38 mm (1.5 in). These precipitation data indicate that the vegetation at Yucca Mountain experienced a drought that was both more severe and prolonged than typically occurs in the northern Mojave Desert.

In February and March 1991, Yucca Mountain received above-normal precipitation. In 1992 and 1993 the October through March periods also had above-normal precipitation (Table 1). Vegetation characterization studies, initiated in 1990 by the U.S. Department of Energy (DOE) at Yucca Mountain, allowed EG&G Energy Measurements to collect data that inferred how both desert vegetation associations and individual perennial plant species were affected by a prolonged and severe drought. The specific objectives of this study were to determine how vegetation associations at Yucca Mountain, Nevada, respond to a prolonged drought, and to determine if plant species that occurred across two or more vegetation associations respond similarly.

Site Description

The Yucca Mountain Site Characterization Project (YMP) area occurs on the southwestern edge of the Nevada Test Site in Nye County, Nevada (Figure 1). The study area occurs exclusively on lands controlled by the Federal government. Ownership and control of the project area is divided among the DOE, which controls the eastern portion of the area through land withdrawn for use as the Nevada Test Site; the U.S. Air Force, which controls the northwestern section of the site through land-use permits for the Nellis Air Force Range (NAFR); and the Bureau of Land Management, which controls the southwestern portion of the site as public trust lands.

Yucca Mountain occurs on the northern edge of the Mojave Desert, in a region that has rugged linear mountain ranges interspersed with broad valleys. Yucca Mountain is a long north-south volcanic ridge with a maximum elevation of 1,494 m, and a steep west slope (15-30°), that tilts

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Table 1—Average monthly and annual precipitation (mm) at station 4JA (elevation 3,422 m) in Jackass Flats, Nevada Test Site. Cumulative record is from 1968 through 1983. Values have been rounded to the nearest millimeter.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	Oct-Mar total
1987	22	M	M	6	21	2	65	0	3	10	21	16	202	112
1988	38	12	0	39	4	0	10	19	6	0	3	1	132	97
1989	2	4	4	0	19	12	0	6	3	3	0	0	53	14
1990	11	4	1	7	8	1	39	10	19	t	7	1	108	19
1991	4	24	43	0	12	t	1	10	9	6	4	25	137	79
1992	30	73	75	0	1	0	t	0	0	19	0	56	225	213
1993	85	84	19	t	t	23							211	263
1987-91 Mean	15	11	12	10	13	3	23	9	7	4	7	8	126	58
1968-93 Mean	16	21	25	5	8	2	15	14	7	7	10	10	137	90
Percent Normal	95	54	47	215	159	133	152	63	111	52	76	87	92	64

M Monthly value is missing but yearly total is available from backup gauges.
t Value is less than 0.5 mm.

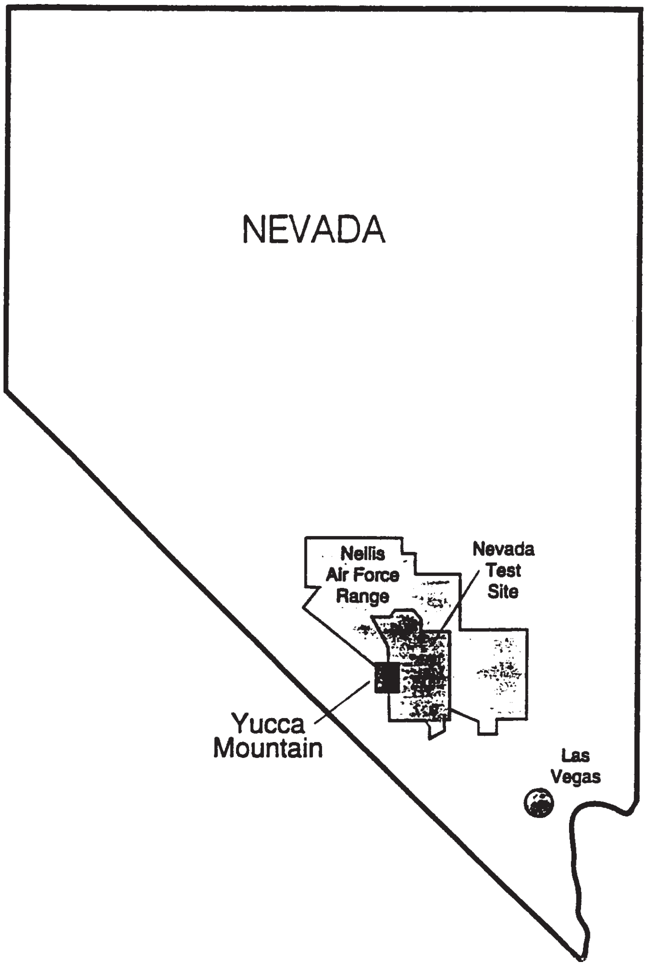

Figure 1—Location of the Yucca Mountain Site Characterization Project area.

towards Crater Flat (about 1,175 m). A gradual east slope (5-10°), composed of a series of highly dissected ridges, tilts towards Jackass Flats (about 1,100 m) (EG&G/EM 1993).

Four primary vegetation associations occur in the Yucca Mountain Project area (Beatley 1976; O'Farrell and Collins 1984). They are: the creosotebush/bursage (*Larrea tridentata-Ambrosia dumosa*), creosotebush/boxthorn/hopsage (*Larrea tridentata-Lycium andersonii-Grayia spinosa*), blackbrush (*Coleogyne ramosissima*), and boxthorn/hopsage (*Lycium andersonii-Grayia spinosa*) associations. The blackbrush association consists of both low and high-elevation phases (i.e., valley bottoms vs. mountain summits). For simplicity and continuity we refer to the low and high-elevation phases of the blackbrush association as the low and high-elevation blackbrush associations. Table 2 provides a relative description of each vegetation association, and the elevation and precipitation gradients that occur at Yucca Mountain.

Methods

Twelve, 200 x 200-m ecological study plots (ESPs) were randomly located in each vegetation association. The blackbrush association had eight ESPs in the low-elevation phase, and four ESPs in the high-elevation phase.

Plant density measurements occurred in eight or ten, 2 x 50-m belt transects, in each ESP. We further subdivided each belt transect into twenty-five, 2 x 2-m quadrats. We found that data collection from contiguous but discrete quadrats located inside each 2 x 50-m belt transect decreased both the frequency of data collectors missing plants, and the accidental inclusion or exclusion of plants from the belt transects. Live and dead perennial plants were counted by species in each 2 x 2-m quadrat. Only plants that had 50% or more of their root crown in a quadrat were counted. Seedlings from the current year were not included in the density measurements. Criteria used

Table 2—General physiographic and abiotic characteristics of the five vegetation associations at Yucca Mountain.

Vegetation association	Elevation range (m)	Landform	Relative precipitation (1992 ave.)	Average soil depth (cm)[1]
Creosotebush	900-1,050	Sandy alluvial plain	Lowest (166 mm)	80+
Creosote/boxthorn/hopsage	1,000-1,200	Young gravelly alluvial outwash	Intermediate (219 mm)	60-100
Low-elevation blackbrush	1,100-1,300	Old alluvial fans	Intermediate (212 mm)	15-45
High-elevation blackbrush	1,400-1,700	Flat mountain tops and mesas	Highest (260 mm)	30-45
Boxthorn/hopsage	1,150-1,500	Ridge tops and mountain sideslopes	Intermediate (220 mm)	30-45

[1] Personal observation of the authors.

to identify seedlings were, plant size, leaf size and number, and stem hardness. Data collection occurred in 1991, the first year that precipitation was sufficient to allow an accurate assessment of live and dead plants.

The number of live and dead plants in each ESP was counted and the ratio of live to dead plants (L:D) for each species in each vegetation association was calculated. The L:D ratio was used as an index to assess how each species responded to drought. Species that had L:D ratios well below 1:1 were considered to have suffered substantial mortality from the drought. Species that had L:D ratios substantially above 1:1 are considered to have endured the drought well. We have assumed that among the vegetation associations the L:D ratios of the individual species, prior to the drought, were more or less equivalent, and that any differences in the L:D ratios of a species among vegetation associations in 1991 were the result of drought conditions.

To test the hypothesis that the drought affected each vegetation association similarly, we classified species that occurred in each vegetation association into two categories (L:D >1:1 and <1:1), and performed a Chi-square test to assess if differences existed among vegetation associations.

Results

Vegetation Association Response

Table 3 shows the number of live and dead plant crowns in each vegetation association in 1991. The percentage of all live plant crowns, across all vegetation associations, after the drought was 63%. The low-elevation blackbrush association had the fewest live plant crowns (46%). The creosotebush/boxthorn/hopsage and the creosotebush/bursage associations had roughly the same percentage of live plant crowns, 57% and 58%, respectively. The high-elevation blackbrush and the boxthorn/hopsage associations had the highest percentage of live plant crowns, 79% and 81%, respectively.

A Chi-square analysis on the L:D ratios suggests that the drought did not affect each vegetation association at Yucca Mountain similarly ($X^2 = 28.0$, $p \leq 0.001$, df = 4, Table 4).

Table 3—Total live and dead plants recorded in the vegetation associations at Yucca Mountain in 1991.

	Vegetation association					
	Creosotebush/ bursage	Creosotebush/ boxthorn/ hopsage	Low-elevation blackbrush	High-elevation blackbrush	Boxthorn/ hopsage	Total
Live plants	13,497	5,938	4,920	2,512	14,324	41,191
Dead plants	9,759	4,478	5,685	662	3,298	23,882
Percent alive	58	57	46	79	81	63

Table 4—Chi-square analysis of live:dead ratios for the 30 most common perennial species in the vegetation associations at Yucca Mountain, Nevada, in 1991. $X^2 = 28.0$, $p \leq 0.001$, df = 4.

		Vegetation association					
Live:Dead Ratio	Observations	Creosotebush	Creosotebush/ boxthorn/ hopsage	Low-elevation blackbrush	High-elevation blackbrush	Boxthorn/ hopsage	Total
		Number of species					
≥ 1:1	Observed	17.0	11.0	11.0	18.0	30.0	87.0
	Expected	15.9	17.4	15.9	15.1	22.8	
< 1:1	Observed	4.0	12.0	10.0	2.0	0.0	28.0
	Expected	5.1	5.6	5.1	4.9	7.2	
Total		21.0	23.0	21.0	20.0	30.0	115.0

The creosotebush/bursage, high-elevation blackbrush, and the boxthorn/hopsage associations had more species than expected with L:D ratios greater than 1:1. The creosotebush/boxthorn/hopsage and low-elevation blackbrush had more species than expected with L:D ratios less than 1:1.

Species Response

Table 5 presents an analysis of how 30 species responded to the drought. The percentage of live plant crowns for each species, summed over all vegetation associations, ranged from a low of 3% for Indian ricegrass (*Oryzopsis hymenoides*), to a high of 98% for galletta grass (*Hilaria jamesii*) and rubber rabbitbrush (*Chrysothamnus nauseosus*). Only two species; Indian ricegrass and desert needlegrass (*Stipa speciosa*), had less than 50% of their plant crowns still alive in 1991. Shadscale (*Atriplex confertifolia*) fared slightly better; 52% of the shadscale crowns were alive in 1991. The median value for all species was 72%.

Twelve of the thirty species analyzed occurred across all vegetation associations. Another eight species occurred across the entire elevation and precipitation gradient (i.e., they occurred in either the high-elevation blackbrush or the boxthorn/hopsage association, but not both). Species that occurred in most of the vegetation associations often did not have the same response in each vegetation association. Generally, species responses can be classified into three categories (Table 6). Category 1 species had L:D ratios >1:1 (i.e., >50% of the crowns present were alive) in every vegetation association in which they occurred. Category 2 species had L:D ratios ≤1:1 in the low-elevation blackbrush and/or the creosotebush/boxthorn/hopsage vegetation associations (i.e., middle elevation associations), and L:D ratios >1:1 in all other associations (i.e., high and low-elevation associations). Category 3 species had L:D ratios ≤1:1 in all but the boxthorn/hopsage association (i.e., highest elevation association).

Seventeen species (57%) had L:D ratios ≥1:1 in every vegetation association in which they occurred (Table 6). Figure 2 shows three species that had this type of response, and how their response varied by vegetation association. Ten species had L:D ratios ≥1:1 in both the lowest and highest elevation associations, and L:D ratios <1:1 in at least one of the two vegetation associations that occur at intermediate points on the elevation/precipitation gradient (Tables 6 and 2). Figure 3 shows two species that had this response, and their variation between associations.

Table 5—The total number of plants (alive and dead) identified by species in the study locations at Yucca Mountain in 1991.

Species	Total live	Total dead	Percent alive
Anderson boxthorn	1,538	388	80
Blackbrush	2,163	979	69
Bladdersage (*Salazaria mexicana*)	221	75	75
Broom snakeweed (*Gutierrezia sarothrae*)	401	143	74
Bursage*	10,477	4,803	69
Cheesebush (*Hymenoclea salsola*)	981	504	66
Coopers goldenweed (*Haplopappus cooperi*)	1,598	956	63
Creosotebush	1,261	49	96
Desert needlegrass	1,439	1,921	43
Desert globemallow (*Sphaeralcea ambigua*)	1,359	76	95
Douglas rabbitbrush (*Chrysothamnus viscidiflorus*)	183	42	81
Fourwing saltbush (*Atriplex canescens*)	60	13	82
Fluff grass (*Erioneuron pulchellum*)	1,338	399	77
Galletta grass	1,119	26	98
Green Ephedra (*Ephedra viridis*)	134	6	96
Goldenweed (*Haplopappus linearifolius*)	113	44	72
Hopsage	1,198	757	61
Indian ricegrass	80	2,288	3
Needleleaf rabbitbrush (*Chrysothamnus teretifolius*)	434	60	88
Nevada Ephedra (*Ephedra nevadensis*)	3,657	724	83
Pale boxthorn (*Lycium pallidum*)	947	112	89
Range ratany (*Krameria parvifolia*)	2,627	253	91
Rubber rabbitbrush	39	1	98
Shadscale	851	777	52
Shockley goldenrod* (*Acamptopappus shockleyi*)	2,099	482	81
Spiny Menodora (*Menodora* spinescens)	2,104	1,162	64
Virgin River Encelia (*Encelia virginensis*)	377	253	60
Winterfat (*Ceratoides lanata*)	1,023	337	75
Wire lettuce (*Stephanomeria pauciflora*)	62	13	83
Yellow buckwheat (*Eriogonum fasciculatum*)	1,304	848	61
Unknown	34	5,391	1
Total	41,191	23,882	72

* The actual percent alive values for these species should be slightly lower. Some dead specimens in the creosotebush/bursage association could not be separated between these two species. Only those that were positively identifiable were used in this analysis.

Table 6—Typical responses displayed by the 30 most common species analyzed for L:D ratios at Yucca Mountain, Nevada.

Response type	Species
1. Species that had L:D ratios ≥ 1:1 in all of the vegetation associations in which they occurred.	Anderson's boxthorn Blackbrush Bladdersage Broom snakeweed[1] Creosotebush Desert globemallow Douglas rabbitbrush[1] Galletta grass[1] Goldenweed[1] Green Ephedra[1] Needleleaf rabbitbrush[1] Nevada Ephedra Pale boxthorn Range ratany Rubber rabbitbrush[1] Virgin River Encelia Wire lettuce
2. Species that occurred across the entire elevation/precipitation gradient and had L:D ratios ≥ 1:1 in vegetation associations at the lowest and highest elevations, and L:D ratios < 1:1 in vegetation associations at intermediate points on the elevation/precipitation gradient.	Bursage Cheesebush Cooper's goldenweed Fluff grass Four-wing saltbush Hopsage Shadscale Shockley goldenrod Spiny Menedora Winterfat
3. Species that had L:D ratios <1:1 in all vegetation associations, except the boxthorn/hopsage (i.e., highest elevation).	Desert needlegrass Indian ricegrass Yellow buckwheat

[1] Species that were present only in the high-elevation blackbrush and boxthorn/hopsage associations.

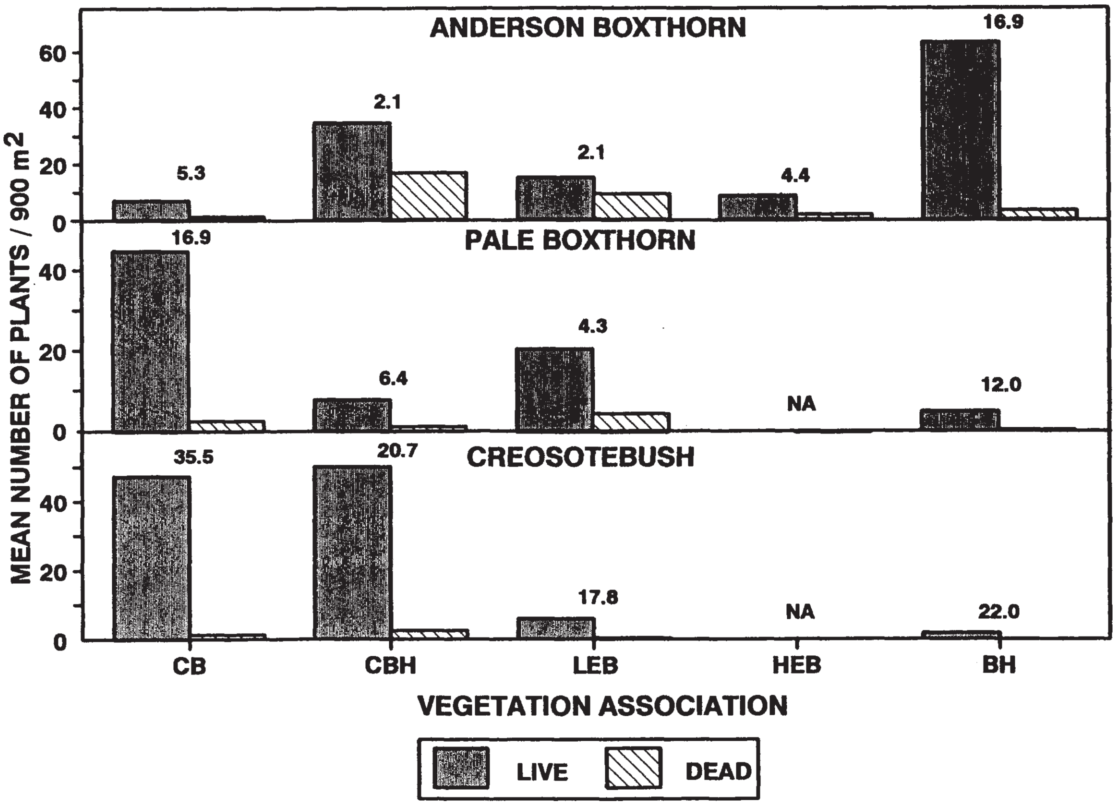

Figure 2—Three of the seventeen species that had L:D rations ≥ 1:1 in each of the vegetation associations in which they occurred, and the variation in species response between vegetation associations. Values above each set of bars are the L:D ratio for the species. Acronyms used to describe each vegetation association are as follows: CB = creosotebush/bursage; CBH = creosotebush/boxthorn/hopsage; LEB = low-elevation blackbrush; HEB = high-elevation blackbrush; BH = boxthorn/hopsage.

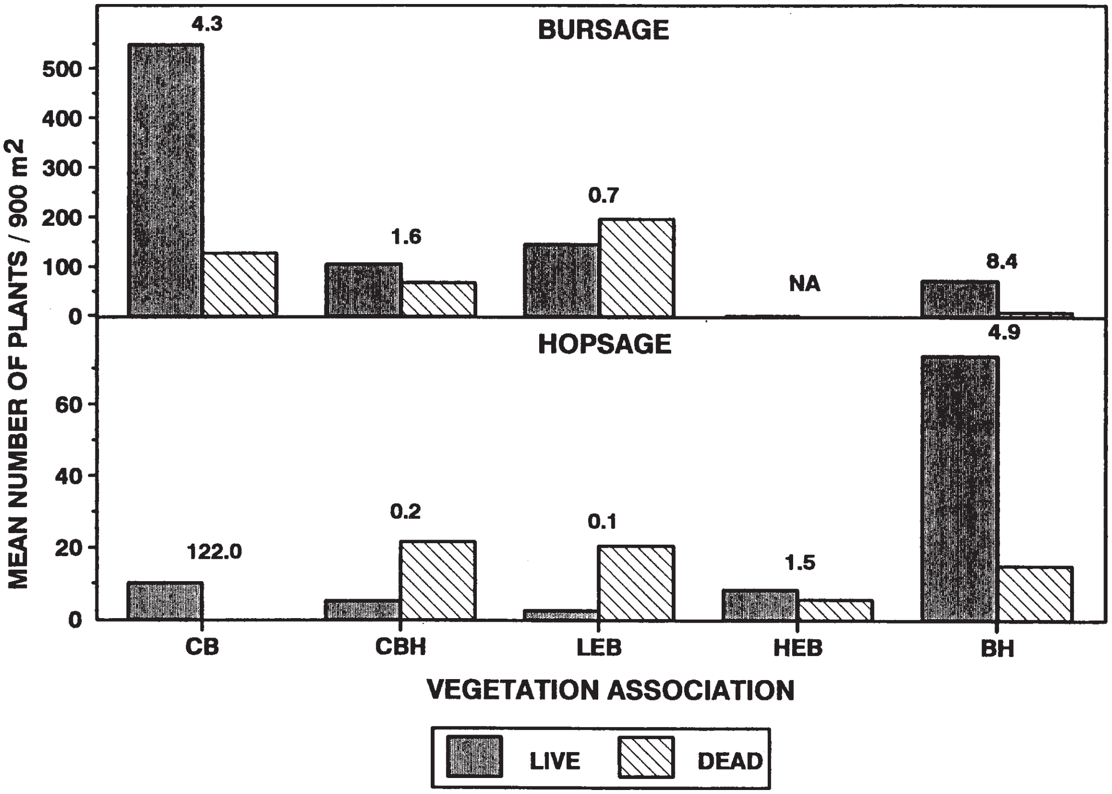

Figure 3—Two of the ten species that had L:D ratios ≥ 1:1 in the vegetation associations at the lowest and highest elevations, and L:D ratios ≤ 1:1 in one or both of the vegetation associations that occurred at intermediate points on the elevation/precipitation gradient. Values above each set of bars are the L:D ratio for the species. Acronyms used to describe each vegetation association are as follows: CB = creosotebush/bursage; CBH = creosotebush/boxthorn/hopsage; LEB = low-elevation blackbrush; HEB = high-elevation blackbrush; BH = boxthorn/hopsage.

Three species had L:D ratios ≥1:1 in only the boxthorn/hopsage vegetation association, and L:D ratios <1:1 in all other vegetation associations (Table 6). The two most common bunch grasses in the project area, Indian ricegrass and desert needlegrass had this response to the drought (Fig. 4).

Discussion and Conclusions

The data from Yucca Mountain, Nevada, indicate that neither vegetation associations nor individual species in the northern Mojave Desert respond similarly to a prolonged and severe drought. One vegetation association had less than 50% of its plant crowns alive in 1991, while another association had over 80% of the plant crowns alive (Table 3). At the species level some species had L:D ratios that were much higher than 1:1 in every vegetation association (Fig. 2), but other species had L:D ratios well above 1:1 in one association and well under 1:1 in another association (Table 6; Figs. 3 and 4).

Precipitation probably explains part of, but not all of, the vegetation response to drought. The four vegetation associations studied occur along an elevation gradient that influences total precipitation levels. As storm systems move over the higher ridges, orographic uplift increases the precipitation. This may explain why the three low-elevation vegetation associations each had more dead plant crowns, a higher percentage of dead plant crowns, and more species with L:D ratios less than 1:1 than did the upper-elevation vegetation associations (Tables 2, 3, and 4). Differences in precipitation, however, do not explain the large difference in the percentage of live plant crowns among the three low-elevation vegetation associations (Table 3), or why the creosotebush/bursage association had substantially fewer species with L:D ratios less than 1:1 (Table 4). The creosotebush/bursage association occurs at the lowest elevations and receives the least precipitation of any vegetation association at Yucca Mountain; however, among the three low-elevation vegetation associations, the creosotebush/bursage association had the highest percentage of live plant crowns, and few species with L:D ratios less than 1:1. If precipitation alone influenced vegetation response to the drought, the creosotebush/bursage association should have had substantially more dead plant crowns than the low-elevation blackbrush association.

When the L:D ratios of each species are grouped by vegetation association (Table 4) there is inferential evidence

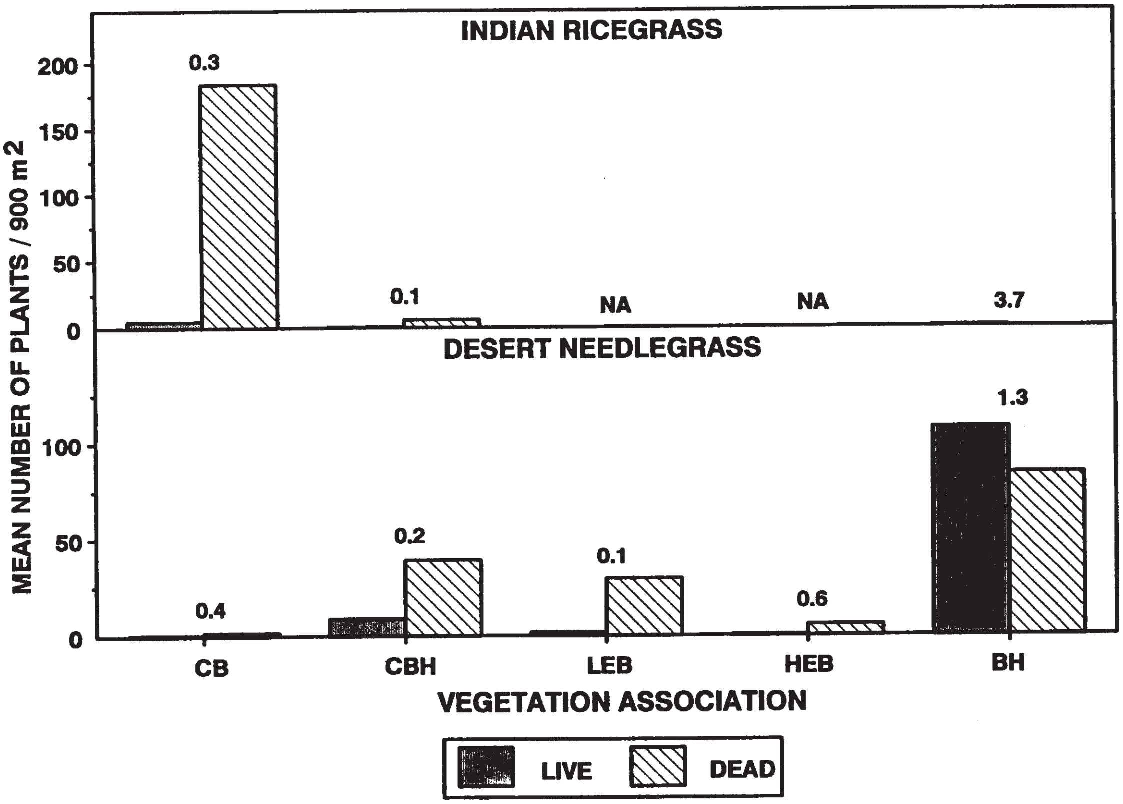

Figure 4—Two of the three species that had L:D ratios ≥ 1:1 in only the boxthorn/hopsage vegetation association. Values above each set of bars are the L:D ratio for the species. Acronyms used to describe each vegetation association are as follows: CB = creosotebush/bursage; CBH = creosotebush/boxthorn/hopsage; LEB = low-elevation blackbrush; HEB = high-elevation blackbrush; BH = boxthorn/hopsage.

that at least one factor besides precipitation influenced both the vegetation association and species response to the drought. The vegetation associations at both the lower and upper ends of the elevation/precipitation gradient had more plant species with L:D ratios ≥1:1 than vegetation associations at intermediate points on the elevation and precipitation gradient (i.e., creosotebush/boxthorn/hopsage and low-elevation blackbrush). Additional evidence that some factor(s) other than precipitation influenced the vegetation's response to drought comes from species that occurred across all five vegetation associations, and particularly, those species that had L:D ratios well above 1:1 in both the driest and wettest vegetation associations, and L:D ratios well under 1:1 in those vegetation associations at intermediate points on the elevation/precipitation gradient (Table 6 and Fig. 3). Bursage and hopsage are two species that illustrate this point (Fig. 3). If only the lack of precipitation influenced their response to the drought, these species should have had L:D ratios near or below 1:1 in the creosotebush/bursage association instead of L:D ratios of 4 and 122:1, respectively.

We believe that one or more soil factors influenced how drought affected both the vegetation associations and individual species at Yucca Mountain. Two soil characteristics that varied among each vegetation association were soil depth and texture (B. Schultz, personal observation), both of which can influence the availability of soil moisture. Most likely soil structure, pH, and the abundance of carbonates and other salts differed among the vegetation associations, and influenced the availability of soil moisture for plant growth. If soil characteristics among the vegetation associations were different enough to influence the availability of soil moisture to plants, then the annual precipitation and available soil moisture may not follow a one-to-one relationship. Vegetation associations or plant communities that receive more total precipitation, but which grow in a soil that has different chemical and physical properties may have less effective moisture available for plant growth. Precisely how soil chemistry and soil physics affect soil moisture availability in Mojave Desert vegetation associations requires additional research.

Additional research on plant-soil relationships, and how drought can affect species mortality, is necessary before more definitive conclusions can be drawn. Additional research on how the L:D ratios change as moisture conditions return towards the long-term average will help determine the population dynamics of perennial species in the northern Mojave Desert.

Acknowledgments

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Species and Community Response to Above Normal Precipitation Following Prolonged Drought at Yucca Mountain, Nevada

Brad W. Schultz
W. Kent Ostler

Abstract—EG&G Energy Measurements initiated a study in 1991 to determine how the perennial species component of vegetation associations and individual perennial plant species in the northern Mojave Desert responded to above-normal precipitation following a prolonged and severe drought. All vegetation associations had a large increase in both absolute and relative cover. Most perennial species increased in cover across all vegetation associations; however, several declined in cover in one or two associations. Plant populations did not show a similar increase in density. Only three species had a large relative or absolute increase in density, but their response was association specific.

Little information is available on how the perennial species component of desert plant communities responds to normal and above-normal precipitation following prolonged drought. Intuitively, one would expect total canopy cover to increase. Whether a concomitant increase in the density of perennial species also occurs is unknown. Even less is known about how individual species respond.

From 1987 through 1991 a prolonged drought occurred in much of the western United States, including the northern Mojave Desert at Yucca Mountain, Nevada. A 25-year precipitation record (1968-1993) from a weather station in Jackass Flats near Yucca Mountain indicates that the mean annual precipitation is 137 mm (5.38 in), and the October through March mean is 90 mm (3.53 in) (Table 1). The October through March period is important because soil-moisture recharge in the northern Mojave Desert frequently begins in October and usually continues through March. Plant growth begins by March, and soil moisture declines. During the drought the average precipitation from October through March was 58 mm (2.27 in), or 64% of the 25-year average. More important, from a vegetation perspective, were the back-to-back dry winters in 1988-1989 and 1989-1990. The respective October through March precipitation in both years was 13 and 19 mm (0.50 and 0.75 in), or less than 21% of normal. Schultz and Ostler (This proceedings) have provided data that indicates that the vegetation associations at Yucca Mountain suffered substantial mortality during this drought.

In February and March 1991 Yucca Mountain received above-normal precipitation. The following two winters (October-March) also had above-normal precipitation (Table 1). Vegetation characterization studies supported by the U.S. Department of Energy (DOE) have provided data that can provide insights into how both vegetation associations and individual species respond to above-normal precipitation following a prolonged drought. Our specific study objectives were to determine: 1) if the collective perennial species component in each of four vegetation associations present at Yucca Mountain responded similarly to above-normal precipitation; 2) how individual perennial plant species responded to above-normal precipitation; and 3) if plant species that occurred in two or more vegetation associations responded similarly in each vegetation association.

Site Description

The Yucca Mountain Site Characterization Project (YMP) area occurs on the southwestern edge of the Nevada Test Site in Nye County, Nevada (Fig. 1), exclusively on land controlled by the Federal government. Ownership and control of the project area is divided among the DOE, which controls the eastern portion of the area through land withdrawn for use as the Nevada Test Site, the U.S. Air Force, which controls the northwestern section of the project area through land-use permits for the Nellis Air Force Range, and the Bureau of Land Management, which controls the southwestern portion of the site as public trust lands.

Yucca Mountain occurs near the northern edge of the Mojave Desert. This region has rugged linear (generally north-south) mountain ranges interspersed with broad valleys. Yucca Mountain is a long north-south volcanic ridge that has a maximum elevation of 1,494 m. A steep west slope (15-30°) tilts towards Crater Flat (about 1,175 m). A gradual east slope (5-10°), composed of a series of highly dissected ridges, tilts towards Jackass Flats (about 1,100 m) (EG&G/EM 1993).

Four primary vegetation associations occur in the Yucca Mountain Project area (Beatley 1976; O'Farrell and Collins 1984). They are: creosotebush/bursage (*Larrea tridentata-Ambrosia dumosa*), creosotebush/boxthorn/hopsage (*Larrea tridentata-Lycium andersonii-Grayia spinosa*), blackbrush (*Coleogyne ramosissima*), and boxthorn/hopsage (*Lycium andersonii-Grayia spinosa*). The blackbrush community

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In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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Table 1—Average monthly and annual precipitation (mm) at station 4JA (elevation 3,422 m) in Jackass Flats, Nevada Test Site. Cumulative record is from 1968 through 1983. Values have been rounded to the nearest millimeter.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total	Oct-Mar total
1987	22	M	M	6	21	2	65	0	3	10	21	16	202	112
1988	38	12	0	39	4	0	10	19	6	0	3	1	132	98
1989	2	4	4	0	19	12	0	6	3	3	0	0	52	13
1990	11	4	1	7	8	1	39	10	19	t	7	1	109	19
1991	4	24	43	0	12	t	1	10	9	6	4	25	137	79
1992	30	73	75	0	1	0	t	0	0	19	0	56	225	213
1993	85	84	19	t	t	23							211	262
1987-91 Mean	15	11	12	10	13	3	23	9	7	4	7	8	126	58
1968-93 Mean	16	21	25	5	8	2	15	14	7	7	10	10	137	90
Percent Normal	95	54	47	215	159	133	152	63	111	52	76	87	92	64

M Monthly value is missing but yearly total is available from backup gauges.
t Value is less than 0.5 mm.

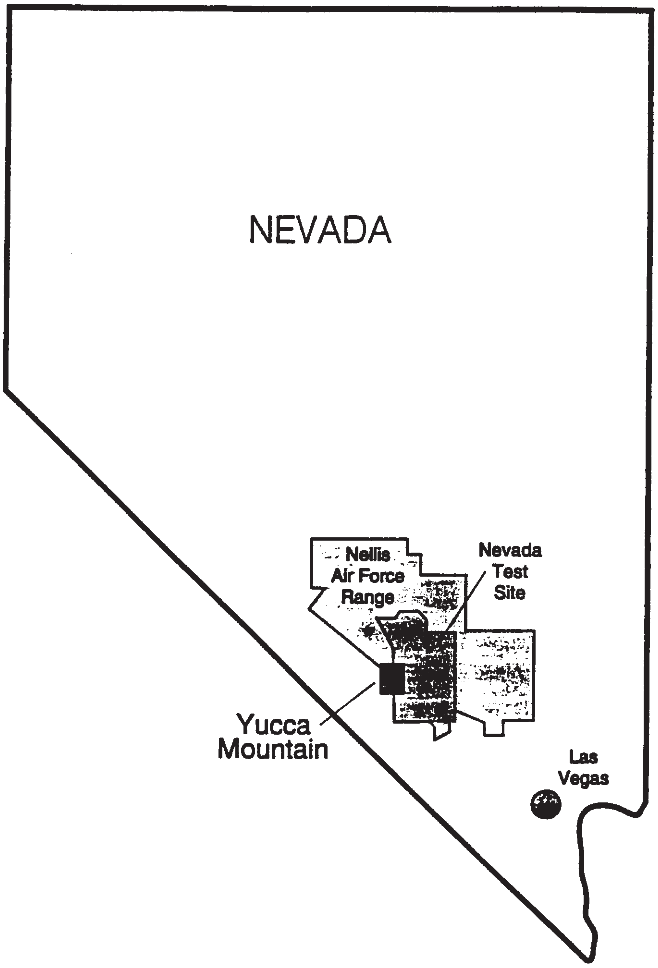


Figure 1—Location of the Yucca Mountain Project area.

consists of both low and high-elevation variations (i.e., valley bottoms versus mountain summits). For simplicity and continuity we refer to the upper and lower elevation phases of the blackbrush association as the low and high-elevation blackbrush associations. Table 2 provides a relative description of the biotic and abiotic conditions that occur in each vegetation association at Yucca Mountain. Table 3 gives the scientific name, common name, and four-letter codes for individual species.

Methods

We randomly located twelve, 200 x 200-m study plots in each vegetation association (48 total plots). The blackbrush association had eight study plots in the low-elevation phase and four study plots in the high-elevation phase (i.e., valley bottoms vs. mountain summits). We measured both the canopy cover and the density of established perennial plants to determine how both vegetation associations and individual species responded to above-normal precipitation, following a drought. Data collection for cover occurred in 1991, 1992, and 1993, and for density in 1991 and 1992.

Canopy cover measurements occurred with the point-intercept method (Bonham 1989) on eight or ten, 50-m line transects. We placed an ocular scope at 1-m intervals along each transect and recorded two point-intercepts, for a total of 100 points per transect (Buckner 1985). We calculated the mean absolute canopy cover of all perennial species, both collectively and individually, in each vegetation association for each year (1991-1993). We also calculated the absolute and relative change in canopy cover for each vegetation association and species, between 1991 and the subsequent year (1992 or 1993) that had the highest cover value.

Density measurements (plants/900 m^2) of all established perennial plants occurred in eight or ten, 2 x 50-m belt transects in each ecological study plot. We further subdivided

Table 2—General physiographic and abiotic characteristics of the five primary vegetation associations at Yucca Mountain.

Vegetation association	Elevation range (m)	Landform	Relative precipitation (1992 ave.)	Average soil depth (cm)[1]
Creosotebush/bursage	900-1,050	Sandy alluvial plain	Lowest (166 mm)	80+
Creosote/boxthorn/hopsage	1,000-1,200	Young gravelly alluvial outwash	Intermediate (219 mm)	60-100
Low-elevation blackbrush	1,100-1,300	Old alluvial fans	Intermediate (212 mm)	15-45
High-elevation blackbrush	1,400-1,700	Flat mountain tops and mesas	Highest (260 mm)	30-45
Boxthorn/hopsage	1,150-1,500	Ridge tops and mountain sideslopes	Intermediate (220 mm)	30-45

[1] Personal observation of the authors.

Table 3—Common and scientific names of species used in the text. Four-letter codes identify species in Figures 3 and 5.

Common name	Scientific name	Code
Anderson's boxthorn	*Lycium andersonii*	LYAN
Blackbrush	*Coleogyne ramosissima*	CORA
White bursage	*Ambrosia dumosa*	AMDU
Cheesebush	*Hymenclea salsola*	HYSA
Cooper's goldenweed	*Haplopappus cooperi*	HACO
Creosotebush	*Larrea tridentata*	LATR
Green Ephedra	*Ephedra viridis*	EPVI
Hopsage	*Grayia spinosa*	GRSP
Indian ricegrass	*Oryzopsis hymenoides*	ORHY
Needleleaf rabbitbrush	*Chrysothamnus teretifolius*	CHTE
Nevada Ephedra	*Ephedra nevadensis*	EPNE
Pale boxthorn	*Lycium pallidum*	LYPA
Shadscale	*Atriplex confertifolia*	ATCO
Shockley goldenrod	*Acamptopappus shockleyi*	ACSH
Spiny Menodora	*Menodora spinescens*	MESP
Virgin River Encelia	*Encelia virginensis*	ENVI
Yellow buckwheat	*Eriogonum fasciculatum*	ERFA

each belt transect into twenty-five, 2 x 2-m quadrats. We found that data collection from smaller quadrats inside each belt-transect decreased both the frequency of data collectors missing plants, and the accidental inclusion or exclusion of plants from the belt transects. Only plants that had 50% or more of their root crown located inside each belt transect were counted. We defined established plants as those individuals that were at least 1-year-old. Among very young or very small plants we used plant size, the number of leaves or leaf blades present, and stem hardness as indicators of plant age. For example, grass seedlings usually had one to three threadlike leaf blades that were less than 5 cm long. Yearling grass plants had substantially more and longer leaf blades, and each were several millimeters wide. Stems on shrub seedlings had not yet hardened. We calculated the collective mean density (plants/m^2) of all perennial species in each vegetation association, and the percent change in the mean density of individual species (plants/900 m^2), between 1991 and 1992. We report the mean density of each vegetation association as the plants/m^2, and the mean density of each species as plants/900 m^2. We selected these scales because species density values at the scale of plants/m^2 were often very small, and were difficult to visualize and interpret. For example, we report shadscale density as 36 plants/900 m^2, instead of 0.016 plants/m^2. Also, the collective size of our belt transects in each ESP averaged 900 m^2.

At the species level, we report the change in cover and density for the 17 most abundant species, across all four vegetation associations. We used a Chi-square test to determine if differences existed among vegetation associations.

Results

Cover

The mean absolute canopy cover (hereafter called cover) of all perennial species, across all study plots was 8.6% in 1991. Cover increased to 11.3% in 1992, and 12.7% in 1993. This represents a relative increase of 48% during the study period.

The collective cover of all perennial species in each vegetation association, except the boxthorn/hopsage association, increased each year (Fig. 2). Absolute cover in the boxthorn/hopsage association increased 4.5% from 1991 to 1992, but was similar in both 1992 and 1993.

Between 1991 and 1993 the absolute cover of the perennial species component in each vegetation association increased at least 3.3%, and the relative cover increased at least 37%. The creosotebush/bursage association had the largest increase in both absolute and relative cover, 5.3% and 62%, respectively (Fig. 2). The boxthorn/hopsage association had the second highest increase in absolute cover (4.5%), but this represented the smallest increase in relative cover (37%). The creosotebush/boxthorn/hopsage and blackbrush associations had the smallest increases in absolute cover, 3.4% and 3.3%, respectively (Fig. 2).

The absolute cover of most species increased between 1991 and 1993 (Figs. 3a-3d). Bursage, Nevada Mormon tea (*Ephedra nevadensis*), hopsage, creosotebush, Anderson's boxthorn, and pale boxthorn (*Lycium pallidum*) were the only species whose absolute cover increased 0.5% or more (e.g., from 2.5% to 3.1%). This level of increase, however, did not occur in each vegetation association. Bursage and creosotebush increased their absolute cover 0.5% or more only in the creosotebush/bursage, creosotebush/boxthorn/hopsage, and low-elevation blackbrush associations. Hopsage, Nevada Mormon tea, and Anderson's boxthorn increased their absolute cover 0.5% or more only in the boxthorn/hopsage community. Pale boxthorn only had a large increase in absolute cover in the creosotebush/bursage association.

Hopsage, Indian ricegrass, and shadscale (*Atriplex confertifolia*) had the greatest relative increase in cover among years (Figs. 3a-3d). The large increase in relative cover, however, was association specific. For hopsage and Indian

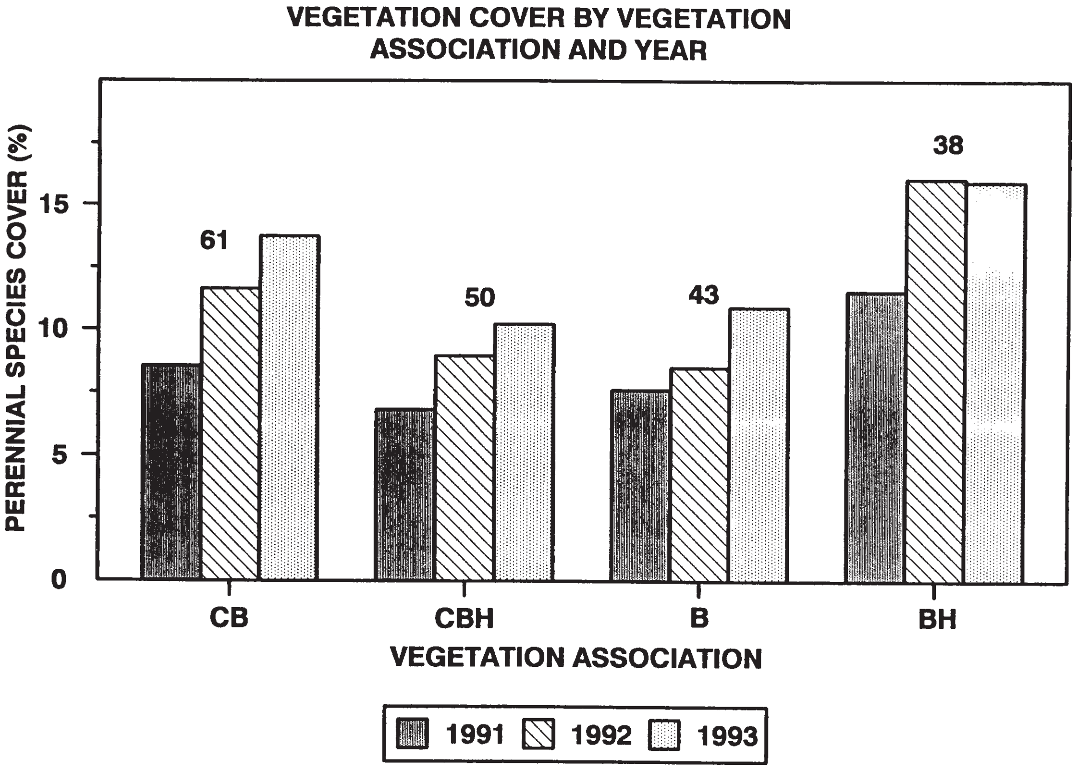
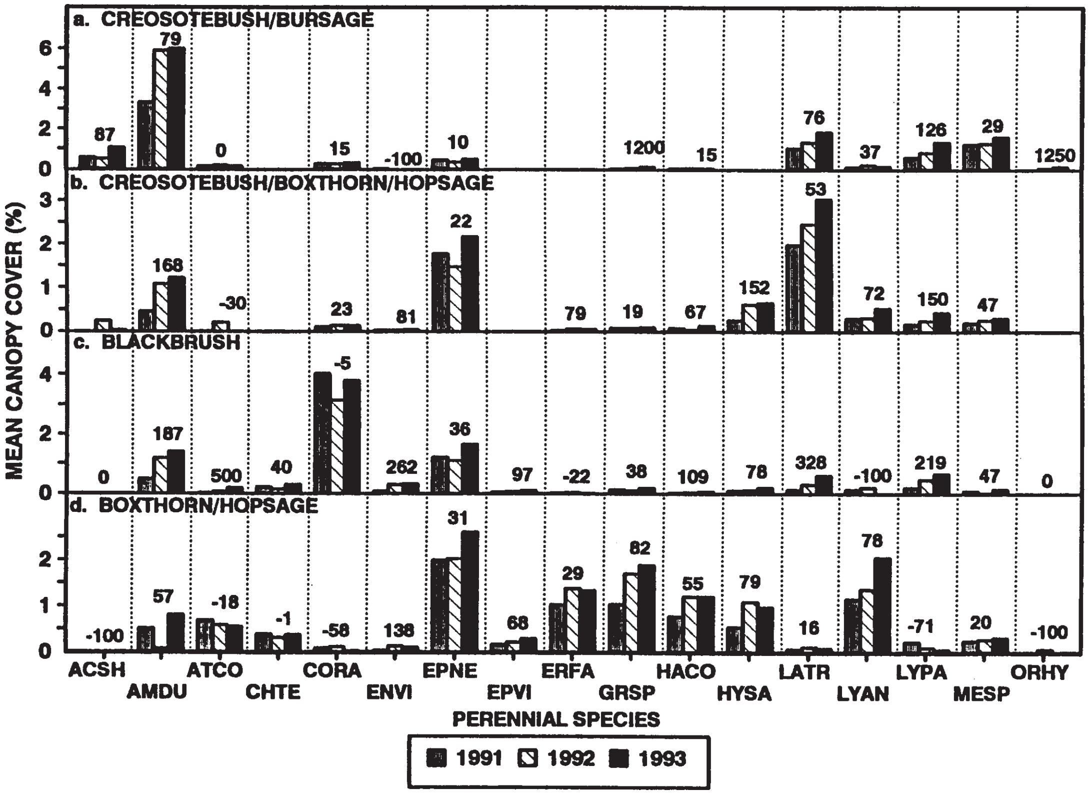


Figure 2—The mean absolute canopy cover of all perennial species in 1991, 1992, and 1993 in the four vegetation associations at Yucca Mountain, Nevada. Values above each bar are the percent change in relative cover between the years that had the lowest and highest absolute cover. Acronyms used to describe each vegetation association are as follows: CB = creosotebush/bursage; CBH = creosotebush/boxthorn/hopsage; B = blackbrush; BH = boxthorn/hopsage.



Figures 3a-3d—The mean canopy cover, in each of three years, of the 17 most common perennial plant species in the four vegetation associations at Yucca Mountain, Nevada. The value above each group of bars is the percent change in total cover between 1991 and 1993. See Table 3 for a description of the species codes.

ricegrass, the increase occurred only in the creosotebush-bursage vegetation association. For shadscale, the increase occurred only in the blackbrush association (primarily the low-elevation study plots). Despite the large increase in the relative cover of hopsage, Indian ricegrass, and shadscale, their increase in absolute cover was small (<0.2%). Other species had a larger change in absolute cover, but their relative increase in cover was comparatively small (Figs. 3a-3d).

Eight species increased their absolute cover across all four vegetation associations (Figs. 3a-3d). Seven additional species had an increase in cover in all but one vegetation association. Two species, shadscale and blackbrush, had a decline in absolute cover in two vegetation associations. None of the seventeen major species present had a consistent decline in cover across all four vegetation associations. The Chi-square test showed that there was no consistent difference in a species increase or decrease in cover among the vegetation associations ($X^2 = 5.3$ with 3 df, p>.1).

Density

Except for the blackbrush association there was little change in the mean density in each vegetation association (Fig. 4). Only three species, bursage, Indian ricegrass, and shadscale had a substantial increase in absolute density (Figs. 5a-5d). Bursage and shadscale increased their density in the blackbrush association, particularly in the low-elevation study plots. Indian ricegrass increased in density only in the creosotebush/bursage association. The remaining species typically had a small change in density. A Chi-square analysis showed no differences in species density increases or decreases among the four vegetation associations ($X^2 = 7.56$, df=6, p>.2).

Discussion

The primary response of the perennial species component of four vegetation associations at Yucca Mountain, when exposed to above-normal precipitation following a prolonged drought, was an increase in absolute cover (Figs. 2 and 4). Each vegetation association had a substantial increase in absolute canopy cover, and except for the blackbrush association no change in density. This result indicates that the existing individuals in these vegetation associations can respond rapidly, with an increase in leaf area, when growing conditions improve (Figs. 3a-3d). Populations of most species, however, increase their numbers at a much slower rate (Figs. 5a-5d).

At the vegetation association level the magnitude of the increase in cover varied widely. The largest increase in both absolute and relative canopy cover occurred in the creosotebush/bursage association, and the smallest increase in the blackbrush association (Fig. 2). The increase in the absolute cover of each vegetation association did not follow the elevation and precipitation gradient present at Yucca

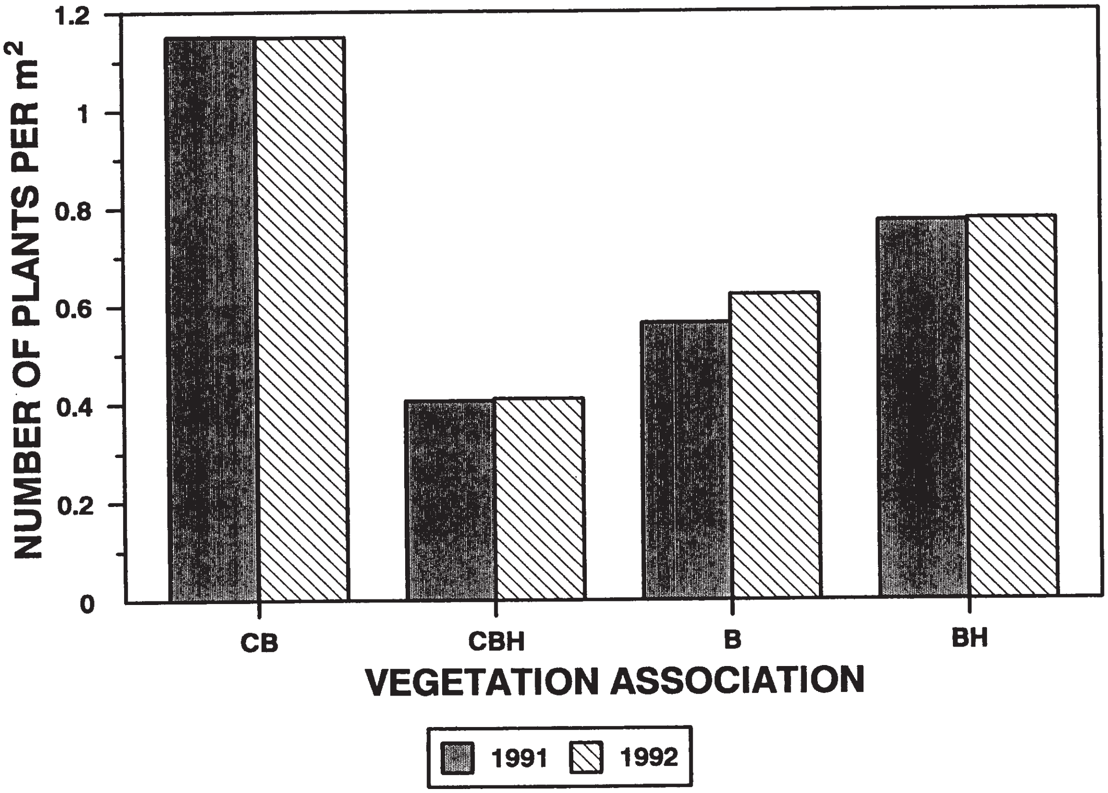
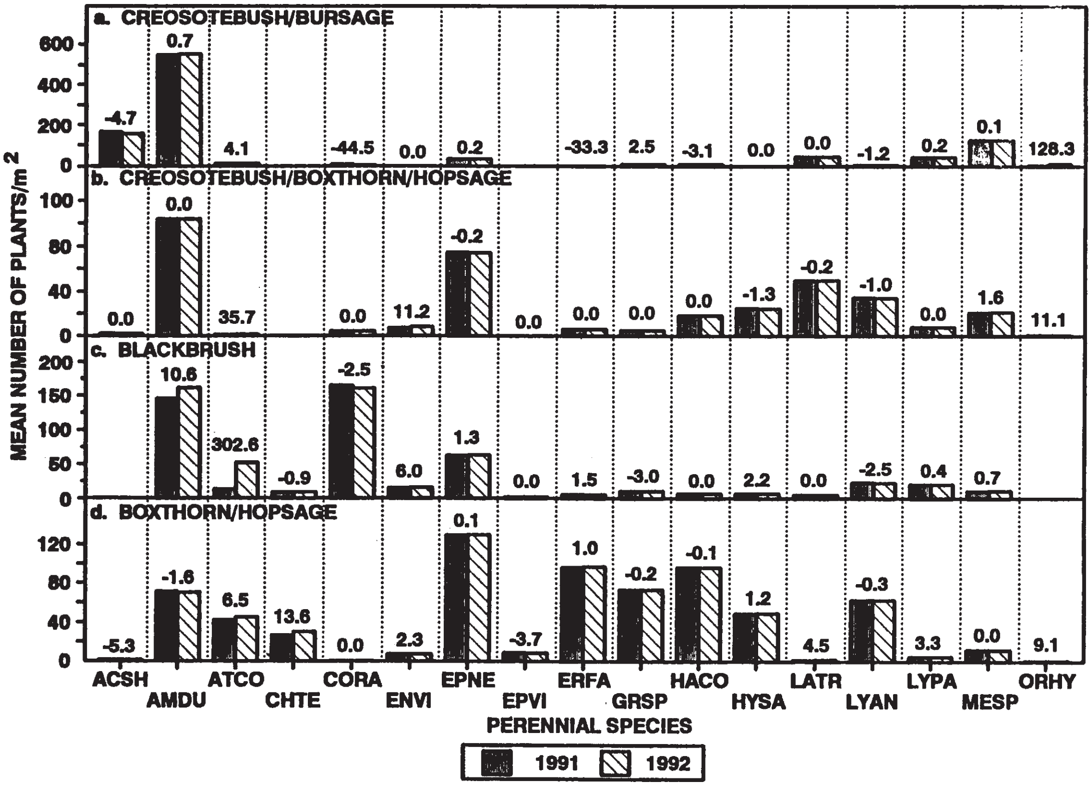


Figure 4—The mean density of the perennial species component of the four primary vegetation associations at Yucca Mountain. Acronyms used to describe each vegetation association are as follows: CB = creosotebush/bursage; CBH = creosotebush/boxthorn/hopsage; B = blackbrush; BH = boxthorn/hopsage.



Figures 5a-5d—The mean density, in 1991 and 1992, of the 17 most common perennial species in four vegetation associations at Yucca Mountain, Nevada. The value above each group of bars is the percent change in density from 1991 to 1992. See Table 3 for a description of the species codes.

Mountain. The creosotebush/bursage association occurs at the lowest elevation, and receives the least precipitation (Table 2); yet this association had the greatest increase in absolute canopy cover (Fig. 2). This may indicate that the creosotebush/bursage association suffered a greater die-back of leaf-producing stems during the drought, and once environmental conditions improved had the greatest potential for community response. An alternative explanation is that bursage, creosotebush, and pale boxthorn, the three species that had the greatest increase in absolute cover in the creosotebush/bursage association, have evolved to increase their leaf area rapidly when growing conditions are optimal. A rapid and comparatively large increase in the leaf area of an individual plant should improve its ability to exploit available resources during brief periods of resource abundance.

Because the increase in absolute cover exhibited by both vegetation associations and individual species did not follow the elevation and precipitation gradient present, and because species performance was not consistent across vegetation associations, factors other than precipitation probably play an important role in how both vegetation associations and individual species respond to above normal precipitation following drought. Two observed differences among each vegetation association were soil depth and texture, both of which influence available soil moisture. Soil structure, pH, and the abundance of carbonates and other salts probably differed among the vegetation associations, and may have affected soil moisture availability for plant growth. If different soil characteristics exist among the vegetation associations, and these soil conditions control the amount of soil moisture available to plants, then the amount of soil moisture available to plants may not follow a one to one relationship with precipitation. Vegetation associations or plant communities that have a greater total precipitation, but which grow in a soil that has a different chemical and physical composition may have less effective moisture available for plant growth. Precisely, how soil chemistry and soil physics affect the availability of soil moisture in Mojave Desert vegetation associations requires additional research.

The change in canopy cover of an individual species does not always follow the general response of the vegetation association in which the species occurs. For example, the absolute cover in all vegetation associations increased (Fig. 2), but several species had a decrease in absolute cover from 1991 to 1993 (Figs. 3a-3d). Without a detailed statistical analysis we can not say for sure if the observed declines in the cover of some species are significant; however, we feel the differential response exhibited by the vegetation associations and some species provides additional evidence that biotic and or abiotic factors other than precipitation influenced the vegetation associations at Yucca Mountain during and after the drought.

Indian ricegrass, shadscale, and bursage were the only species that had a substantial increase in both cover and density (Figs. 3a-3d and 5a-5d). Their respective increase in cover and density only occurred in the creosotebush/bursage and low-elevation blackbrush vegetation associations, and may reflect their initial stage of recovery from the high mortality they suffered during the drought (Schultz and Ostler, this proceedings). Other research at Yucca Mountain (Hall and others, this proceedings) found that only Indian ricegrass had good seedling survival (43%) from 1992 to 1993. The large increase in the mean density of shadscale in the blackbrush association, between 1991 and 1992, indicates that shadscale probably had relatively good seedling survival in this association. We noted that Indian ricegrass seedlings often occurred in interspaces between shrubs, but that shadscale seedlings were most frequent under the skeletons of dead shrubs, most of which had been shadscale plants.

Several implications and conclusions can be drawn from these observations. Indian ricegrass appears to be well adapted to the creosotebush/bursage vegetation association, and can rapidly increase in density when climatic conditions are good. Indian ricegrass had good seed germination and seedling survival in the interspaces between shrubs, an area considered inhospitable to plant growth in arid environments. Indian ricegrass, at least in the creosotebush/bursage vegetation association, is a climatic opportunist. In the other vegetation associations, all of which receive higher annual precipitation, the density of Indian ricegrass appears to be limited by other factors. These may include interspecific competition, soil characteristics, or a lack of safe-sites for either seed germination or seedling survival. Hall and others (This proceedings) provide evidence that interspecific competition with annuals may limit the presence of Indian ricegrass in the other vegetation associations.

Shadscale is well adapted to the low-elevation blackbrush association, but appears to require a die-off of existing plants before a large number of seedlings will survive. The low number of shadscale seedlings in interspaces, the high number of seedlings under living shrubs, and the higher abundance of yearling shadscale plants under dead shrubs (Brad Schultz, personal observation) indicates that shadscale has different and probably narrower micro-habitat requirements than Indian ricegrass. The best micro-habitat for seed germination does not appear to be the best habitat for seedling survival. Either intra- or interspecific competition appears to limit seedling survival, primarily to locations under dead shrubs.

Conclusions

The perennial species component of each vegetation association responded similarly to above-normal precipitation following drought. Each association expressed a large increase in absolute cover; however, the magnitude of the increase varied among the vegetation associations. None of the vegetation associations had a comparatively large change in mean density.

Individual species did not always respond similarly across vegetation associations. Some species (e.g., bursage) increased their absolute cover in every vegetation association in which they occurred. Other species (e.g., shadscale) had an increase in cover in one association, and a decrease in cover in another association. Only two species saw a large increase in absolute density.

Individual plants appear to respond rapidly to improved growing conditions, and sharply increase their canopy cover. Plant populations respond at a much slower rate, and each species appears to have a specific set of biotic or abiotic conditions that must be present before density can increase. Factors other than just precipitation appear to control how both vegetation associations and plant populations respond to above-normal precipitation following a drought.

Acknowledgments

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Predicting Plant Growth Rates From Dark Respiration Rates: an Experimental Approach

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Abstract—A desirable quality in native plants used for revegetation is the ability for rapid growth and establishment, whether transplanted as seedlings or directly seeded. Photosynthetic rates are variable but not correlated with growth rate. Dark respiration rates measured by microcalorimetry, infrared gas analysis (CO_2), or oxygen electrodes are strongly correlated with growth rate for desert shrubs and crop plants. Respiration of germinating seeds effectively predicts performance not only of seedlings but also mature plants. This allows for rapid screening of available accessions to predict growth performance. This method is faster and less expensive than determining $^{13}C/^{12}C$ ratios of plant tissue and works for C_4 plants as well as C_3 plants.

Revegetation in arid environments requires plants that can grow rapidly under harsh conditions. Metabolic measures made at an early stage that indicate future rapid growth would thus be of great value. Photosynthetic differences exist but do not seem to be correlated with growth rate (Frank and others 1986). Water use efficiency, as measured by $^{13}C/^{12}C$ ratios, has been widely used to predict growth rate (Condon and others 1987; Farquhar and others 1982), however this test is expensive and works only for C_3 plants under water stress. Dark respiration has been said to be positively correlated with plant growth (Hay and Walker 1989), but others hold a contrary view (Amthor 1989). Thornley (1970) proposed a model for plant growth based on respiration: $P - R_m = R_x + \text{storage}$, where P is the gross photosynthetic rate, R_m is the respiration rate needed to maintain life processes, R_x is the rate of carbon metabolized for growth, defense, stress reduction, etc., and storage is the rate of production of starch, lipid, or biomass which can be converted to energy. In practice, several of these parameters, especially R_m, are difficult to measure. This research is an attempt to experimentally define parameters that may prove useful in predicting plant growth.

Materials and Methods

Shrub seeds were obtained from Durant McArthur at the Intermountain Research Station's Shrub Science Laboratory and from Howard Stutz of Brigham Young University. Other plant materials were obtained from the Botany greenhouse and from commercial sources. Specific respiration and photosynthetic rates were measured using a Lycor-2600 infrared gas analyzer, a Hansatech oxygen electrode, and a Hart Scientific model 7707 differential scanning calorimeter. Isotope ratios were determined on an isotope ratio mass spectrometer.

Results and Discussion

Bushbean (*Phaseolus vulgaris* L.) cv. Tendergreen seed was soaked for one hour in aerated, distilled water, then planted in a light soil mix and placed in a growth chamber with 15 hours in light at 23°C and 9 hours in dark (21°C). Gas exchange was measured on whole seedlings, or leaves, with an infrared gas analyzer at 24°C. The dry seed had a very low rate of dark respiration. As seen in Table 1, respiration increased rapidly and continuously with seedling growth and development. Green tissue appeared after 7 days with some fixation of CO_2. However CO_2 uptake in the light did not exceed CO_2 evolution in the dark until the plants were nearly two weeks old. The photosynthesis to respiration ratio is an indication of energy available from photosynthesis.

Another way to follow development with time is to use leaves of different ages from the same plant. The smallest

Table 1—Photosynthetic rate (P_{CO2}) and dark respiration rate (R_{CO2}) in leaves from Bushbean cv. Tendergreen germinated and grown in a growth chamber

	µg CO_2/g fr wt/min		
age (days)	P_{CO2}	R_{CO2}	P_{CO2}/R_{CO2}
dry seeds		+0.04	
0 (1 hr soak)		+1.1	
1		+4.6	
2		+7.8	
7	+8.7	+16.5	
11	+7.8	+20.3	
13	-24.2	+23.5	1.0
14	-45.8	+27.5	1.3
15	-83.5	+34.9	2.4

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and youngest leaves are at the stem tip and leaves become progressively larger and older down the stem. Leaves may be retained for a very long time. Leaves from a six-month old hybrid of *Atriplex canescens* x *A. obovata* grown in the greenhouse were removed in order of growth (and size) and analyzed for metabolic activity with an infrared gas analyzer at 24°C. Table 2 shows that the youngest leaves had the highest rates of dark respiration, decreasing with leaf number to a low and steady rate. By contrast the photosynthetic rate was much lower in younger leaves and higher in older leaves. There was a fair correlation between leaf number and leaf area, the older leaves becoming much larger (Table 2). Ratios of photosynthesis to respiration increased with leaf age to very high values.

Plumeria is a small tropical understory tree with tufts of leaves at the ends of branches. New leaves are formed at the apex as older leaves senesce and fall off, retaining the tufted appearance. The leaves are large, dark green and leathery. Table 3 shows both similarities with and differences from the data in Table 2. Younger leaves have higher rates of respiration than older leaves, and photosynthetic rate is lower in the younger leaves and increases with leaf number up to about 12. In contrast to *Atriplex*, in *Plumeria* the very oldest leaves are smaller and have decreasing rates of photosynthesis (Table 3). Differences between *Atriplex* and *Plumeria* can be understood and explained on the basis of growth habit. *Atriplex* is a sun plant with higher rates of photosynthesis and higher photosynthesis to respiration ratios in the oldest leaves while *Plumeria* is a shade plant. As the older *Plumeria* leaves begin to senesce, nutrients are reabsorbed and distributed to growing tissue. As the old leaf becomes chlorotic, it falls off the stem.

Seedlings of the three subspecies of big sagebrush (*Artemisia tridentata*) and two geographic races of *Kochia prostrata* were grown in the greenhouse for four months under well-watered conditions. Shoot length was measured, carbon isotopes determined in leaf tissue and dark metabolic heat rates determined using a differential scanning microcalorimeter in the isothermal mode at 25°C. Results are shown in Table 4. Within species the metabolic heat rates were clearly a much better indicator under these conditions of plant growth rates than were $^{13}C/^{12}C$ ratios.

Table 3—Photosynthetic rate (P_{CO2}) and respiration rate (R_{CO2}) as a function of leaf number and leaf area starting from the stem tip of *Plumeria*. Photosynthesis means CO_2 uptake (–), while respiration means CO_2 production (+). Photosynthesis to respiration ratios (P_{CO2}/R_{CO2}) are an indication of energy from photosynthesis available for growth.

		μg CO_2/g fr wt/min		
leaf #	leaf area cm^2	P_{CO2}	R_{CO2}	P_{CO2}/R_{CO2}
3	182 cm^2	–70.7	+63.0	1.1
6	410	–96.9	+34.0	2.9
9	506	–82.6	+49.6	1.7
12	654	–101.2	+40.4	2.5
15	570	–54.4	+33.5	1.6
18	330	–38.6	+25.3	1.5

Pea plants (*Pisum sativum* L. cv. Azad) were grown in natural light for 15 to 20 days. Disks (7 mm diameter) were cut under water from the first (young) and fourth (old) pair of leaves counting from the top. Disks were incubated in Petri dishes containing a medium of 0.02 mM $CaCl_2$, 2 mM bicarbonate in 10 mM HEPES-KOH at pH 7.8 under weak light (75-100 μE m^{-2} s^{-1}) for 12 hours followed by 12 hours dark with continuous shaking. The area of leaf disks immediately after cutting and after 24 hours in the Petri dishes was measured on enlarged xerox copies of the disks. Oxygen uptake or production was monitored at 25°C using a Clark-type oxygen electrode. Light intensity of 1,000 μE m^{-2} s^{-1} was used for photosynthesis. Disks were incubated with metabolic inhibitors for one hour. Gas exchange measurements were made with inhibitor present.

Disks from younger leaves of pea plants expanded five times as rapidly as disks from older leaves. As seen in Table 5, rates of photosynthesis and dark respiration were more than twice as great in young leaves as in old leaves. Plant species either possess or can develop an alternative oxidase system (the physiologic function is still not understood). Sodium azide (NaN_3) inhibits cytochrome activity

Table 2—Photosynthetic rate (P_{CO2}) and respiration rate (R_{CO2}) as a function of leaf number (age) and leaf area from tip to base of a six–month old seedling of an *Atriplex* hybrid (*obovata x canescens*). Photosynthesis (P_{CO2}) means CO_2 uptake (–), while dark respiration (R_{CO2}) means CO_2 production (+). Photosynthesis to respiration ratios are an indication of energy available from photosynthesis for growth.

		μg CO_2/g fr wt/min		
leaf #	leaf area cm^2	P_{CO2}	R_{CO2}	P_{CO2}/R_{CO2}
3,4	0.75 cm^2	–96.9	+42.1	2.3
5,6	1.52	–100.8	+25.2	4.0
7,8	1.35	–92.1	+20.3	4.5
9,10	3.08	–128.0	+9.1	14.1
22,23	5.61	–134.9	+8.1	16.7

Table 4—Shoot growth, carbon isotopic ratios, and metabolic heat rates from leaves of races or subspecies of *Artemisia tridentata* and *Kochia prostrata*.

subspecies	shoot length (cm)	$\partial^{13}C$ vs PDB (o/oo)	metabolic heat rate (μw/mg)
Artemesia tridentata			
wyomingensis	4.66	–34.91	8.46
tridentata	7.24	–35.01	10.56
vaseyana	7.57	–34.96	10.74
F_2 hybrid			
tridentata x vaseyana	7.65	–34.21	12.69
Kochia prostrata			
U 10	8.15	–23.88	9.36
U11	9.01	–18.28	14.27

Table 5—Photosynthetic rates (P_{O2}) and respiration rates (R_{O2}) in young and old pea leaves inhibited by 1 mM NaN_3 and 10 mM salicylhydroxamic acid (SHAM)

	young leaves		old leaves	
	rate	inhibition %	rate	inhibition %
P_{O2} (μmol O_2 produced m^{-2} s^{-1})				
control	5.53	0	2.17	0
+ NaN_3	0.56	90	0.80	63
+ NaN_3 + SHAM	-0.40	107	0.08	96
R_{O2} (μmol O_2 consumed m^{-2} s^{-1})				
control	1.86	0	0.83	0
+ NaN_3	1.33	28	0.51	39
+ NaN_3 + SHAM	0.21	89	0.24	71

Table 6—Respiraton rates (R_{CO2}) in younger and older phyllodes from a single leaf of *Acacia auriculariformis* after exposure to metabolic inhibitors. For dark-adaptation, an entire leaf was removed from the tree and kept with the petiole in water in the dark for 24 hours.

	young		old	
	R_{CO2} (μmol CO_2/m²/s	inhibition (%)	R_{CO2} (μmol CO_2/m²/s)	inhibition (%)
light-adapted				
control	8.10	0	3.26	0
+ NaN_3	6.83	16	2.90	11
+ NaN_3 + SHAM	4.24	48	0.52	84
+ NaN_3 + SHAM + NaF	3.10	62	0.52	84
dark-adapted				
control	4.13	0	3.84	0
+ NaN_3	2.53	39	3.31	14
+ NaN_3 + SHAM	7.44	0	5.30	0

while salicylhydroxamic acid (SHAM) inhibits the alternative pathway of electron transport in mitochondria. Photosynthesis proved to be very sensitive to both inhibitors, even more so than dark respiration. The difference in respiration between young and old leaves was largely due to the alternative path. Maintenance respiration has been estimated as the steady-state flux of CO_2 after 48 hours in the dark at a constant temperature (McCree 1974). Such treatment in older leaves caused a complete elimination of the cytochrome path that returned with recovery in the light. Starvation (48 hours in the dark) in younger leaves mostly decreased the alternative path. Our results indicate this method of measuring maintenance respiration is severely flawed.

Similar results were obtained by comparing younger and older phyllodes from a single, large compound leaf from six-year old trees of *Acacia auriculariformis* A. Cunn. ex Benth. In this case gas exchange was measured with an infrared gas analyzer. Juvenile phyllodes from near the leaf tip had twice the rate of dark respiration as did mature phyllodes from near the leaf base (Table 6). Keeping the phyllodes in the dark for 24 hours completely eliminated the alternative path from both juvenile and mature phyllodes. The difference in respiration between juvenile and mature phyllodes was due to cytochrome respiration, glycolysis and basal respiration. Carbon dioxide evolution in the presence of all three inhibitors (NaN_3, SHAM, and NaF), termed basal respiration, is probably due to direct oxygen uptake by phenol oxidases, ascorbic acid oxidases, etc.

In conclusion, dark respiration can predict plant growth but is complex enough that one must know a great deal about the biology of the particular plant. Thornley's model (1970) for respiration and growth is too simplistic and needs drastic revision. We intend to pursue this idea in several other systems in the coming months.

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Structure of Woody Riparian Vegetation in Great Basin National Park

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Abstract—The community composition and population structure of the woody riparian vegetation in Great Basin National Park are described. Community analyses were accomplished by sampling 229 plots along an elevational gradient of 8 major stream systems in the Park. TWINSPAN analysis identified 4 primary species groups that were characterized by *Populus tremuloides* (aspen), *Abies concolor* (white fir), *Rosa woodsii* (Woods rose), and *Populus angustifolia* (narrowleaf cottonwood) as dominants, respectively. Detrended Correspondence Analysis (DECORANA) showed that the most important environmental factors associated with the distribution of species were elevation and slope, with flood-related physiographic factors having a secondary effect. Analysis of size-class distributions of the four major riparian tree species in the Park indicated that each dominant shows good recruitment on most watersheds. Overgrazing by domestic livestock and stream diversion are the two primary disturbance factors affecting riparian vegetation in Great Basin National Park.

Riparian ecosystems are located at the functional interface between aquatic and upland terrestrial ecosystems. Although they occupy less than 1% of the total landscape in the western United States (Knopf et al. 1988), the biological and hydrological importance of riparian ecosystems in overall landscape function is substantial. In the arid/semiarid West, riparian areas typically exist as a narrow corridor of taxonomically distinct, dense plant populations relative to surrounding upland areas, with the resultant oasis effect leading to an enrichment of resident and migratory wildlife (Knopf et al. 1988, Szaro 1989). Riparian zones are also key management areas for water resources, as agricultural and recreational demands for water are placed on these systems due to the fact that water is limiting in most upland areas of the arid/semiarid West.

The central role played by arid land riparian areas in regional ecological processes, together with the unique attributes of riparian systems, has recently resulted in increased attention while at the same time underscoring the need for appropriate vegetation classification and quantitative descriptions in riparian zones. Management of riparian forests depends on knowledge of recognizable community types and their environmental determinants, as well as knowledge of individual species interactions, population structures, and the interaction of those factors with stream channel stability and other disturbance factors (Miller and Johnson 1986). Recognition and classification of discrete vegetation units will allow information to be digitized into a Geographic Information System (GIS) framework that will aid in the production of spatial maps that can integrate riparian systems into the landscape as a whole (Delong and Brusven 1991).

Quantitative descriptions of riparian communities in the arid land West are generally lacking. Szaro (1989) suggested that efforts to classify riparian vegetation are necessary in order to fully understand the distribution and dynamics of many bird, fish, and other vertebrate populations, and that much ecological work in this area has been plagued by oversimplification. Several studies have been conducted that have resulted in classification systems of riparian vegetation across broad geographic areas (Johnson et al. 1976, Szaro 1989, 1990). Although more localized studies have been conducted in a number of geographic areas of the arid land West and Intermountain Region, we presently know little of the structure and function of riparian ecosystems in the Great Basin.

In this study, we described the structure of woody riparian vegetation within the boundaries of Great Basin National Park in Nevada (hereafter referred to as the Park). We concentrated our analyses on woody riparian species due to the fact that true riparian meadows are not well represented in the Park, and many of those that do exist have a long history of grazing pressure that has converted them into more xeric meadows that are largely dominated by exotic species, such as *Bromus tectorum*. The primary objectives of this study were to (1) determine the relative cover values for all woody shrub and tree species in riparian corridors within the Park, (2) identify, through multivariate statistical techniques, the primary riparian community types (species groups) that occur predictably within the Park, (3) determine the relationship between the distribution of riparian plant species groups and environmental factors such as elevation, aspect, and stream physiography, and (4) quantify stand demographics, specifically population size structures, of the major tree dominants to determine population recruitment patterns in the Park.

Previous studies that have attempted to classify riparian plant communities and relate these communities to

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physical site characteristics (Minckley and Brown 1982, Szaro 1989) have considered geographically and physiographically diverse areas. In this study, we focused on a set of streams in exclusively mountainous terrain at relatively high altitudes, which has permitted a degree of resolution and detail that is not possible at much larger scales of inquiry. An applied goal of the study was that the detailed patterns provided herein would aid the National Park Service in future research and resource management efforts, such as vegetation mapping, GIS-based habitat classification, and long-term monitoring of the biodiversity and stability of riparian ecosystems in Great Basin National Park.

Methods

Studies were conducted in Great Basin National Park during the summers of 1991 to 1993. The 31,081 ha Park is located in the South Snake Range of eastern Nevada, a north-south trending fault-scarp mountain system exhibiting a steep, dry west face, with a moister eastern slope. Eleven major drainage systems are found within Park boundaries (Figure 1), offering in excess of 155 km of riparian habitat that extend through a 1,350 m elevational gradient from altitudes of 1,900 to 3,170 m (summits reach almost 4,000 m). The longest and best developed riparian corridors are located along perennial streams (e.g., Lehman and Baker Creeks) on the east flank of the Snake Range, where visitor use is most concentrated. Less well developed riparian corridors, often with shrubby vegetation, can be found along more ephemeral streams that are found on the western and southern flanks of the mountain range.

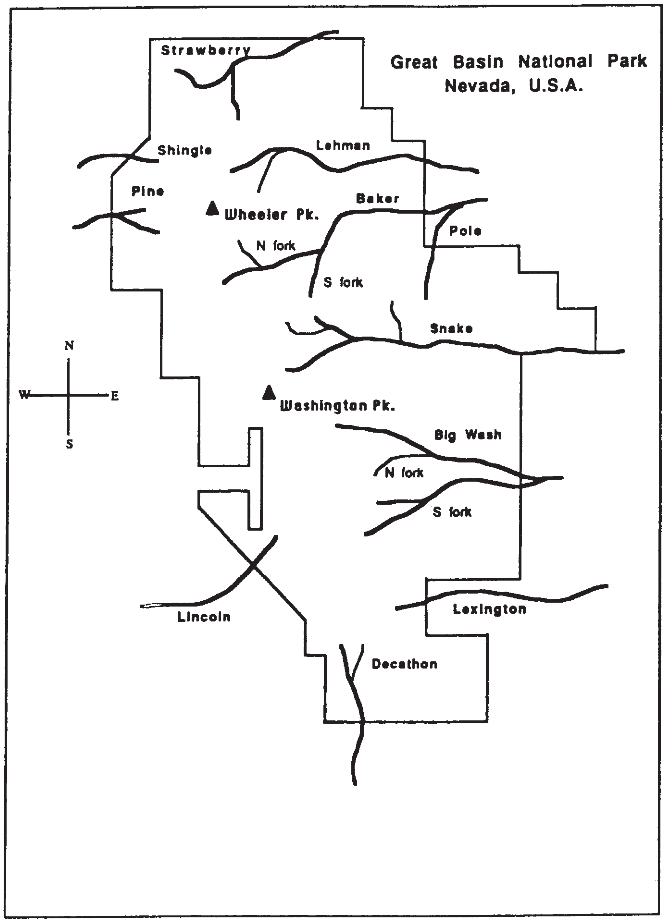

Figure 1—Map of Great Basin National Park, showing the primary stream systems that drain the South Snake Range.

Eight major riparian systems (Baker, Big Wash, Lehman, Pine, Pole, Shingle, Snake, and Strawberry Creeks) were selected for quantitative analyses of vegetation structure (Fig. 1). They were selected because they offered a range of environmental conditions that typify the Park, given their variation in elevation, aspect, gradient, and valley form. For example, two of the streams (Pine and Shingle Creeks, both of western aspect) are Type 1 streams (Frissel and Liss 1993), streams draining steep canyons that lack glaciation signature and wide valley floors; two of the streams (Baker and Lehman Creeks) are Type 2 streams, which drain glacial landforms underlain by granitic rocks that yield boulder-sized and cobble-sized clasts with weathering; and four of the streams (Big Wash, Pole, Snake, and Strawberry Creeks) are Type 3 streams, which drain alluvial landforms with wide valley floors that lack glacial signature, and are underlain by limestones and shales that weather rapidly into gravel- and sand-size particles that are easily transported by fluvial processes.

All vegetation sampling efforts were based on a functional definition of riparian ecosystems as three-dimensional zones of direct interaction between aquatic and terrestrial ecosystems, which extend outward from the stream edge to the limits of flooding and upward into the canopy of streamside vegetation (Gregory et al. 1991). A total of 229 sample plots were placed at a minimum of 250 m intervals along each of the study streams. Each 50 m^2 plot was a 10 x 5 m rectangular quadrat placed perpendicular to the stream flow direction, with two 5 x 5 m subplots placed on opposite stream banks. The large number of plots from multiple stream systems were sampled in order to adequately represent the diversity of watersheds found in the Park, and to ensure a statistically valid sample given the high species richness and patch structure that typify riparian vegetation (Szaro and King 1990).

Within each sample plot, percent cover was estimated for all species of woody plants, and a combined cover estimate was made for grasses/sedges, forbs, plant litter, standing dead, and bare ground. Cover for each woody species or other category was estimated visually by two experienced observers and a cover estimate was recorded as one of the following transformed cover classes: 0 = absent; 1 = < 1% cover; 2 = 1-5% cover; 3 = 6-25% cover; 4 = 26-50% cover; 5 = 51-75% cover; 6 = 76-95% cover; and 7 = > 95% cover, a scheme based on the releve method of Daubenmire (1959). Species nomenclature follows that of Welsh et al. (1987).

Elevation, aspect, stream gradient, and stream bank height were measured in the field and verified with USGS 7.5 minute topographic maps. Other physiographic features collected at each sample plot (collected by C. Frissel and colleagues, Oregon State University) included flow state (from dry to gaining reaches), channel pattern (from straight to lake or pond), valley form (from narrow V-shaped valleys to wide valleys with distinct floodplains), floodplain and terrace width, and valley fill texture (Frissel and Liss 1993).

Two-way indicator analysis (TWINSPAN) was employed in the classification of community types. TWINSPAN is a polythetic, divisive program for arranging multivariate data into an ordered two-way table of classification of species and attributes (Hill 1979). The program organized sample stands into compositional groups based on species transformed cover values, and produced a set of species groups based on floristic similarities among the sampled stands. For more details of the TWINSPAN procedure, see Murray et al. (1995).

Detrended correspondence analysis (DECORANA; Hill and Gauch 1980) was used to arrange species and stand groups identified by the TWINSPAN procedure along ordination axes representing different environmental gradients. A rotational correlation analysis (Dargie 1984) was used to determine the vector direction of environmental and physiographic gradients that best correlated with DECORANA ordination axes. Parameters used to depict environmental and physiographic factors in the gradient analysis included: elevation, gradient, aspect, flow state, channel pattern, valley form, stream bank height, floodplain width, and terrace width, as described by Frissel and Liss (1993).

The population size structures of the four major riparian tree taxa in the Park (*Abies concolor*, *Picea engelmannii*, *Populus angustifolia*, *Populus tremuloides*) were surveyed at 21 sites, on six major watersheds, in the Park. Sites were selected subjectively in order to sample vegetation types that represented (1) homogeneous stands of the species or its characteristic species-group, (2) the diversity of community types with low, intermediate, and high elevations in the Park, and (3) riparian corridors that were not excessively disturbed by human activities. At each site, a 5 m wide plot was laid down adjacent and parallel to the stream through the riparian corridor. Within each plot, all individuals of the species were counted, and their diameters measured. For mature trees, diameters were measured at 1 m height above the ground surface (approximating diameter breast high); diameters of seedlings and saplings were measured just above the ground surface.

Results and Discussion

Riparian vegetation within Park boundaries consisted of 41 woody plant taxa, including a large number of species that primarily occur in upland habitats. Species richness (mean number of species per plot) varied between streams (Figure 2), ranging from 4.92 (Baker Creek) to 6.94 (Big Wash) woody species per 50 m^2 plot. These low richness values indicate that there is a finite number of woody species that have widespread distribution and reach dominant or co-dominant status at numerous sites. Species which have this status include three tree species, *Populus tremuloides* (aspen), *Abies concolor* (white fir), and *Picea engelmannii* (Engelmann spruce), and five shrub species or species complexes, *Rosa woodsii* (Woods rose), *Symphoricarpos oreophilus* (mountain snowberry), *Betula occidentalis* (water birch), *Salix* spp. (broadleaf willows; at least 3 species), and *Mahonia repens* (Oregon grape) (Table 1). Of interest is the fact that these dominants do not change across different stream types. Interesting localized distributions include well developed gallery forests of *Populus angustifolia* (narrowleaf cottonwood) at lower elevations along Big Wash and Snake Creek, and extensive stands of *Pinus ponderosa* (ponderosa pine) along Shingle Creek, *Equisetum hymenale* (common scouring rush) along Big Wash and *Equisetum arvense* (meadow horsetail, included here because of its structural contribution to the shrub canopy) along Strawberry Creek, and dense stands of *Cornus sericea* (Red-osier dogwood) along Big Wash and *Amelanchier alnifolia* (serviceberry) along Shingle Creek.

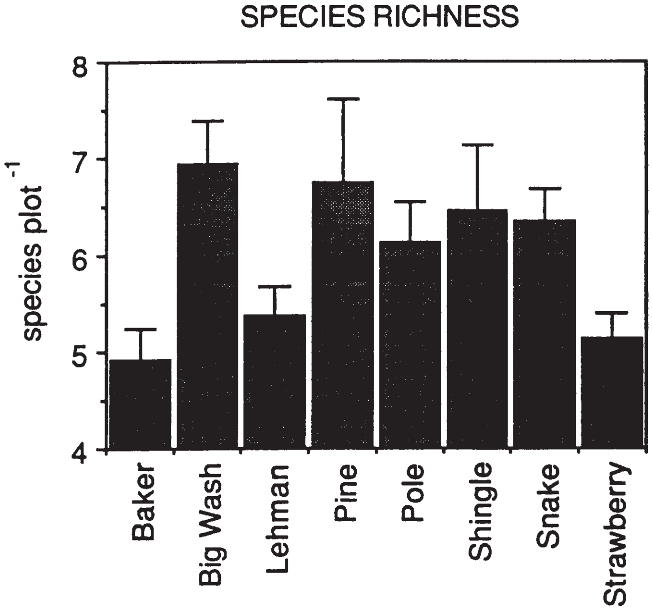

Figure 2—Species richness (mean number of species per 50 m^2 sampled plot) for each study stream in Great Basin National Park. Vertical bars indicate standard error of the mean.

Four stable species groups were identified by TWINSPAN analysis of the releve data (Table 2). Species Group A was dominated by tree species such as aspen, Engelmann spruce, and limber pine, with an understory dominated by *Juniperus communis* (common juniper), and represented the highest elevation community type. Species Group B was characterized by a white fir tree canopy and a shrub layer dominated by snowberry, willow, and Oregon grape, and typified upper intermediate elevation stands. Species Group C lacked a well developed tree canopy, was characterized by an abundance of shrub species such as Woods rose, water birch, and chokecherry, and occupied lower intermediate elevations. Species Group D was distinct owing to the frequency of upland species such as big sagebrush, pinyon pine, and rabbitbrush, but also to the presence of obligate riparian taxa such as narrowleaf cottonwood and dogwood.

The TWINSPAN procedure was successful in producing a structural framework for classification of riparian community types in the Park. Although vegetation differed

Table 1—Dominant woody riparian species in Great Basin National Park (whole Park; pooled data from the eight study streams) and the three primary type streams in the Park. Species are listed in declining order of relative frequency in sampled stands (n = 229 for the whole Park). See text for a description of stream types; Pine and Shingle Creeks are Type 1 streams, Baker and Lehman Creeks are Type 2 streams, and Big Wash, Pole, Snake and Strawberry Creeks are Type 3 streams (see Figure 1).

Stream type	Tree species	Shrub species
Whole Park	*Populus tremuloides* *Abies concolor* *Picea engelmannii*	*Rosa woodsii* *Symphoricarpos oreophilus* *Betula occidentalis* *Salix* spp. *Mahonia repens*
Type 1 Streams	*Populus tremuloides* *Abies concolor* *Picea engelmannii*	*Betula occidentalis* *Amelanchier alnifolia* *Rosa woodsii*
Type 2 Streams	*Populus tremuloides* *Picea engelmannii* *Abies concolor*	*Rosa woodsii* *Salix* spp. *Mahonia repens*
Type 3 Streams	*Populus tremuloides* *Abies concolor* *Picea engelmannii*	*Rosa woodsii* *Symphoricarpos oreophilus* *Cornus sericea*

Table 2—Species groups determined by TWINSPAN analysis using data from eight sampled streams in Great Basin National Park (N = 229 stands).

Species group	Tree dominants	Shrub dominants
Group A	*Populus tremuloides* (quaking aspen) *Picea engelmannii* (Engelmann spruce) *Pinus flexilis* (limber pine)	*Juniperus communis* (common juniper) *Sambucus cerulea* (elderberry) *Arctostaphylos patula* (greenleaf manzanita)
Group B	*Abies concolor* (white fir) *Pseudotsuga menziesii* (Douglas-fir) *Pinus ponderosa* (ponderosa pine)	*Salix* spp. (broadleaf willows) *Symphoricarpos oreophilus* (mountain snowberry) *Mahonia repens* (Oregon grape)
Group C	*Juniperus osteosperma* (Utah juniper)	*Rosa woodsii* (woods rose) *Betula occidentalis* (water birch) *Prunus virginiana* (chokecherry)
Group D	*Populus angustifolia* (narrowleaf cottonwood) *Pinus monophylla* (single-leaf pinyon)	*Artemisia tridentata* (big sagebrush) *Cornus sericea* (red-osier dogwood) *Salix exigua* (narrowleaf willow) *Chrysothamnus nauseosus* (rabbitbrush)

across watersheds, the fundamental species groups consistently emerged when TWINSPAN analysis was conducted on the riparian vegetation of individual watersheds (Murray et al. 1995). As a result, we view these species groups as community types that show excellent fidelity across riparian ecosystems in the Park. Riparian systems can be extremely diverse and vegetation structure is usually patchy (Hanson et al. 1990), but we found that the classification presented here has good field-truth and would be highly useful in efforts to map riparian communities in the Park as a whole.

Ordination of the 229 sampled stands by DECORANA resulted in significant stand group segregation along two orthogonal axes (Murray et al. 1995). DECORANA Axis 1, the axis which explained the highest amount of variation in the data set, was significantly correlated with elevation and slope (Table 3). Elevation and slope covary in a predictable fashion, with slope generally increasing with elevation. Zonation of riparian communities with respect to elevation is well recognized (Minckley and Brown 1982, Medina 1986), and we conclude that elevation is undoubtedly the most important environmental factor determining the distribution of species groups in the Park. From a functional perspective, the upper elevational distribution limits of species along the elevational gradient is primarily a temperature response, whereas the lower elevational limits are probably related to seasonal water stress (or episodic droughts) and/or competition. Stream bearing and stream gradient have also been shown to influence riparian community types (Szaro 1989). However, we found no significant relationship between the ordination of stands and stream aspect, probably because a majority of streams in the Park occur on the east-facing escarpment of the Snake Range, and individual streams are generally uniform in flow direction (i.e., they exhibit low sinuosity). However, riparian vegetation is clearly more reduced and assumes more of a shrub-like physiognomy on the west-facing side of the escarpment.

DECORANA Axis 2, which was orthogonal to Axis 1 and explained less total variation in the data set, was significantly, but weakly correlated with channel pattern, terrace width, stream bank height, flow state, and valley form (Table 3). However, when the individual factors are taken together, we interpret Axis 2 to represent a flood frequency/stream flow volume gradient. Channel pattern and terrace width are related to flow volume since terrace development is controlled by the frequency, seasonality, and magnitude of stream discharge events sufficient to cause overflow of the primary stream channel. Other investigators have shown that the distribution of riparian plant species is closely related to terrace development (Minckley and Clark 1984). Flooding is a common, naturally occurring form of disturbance in riparian systems which can strongly influence vegetation patterns (Johnson et al. 1976, Hupp and Osterkamp 1985). The ordination results from this study are similar to those found in other riparian studies in the region. In an analysis of 153 sites in the southwestern U.S., Szaro (1990) found elevation, stream direction, stream gradient, and valley cross-sectional area (in that order) to be the primary determinants in the ordering of 28 riparian community types.

Table 3—Coefficients of determination (r^2 values) of component loadings of the first and second axes obtained from DECORANA ordination of riparian vegetation in Great Basin National Park with environmental/physiographic factors. Coefficients of determination are based on the analysis of 229 stands located on eight major watersheds in the Park. Only statistically significant r^2 values are reported.

Factor	First axis	Second axis
Elevation	0.82	n.s.
Slope	0.40	n.s.
Aspect	n.s.	n.s.
Channel pattern	n.s.	0.25
Terrace width	n.s.	0.17
Streambank height	n.s.	0.14
Flow state	n.s.	0.12
Valley form	n.s.	0.11
Texture valley fill	n.s.	n.s.

In an analysis of riparian vegetation from Hells Canyon (Snake River Gorge, Idaho), Miller and Johnson (1986) found that their first ordination axis of riparian stands represented a temperature (i.e., elevation) gradient while the vertical axis represented a gradient of stream channel stability (i.e., disturbance). Therefore, the consistency of these results suggest that elevation exerts the strongest influence on the zonation of riparian vegetation within the montane West, but that flood-related disturbances are also important in the zonation of riparian vegetation along individual stream reaches.

The size class frequencies of four dominant tree species (aspen, white fir, Engelmann spruce, and narrowleaf cottonwood) all showed a majority of individuals to occur in the smaller size classes, with a very high percentage of seedlings and saplings and a gradually reduced frequency in each consecutive size class (Table 4). Engelmann spruce exhibited a distribution out to very large size classes, whereas white fir did not. There were, however, anomalous size frequency distributions for several of the species on individual watersheds. For example, there were no individuals of white fir between 20 and 55 cm trunk diameter on Pine Creek, and Engelmann spruce showed poor recruitment at higher elevations on both Lehman and Baker Creeks.

Table 4—Relative frequencies of individuals in different diameter size classes for the four dominant tree species in Great Basin National Park.

	D.b.h. (upper limit)							
Species	2	10	20	30	40	50	60	>60
	- - - - - - - - - - - - - - - - *cm* - - - - - - - - - - - - - - - -							
Abies concolor	.68	.20	.09	.02	.01	0	0	0
Picea engelmannii	.34	.28	.16	.09	.06	.03	.02	.02
Populus angustifolia	.58	.14	.10	.09	.06	.02	.01	0
Populus tremuloides	.55	.27	.13	.04	.01	0	0	0

Plant populations with a “normal” population structure exhibit a frequency distribution which is characterized by most individuals in the population occurring in the smaller size (age) classes, and a declining number of individuals in each successively larger size class. The dominant riparian trees of Great Basin National Park clearly exhibit such a population structure. The high frequency of seedlings and saplings encountered at many of the sampled stands indicates good recruitment of tree species within riparian systems of the Park. This was particularly evident at low elevation sites within the Park, whereas several high elevation sites exhibited low recruitment of several tree species. Although this is perhaps counter intuitive given the dry climate of Nevada, simulations of long-term cyclic dynamics of riparian forest stands indicate that warmer/drier conditions result in more diverse riparian forest with less distinct cyclic behavior than in cooler/wetter conditions, which tend to support one or two dominant species (Liu and Malanson 1992). Our demographic data tend to support these simulations, and suggest that recruitment processes and population turnover are perhaps more rapid events at lower elevation sites that are dominated by broadleaf trees and shrubs, than in the cool, conifer-dominated forests at higher elevations.

Although many of the riparian ecosystems in the Park are in fair general condition, there is strong evidence that domestic livestock are stressing riparian systems and thus not allowing them to reach their ecological potential (relative to biodiversity, productivity, etc.). Invasive taxa that preferentially occupy disturbed sites, such as *Bromus tectorum* (cheatgrass) and *Chrysothamnus nauseosus* (rabbitbrush), are very common along many of the riparian corridors of the Park, particularly at lower elevations. Extensive coppicing of cottonwood saplings also indicates a potential negative impact of cattle browsing on tree regeneration.

A second anthropogenic disturbance in the Park is streamflow diversion, which only affects a lower, about 5 km, segment of Snake Creek. In comparison to most western watersheds, Great Basin National Park is relatively free of diversion effects. Nevertheless, the diverted stretch of Snake Creek shows typical diversion effects, with little or no recruitment of the dominant tree, narrowleaf cottonwood, and accelerated senescence of mature trees along that stretch of the stream. This dewatered segment of Snake Creek appears to be in imminent danger of decline, which can only be alleviated by the return of instream flows to the diverted stretch of the creek.

The continued practices of grazing and streamflow diversion in Great Basin National Park illustrate the inherent conflicts that are presented to the Park Service when attempting to manage riparian systems for both commodity (grazing, water) and non-commodity (recreation) uses in a National Park setting.

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Differential Establishment of Perennial Grass and Cheatgrass Following Fire on an Ungrazed Sagebrush-Juniper Site

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Abstract—After one fire in a bunchgrass-dominated juniper woodland, cheatgrass became dominant under the remnant crowns of burned juniper, but native bunchgrass dominated the inter-spaces. In a second burn across a ridge bunchgrass dominated both under burned juniper crowns and interspaces. Vegetation variables of species crown cover, average perennial plant size, and perennial plant and cheatgrass densities did not differ between interspace areas for the two burn locations or between interspace areas and the area under juniper crowns of the second burn. Several soil surface variables, and total soil organic carbon and organic nitrogen differed between tree and interspace areas but not between burns within tree or interspace areas. The variables analyzed did not explain why two stable communities with a threshold between them occurred on this site following fire.

The existence of several stable states of plant species composition with thresholds, or barriers to change, between them is now known to exist within many plant communities (Friedel 1991; Laycock 1991). The reasons for the stable states and intervening thresholds can involve many biotic and abiotic factors. Understanding the mechanisms that permit multiple stable states in community composition, and that can cause the thresholds between them, is important for managing rangelands (Johnson and Mayeux 1992; Tausch and others 1993). For many communities, thresholds were crossed during the late 19th and early 20th centuries as a result of heavy livestock use. The introduction of cheatgrass (*Bromus tectorum* L.) in many areas has formed an additional stable state community and a threshold between it and the former plant composition. If present in a community, cheatgrass usually remains a part of the herbaceous layer until a fire occurs (Young and Tipton 1990; Young and others 1987). Fire alters the biotic and abiotic factors enough that the plant community crosses a threshold from a perennial-dominated to an annual-dominated community. This dramatic shift in species composition alters competitive and fire dynamics to maintain annual dominance on the affected sites (Billings 1990; Tausch and others, 1994a; Young and Evans 1973; Young and others 1987). Such major changes in community composition to new stable communities are examples of a largely unappreciated component of global change (D'Antonio and Vitousek 1992).

It is important for managers to understand the processes and factors behind the largely irreversible conversion of range vegetation from perennial dominance to cheatgrass dominance. Cheatgrass currently dominates more than 41 million hectares in the Intermountain West (D'Antonio and Vitousek 1992; Mack 1981; Young and others 1987) and is continually expanding (Young and Tipton 1990). The conversion has occurred on extensive areas of western and northern Nevada rangelands (Morrow and Stahlman 1984). Cheatgrass is also invading undisturbed sites (Morrow and Stahlman 1984; Young and Evans 1973) where a slow conversion to annual dominance can then occur (Svejcar and Tausch 1991; Tausch and others, 1994b).

Is the barrier to the return of perennial dominance controlled by the presence of cheatgrass? What has been the role of fire or other environmental factors, either alone or in combination, in the establishment and persistence of cheatgrass? Many factors such as soil physical, microbiological, and nutrient characteristics, are potentially involved in the change from perennials to annuals following fire. These factors are all modified by the level and duration of disturbance (Klopatek and others 1988).

However, some known characteristics of cheatgrass are definite factors. Once present, the dominance of cheatgrass seems related to its ability to effectively compete with native perennials for limited soil moisture (Melgoza and others 1990). Cheatgrass is also an example of an invading species for which close climatic similarity to its region of origin is not necessary (Roy and others 1991).

In Nevada the dominance of cheatgrass following disturbance varies with the environmental conditions and plant species composition of the site (Tausch and others 1994b). Higher elevation sites and sites with a high cover of perennial grass are more likely to return to perennial dominance following fire than shrub-dominated lower elevation sites. This pattern, however, can be modified by

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the grazing history of the site (Tausch and others, 1994a). To control these changes, a better understanding of the environmental and vegetation conditions that allow the conversion is needed. Particularly needed is information on how community composition, precipitation amount and seasonality, nutrient dynamics, and microbiological relationships of a site affect the competitive balance between cheatgrass and perennial species.

In a mid-elevation Utah juniper (*Juniperus osteosperma* [Torr.] Little) woodland with a bunchgrass-dominated understory, cheatgrass dominance appeared to vary by micro-site following fire. Areas under remnant juniper crowns (crown sites) on one burned area were cheatgrass dominated; the interspace areas (interspace sites) were dominated by bunchgrasses. On a second burn across a ridge both crown and interspace sites were dominated by bunchgrasses. We hypothesized that some combination of the presence of juniper, characteristics of the fire, soil conditions, and effects on nutrient conditions was sufficient to push the plant community across a threshold to a stable community dominated by cheatgrass. The fire, in combination with the other possible factors, did not result in the environmental conditions necessary for cheatgrass dominance in the interspace areas of the first burn or on any part of the second burn.

The two burns offered a rare opportunity to study the microscale conditions that alter cheatgrass and perennial grass dominance following fire. The objectives of this study were to document possible vegetation differences, and to examine some of the potential abiotic factors that may lead to cheatgrass dominance following fire in a relic juniper community. Efforts were focused on answering two questions. First, were there biotic and edaphic factors that differed under the crowns of unburned juniper, or in unburned interspace areas adjacent to the two burns, to explain the post-fire differences? Second, were there biotic or edaphic factors that differed between crown and interspace areas after burning that coincided with cheatgrass dominance?

METHODS

Study Site Description

Two sites in an area of ungrazed relic vegetation were used for this study. These sites are on the upper elevations of the south end of the Virginia Mountains west of Pyramid Lake in Nevada. Patterns of cheatgrass dominance following fire in this area are variable with location (Tausch and others, 1994b). The relic communities are dominated by an overstory of scattered Utah juniper. Trees cover the full range of age classes from seedlings to trees several hundred years old, but total tree cover is less than 15 percent of the area. The understory for most of the area is dominated by bluebunch wheatgrass (*Pseudoroegneria spicatum* [Pursh] A. Young). Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Bettle & A. Young) is scattered throughout the area. The two burns are separated by the main north/south ridge of the mountains. The west side, with cheatgrass under remnant juniper crowns, burned in 1974 and the east side burned in 1981. All of the burned area on the east side, and the upper elevation portion of the burn on the west side, are on the same parent material, a residuum and colluvium from basalt. They also have the same soils—loamy-skeletal, mixed, mesic, aridic argixerolls (SCS 1983). Only the part of the west side burn that has the same soil type as the east side burn was used for the study. Both burns were patchy with unburned areas surrounded by burned area.

The studied area of the west side burn covers an elevation range from just under 1,900 m to 1,950 m. Most of the site is on northwest- to north-facing slopes with limited south slope involvement. Sampling on the east side burn was over an elevation range of 1,950 m to 2,100 m and on mostly east-facing slopes.

Data Collection

Vegetation and soils were sampled in August 1993 using circular study plots 10 m^2 in area (3.57 m diameter). The woody portions of the crowns of the burned juniper are still standing on both burns. All burned juniper trees on both burns with crowns large enough to contain the circular plot were located and mapped. Five of these trees were randomly selected on each burn. Three additional plots were then located for each burned tree plot. A burned interspace plot was randomly located adjacent to each burned tree plot. The unburned tree of sufficient size nearest to each selected burned tree, on the same slope and aspect, and similar in elevation to the burned tree plot, was selected as a paired unburned tree plot. Last, an unburned interspace plot was randomly located adjacent to each unburned tree plot. This gave a total of five sets of four plots (burned and unburned tree and burned and unburned interspace), or a total of 20 plots on each burn. Plots located under burned or existing juniper crowns were centered within the area covered by the crown. Interspace plots adjacent to each burned or unburned tree plot were located at least 2 m, but not more than 5 m, away from the edge of the nearest burned or unburned tree crown.

Plant crown cover was estimated in four 0.5 m^2 quadrats that were randomly selected from eight possible quadrats. One quadrat was randomly selected from each of four pairs located on the uphill, downhill, and on either side of the circular plot. An estimation guide representing 1 percent of the quadrat was used to determine cover. Cover data were averaged by species for each circular plot.

Shrub and perennial grass density and average crown area were sampled in the full 10-m^2 circular plot. Two crown diameters were measured on each perennial plant: the longest and the one perpendicular to the longest. Measurements for each plant were converted to crown area using the equation for an ellipse; average crown area was determined for each species in each circular plot. Soil surface characteristics of litter, bare ground, gravel, cobble, stone, and cryptograms were determined from six points along each side of each quadrat (48 points per plot). Percent of the total number of points was computed for each category for each circular plot.

Four soil samples of the 0-5 cm surface mineral layer were randomly sampled within each 10-m^2 circular plot and composited for analysis. The Walkley-Black procedure was used to quantify soil organic carbon (Nelson and Sommers 1982). Total organic nitrogen was quantified with the Kjeldahle method (Bremmer and Mulvaney 1982). Nitrogen is possibly the most limiting nutrient in juniper woodlands (Klopatek 1987).

Data Analyses

Two areas of possible differences were the focus of the analyses. First, were there differences between east and west unburned tree plots that might explain the post-burn differences in vegetation composition of the burned tree plots? A supplemental analysis was a comparison of east and west differences between unburned interspace plots. Second, were there differences among the east and west side burned interspace plots plus the east side burned tree plots, and differences between these three sets of plots and the west side burned tree plots as a separate group?

Vegetation and soils data were analyzed by dividing the data into burned and unburned sets to directly focus on these differences. Each set was analyzed separately with one-way analysis of variance. Each AOV analysis contained four treatments. Burned site treatments were east side burned tree (EBT), east side burned interspace (EBI), west side burned tree (WBT), and west side burned interspace (WBI) plots. Unburned treatments were east side unburned tree (EUT), east side unburned interspace (EUI), west side unburned tree (WUT), and west side unburned interspace (WUI) plots. Significant differences for all analyses were at the $P \leq 0.05$ level. Differences between treatments within each analysis were by Tukey's method of pairwise comparisons.

The classification program TWINSPAN from the Cornell Ecology package (Ludwig and Reynolds 1988) was used to evaluate the degree of similarity among the 40 sampled plots. Classification was based on the percent vegetation cover for the individual species.

Results and Discussion

Seven shrub, seven grass, and 22 forb species were sampled on the east side burn (table 1). The west side burn had five shrub, seven grass, and 17 forb species. A total of 42 species were identified with seven more species sampled on the east side than the west side.

Table 1—Tree, shrub, grass, and forb species sampled on two burns on the Virginia Mountains, NV

Species	West	East
Trees		
Juniperus osteosperma (Torrey) Little	X	X
Shrubs		
Artemisia nova Nelson	X	X
A. tridentata wyomingensis Beetle & A. Young	X	X
Chrysothamnus viscidiflorus (Hook) Nutt.	X	X
Ephedra viridis Cov.	X	X
Eriogonum microthecum Nutt.		X
Ribes velutinum E. Greene	X	X
Tetradymia canescens DC.		X
Grass		
Achnatherum hymenoides (Roemer & Schultes) Barkworth		X
A. thurberianum (Piper) Barkworth	X	X
A. webberi (Thruber) Barkworth	X	X
Bromus tectorum L.	X	X
Elymus elymoides (Raf) Swezey	X	X
Melica stricta Bolander		X
Poa secunda J.S. Presl.	X	X
Pseudoroegneria spicata (Pursh) A. Love	X	X
Forb		
Allium sp.		X
Antenaria sp.	X	
Arabis holboellii Hornem.	X	X
Astragalus sp.		X
Aster sp.		X
Balsamorhiza hookeri Nutt.		X
Castilleja chromosa Nelson		X
Calochortus bruneaunis Nelson & J.F. Macbr.	X	X
Chorizanthe brevicornu Torrey		X
Crepis acuminata Nutt.	X	X
Cryptantha micrantha (Torrey)	X	X
Eriastrum sparsiflorum (Eastw.) H. Mason	X	
Erigeron sp.	X	
Galium sp.	X	
Gayophytum sp.	X	X
Gilia inconspicua (Smith) Sweet	X	X
Lactuca sp.	X	X
Lomatium sp.		X
Lupinus caudatus Kellogg	X	X
Lygodesmia spinosa (Nutt) Tomb.	X	X
Machaeranthera canescens var. *leucanthemifolia* (E.Greene) Welsh	X	
Mentzelia albicaulis Hook.	X	X
Phacelia bicolor S. Watson	X	
Phlox stansburyi (Torrey) A.A. Heller	X	X
Senecio multilobatus A. Gray	X	
Sisymbrium altissimum L.	X	X

Vegetation cover differences between east and west side unburned tree plots were not significant. Unburned interspace plots on the west side, however, had significantly higher total vegetation cover than the east side plots because of higher sagebrush and total perennial grass cover (table 2). Over 97 percent of the total plant cover on burned tree plots on the west side was cheatgrass or annual forbs; these species comprised less than 9 percent of the cover on burned tree plots on the east side. Cheatgrass plus annual forbs comprised 17 and 11 percent of the burned interspace plots on the west and east sides, respectively. The west side fairly consistently had the highest total plant cover across burned and unburned plots compared to east side plots.

Bluebunch wheatgrass density on the west side unburned tree plots was only slightly higher than on the east side (table 3). All unburned interspace plots and east side burned tree plots were similar in bluebunch wheatgrass density. The burned tree plots on the west side had

Table 2—Average percent vegetation crown cover for unburned and burned, east and west, and tree and interspace plots. Means with different letters across rows are significantly different ($P \leq 0.05$). Species with less than 0.1 percent cover are indicated with 't'

	Tree		Interspace	
Unburned	**East side**	**West side**	**East side**	**West side**
Total cover	2.2_a	6.5_a	26.0_b	39.5_c
A. tridentata wyomingensis	0.2_a	0.1_a	5.7_b	11.0_c
Total shrub	0.2_a	1.3_a	10.7_b	16.8_b
Pseudoroegneria spicata	0.8_a	1.2_a	13.4_b	19.9_b
Elymus elymoides	t_a	0.3_a	t_a	0.6_a
Poa secunda	0.3_a	0.7_a	0.5_a	1.2_a
Total perennial grass	1.1_a	2.2_a	13.9_b	21.7_c
Bromus tectorum	0.2_a	0.2_a	0.6_a	0.2_a
Forbs	0.8_a	2.8_a	1.4_a	1.0_a
Burned				
Total cover	47.5_{ab}	66.3_a	40.4_b	50.2_{ab}
A. tridentata wyomingensis	2.3_a	0.0_a	t_a	t_a
Total shrub	4.2_a	0.6_a	0.6_a	2.4_a
Pseudoroegneria spicata	39.0_a	0.9_b	35.4_a	37.7_a
Elymus elymoides	0.0_a	0.2_a	$t4_a$	0.5_a
Poa secunda	0.1_a	0.0_a	t_a	0.9_b
Total perennial grass	39.1_a	1.1_b	35.4_a	39.2_a
Bromus tectorum	1.1_a	47.7_b	2.6_a	0.8_a
Forbs	3.1_{ab}	16.9_a	1.9_b	7.8_{ab}

Table 3—Average plant density (no./10 m^2) for unburned east and west, tree and interspace plots. Means with different letters across rows are significantly different ($P \leq 0.05$)

	Tree		Interspace	
Unburned	**East side**	**West side**	**East side**	**West side**
A. tridentata wyomingensis	0.8_a	1.6_{ab}	5.0_{ab}	5.6_b
Pseudoroegneria spicata	9.6_a	17.0_a	69.6_b	54.6_b
Elymus elymoides	0.4_a	9.0_b	0.2_a	0.8_a
Total perennial grass	11.0_a	26.8_{ab}	70.6_c	57.2_{bc}
Bromus tectorum (no./m^2)	18.0_a	14.7_a	22.4_a	9.5_a
Burned				
A. tridentata wyomingensis	0.4_a	0.0_a	0.0_a	0.2_a
Pseudoroegneria spicata	49.8_a	3.2_b	72.6_a	50.8_a
Elymus elymoides	0.0_a	1.8_a	0.2_a	1.2_a
Total perennial grass	49.8_{ab}	16.0_b	72.8_a	53.2_{ab}
Bromus tectorum (no./m^2)	42.9_a	284.6_b	74.2_a	79.3_a

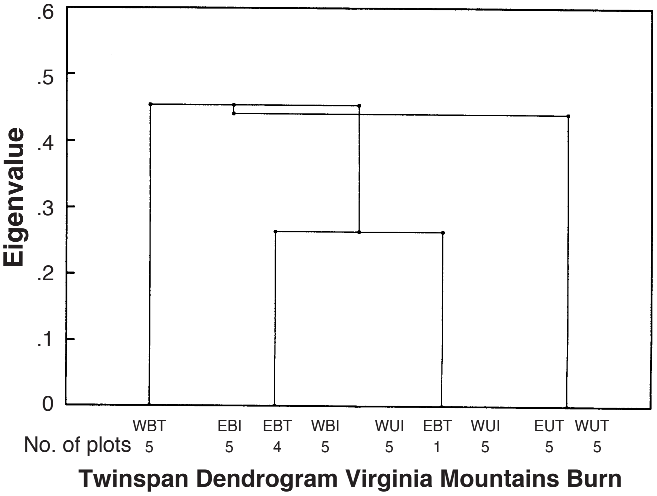

Figure 1—Dendrogram of TWINSPAN analysis results for the 40 circular plots sampled on two burns on the Virginia Mountains, NV. Only the first three levels of division are shown. Sample site abbreviations are: WBT = west side burned tree, EBI = east side burned interspace, EBT = east side burned tree, WBI = west side burned interspace, WUI = west side unburned interspace, EUT = east side unburned tree, WUT = west side unburned tree.

less than a third of the bluebunch wheatgrass density and were an order of magnitude greater in cheatgrass density than all the other plots.

Sagebrush plants tended to be larger on the east side while both bluebunch wheatgrass and squirreltail (*Elymus elymoides*) were generally larger on the west side (table 4). Overall, differences in the results between east and west sides, with the exception of species composition on the west side burned tree plots are small, indicating the two sites share the same basic community.

Classification of the 40 sample plots based on vegetation cover indicated four groups (fig. 1). The first division separated the unburned tree plots from the rest, and the second separated the burned tree plots on the west side. At no level of division were the unburned tree plots on the east and west sides separated. The final two groups separated the remaining unburned plots from the remaining

Table 4—Average plant crown area (cm^2) for unburned and burned, east and west, and tree and interspace plots. Means with different letters across rows are significantly different ($P \leq 0.05$)

	Tree		Interspace	
Unburned	**East side**	**West side**	**East side**	**West side**
A. tridentata wyomingensis	593_a	$1,187_a$	$1,313_a$	880_a
Pseudoroegneria spicata	4_a	9_a	47_b	54_b
Elymus elymoides	16_a	5_a	6_a	80_a
Burned				
A. tridentata wyomingensis	$1,891_a$	0_a	0_a	113_a
Pseudoroegneria spicata	124_a	23_b	104_a	122_a
Elymus elymoides	0_a	19_a	19_a	35_a

Table 5—Total soil organic nitrogen (percent), total soil organic carbon (percent) and C/N ratios for unburned and burned, east and west, and tree and interspace plots. Means with different letters across rows are significantly different ($P \leq 0.05$)

	Tree		Interspace	
Unburned	**East side**	**West side**	**East side**	**West side**
Nitrogen	0.32_{ab}	0.56_a	0.10_b	0.15_{ab}
Carbon	4.86_a	7.33_a	1.28_a	1.87_a
C/N ratio	15.56_a	12.32_a	13.65_a	13.68_a
Burned				
Nitrogen	0.33_{ab}	0.51_a	0.17_b	0.16_b
Carbon	3.86_{ab}	5.80_a	1.70_b	1.65_b
C/N ratio	11.99_a	11.44_a	10.64_a	10.47_a

Table 6—Percent ground cover for litter, bare ground, gravel, cobble, stone, and cryptogram for unburned and burned, east and west, and tree and interspace plots. Means with different letters across rows are significantly different ($P \leq 0.05$)

	Tree		Interspace	
Unburned	**East side**	**West side**	**East side**	**West side**
Litter	80.00_a	84.58_a	41.66_b	37.10_b
Bare	0.42_a	0.00_a	7.50_a	10.42_a
Gravel	2.08_a	0.82_a	14.58_b	4.16_a
Cobble	2.97_{ab}	0.84_a	7.08_{ab}	9.16_b
Stone	5.84_a	4.18_a	18.76_b	20.84_b
Cryptogram	7.92_a	8.34_a	9.58_a	16.82_a
Burned				
Litter	68.34_a	65.42_{ab}	50.42_b	55.00_{ab}
Bare	0.84_a	0.84_a	7.08_a	6.68_a
Gravel	4.46_a	0.00_a	9.18_a	4.58_a
Cobble	0.84_a	1.26_a	3.76_a	4.16_a
Stone	25.84_a	32.50_a	26.68_a	25.00_a
Cryptogram	0.42_a	0.00_a	3.32_a	4.58_a

burned plots, with one exception. The east side burned tree plot with the highest shrub cover ended up with the unburned interspace plots from both the east and west sides. Except for the burned tree plots on the west side that had been cheatgrass dominated for 19 years, east and west side plots did not separate at any level of the classification analysis.

Overall, the east and west sides were not significantly different for any carbon or nitrogen measures (table 5). Levels were largely the same on the burned plots, even the burned western tree plots. Carbon/nitrogen ratios were slightly lower on the burned plots.

Litter cover in the unburned tree plots was higher than in the interspace plots, as may be expected from tree litter (table 6). Cryptogram cover was lower in the burned plots compared to the unburned plots, particularly in the tree plots. Within both the interspace and tree plots, the eastern and western sides were not significantly different for any of the ground cover variables.

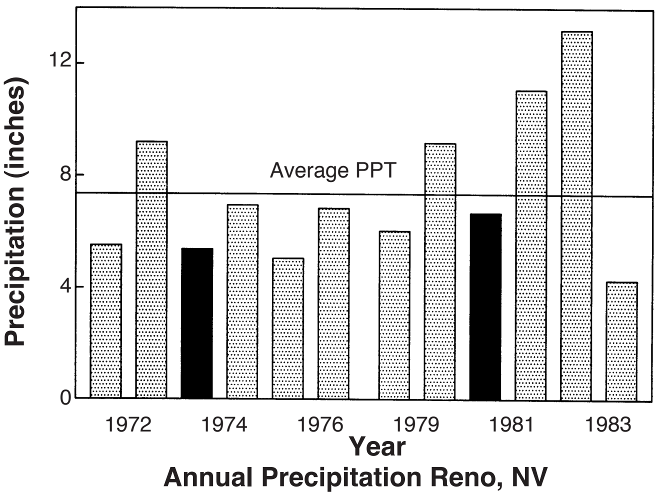

Figure 2—Histograms of annual precipitation for Reno, NV, for the years 1972 to 1984. Precipitation histograms coinciding with years of the two burns on the Virginia Mountains, NV, are filled in solid.

An investigation of the associated precipitation patterns at Reno, NV, revealed an interesting pattern (fig. 2). Two years prior to the date of each burn precipitation was below average. The year prior to the year of each burn had above average precipitation and the precipitation of the year of the burn was below average for both. However, the 2 years following the burn on the west side (1974) were below average while those following the burn on the east side (1981) were two of the wettest on record. Direct experimentation will be necessary to determine if these differences were an important factor in the dominance of annuals under the burned western trees.

Conclusions

The existence of microscale patterns of alternate perennial bunchgrass- or cheatgrass-dominated stable communities in an area of woodland vegetation represented a rare opportunity for investigating some of the processes involved. Similar to many areas of the Great Basin (Young and others 1987), where either annual or perennial species dominated the site, seedling establishment by the other group was very limited. Differences might still persist because cheatgrass dominance may be preventing bunchgrass establishment on the soils under burned juniper, and bunchgrass dominance may be preventing cheatgrass establishment on the interspace soils. If the vegetation or soil factors sampled for this study had been modified by the previous fire, these changes were no longer present at sampling. While different stable states in community composition are common, and potentially important, the reasons for their existence and for the threshold between them can be subtle and difficult to identify.

Several possibilities may be involved. Fire, in combination with the presence of large juniper, may have modified the physical, chemical, or microbiological characteristics of the soil. Nutrient islands form beneath juniper canopies and result in different nutrient dynamics between canopy and interspace soils. Nitrogen mineralization and nitrification can also be higher beneath the canopy than in the interspace (Klopatek 1987; Klopatek and others 1990). Soil N had a small but significant increase in canopy versus interspace soils following fire in woodlands (Klopatek and others 1991). Nitrogen and other soil nutrients also showed increases under burned debris piles (Gifford 1981). Juniper as well as most of the understory species are dependent on vesicular-arbuscular endomycorrhizae (VAM) species that can be substantially reduced by fire (Klopatek and others 1988). Cheatgrass and other introduced annuals, by contrast, are not mycorrhizal dependent and are unaffected by mycorrhizal reduction by fire. Other possibilities can include different grazing regimes, differences in the intensity and timing of fire or other disturbance, and other environmental differences at the time of both the disturbance and subsequent plant reestablishment.

More detailed studies of the changes in key soil factors and the patterns of plant establishment that immediately follow fire are needed to better understand the processes involved. Future studies would also need to be conducted in different community types and locations to verify the processes involved.

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Juniper Decline in Natural Bridges National Monument and Canyonlands National Park

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Abstract—Extensive foliar damage to Utah juniper (*Juniperus osteosperma* [Torr.] Little) has been observed in southern Utah. The distal foliage becomes chlorotic and dies. While junipers are plagued with a number of disease problems, no pathogenic agents or soil minerals appear to be responsible for the decline. Some chlorotic branches were due to insect twig cutters, but these insects do not appear to be the cause of decline. Juniper decline could be the combination of drought and temperature stress, which reduce the water resources and increase the uptake of salts by the trees. This effect, along with the crystal formation of iron, magnesium, and calcium could result in decline symptoms.

The pinyon-juniper woodland is a widespread vegetation type in the southwestern United States that is estimated to cover from 30 to 40 million hectares (Allred 1964, Tausch and Tueller 1990). The pinyon-juniper vegetation provides a source of fuel, building materials, charcoal, pine nuts, Christmas trees, and folk medicines (Tueller et al. 1979, Hurst 1977, Lanner 1975, Cronquist et al. 1972, Gallegos 1977). About 80% of the acreage is grazed by livestock and wildlife (Clary 1975, Bunderson et al. 1986b). In Utah, this ecosystem is a large component (62,705 km^2 or 28.6%) of the vegetation (Kuchler 1964). Particularly, in the Utah National Parks, the pinyon-juniper woodlands are valued for their watershed, aesthetic, and recreational values (Gifford and Busby 1975).

Over the past several years an extensive foliar damage to Utah juniper (*Juniperus osteosperma* [Torr.] Little) has been observed in the Natural Bridges National Monument. The characteristic pattern is for distal foliage to become chlorotic and die. Mortality progresses along twigs until whole branches or the entire tree dies. Reports of similar foliar damage have been reported in Canyonlands National Park, Arches National Park, Mesa Verde National Park, Colorado National Monument, areas near Cedar City in southwestern Utah and in eastern Nevada, which would indicate that the foliar damage is a widespread problem. The cause for the foliar damage is not known. The loss of juniper trees in the national parks in southern Utah would have a dramatic ecological impact and would be an aesthetic blight in the parks. There is a need to determine the cause of the decline of Utah junipers.

In 1985, Bunderson et al. collected Utah juniper foliage and soil samples from 17 sites previously selected by Perry Plummer of the USDA Forest Service as typical of pinyon-juniper communities in Utah. Bunderson and Weber (1986) analyzed 255 Utah juniper (*Juniperus osteosperma*) trees for foliar mineral composition, total soluble carbohydrate and total chlorophyll content. The foliar concentrations of N, P, and K were consistent with other forest species. The concentration of Ca varied while the amount of Na and Fe were present at higher concentrations.

The soil mineral composition of the 17 sites was determined (Bunderson et al. 1985). The results suggested that Utah juniper was salt sensitive. The three growth limiting factors were nitrogen, phosphorus, and potassium.

The diseases associated with Utah juniper at the 17 different sites were also determined (Bunderson et al. 1986a). The most common rust was *Gymnosporangium inconspicuum* followed by *G. nelsoni, G. kernianum,* and *G. speciosum* (Peterson 1967). Needle blight and tip dieback were two unidentified diseases that were common at the different sites. In some sites, 80% of the trees had needle blight and tip dieback (Bunderson et al. 1986a). The parasite, mistletoe, weakened juniper trees and in many cases resulted in death of the junipers (Hreha and Weber 1979).

Materials, Methods, and Study Sites

There are several possible hypotheses for the cause of juniper decline.

1. Pathogenic agents (viruses, mycoplasma, bacteria, fungi, mistletoe, and insects).
2. Nonpathogenic factors (minerals, salts, etc.).
3. A combination of drought, higher salts, and temperature stress.

In order to evaluate the extent of juniper decline, reference transects were established in Natural Bridges

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In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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National Monument and in the Needles area of Canyonlands National Park. At each site, 40 Utah juniper trees were randomly selected by the quarter method (Phillips 1959). Each tree was measured for height, trunk diameter, signs and symptoms of diseases, insect damage, nonparasitic injury, decline symptoms, vigor, and percent of decadence. Tissue samples were taken from five trees at each site by clipping 5 terminals at equidistant points around the tree. The samples were ground using liquid nitrogen and a mortar and pestle. The ground samples were frozen until analyzed. Nitrogen and phosphorus were determined by the Kjeldahl procedure using sulfuric acid digestion (Horwitz 1980) and the concentrations of the following minerals (K, Ca, Mg, Na, and Fe) were determined by using nitric-perchloric acid digestion and atomic absorption spectroscopy (Johnson and Ulrich 1959). Total chlorophyll of leaf tissue was determined by the dimethyl sulfoxide method of Hiscox and Israelstam (1979). Plant tissues from the different sites were analyzed for major elements. Healthy, diseased green and diseased yellow leaves were analyzed for major elements. Three soil samples were taken from each transect at each site. Each of the three soil samples was the composite of soil obtained from three dig spots at the sample location. The soils were dried, ground, and analyzed for mineral composition, pH, soil texture, moisture, and soil type. The data obtained from the soil and tissue analyses were analyzed by statistical methods using Statview II and Data Desk computer statistical packages.

Classic isolation of organisms (bacteria, mycoplasma and fungi) using standard isolation procedures was done (Kelman 1967). No particular organism was consistently isolated. Since some mycoplasma can not be cultured, roots of healthy and symptom-expressing trees were observed for mycoplasmas. Endomycorrhiza and ectomycorrhiza have been reported to be present on Utah juniper (Reinsvold and Reeves 1986, Reeves et al. 1979, Klopatek and Klopatek 1987). The mycorrhiza increase the water absorption and mineral uptake capacity of Utah juniper. Soil and fine roots from the Utah junipers growing at the different transects were collected and the amount of VA (vesicular-arbuscular) mycorrhiza was determined using the methods of Schenck (1982). Samples of healthy and diseased twig and root tissue were fixed in 0.1 M sodium cacodylate buffer (pH 7.2-7.4) for 2 h at room temperature. After fixation, samples were washed 6 times with 1:1 vol./vol. water-buffer solution and post fixed and stained with buffered 1% osmium tetroxide for 2 h at 0-4 °C The samples were then stained overnight with aqueous 0.5% urnayl acetate, dehydrated in a graded series of ethanol and embedded in Spurr's resin. Sections were cut using a Sorvall MT 2B ultramicrotome, stained with Reynold's alkaline lead citrate and examined with a Phillips EM 400 transmission electron microscope (Upadhyay et al. 1991). Sections (3 m thick) were also cut and analyzed with energy dispersive X-Rays using an Oxford instrument (LinK Analytical Group) eXL with the Pentefet ST detector on a JEOL-JSM 8LIOA Scanning electron microscope. The thick sections were mounted on glass slides on aluminum stubs.

Predawn water measurements were made in the Natural Bridges and Needles area. Branch stems were collected and placed in sealed containers. The water in the branch stem samples were analyzed by isotope mass spectrometry in Elringer's laboratory at the University of Utah to obtain the delta values.

Results and Discussion

Juniper decline was so common in all the transects in Natural Bridges and in the Needles area of Canyonlands that it was difficult to find a healthy tree (table 1). Many other diseases were detected in the transects as shown in table 1. The average values of different diseases were obtained by sampling 240 trees in the seven transects of the Natural Bridges area and 200 trees in the Needles area.

Hypothesis one: pathogenic agents.

While a number of diseases were recorded such as rusts, witches broom, mistletoes, and insect galls, none was consistently associated with twig blight and tip dieback. Efforts to isolate a bacterial or fungal pathogen from the leaves of the diseased juniper were not successful. Analyses of root tissue provided no evidence for mycoplasma in the vascular tissue. No viruses were observed with the electron microscope in thin sections of the diseased tissue. While fungal diseases such as rusts were found, there was no correlation between rusts and juniper decline. Juniper roots did not contain any pathogenic fungi, but mycorrhizal fungi appeared to be present on healthy roots. Mistletoe was detected but was not associated with the twig blight and tip dieback. Insect galls and insect borers were present in the transects (table 1) but there was little correlation with juniper decline.

In the Needles area of Canyonlands, twig cutter larvae which girdle the tissue beneath the bark were identified as *Styloxus bicolor*. The number of insect twig cutters is shown in table 1 for the Needles area. In contrast, little twig cutter activity was observed in the Natural Bridges

Table 1—Diseases observed in Natural Bridges and Needles areas.

Diseases	Ratings	Nat Bridges	St. error	Needles	St. error
Needle blight	Tree rating*	1.30	.038	00.68	0.079
Tip dieback	Tree rating	0.86	.082	01.01	0.086
Senescence	Tree rating	2.40	.101	00.81	0.219
Needle cast	Tree rating	0.57	.112	00.80	0.127
Wood rot	Tree rating	0.00	.000	00.00	0.000
Foliage fungi	Tree rating	0.01	.107	00.14	0.009
Rust galls	No/tree	0.86	.154	00.19	0.127
Fusiform rust	No/tree	0.44	.149	00.01	0.008
Witches broom	No/tree	0.02	.012	00.58	0.079
Mistletoe	No/tree	0.05	.002	00.31	0.113
Insect tree cutters	No/tree	0.00	.000	06.80	1.672
Insect bores	No/tree	0.05	.002	01.31	0.045
Pear insect galls	No/tree	0.06	.167	02.08	0.467
Burr insect galls	No/tree	0.64	.020	10.16	2.093

*Ratings show percent of tree affected: 0=0%; 1=1-20%; 2=21-40%; 3=41-60%; 4=61-80%; 5=81-100%; 6=dead (no foliage).

Table 2—Composition of soils from transects in Needles and Natural Bridges area.

Soil analyses of transects in Canyonlands and Natural Bridges				
Elements	**Nat. bridges**	**St. error**	**Needles**	**St. error**
Soil pH	7.83	0.045	8.18	0.100
% sand	69.90	1.720	74.87	1.617
% clay	15.66	1.510	11.06	0.897
% silt	15.37	1.230	0.53	1.349
% moisture	4.06	0.195	3.21	0.106
% OM	1.17	0.135	1.01	0.104
ppm NO3-N	2.14	0.132	1.53	0.157
ppm Fe	1.85	0.156	1.56	0.170
ppm K	88.28	12.911	85.00	15.373
ppm Ca	9539.00	156.243	6637.00	181.888
ppm Mg	410.00	56.626	98.33	9.779
ppm Na	42.48	13.819	3.90	2.941

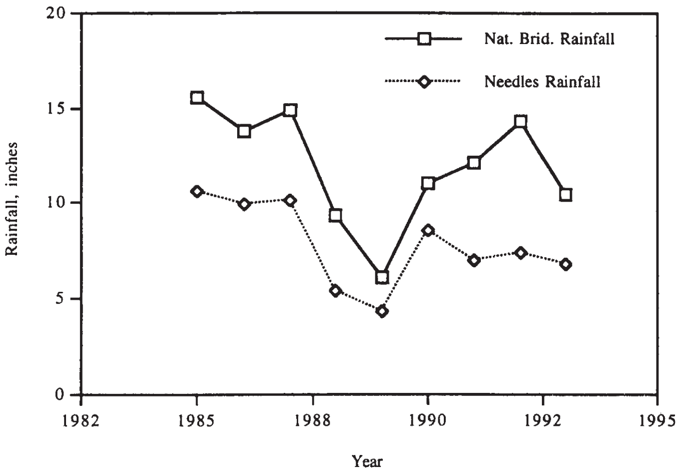

Figure 1—Amount of rainfall in Natural Bridges and Needles area.

area. The twig cutters contributed significantly to chlorotic branches on the juniper trees; however, the symptoms of twig blight were different and not due to twig cutting insects. Twig blight was also present on branches of trees in the Needles area of Canyonlands not infested with twig cutters.

Hypothesis two: nonpathogenic agents (minerals).

The elemental composition of the soil from the different transects was determined (table 2). Juniper decline did not correlate highly with any single element in the soil. The elemental composition of the tree tissue was determined (table 3) and the concentration of the individual elements in the tissues did not correlate highly with the juniper decline.

Hypothesis three: a combination of drought, higher salinity, and temperature stress.

The southwestern part of Utah has been experiencing a severe drought over the past several years followed by a period of increased rainfall. However, rainfall in Natural Bridges and Needles areas have not reached high levels (figure 1). From 1991 to 1992, there was a reduction in the amount of twig blight in Natural Bridges National Monument. In 1993 there was a small increase in twig blight, but it was lower than the 1991 level. Prior to 1991 there had been a drought for several years. 1992 was a wet year. The rainfall in 1993 was 28% lower than in 1992. This suggests an association of the disease symptoms with the rainfall level in Natural Bridges National Monument.

As drought occurs, salts tend to move up to the upper layers of the soil. Since Utah junipers are salt sensitive, it is possible that these combinations could be contributing to the decline problem. Mycorrhiza were present in the root samples collected. No correlation of mycorrhizal populations with juniper decline was obtained.

Isotope analyses of the water in the juniper trees in Natural Bridges National Monument indicated that the water in the trees was coming mainly from the ground water, not the summer surface rains (table 4). In the Needles area, the isotope analyses of the water in the juniper trees indicated that the water was coming mainly from the surface water such as the summer rains (table 4).

The element composition of healthy, green diseased and yellow diseased leaves was determined by atomic absorption spectrometry. Yellow diseased leaves had high concentrations of iron, calcium and magnesium (figure 2, 3, and 4).

Thin sections of healthy, green diseased and yellow diseased leaves were made and observed with the electron microscope. Crystals were detected in the yellow diseased

Table 3—Mineral composition of the juniper leaves.

Leaf analysis data for the juniper decline transects				
	Nat. bridges	**St. error**	**Needles**	**St. error**
% Ca	0.97	0.06	0.63	0.03
% K	0.23	0.01	0.28	0.01
% Mg	0.11	0.01	0.08	0.01
% N	0.44	0.01	0.63	0.03
% P	0.04	0.01	0.04	0.01
Cu ppm	1.37	0.06	4.95	0.16
Fe ppm	66.39	1.65	37.06	5.59
Mn ppm	11.54	1.14	15.61	2.60
Zn ppm	**11.93**	**0.46**	**8.37**	**0.57**

Table 4—Water sources in juniper stems.

Comparison of the -delta values of water from stem sap in junipers in the Needles area of Canyonlands National Park and Natural Bridges area				
	Needles area		**Natural Bridges area**	
Treatment	**Delta values**	**St. error**	**Delta values**	**St. error**
Ground water	–96.00	3.0	–96.00	3.0
Summer rain	68.00	3.1	68.00	3.1
Healthy	85.67	5.9	–93.50	3.9
Diseased	–73.83	6.1	–99.33	3.6

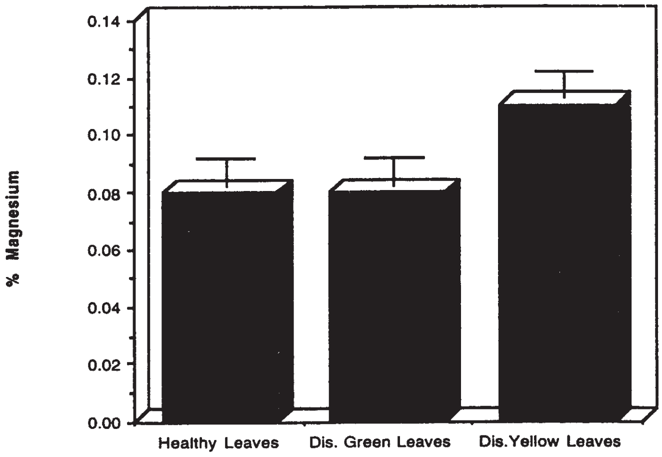

Figure 2—Magnesium concentration in healthy, diseased green, and diseased yellow leaves.

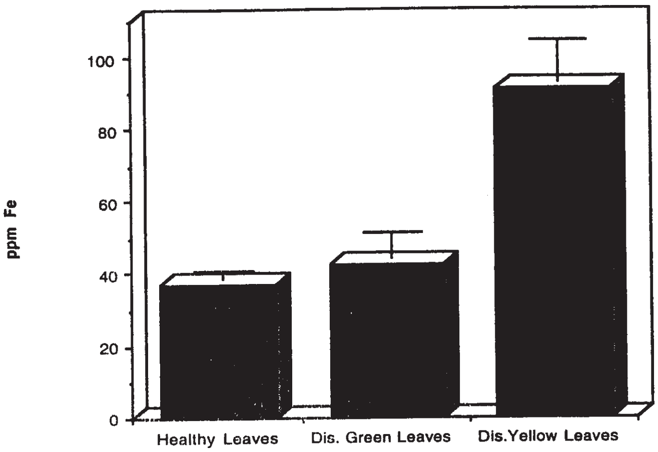

Figure 4—Concentration of iron in healthy, diseased green, and diseased yellow leaves.

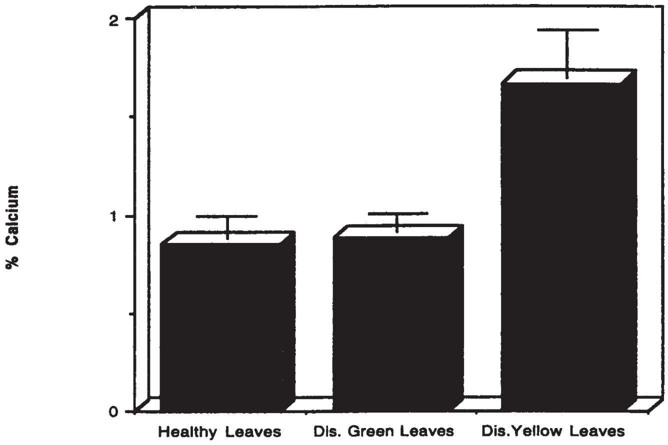

Figure 3—Concentration of calcium in healthy, diseased green, and diseased yellow leaves.

tissue (figure 5). The crystals and tissue were analyzed with energy dispersive X-ray microanalysis. The elements chlorine, osmium and uranyl were detected but were due to the fixatives and stains used. The major elements detected were silicon, aluminum, calcium, potassium, sodium and magnesium. The elemental analyses do not determine whether the elements are in certain complexes. It is possible that silica complexes of elements such as calcium, iron and magnesium could make the elements unavailable to the growing plant tip. The resulting effect would be a deficiency symptom of chlorosis (Brown, 1978). Young tips are probably the most susceptible areas because they need the minerals for new growth.

Figure 5—Thin sections of yellow leaves of diseased junipers showing the presence of crystals.

Summary

While junipers are plagued with a number of disease problems, no pathogenic agents appear to be responsible for the decline problem. There do not appear to be any high correlations with high or low amounts of minerals in the soil.

Some of the chlorotic branches that were present are due to insect twig cutters. While the twig cutters are a problem, they do not appear to be the cause of decline.

One logical explanation of juniper decline is that the combination of drought and temperature stress reduce the water resources and increase the uptake of salts by the trees. This effect along with complexing of iron, magnesium and calcium to form complex crystals result in decline symptoms. While ground water appears to be the major water source for Natural Bridges, the long drought could have reduced the ground water reserve and it is slowly being replenished.

Acknowledgments

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Genetic Integrity

Genetic Integrity: Why Do We Care? An Overview of the Issues

Jayne Belnap

Abstract—There are many reasons to be concerned about the use of non-native species or non-local genetic material in restoration efforts. An overview of these issues is presented. It is argued that site restoration is more than just successful vascular plant establishment, and that local plant material should be used whenever possible. However, it is recognized that time and money often constrain restoration efforts, and that maintenance of genetic integrity is often an issue of project scale.

Much debate is occurring on the importance of using native plants or locally collected plant material for revegetation efforts. As scientists learn more about the complex and interdependent nature of ecosystems, it is increasingly apparent that alteration of system components can have serious ramifications for continued natural functioning of these systems. The vascular plant community is critical in determining habitat attributes. Consequently, any alteration of this component needs to be approached with caution. Changes in the vascular plant communities can result from planting different species or different genotypes or altering relative species abundance or plant spacing. Since successful restoration is of critical concern to land managers, the effects of using different plant materials needs to discussed by scientists and managers together. For this reason, it was decided to have a symposium addressing this topic.

There are many potential issues associated with changing the structure of vascular plant communities, whether physically or genetically. Unfortunately, there are few long-term data sets to highlight which of these may become problems. Also, since basic aspects of many ecosystems have not been studied, the effects of vegetation changes on these facets cannot be documented. However, there are enough studies and evidence to alert us that problems can, and do, occur. These problems range from unsuccessful plant establishment to effects on other system components.

Long-term plant establishment has historically been the primary goal of restoration efforts. While many plantings of non-native or non-local genotypes appear successful in the short time for which we have data, many problems have occurred as well. These problems have ranged from invasion of neighboring communities by the planted material (such as, *Tamarix*, *Euryops*, *Bromus*, *Eragrostris*) to eventual failure of the plantings, whether through mass die-offs from unfavorable conditions (*Agropyron desertorum*, *A. cristatum*, and *Atriplex canescens* var. *rincon*) or through gradual replacement by less desirable exotics (*Bromus inermis*, *Phleum pratense*, *Dactylis glomeratus* and other seeded non-natives replaced by *Madia glomerata*; *B. tectorum* replacing planted material). Problems have also occurred for non-local native species that germinate, flower or seed set at inappropriate times. In addition, root deployment patterns can vary within plant species. Variations in any such characteristics may mean that non-local plant material dies under conditions that local populations are adapted to, even though the same species is used.

Using non-local (native or not) material can also have a significant effect on surrounding native plant communities. Planted material may use water or nutrients needed by local natives to successfully establish, or may otherwise compete with natives for favorable sites. Use of non-local material may lead to soil, microorganism or nutrient loss. Such site degradation may negatively affect the ability of local material to reclaim the area.

Many attributes of plants determine the micro- and macrobiota associated with them. While it is known that these attributes vary widely among species, less is known about interspecific variation. It is these attributes that we are concerned with when planting non-native plants, or plants with different genetic stock. Examples of these attributes include root mucilage secretion rates, root structure, or root deployment patterns, all of which heavily influence soil food webs (bacteria, fungi, nematodes, protozoa, and microarthropods). Chemical composition of plant litter varies within and between species. Many decomposers are specialists, and changing the types of litter available can affect soil food webs as well. Soil food webs are a critical part of the nutrient cycles in ecosystems. Since different species play distinct roles in nutrient processing, species composition and abundance can heavily influence the type and rate of nutrient processes that occur, thereby affecting nutrient availability by altering rates of nutrient input and plant litter decomposition. In addition, changes in soil communities can affect the rate of nutrient uptake by plants through altering mycorrhizal or nitrogen-fixing bacterial populations.

Aboveground faunal populations are affected as well by changes in the vascular plant community. The type, quantity, and timing of germination, growth, and reproduction of vascular plants is often highly variable both among and between species. Since many pollinators, dispersers and consumers are tightly tied to one or more of these aspects, variation in these characteristics may result in the failure of the system to support the plant or the animal. Chemical composition of plant tissue is used by many invertebrates

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as a cue for oviposition, herbivory and other activities. Since chemical composition is variable among individuals, populations, and species, using non-local plant material may affect dependent organisms. Animal species composition and abundance patterns are also affected by the physical structure of the vascular plant community. This has been shown repeatedly for bird and invertebrate species. It can also be true for larger mammals, as was recently found when coyote predation rates on sage grouse increased dramatically where grasses were planted in rows as opposed to a naturally staggered pattern.

In light of the above discussion, there are many reasons to use all possible resources to preserve genetic integrity in restoration efforts. However, even the best of intentions to preserve genetic integrity of communities are often limited by lack of local material, insufficient financial resources or degraded site conditions. Concern levels need to be matched with the reality of the land managers' position. Project scale generally is the determining factor. For small projects with readily available seed sources, all possible efforts should be made to maintain the genetic integrity of plant populations by using locally obtained plant materials. For large areas, or areas where no original plant material remains (such as vast areas in southern Idaho), concerns for genetic integrity may be limited to the use of native species. Most projects lie somewhere in between these two extremes.

The more we learn about the long- and short-term effects of introducing new genetic material into ecosystems, the more we find that we need to exercise caution. There is much about ecosystem functioning that we do not understand, and unintentional changes are often detrimental. Clearly, judgments on the extent to which genetic integrity will be preserved in any particular instance will have to be made on a case-by-case basis. However, given the lack of long-term data, a conservative approach should be used until we better understand the effects of our actions. Emphasis should be given to preserving, within the limits of our resources, what genetic integrity we can, remembering that ecosystem restoration is more than successful vascular plant establishment.

Molecular Analysis of Genetic Diversity: Advantages and Limitations

D. J. Fairbanks
W. R. Andersen

Abstract—Genetic diversity in plant materials used for revegetation of disturbed sites is important to allow natural selection and adaptation to occur. Several methods for estimation of genetic diversity using molecular markers are available. Protein markers, such as isozymes and seed storage proteins, have been used extensively, but their use has declined in recent years in favor of DNA markers. Use of protein markers is limited by lack of polymorphisms, number of markers available, and the need to use different detection methods with isozymes. DNA markers, including RFLP and RAPD analyses, are reliable methods that are widely used. The major limitation is the cost of labor and supplies.

Genetic diversity is an essential part of nature. It provides populations with adaptive plasticity allowing them to change genetically in response to environmental fluctuations. Without genetic variation, natural selection is ineffective. Genetic uniformity, on the other hand, is often the rule for cultivated species. Large-scale marketing typically requires a product with predictable characteristics including such factors as high yield, predictable seed or fruit size, known nutritional aspects, harvestability, and characterized disease and pest resistance. Numerous well-tested varieties are available commercially to fill specific environmental niches and to meet specific market demands. Variety registration and seed certification have been instituted to insure that varieties are genetically uniform, well characterized, and predictable. Nonetheless, genetic uniformity in cultivated species has its costs. Widespread use of a single variety or a few related varieties can select for emergence of virulent races of pathogens. Once a virulent race emerges, it can infect plants in epidemic proportions since the uniform plants are uniformly susceptible. The 1970 southern corn leaf blight epidemic in the United States, and the 1976 stem rust epidemic in Northwest Mexico's wheat crop are examples.

Plant species used in arid land revegetation straddle the fence between native species and cultivated species. On one hand, plants used in revegetation are often seeded, cultivated, irrigated, and harvested for seed much like their field-crop counterparts. On the other hand, the environments in which they are ultimately planted are much more varied than prepared fields. However, there is little question of the need for genetic diversity. The diverse environments faced in revegetation are very different from the more uniform conditions of cultivated fields. Nor is there any market demand for uniform products to deter the use of diverse material, as is the case with cultivated plants. Consequently, in selecting and developing materials for land restoration, genetic diversity should be among our primary concerns. It serves as a buffer against uniform susceptibility to pathogens and insects. It also provides genetic plasticity, allowing natural selection to work on plants from a single seed source in a variety of environments. Genetically diverse seed sources can be self-adapting, where those plants most adapted to the environment survive and reproduce while the less adapted are eliminated.

If we accept the premise that genetic diversity in plant materials used for revegetation is essential, then there is a clear need to assess, at least to some degree, the amount of genetic diversity in the materials we use. Unfortunately, little is known about the genetic diversity of seed currently used in revegetation. Most seed is collected from wild populations that may or may not be genetically diverse. Genetic uniformity is probably a major contributing factor to the frequent problem of dieback in large-scale revegetation projects. As the demand for seed from certain species commonly used in revegetation increases, seed sources will probably tend to move toward commercial seed production and away from collection in wild populations. Also, stricter regulation of seed collection on federal land may further contribute to this shift. Already, the demand for four-wing saltbush (*Atriplex canescens*) seed is sufficient to warrant commercial seed production. Will commercial seed production reduce or increase genetic diversity? The answer probably depends on the amount of attention aimed at insuring a high degree of genetic diversity in the seed crop. Uniform characteristics, such as high seed yield, harvestability, uniform plant height, and coordinated maturity are all desirable in a commercial seed production scheme, but selection for these characteristics may compromise the overall genetic diversity that is essential for successful revegetation. Several ways of increasing genetic diversity have been proposed. Mixtures of seed collected from distant sites and hybridization of genetically diverse materials are simple, yet effective ways to increase the diversity of a seed source.

Assessment of Genetic Diversity

Morphological diversity is a good indication of genetic diversity, but at times it can be misleading. Morphological

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traits are subject to environmental variation, as many a botanist has observed when plants are grown in a uniform garden. Also, morphological uniformity is not necessarily indicative of genetic uniformity, and morphological diversity for one or two traits can be due to very little genetic diversity.

Molecular markers, particularly DNA genetic markers, are valuable in that they are not subject to environmental influences, and represent underlying genetic diversity. They provide a reasonable estimation of genetic diversity provided a sufficient number of markers have been analyzed in a sufficient number of individuals to adequately represent the true genetic diversity of a population. Because of time and resource limitations, this ideal is not always possible. In fact, the greatest obstacle to using molecular markers for estimation of genetic diversity is the lack of facilities, time, and financial resources. The remainder of this paper will be devoted to a discussion of several of the various molecular marker analysis methods that are available, focusing on their advantages and limitations.

Protein Markers

Isozymes—Isozymes have been used for decades to estimate genetic diversity (Tanksley and Orton 1983). They represent native enzymes that have slightly different amino acid sequences contributing to different electrophoretic mobilities. Typically, proteins are isolated from a plant tissue, dissolved in a buffer solution, then separated electrophoretically in starch gels. The reason for using starch gels instead of polyacrylamide, which provides superior resolution, is the ability to slice a thick starch gel into several thin slabs in order to test several isozymes with a single electrophoretic step. Each gel slice is incubated in the substrate for the enzyme being tested. The active enzyme converts the substrate into the product at the site in the gel where the enzyme is located. The product is usually detected by chemical methods that cause a color change.

Differences in electrophoretic mobility represent underlying differences in the DNA that coded for the enzyme. Each enzyme represents one locus. After several enzymes have been analyzed, similarities and differences in enzyme mobility can be compared among the genotypes tested. The data can then be subjected to various forms of statistical analysis, usually some form of hierarchical cluster analysis, to determine the relative genetic distances.

Isozyme analysis is effective and has been used in many studies. In general, it is not expensive and requires little in terms of equipment and expertise. However, its use has declined significantly in recent years as DNA methods have replaced it. It has two primary limitations. First, since it involves enzymes that presumably are subject to natural selection favoring the most adaptive types, the degree of polymorphism (genetic difference) is low compared to other methods. It is not uncommon to compare a variety of isozymes among different populations and find that there are no genetic differences in the isozymes even though there may be obvious morphological differences. Isozymes are often more valuable for comparing related species than for assessing genetic diversity within a species. Second, each isozyme requires a different method for detection, meaning that a variety of chemicals must be purchased and a variety of techniques applied to obtain data from several isozymes. DNA methods use a single procedure for all DNA markers, providing a significant advantage over isozyme analysis when large numbers of markers are compared.

Seed Storage Proteins—Seed storage proteins have also been used to compare genetic diversity (Fairbanks and others 1990). Seed storage proteins are deposited in relatively large quantities in mature seeds and typically remain stable until the seed germinates. Their purpose is to provide the germinating seedling with a source of amino acids until it is able to begin photosynthesis and synthesize its own amino acids from photosynthate precursors. Since seed storage proteins are an amino acid source, rather than enzymes or structural proteins, alterations in their amino acid sequences are not as critical to the plant. Thus, they are not as subject to natural selection as their isozyme counterparts and may have higher levels of genetic polymorphism.

Seed storage proteins can be easily extracted from seeds and analyzed electrophoretically using polyacrylamide gel electrophoresis. Polymorphisms are detected as differences in electrophoretic mobilities and can be analyzed statistically just as isozymes are. Additional polymorphisms can be detected by subjecting the proteins to proteolytic cleavage using enzymes such as trypsin, chymotrypsin, and *Staphylococcus aureus* V8 protease, or chemicals such as cyanogen bromide that cleave polypeptides at specific amino acid sequences. The proteolytic fragments can then be separated electrophoretically to reveal additional genetic polymorphism.

The advantages of seed protein analysis are ease and economy. Relatively little is required in terms of laboratory equipment and the procedure is rapid. The one disadvantage is a distinct lack of available markers. The number of seed storage proteins that can be resolved by electrophoresis in any particular species is usually less than 20 and typically many of them are not polymorphic. While seed protein markers are useful, they usually must be augmented with other types of markers, such as isozymes or DNA markers for reliable estimates of genetic diversity.

DNA Markers

Restriction Fragment Length Polymorphism (RFLP) Analysis—RFLP analysis is now a standard, well-tested procedure for estimation of genetic diversity. It has been used in thousands of studies in a variety of species. Virtually every university has more than one laboratory with RFLP capabilities. RFLP analysis is based on the ability of restriction enzymes (also called restriction endonucleases) to cleave DNA at specific target nucleotide sequences consisting usually of a four or six nucleotide pair target. For example, one of the more commonly used enzymes, *Eco* RI, cleaves DNA at the target sequence GAATTC. Each time the enzyme encounters this sequence, it cleaves the DNA molecule at that point.

When cellular DNA is subjected to restriction enzyme digestion, the enzyme cleaves the DNA into thousands of fragments, each defined by the target sequence. Differences in nucleotide sequences at target sites, or in the number of nucleotides between target sites generate fragments of different sizes. These different-sized fragments are called restriction fragment length polymorphisms or RFLPs. They can be separated from each other by gel electrophoresis, and then detected by hybridization of blotted DNA fragments with a labeled probe.

RFLP markers have been used extensively for genome mapping and for analysis of genetic diversity (see Tanksley 1993 and references cited therein). They have also been used in plant breeding programs for marker-assisted selection. RFLP markers tend to be inherited as simple Mendelian codominant alleles, and are not influenced in any way by environmental factors. Therefore, their heritabilities are invariably 100%.

There are three major advantages to RFLP analysis over protein markers. First, the number of polymorphic markers that can be generated is virtually limitless. No laboratory has ever exhausted the supply of potential RFLPs. Second, the procedure is the same for every marker, so once a laboratory is set up for RFLP analysis, no major changes need to be made for analyzing different markers. Third, the level of polymorphism is greater in RFLPs than in protein markers. Since RFLPs do not necessarily represent sequences that are expressed as genes (as proteins do), their DNA sequence is not as subject to preservation by natural selection, resulting in higher levels of polymorphism. Consequently, the amount of useful information obtained per marker tends to be higher with RFLPs than with protein markers.

There are disadvantages, however. RFLP analysis is more complicated and expensive than protein analysis. It requires more time and expertise. Until recently, RFLP analysis also required the use of radiolabeled DNA, which imposed the added safety precautions needed in working with radioactive materials. However, recent advances in recombinant DNA technology have made reliable nonradioactive labels available that work well for RFLP analysis. Another significant disadvantage for RFLPs is probe availability. For major field crops, sets of RFLP probes were once sold for as much as several hundred-thousand dollars. Now they are often available for the asking. Each time an RFLP program is initiated in a new species, a new set of probes often needs to be developed. In a few cases, probes from a related species may be used if they are available. For instance, most tomato probes can be used in potato. Probe generation by cloning and testing can be laborious and expensive. If probes are not readily available, RFLP programs may require a substantial initial investment of time and money before reliable data are available. Nonetheless, RFLP analysis remains a reliable and much-used technique for analysis of genetic diversity.

Random Amplified Polymorphic DNA (RAPD) Analysis—RAPD analysis is a relatively new method designed to do essentially the same thing as RFLP analysis does with less effort and expense (Williams and others 1990). It is similar to the polymerase chain reaction, but relies on a single decanucleotide primer to amplify DNA fragments that can be used for genetic analysis. Its use in genetic diversity analysis has been explained in detail in a number of sources (Fairbanks and others 1993; Joshi and Nguyen 1993; Dweikat and others 1993; Vierling and Nguyen 1992; Heusden and Bachman 1992; Williams and others 1990; Andersen and Fairbanks 1990).

The advantages to RAPD analysis are numerous. RAPD markers are typically inherited as simple dominant Mendelian alleles and for this reason can be used for most genetic marker applications. The procedure is streamlined compared to RFLP analysis. RFLP analysis requires digestion of DNA with a restriction enzyme, separation of fragments on an agarose gel, blotting onto a filter, probe hybridization, and fragment detection, a procedure that typically requires several days. RAPD analysis requires amplification of DNA in a thermocycler and separation of fragments on an agarose gel, a procedure that requires about six hours. The cost of RAPD analysis is about the same for supplies as RFLP, but less for labor. About 60% of the cost comes from a single reaction component, the enzyme Taq polymerase (Fairbanks and others 1993). There is no need for probe development since the same set of random primers may be used for all species. The only adaptation required is a few initial experiments to determine the ideal DNA and magnesium concentrations for the species in question. These many advantages have made RAPD analysis quite popular in the past few years.

In spite of the numerous advantages, there are some disadvantages. Alterations in DNA, the concentrations of template DNA, polymerase, primers, and magnesium can cause different fragments to be produced. For this reason, RAPD results are not always repeatable when conducted in different laboratories. Generally, it is best to replicate experiments and use appropriate controls when comparing one experiment with another. Also, there is often a tendency to produce non-specific amplification as a background smear of DNA, or fragments of DNA that are not present in high amounts and appear as faint bands in the gel. Often it is a matter of guesswork to determine which DNA fragments truly represent genetic polymorphism and which polymorphisms among less visible bands represent artifacts of the procedure. In spite of these limitations, most RAPD studies confirm the results of previous studies done using other types of molecular markers and morphological or agronomic traits, indicating that the RAPD analyses were reliable (Transue and others in press). Also RAPD markers mapped to a particular site on a chromosome typically map to the same site when converted to RFLPs, a further indication of reliability (Williams and others 1990).

Several refinements of RAPD analysis have been proposed to overcome some of these limitations. Nonspecific amplification can be reduced in some cases by prior digestion of template DNA with restriction enzymes (Riede and others in press; Sharma and others 1992). Artifacts due to variations in magnesium concentration can be reduced by using the Stoffel fragment (a genetically engineered polymerase) in place of Taq polymerase (Sobral and Honeycutt 1993). Additional polymorphisms can sometimes be visualized using denatured RAPD markers and polyacrylamide gel electrophoresis (Dweikat and others

1993). Each of these procedures is somewhat more laborious than standard RAPD analysis.

In order to provide markers that can be reliably transferred from one laboratory to another, Paran and Michelmore (1993) recommended that the nucleotide sequence of selected RAPD markers be determined and this information used to synthesize long primers that are specific for the marker. Then true PCR can be used to amplify the markers avoiding the possibility of artifacts. While this procedure requires a substantial investment of time and resources, it may be worthwhile if markers need to be compared in several different laboratories.

Conclusions

Several valuable methods for molecular marker analysis are currently available for estimation of genetic diversity. DNA marker analysis, including RFLP and RAPD analyses, are now the most frequently used methods due to their advantages over protein markers. Perhaps the greatest limitation for using DNA markers is the cost associated with laboratory set up, labor, and supplies.

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Restoration, Revegetation, and the Importance of Genetic and Evolutionary Perspectives

Yan B. Linhart

Abstract—Sound biological principles must provide the framework of revegetation projects. Propagules of native species must be used, and these propagules must represent genetic material from sites that match the area to be revegetated as closely as possible. Such matching can be best achieved by using materials from nearby plants growing in nature or propagated in nearby nurseries. The closeness of matching will depend on the type of site to be revegetated. Within National Parks, whose mandate is to maintain the ecological and genetic integrity of the biota, plants or their progeny must come from nearby sites. At other locations, matching may not need to be so conservative. The primary reason for this cautious approach is that plant genomes show very precise adaptations to local conditions. Introduction of non-local materials may lead to failure of the revegetation project and endanger the long-term biological health of nearby populations.

The primary conclusions I wish to draw from the extensive scientific evidence available on these topics involve five recommendations.

1. *Whenever practicing restoration, use native species*. This is important primarily for ecological reasons. The world is already too full of introduced, "exotic" species that have run amok in their new environments and modified these environments so thoroughly as to render them unfit for many of the original, native species. The impacts of various introduced species on the grasslands of western North America provide excellent examples of these negative effects, and have been documented extensively (Baker 1978; Bock and others 1986; Joyce and others 1991; Mack 1981).
2. *The use of "native" species is not enough*. Just because two plants have the same Latin binomial does not make them "equal under the laws" of restoration and revegetation. For example, *Deschampsia caespitosa* grows in Colorado, Washington, and Germany. This does not mean that it can be moved with impunity among those locations.
3. *The best possible option is to use seeds or clones from nearby plants*. "Nearby" should be, if possible, about 100 m for herbs and 1 km for woody plants. In some revegetation projects, even these values may be too optimistic because significant genetic differentiation has been documented over shorter distances.
4. *If you wish to restore locale A, do not collect seeds or plants at A, grow them in a very different environment at locale B (50 km away across the Continental Divide), and return the progeny, after 4 generations to locale A*. Locale B may be so different in both physical and biotic features that it will create specific selective pressures that alter the original gene pools from locale A.
5. *Restoration methods are often species-specific, because different species have different life histories. These life histories must be taken into consideration when planning the work*. For example restoration with annual species, rhizomatous grasses, shrubs and coniferous trees all require somewhat different approaches.

The rest of this essay is devoted to providing evidence to back up these recommendations. The evidence is extensive: several hundred papers and several book-length treatments deal with these topics. I hope to convince readers with this evidence; consequently, this article is long. If the reader wants only the "bottom line," go directly to section IV "Management Applications" at the end. I would also like to hear opinions about what other research is needed to fine-tune these recommendations and develop others.

The organization will be as follows.

In "Life Histories of Plants," I will deal with a discussion of recommendation 5, "Life Histories," because it provides a convenient framework within which to think about plants.

In "The Genetic Structure of Plant Populations," recommendations 2 to 4 will be addressed in detail, as this is really what most of this essay is about, and various kinds of evidence for recommendations 2 to 5 are intermixed with each other in the context of genetic structure of plant species.

Recommendation 1, the importance of native species, will not be expanded primarily because it is self-evident and because of space constraints. It is self-evident in the context of extensive documentation of the negative impacts of the invasion of exotic species. Some of these species were introduced because they were thought to provide "quick fixes," often by virtue of their rapid growth or establishment in stressful ecological settings created as a result of severe human modification of native ecosystems. Some references to these introductions, and a discussion of the serious problems caused by these species, include annual grasses in the central valley of California (Baker 1978) and species of the genera *Bromus* (Mack 1981) and *Eragrostis* (Bock and others 1981). Incidentally, despite the problems caused by introduced species, there are still those who will argue that such species are not only acceptable, but often better than native species for revegetation. In this context, there is talk of a "New Range War" over the suitability of exotic species, and such species are said by some to be perfectly acceptable for revegetation, because they often resemble native species

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In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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morphologically, and because one should not base "acceptability of plants according to a foreign gene or two" (Anon. 1992).

Life Histories of Plants

The life history of plants used in revegetation and ecosystem restoration involves a variety of features which must be taken into account in order to be successful at reestablishing species and reconstructing communities. The list below is a compendium of the various features of a plant species' life history.

Stages of Life Span

Pollination—Stationary plants need mobile pollinators to ensure that gametes meet to produce seed. Native pollinators are needed for proper seed set in many native plants. In addition, breeding systems are relevant because species which are able to self-pollinate (self-compatible) will have very different genetic structures from species which are obligately cross-pollinated (self-incompatible).

Seed Dispersal—At this stage, seed dispersers are of paramount importance to plants, and both birds and mammals play important roles. Their behavior affects establishment and genetic structure of plant populations.

Germination—Most wild species have various dormancy mechanisms whose primary roles are to ensure that seeds germinate at the proper time and not all seeds germinate simultaneously, so that some are left in a "seed bank" for future years. These mechanisms are typically under genetic control, but respond to ecological cues such as day length, total rainfall and many others.

Stand Structure—As plants grow they are exposed to both intra-specific and inter-specific competition, a variety of soil conditions and other forms of landscape heterogeneity. Most plant species also need some species of mycorrhizal fungi to be healthy. The landscape is patchy, and plant populations reflect these patchy habitats with a patchy structure. All these factors create selection pressures that help shape genetic variability.

Maturation and Reproduction—As plants become larger, they are increasingly attractive to herbivores, parasites and seed eaters. All these species, in turn, generate selection.

Life Spans and Life Styles

Plants can be bryophytes, ferns, gymnosperms, or angiosperms, and can reproduce once (monocarpic or semelparous) or many times (polycarpic or iteroparous). If monocarpic, they are usually annual or biennial. If polycarpic they can live a few or many years. Plants can be herbaceous or woody, can have one or many trunks, and can have extensive vegetative spread by runners, rhizomes or other subterranean growth or have little or no such spread.

All these variables will affect revegetation strategies (annuals must set seed yearly or they will die out unless a seed bank is available in the soil) and genetic structuring (small annual plants can show genetic heterogeneity on scales of less than 10 m, whereas populations of tall trees are genetically substructured at scales of 100-1,000 m). Plants with extensive vegetative growth (many Poaceae, Cyperaceae, *Populus*) can be replanted with clonal material, genetically identical to their parents; in contrast, annuals, biennials, and most conifers must be regenerated from genetically heterogeneous seeds.

Ecological Settings

By "settings" I mean the sum total of physical and biotic features characterizing the niches of populations. These include both the total precipitation and its timing, soil conditions, light, above- and below-ground temperatures, pollinators, seed dispersers, herbivores, parasites, mycorrhizae, symbiotic bacteria, and other associated species.

These settings define the selective pressures encountered by various populations of a species, and contribute to the variable, genetically controlled features of these populations. For example, a given species, be it *Artemisia tridentata*, *Yucca glauca*, *Eriogonum niveum* or *Pinus ponderosa*, can grow on north-facing or south-facing slopes, in alkaline or neutral soils, or at sites differing in latitude by many hundreds of kilometers. At each site, it will encounter specific physical and biotic conditions that help shape its gene pool.

Genetic Events

The primary factors that shape the genetic variability in a species are:

1. Breeding Systems—Whether a species is self-compatible or self-incompatible will dictate whether it can or cannot self pollinate. This in turn may determine how much dependence it will have upon natural pollinators. As will be seen below, various species, such as *Yucca glauca*, can be one or the other, depending upon the populations tested. Whether a species is self-compatible or not will also affect the patterns of genetic structuring within and among populations. Self-compatible species, especially those that are self pollinated, tend to show more localized genetic heterogeneity than do self-incompatible species.

2. Natural Selection—These processes shape the gene pools of most species more strongly than other evolutionary forces and will be discussed in detail below.

3. Genetic Drift—This describes what happens when populations are reduced, either by nature or by humans, to very small sizes. Much of the genetic variability is then lost by accident, and when this is coupled with the associated repeated matings between surviving relatives and self pollination, genetic erosion is even greater.

   A practice which can lead to very serious loss of genetic variability in the context of revegetation involves the use of seeds from few parents which were sometimes propagated vegetatively themselves to establish nursery stock or seeding stock.

4. Gene Flow—Genetic exchange among individuals and populations can counteract the effects of selection, and genetic drift, prevent differentiation and maintain genetic integrity within a species.

The Genetic Structure of Plant Populations

Background

A species is more than just a Latin binomial name. As biologists and land managers, we have been taught that whenever we study a species, we must provide its Latin binomial. Having done so, we sometimes feel that we have described the species adequately. This perspective has many pitfalls. For example, at the scientific level, there is a tendency to believe that if you have characterized some few individuals, collected in one location, in terms of their physiology, ecology or genetics, you have characterized the whole species. At the practical level, there is a tendency to feel that if you need to replant a species in a given location, seeds carrying that same Latin binomial will be adequate whether they come from 10 m or 10,000 km away.

The primary objective of this section is to convince the reader that this simplistic perspective is incorrect and that, in fact, at all scales, from that of the species as a whole to that of the local population, there is a tremendous amount of genetic variability, organized or at least shaped, by a combination of all the forces that produce evolution—primarily selection, gene flow, breeding structure, and drift. The conclusion will be that every population is unique because it consists of a genome shaped by the interaction of the biological and physical features of its environment. This has very important implications for revegetation because it means that whenever possible, a very conservative approach must be taken, so that the most appropriate plants to use are those from nearby sources, and that the more pristine the conditions desired (inside a National Park) the more conservative one needs to be.

This section is organized to stress the fact that there are three important themes in discussions of genetic organization. First, there needs to be genetic variation in a species. Second, the variation is known to be shaped by the interplay between the homogenizing effects of gene flow and the opposing effects of selection. For this reason, the next two subsections will describe gene flow and other aspects of genetic recombination, and will be followed by a third section which describes selection and its impacts. In the concluding segment, I will address the consequences of the interplay between various evolutionary forces in the context of plant variation, evolution, and revegetation.

The literature associated with the various topics to be dealt with is truly vast, and growing daily. For example, several new book-length treatments of evolutionary ecology of plants have appeared within the last two years. Reviews of many topics are also plentiful. For this reason, such topics as large scale (many kilometers) geographic variation within species, gene flow, and phenotypic plasticity will not be discussed in detail beyond providing references to pertinent reviews. The major topic that has not been reviewed to date in the published literature is that of genetic differentiation between adjacent subpopulations or micro-differentiation. This will be discussed in most detail here because of its relevance to revegetation.

The information provided deals with plant species. Please note that it is equally valid for animal species, although the varying amounts of mobility, especially of birds, mammals and flying insects alter the details of some conclusions.

The tools used to study genetic variation have traditionally involved the analysis of morphological, physiological and breeding system variation in common gardens. Such gardens are very costly of funds and effort, and are not very suitable for large or long-lived species. Within the past 20 years, analyses of variation, gene flow and genetic structure have been aided tremendously thanks to biochemical techniques such as protein electrophoresis and various DNA-based molecular methods. There is concern in some places that much of this biochemical and molecular variation is neutral and therefore uninteresting. It is important to recognize that this is not so. Variation can be neutral and still be very useful and interesting, for instance, in studies of gene flow and population architecture. There is also concern that morphological, electrophoretic and DNA-based molecular variation show different patterns. This is true, and a "fact of life" (Bruce and Ayala 1979; Grant and others 1989). Consider the remarkable morphological and behavioral differences among humans, chimpanzees, gorillas, and orangutans. Yet biochemically, they are remarkably similar to one another. The contrast between the patterns at the biochemical, morphological and behavioral levels underscores some of the complexities of evolutionary dynamics and suggests that variation at all three levels needs to be studied if one wants to have a complete understanding of a species' genome.

Incidentally, the new molecular techniques are currently most useful in studies of systematic relationships among taxonomic entities from varieties on up. The techniques' relative complexity means that they are time-consuming, expensive, and therefore still difficult to apply to population-oriented questions such as patterns of within-species variability, gene flow and selection. Protein electropheresis is still the cheapest and best-developed methodology available for such work.

Genetic Variability

In order for species to survive and evolve, they must be genetically variable. Indeed one of the basic principles of evolutionary biology is that the rate of evolutionary change is proportional to the amount of genetic variability present in a species (Futuyma 1979).

Exact amounts of variation are difficult to measure in an absolute sense, because we cannot use the same methods for all plants and at all levels of biological organization from biochemistry to morphology. However, electrophoretic analyses allow us to make interspecific comparisons at the single gene level. There exist several reviews of this ever-growing literature (Brown 1979; Hamrick and Godt 1990; Hamrick and others 1979, 1991, 1992; Loveless and Hamrick 1984). These reviews have demonstrated the existence of very high levels of genetic variation (between 20 and 50% of loci sampled are commonly polymorphic) and significant correlations between the amount and distribution of genetic variability and various life history attributes of species. The number of species sampled as of 1992 was 448, representing 165 genera. Some of the major conclusions of these surveys are as follows:

1. In the overall analyses, geographic range alone accounted for the largest proportion of interspecific variation in genetic variability. As a result, species with large ranges are more variable than narrow endemics.
2. Woody, long-lived species are more genetically variable than short-lived ones.
3. Patterns of genetic organization within species are strongly influenced by the breeding system: for example, self-pollinated species had over 50% of their total genetic variability distributed among populations, while strongly outcrossed, wind-pollinated species had less than 10% of total variation among populations.

The final result must be interpreted with caution. It does mean that interpopulation differences tend to be more pronounced in self-pollinated than in outcrossed species. This is logical, since the essence of selfing is reduced gene flow and the associated recombination. It does not mean, however, that, since 90% of electrophoretically measured variation in certain species is within populations, one population is as good a seed source for revegetation as any other. This is because a small proportion of genes (meaning perhaps 500 out of a total genome of 5,000 genes) may be critical in terms of determining patterns of germination, or flowering time, root elongation, hardening off at the end of the growing season, or of other features critical to the well-being of a specific population in a specific site.

One result is worthy of specific mention in the context of species' management and protection. Endemic, therefore often rare, species are usually much less variable than more widely distributed ones.

Patterns of Recombination

Gene Flow—Gene flow can take place by pollen, seeds and other plant parts such as bulbils or other propagules. Studies of pollen and seed dispersal have been, and continue to be, very common. The two major reasons are that:

1. Gene flow is recognized as the primary homogenizing force of a species' genome. Gene exchange is what keeps a species together. For these reasons it is of basic scientific interest (Futuyma 1979).
2. Gene flow can involve the modification and dilution of a carefully selected and bred variety, it represents contamination.
3. Genes may "escape" from genetically engineered plants into nearby weeds with interesting, perhaps worrisome, consequences (Ellstrand and Hoffman 1990; Raybould and Gray 1994). For these reasons, it is of significant agronomic interest.

Recent reviews, providing genetic, ecological and evolutionary interpretations are available in Levin and Kerster (1974), Levin (1981, 1984), and Slatkin (1985). Pollen can be dispersed by wind, water, or animals. In most cases, the majority of the pollen dispersed travels a few meters. The rest can travel a few to many hundreds of meters. The shapes of the dispersal curves vary with pollination mode. Wind pollination generally produces so-called leptokurtic distributions. That means that, in comparison to a normal (bell-shaped) distribution, significantly larger than expected quantities travel short distances or very long distances, while smaller than expected amounts travel intermediate distances. This same leptokurtic pattern is often observed in plants pollinated by relatively small- to medium-sized insects (honey bees). In contrast, larger insects such as bumble bees, hawk moths, bats and birds, can fly very long distances, providing the potential for more extensive pollen dispersal. Water pollination, or hydrophily, is very poorly studied. Studies of distances of water-mediated pollen dispersal are not reported but one can expect distances to be generally more extensive than in land plants, at least in moving water.

Most pollinators whose behavior has been studied in detail are primarily small bees and butterflies, and have short flight distances. Consequently the pollen they disperse does not travel very far, and provides the potential for mating between few individuals. These mating opportunities are described with Wright's (1978) neighborhood model. A neighborhood is defined as the area from which the potential parents of some individual in the center of the area can be drawn at random. A related perspective is that a neighborhood area encompasses all individuals that can mate at random within the area. Neighborhoods are calculated from known distances of pollen and seed dispersal. In herbaceous, insect-pollinated species, neighborhood areas (and numbers of individuals) have been reported as follows: *Primula vulgaris* 30 m^2 (175); *Viola rosstrata* 25 m^2 (167); *Phlox pilosa* 108 m^2 (1,409); *Liatris cylindracea* 63 m^2 (1,260); and *L. aspera* 38 m^2 (176). Within *L. aspera*, neighborhood size varied with plant density from 45 m^2 at 1 plant/m^2 to 363 m^2 at 11 plants/m^2. Note also that the two species of Liatris have very different neighborhood sizes (Levin 1986). For wind-dispersed forest trees, neighborhood sizes have also been estimated for a few species, sometimes from pollen dispersal data alone. Although the areas can be much higher than those noted above, in the hundreds of square meters, the numbers of individuals involved are generally comparable, tens to hundreds (Brunel and Rodolphe 1985; Levin 1981; Richards and Ibrahim 1978; Wright 1965). As noted above, species with large flowers, and pollinated by large, strong-flying animals (large Hymenoptera, Sphingidae, certain hummingbirds or bats) can be expected to have rather different population structures because of the long distances traveled by their pollinators (Emerson 1939; Linhart and Mendenhall 1977). For example, larger neighborhoods can be expected to have less inbreeding, and this appears to be true (Linhart and others 1987), although data are scarce.

Studies of seed dispersal are often anecdotal, poorly quantified, and hence difficult to be precise about (but see Williams 1994). This problem is further complicated by the fact that seed dispersal cannot be equated with plant establishment. Three general patterns of genetic relevance can, however, be stated fairly confidently:

1. Much seed dispersal is restricted to a few meters, especially in herbaceous species (Bannister 1965; Levin 1981).
2. Some establishment can occur over very long distances (Linhart 1988a; Linhart and Premoli 1994; Tomback and Linhart 1990).
3. The preponderance of short-distance dispersal means that plant populations often consist of groups of genetically related individuals living in close proximity to each other. These patterns of genetic substructuring have been identified in a variety of herbaceous and woody species (Brunel

and Rodolphe 1985; Hamrick and Allard 1972; Linhart 1989; Linhart and others 1981; Schaal 1975; Turner and others 1982; Wright 1943).

Breeding Systems—Plants are remarkably variable in their breeding systems. From the point of view of genetic recombination, this means that everything from a very conservative maintenance of specific genotypes to a complete genetic reshuffling every generation is possible. It must also be stressed that breeding systems are highly variable within taxa, so that patterns are seldom as clear as they seem. For example:

- Certain *Taraxacum* taxa are triploid, and thought to be strictly apomictic (asexually reproducing) and therefore rather genetically uniform. In fact, some triploid *Taraxacum* populations show sexual reproduction, and contain important amounts of genetic variation (Richards 1986).
- *Yucca* species are commonly perceived as being obligately associated with *Tegeticula* moths, needing these moths for pollination, as the plants are self-incompatible. Yet in Colorado, *Y. glauca* are self-compatible, and attract other insects that serve as potential pollinators (Dodd and Linhart 1994).
- Dioecy, because it requires the presence of individuals of separate sexes, is thought to be uncommon in colonizing species. Yet many island species are dioecious. A paradox? Not really, since many of these island species have "leaky dioecy"; they are able to circumvent the need for separate sexes under some circumstances (Cox 1989).

Variability in the breeding system, and the associated outcrossing rates, has been demonstrated in a wide variety of plant species, and is often affected by obvious landscape features such as elevation, exposure, and plant density, and may vary from year to year. In at least some cases, such variation can be observed between populations separated by distances of 100 m or less; under these circumstances it can be thought of as another suite of characters that are subject to the effects of selection (Antonovics 1968; Arroyo 1973; Baker 1966; Brown and others 1975; Cheliak and others 1985; Cuguen and others 1989; Ellstrand and Foster 1983; Ellstrand and others 1978; Ennos 1985; Ennos and Clegg 1982; Farris and Mitton 1984; Jain 1976; Lloyd 1965; Moore and Lewis 1965; Moran and Brown 1980; Neale and Adams 1985; Sander and Hamrick 1980; Wyatt 1984a,b, 1988). These interpopulation differences illustrate why the maxim "local seed sources are best" is important. Importing non-local populations may mean that plants with non-local, perhaps maladapted breeding systems, get established and disrupt locally-developed, specific features of genetic recombination.

Genetic Organization by Selection

Geographic Variation—The study of geographic variation in plants is really an analysis of the interplay between the four classes of events noted above. Selection obviously occupies a predominant role in the shaping of this variation, and I will assume so here. The earliest studies of morphological variation in plants were not motivated by evolutionary concerns but very pragmatic commercial and military ones. The French Navy was especially concerned about having adequate supplies of timber for its ships. The Inspector General of the Navy was not an admiral but a well-known botanist, H. L. Duhamel de Monceau. He started to grow plantations of *Pinus sylvestris* for masts and oaks for hulls, from seeds collected in various parts of Europe. These studies demonstrated forcefully that trees from different geographic sources showed different morphologies (Langlet 1971). The results were so striking that they were used by Darwin (1872) to buttress his arguments about the reality of selection as an agent of evolutionary change. Geographic variation continued to be studied on a large scale by forest biologists who were interested in reforestation with proper material. Reviews are available in Langlet (1971), Libby and others (1969), Dorman (1974), and Stern and Roche (1974).

The best analyses of geographic variation in plants were initiated by Clausen, Keck, and Hiesey of the Carnegie Institution in California. They stand out because they were by far the largest, most complete analyses of morphological variation, and involved a variety of species such as *Achillea lanulosa*, *Potentilla glandulosa*, and several species of *Viola* and *Mimulus* (Clausen and Hiesey 1958; Hiesey and Milner 1965). Later, these studies were expanded to include physiological characters (Björkman 1968, Björkman and others 1969; Hiesey and Milner 1965). The most important lesson from all these studies is that every species studied shows significant levels of genetically based differentiation. The genome of species is not a fixed homogeneous entity, but a deeply fissured, rapidly changing assembly of shapes. Various features of the physical landscape provide good clues about the nature of genetic structure in a species. Differentiation as a function of distance is more dramatic along steep mountain slopes than in rolling hills. Abrupt differences in elevation, exposure (especially north vs. south faces) shifts in bedrock or soil characteristics, and water availability are all sources of selection-induced changes in this genome.

Differentiation usually involves large segments of the genome, because it involves many characteristics associated in some way with fitness and survival. For example, in *Potentilla glandulosa*, the following characters (and estimated numbers of loci involved) showed significant differentiation between populations from different localities: winter dormancy (3); seed weight (6); seed color (4); petal length (4); width (2); color (1); pubescence (5); anthocyanin levels (4); flowering time (many); stem length (many); and leaf length (many) (Clausen and Hiesey 1958).

In early studies of geographic variation, one major focus of the analyses was whether the variation showed a clinal (continuous) pattern or an ecotypic (discontinuous) one. The same results were sometimes interpreted as clinal or ecotypic by different groups of researchers. This dichotomy of views reflects the fact that, for taxonomically inclined botanists, ecotypes were far easier to interpret and deal with than clines. That is because, being discrete entities, ecotypes could be considered as hierarchies of classification, below varieties in order of importance. Clines however were "messy" from this perspective. Detailed analyses of variation now show that, within the same species, some characters can vary gradually, others discontinuously, depending on gene flow, intensity of selection, number of genes involved, or terrain configuration; the controversy is not useful and has died down (Langlet 1971).

Another general conclusion is that most species studied are very variable and extensively differentiated on a geographic scale, whether it be at the morphological (Clausen and Hiesey 1958; Libby and others 1969), electrophoretic (Guries and Ledig 1982; Hiebert and Hamrick 1983; Li and Adams 1989; Loukas and others 1983; Lundkvist 1979; Plessas and Strauss 1986; Yeh and El Kassaby 1980; Yeh and Layton 1979; Yeh and O'Malley 1980; Yeh and others 1985), or physiological (Björkman 1981; Denno and McClure 1983; Hiesey and Milner 1965; Mooney and Dunn 1970) levels.

Exceptions to this pattern of extensive differentiation do exist. They tend to involve species with little genetic variability, species that live in aquatic environments, and those with large amounts of phenotypic plasticity. These exceptions will be dealt with in more detail in a subsequent section.

Microgeographic Differentiation—This section will focus on genetic differentiation on a small scale: tens to hundreds of meters. The primary concern will be a review of the studies that have analyzed differentiation either between adjacent sub-populations occupying contrasting habitats or within populations exposed to diversifying selection. These studies have dealt with herbaceous species, whose populations can show genetic heterogeneity on a scale of tens of meters or less, and with larger woody species which generally show such heterogeneity on a scale of 100 to 300 m. Species for which genetic differentiation has been demonstrated on scales of 300 m or less are listed in table 1.

In general, physical components of the environment (moisture, soil conditions, exposure) vary spatially either in a gradient, or abruptly. Consequently, they produce differentiation between adjacent populations. Conversely, biotic components (competition, herbivory, parasitism) vary much more dynamically, because the elements providing the selection (competitors, herbivores, and parasites) can move about within a given area (plant competitors or parasites can move about via seed or spores, from one generation to the next). Consequently, they usually produce differentiation within populations.

Agents of Selection

Toxic Soils—These human-induced patterns of genetic differentiation are worth mentioning because they may be relevant in the context of revegetation of old mines and other toxic habitats. Mining activities, especially for toxic metals such as copper, zinc, lead and tin have produced large tailings of refuse, consisting of soils mixed with high concentrations of these metals. Many of these mines have been abandoned, and the heaps have been colonized. Studies of the evolution of this tolerance are abundant, and among the most detailed, complete, and elegant in evolutionary biology. Some of the most important results are as follows.

- Selection has been very intense. As a result, metal tolerant "races" have evolved very rapidly, within hundreds of years or less (Antonovics and others 1971; Bradshaw 1976; Gibson and Pollard 1988; Jain and Bradshaw 1966; Shaw 1990).
- Selection can produce differentiation on a scale of 10 m or less. Boundaries of mine heaps are very abrupt, and plants on either side of a boundary, 1 to 2 m apart, can be very different.
- Adaptation to heavy metals evolves at some cost: individuals that are metal-tolerant are generally competitively inferior to individuals that grow on adjacent, non-metalliferous soils, when grown on this latter soil type (Antonovics and others 1971; Bradshaw 1976; Hickey and McNeilly 1975). The same pattern appears to be true in plants that are tolerant of serpentine soils (Kruckeberg 1954), and may be a generally applicable conclusion.
- Evolution of metal tolerance has occurred in a wide variety of plant species with many different life histories and characterized by different (wind and insect) pollination systems and life spans. Most are herbaceous, but tolerance has evolved in at least one tree (Betula) (Bronn and Wilkins 1985). The species include *Armeria maritima* (Lefebvre 1989), *Agrostis tenuis* (McNeilly 1968), *Anthoxanthum odoratum* (Antonovics and others 1971), *Agrostis stolonifera* (Wu and others 1975), *Arrhenatherum elatius* (Ducousso and others 1990), *Silene cucubalus* (Verkleij and others 1985), *Mimulus guttatus* (Allen and Shepard 1971), the legume *Lotus purshianus* and its symbiont *Rhizobium loti* (Wu and Lin 1990), and a variety of mosses and other bryophytes. In many bryophytes evolution has not necessarily occurred with the speed documented for angiosperms, nor has the existence of adjacent metal-tolerant and intolerant populations been demonstrated (Shaw 1987a,b, 1990; Shaw and others 1987).

Herbicides—Just as insects have evolved resistance to insecticides, and rodents have evolved resistance to rodenticides, so have plants evolved resistance to herbicides. These are typically weedy plants, such as *Convolvulus arvensis*, *Tripleurospermum inodorum*, *Daucus carota*, *Echinocloa crusgalli*, *Senecio vulgaris* and *Amaranthus retroflexus*. Resistance has been found to most important herbicides, including, 2,4-D, Atrazine and Simazine. Such resistance is becoming a problem, as resistant populations of *S. vulgaris* occupy hundreds of thousands of acres in the Western United States, and resistant *A. retroflexus* are found in Washington, Maryland, Pennsylvania, Ontario and Nova Scotia (Holliday and Putwain 1977, 1980; Lebaron and Gessel 1982). These results are worrisome, as they suggest that the use of herbicides in the context of revegetation manipulations is probably counterproductive.

Nursery Conditions—The rearing of plants in greenhouses, nurseries or well-fertilized fields or fish in hatcheries and of other animals in "captive" domesticated conditions, where food and shelter are easy to obtain, and where natural conditions never prevail have led to adaptation by these populations to their domesticated situations (Davies and Snaydon 1975; Schontz and Schontz 1975; Briggs and Walters 1984). Such genetic changes have led to problems whenever these species are planted or released in the wild. After even a few generations of leading a comfortable, protected lifestyle, the species in question have clearly become

Table 1—Examples of species for which significant genetic differentiation among adjacent subpopulations has been demonstrated. For annual and herbaceous perennial species, the scale of differentiation is usually 5 to 20 m. For forest trees, the scale is usually 100 to 300 m. Only one reference is cited, but more than one is available for most species.

ANNUALS

- Graminae
  - *Hordeum spontaneum* (Nevo and others 1986)
  - *Avena barbata* (Hamrick and Allard 1972)
  - *Poa annua* (Law and others 1977)
- Polemoniaceae
  - *Linanthus parryae* (Epling and Dobzhansky 1942)
- Balsaminaceae
  - *Impatiens pallida* (Schemske 1984)
  - *I. capensis* (Schmitt and Gamble 1990)
- Compositae
  - *Galinsoga ciliata* (Shontz and Shontz 1972)
  - *Lasthenia fremontii* (Linhart 1976)
- Limnanthaceae
  - *Limnanthes floccosa* (Arroyo 1973)
- Lobeliaceae
  - *Downingia concolor* (Linhart 1976)
- Onagraceae
  - *Boisduvalia glabella* (Linhart 1976)
- Scrophulariaceae
  - *Veronica peregrina* (Linhart 1988b)

HERBACEOUS PERENNIALS

- Graminae
  - *Anthoxanthum odoratum* (Grant and Antonovics 1978)
  - *Agrostis tenuis* (McNeilly 1968)
  - *A. stolonifera* (Aston and Bradshaw 1966)
  - *Arrhenatherum elatius* (Ducousso and others 1990)
- Plantaginaceae
  - *Plantago lanceolata* (Gregor and Lang 1950)
  - *P. major* (Warwick and Briggs 1980b)
- Compositae
  - *Liatris cylindracea* (Schaal 1978)
  - *Taraxacum officinale* (Solbrig and Simpson 1974)
  - *Bellis perennis* (Warwick and Briggs 1980a)
  - *Achillea millefolium* (Warwick and Briggs 1980c)
  - *A. borealis* (Kruckeberg 1954), *Lysimachia volkensii* (Agnew 1968)
- Leguminosae
  - *Trifolium repens* (Turkington and Aarrsen, 1984)
  - *T. hirtum* (Jain and Martin 1979)
  - *Lotus alpinus* (Urbanska 1984)
  - *L. purshianus* (Wu and Lin 1990)
- Ranunculaceae
  - *Ranunculus montanus* (Dickenman 1982)
- Labiateae
  - *Prunella vulgaris* (Warwick and Briggs 1979)
- Rosaceae
  - *Potentilla erecta* (Watson 1969)
  - *Dryas octopetala*, (McGraw and Antonovics 1983)
- Caryophyllaceae
  - *Silene cucubalus* (Verkleij and others 1989)
  - *Armeria maritina* (Lefebvre and Vernet 1989)
- Scrophulariaceae
  - *Mimulus guttatus* (Allen and Sheppard 1971)
- Viscaceae
  - *Arceuthobium vaginatum* (Linhart and others 1994)
  - *A. americanum* (Linhart and others 1994)
  - *Viscum album* (Paine 1950)
  - *Phoradendron tomentosum* (Clay and others 1985)

FOREST TREES

- Pinaceae
  - *Pinus ponderosa* (Mitton and others 1977)
  - *P. sylvestris* (Gullberg and others 1982)
  - *Pseudotsuga menziesii* (Herman and Lavender 1968)
  - *Picea abies* (Tigerstedt 1973)
  - *P. engelmannii* (Grant and Mitton 1977)
  - *Abies lasiocarpa* (Grant and Mitton 1977)
- Cupressaceae
  - *Cryptomeria japonica* (Sakai and Park 1971)
- Myrtaceae
  - *Eucalyptus urnigera* (Thomas and Barber 1974)

genetically modified. As a result, they may do poorly and die off in large numbers following planting in nature. This "nursery effect" has been of concern to a number of people involved in revegetation, but needs some serious scrutiny to develop potential solutions to the problem (Kitzmiller 1993).

Maritime Exposure—Plants growing on cliffs, dunes and other seaside habitats are exposed to extremes of light, wind, salt deposition, wave action and other difficult conditions, and were the object of study of some of the earlier investigations of intra-specific differentiation by Turesson (1922, 1930). On a finer scale, Gregor (1946, and his collaborators, Gregor and Lang 1950) were the first to demonstrate genetic differentiation between populations separated by a few meters. Seaside *Plantago* were more tolerant of high winds and salt spray, and generally markedly more prostrate than *Plantago* in adjacent meadows.

Moisture, Temperature, Elevation—These factors are often interrelated. Several studies of differentiation have been done in habitats that contrast in one or more of these features. Inevitably, associated features are known to, or can be expected to, contribute to the differentiation observed. In these cases, the effects of single factors cannot be isolated, or, when several factors are involved, they cannot be ranked in terms of their relative importance. For example, genetic differentiation has been demonstrated between trees in forests and their conspecifics growing nearby as shrubby "Krummholtz" at tree line (Grant and Mitton 1977). Differences between these habitats include temperature extremes, snow accumulation, insolation, competition and herbivory on seedlings, wind and probably soil factors such as fertility and mycorrhizae. We cannot determine which of these factors is most important in producing the genetic differences observed. Nonetheless, we can at least conclude that, in *Abies lasiocarpa* and *Picea engelmanii* there are significant genetic differences associated with growth morphology, detectable at the scale of 100 to 200 m. On a similar scale, there is significant genetic differentiation in *Pinus ponderosa* occupying north and south-facing slopes in the Colorado Rocky Mountains (Mitton and others 1977), and in *Pseudotsuga menziesii* where roots of plants from south-facing slopes show genetically based greater growth rates than those from north-facing slopes with more plentiful water supplies (Herman and Lavender 1968). This observation led these authors to suggest that "aspect races" have evolved in Douglas-fir. Similar results have also been reported in *Pseudotsuga menziesii* (Campbell 1979), *Pinus sylvestris* (Gullberg and others 1982), and several species of *Eucalyptus* (Barber 1965; Barber and Jackson 1957).

In herbaceous species, the observed differentiation is on a smaller scale. For example, *Avena barbata* is an annual plant in California introduced primarily in the past 100 years. It shows significant genetic differentiation both in allozyme patterns and in morphology, between cool, mesic northern California, and the hot, xeric southern parts of the state. When the variation was analyzed on the scale of a single hillside, genetic differentiation was also demonstrated between locations 5 to 50 m apart. The pattern was consistent with the large-scale, state-wide analyses. Genotypes characteristic of the mesic sections of the state were also most common in the mesic sections of the hillside bottom. Conversely, the genotypes and allele frequencies characteristic of southern California were also found in the xeric hilltop (Hamrick and Allard 1972; Hamrick and Holden 1979). Note that, as in the *P. ponderosa* results discussed above, large-scale patterns and small-scale patterns are consistent with each other, providing stronger evidence that selection is involved in the differentiation observed. Given the recent arrival of *A. barbata* in California, differentiation has obviously occurred in less than 100 generations.

Gradients of environmental variability can span very small distances, no more than 10 m, and still create genetic differentiation over these distances. For example, small depressions that fill with water seasonally, and then dry out, provide microhabitats that vary from one another in many characteristics, including moisture availability, soil pH, temperatures, soil aeration and vegetation composition. Such depressions, called vernal pools, are important sites of endemism of the California flora; their existence is threatened because of agricultural activities (Jain and Moyle 1984). Several species have been studied in these pools, especially along the microgradients found along pool sides. Differentiation associated with environmental heterogeneity has been demonstrated in *Limnathes* spp. (Arroyo 1973; Jain and Moyle 1984) and in *Downingia concolor*, *Boisduvalia glabella*, *Lasthenia fremontii* and *Veronica peregrina* (Linhart 1976). *V. peregrina* was studied in most detail, and there was demonstrable differentiation between plants occupying the central, moist to water-logged, densely populated sections of pools and plants occupying the drier periphery, where *Veronica* are few (intra-specific competition is minimal) but where taller grasses are common (interspecific competition is severe). The differentiation involved a combination of responses to water-logging (Linhart and Baker 1973), phenology, reproductive output, plant size, seed size and seed number (Linhart 1974, 1976, 1988b), and electrophoretic variability (Keeler 1978). Plants at the center and periphery had adapted to the different moisture regimes and especially to the competition regimes prevalent in their original habitats. The larger, fast-germinating seed of center plants provided a significant early advantage in intra-specific competition. Periphery plants flowered later and grew taller, providing an advantage in inter-specific competition. Gene flow via seed was potentially important, in that, within a vernal pool that was plowed yearly, but retained its general physical and biological features, center-periphery differences in *Veronica* sub-populations were much less pronounced than in an undisturbed population.

Soils—Whenever edaphic conditions are somewhat extreme in terms of pH, mineral contents, or other features, they can be expected to generate selection pressures of the sort documented in the section dealing with mine tailings above. Among the best examples of such soils are serpentine-derived ones, which, among other features, have high levels of magnesium and low levels of calcium. Such conditions can lead to the formation of strongly differentiated populations, as in *Achillea borealis* (Kruckeberg 1954). These unusual soils are especially interesting in the long run, because they form sites for potential endemism. For example, there are serpentine-associated endemic species in Zimbabwe, New Caledonia (where 2 families, over 30 genera and 900 species are restricted to serpentine outcrops), Yugoslavia, and California. There are also edaphic endemics on other unusual soil formations. *Astragalus phoenix* is restricted to calcareous alkaline soils in Nevada. *Hudsonia montana* is restricted to quartzite ledges in Burke County, N.C. These endemics also illustrate another reason why the study of genetic differentiation can be important: it can provide clues to the formation of new species via selection, and perhaps random events, coupled with barriers to gene flow.

Less extreme variation in soil conditions is more common in nature than are serpentine outcrops. Differentiation associated with such variable soil conditions has also been documented. In the Swiss Alps, variation in frequencies of acyanogenic and cyanogenic morphs of *Lotus alpinus* (Urbanska 1984) and *Ranunculus montanus* (Dickenman 1982) was demonstrated in adjacent populations occupying soils characterized as with "acidic silicate" or "carbonate."

Competition—Plants may compete with one another for light, water, nutrients, space and other features of their "living space." Therefore, competition can involve many different kinds of competitive interactions. For example, intra-specific and interspecific competition differ from each other, and *Veronica peregrina* sub-populations exposed to these two regimes showed adaptive differentiation in seed size, timing of germination, growth rate, branching patterns and overall plant size as a result (Linhart 1988b). In addition, interspecific competition involves competitive interactions with many species. *Trifolium* repens in competition with *Lolium*, *Agrostis*, *Phleum* and *Dactylis* showed differentiation in response to being associated with these four species (Turkington and Aarssen 1984).

Herbivory, Predation, Parasitism—All these factors have demonstrable selective effects upon plants. What is especially important is to understand how these factors act in concert to affect evolutionary change in plants. In the juvenile part of its life, a plant is likely to be chewed by caterpillars, rasped by mollusks, clipped by beetle larvae, invaded by fungal mycelia, colonized by bacteria, or play host to viral infection. With the onset of maturity, a plant can, in addition, be mined, drilled, defoliated, grazed, shredded and uprooted. If it reaches sexual maturity, its flowers, fruits, and seeds may be robbed, eaten, parasitized, or otherwise harmed. This is but a small sample of the possible fates which a plant may experience due to its position in the natural food web of the community in which it grows.

Ford (1942) and Haldane (1949) were among the first biologists to suggest that diseases and parasites play a significant role in evolution. The Ford-Haldane perspective has been largely validated for various animals. For plants, the important roles of fungi and arthropods (Denno and McClure 1983; Fritz and Simms 1992) in shaping evolutionary change have also been demonstrated.

Parasites and disease organisms are of particular interest to students of evolution because the modes of selection they are capable of exerting on their potential hosts differ from the selective patterns often exerted by physical components of the environment. Whereas temperature and soil moisture, salinity and heavy metal status exert directional selection which then generate evolutionary change, parasitism and disease are often apt to create various forms of diversifying selection. One reason for this is that, very often, rare biochemical genotypes of the host plant, because they possess novel or at least uncommon defenses in the form of secondary compounds, are less likely to suffer harmful attack (Haldane 1949). Among the evolutionary consequences of this type of selection are the maintenance (preservation) of large numbers of alleles at particular loci, and the possibility of selection favoring mechanisms which generate genetic change, such as intragenic recombination and mutation. Furthermore, the various allelic combinations at one or more loci which may bestow a resistance to certain parasites may simultaneously render the host susceptible to attack by other parasites.

One evolutionary consequence of this selection pattern is the maintenance of variability via diversifying selection, since alternative genotypes at a given locus or loci will be favored under different conditions. Diversifying selection can also operate if one allele or genotype is selected against by the dependent species but is selected for in the absence of the dependent species because it is associated with a higher growth rate, reproductive output, or some other component of total fitness (Denno and McClure 1983; Linhart 1989, 1991).

Plants can serve as hosts to a wide variety of disease organisms, parasites, herbivores, commensals, symbionts and other life styles. For the sake of simplicity these species in the aggregate are referred to as dependent species. The number of dependent species that can be associated with a species of host plant is often large: more than 200 insect species have been identified for several tree species (Furniss and Carolin 1977). In addition, a plant species is usually susceptible to viral, bacterial and fungal diseases, plant parasites and mammalian herbivores, although not all these dependent species will be active simultaneously. Neither is it likely that every dependent species has a unique suite of physiological and behavioral characteristics, and can thereby generate a unique set of selection pressures. Nevertheless, variation in the direction of selection can be expected. These differences engender what is referred to as species-specific host selection. The life-forms for which species-specific host selection has been documented include algae, herbaceous plants, and forest trees. In some cases, preference by dependent species, or susceptibility by a host, has not been related to precise features of the host phenotype. However, in some cases, a class of compounds has a deterrent effect upon one herbivore, but stimulates feeding by another herbivore species. In other cases, variability in morphology is associated with resistance to some and susceptibility to other dependent species (Linhart 1989, 1991).

Comments on Patterns of Differentiation

Selection Over Time—Such selection is important in two contexts. The great majority of studies documenting rapid evolutionary change have involved comparisons of spatially adjacent groups. In some cases, analyses of populations residing on mine soils or fertilized plots of known date of origin, the rate of change can be given a time frame. In most cases, the time frame is imprecise or unknown. However, such a time frame is important to know, because it gives us information about rates of evolution.

Many plants live long periods of time. As a result, populations often consist of cohorts of different ages, established under different conditions, and therefore subject to different selection pressures. This also provides the opportunity for genetic differentiation among such cohorts. This means that such age-structured populations can consist of groups occupying the same site but having very different genetic constitutions despite the fact that the younger plants are descended from the older plants on the site, and are therefore genetically closely related to these older plants. The theoretical consequences of this possibility have been explored by Charlesworth (1980), and there is evidence for such temporal differentiation in both herbaceous (Gray 1987) and woody species (Beckman and Mitton 1984; Linhart and Davis 1991).

Spatial Scale of Differentiation—This scale depends primarily on two sets of factors. One has to do with the relationship between the intensity of selection, whose effect is to disrupt a gene pool, and the extent of gene flow, whose effect is to homogenize the gene pool, thereby counteracting the impact of selection. The finest scale of differentiation, 10 m or less, has been found in situations with extremely strong selection pressures, either human-related, such as mining (Antonovics and others 1971; Shaw 1990), or natural such as those on the sides of temporary pools (Linhart 1988b). However, even in these situations, gene flow has been documented as reducing the extent of differentiation. All these cases involve annual or short-lived perennial plants of small stature.

The second factor has to do with plant size. Forest trees, because of their stature, typically have much more extensive gene flow than do herbs. In addition, they tend to be primarily outcrossing, and therefore have a more open breeding system. For these reasons, the selection-associated differentiation documented to date between adjacent sub-populations is usually on a minimum scale of 100 to 300 m (Grant and Mitton 1977; Herman and Lavender 1967; Mitton and others 1977). However, strong differentiation on a scale of 10 to 50 m can be found, usually as a result of very localized seed dispersal, generating the existence of family groups (Brunel and Rodolphe 1985; Linhart 1989; Linhart and others 1981).

Life History and Systematic Position—Microgeographic differentiation has been demonstrated in bryophytes (Shaw 1990), in coniferous trees (Grant and Mitton 1977; Moran and Adams 1989; Tigerstedt 1973), and among angiosperms, in plants of all life forms including annuals, herbaceous perennials and forest trees (table 1). Among herbs, there is evidence of differentiation among species with the potential for extensive vegetative propagation, such as *Mimulus guttatus* (Allen and Sheppard 1971), *Agrostis stolonifera* (Aston and Bradshaw 1966), and *Trifolium repens* (Turkington and Aarssen 1984). Breeding systems vary among all the species. Both self-pollinated and outcrossed species are clearly capable of having significantly differentiated sub-populations adjacent to one another, especially if selection is intense enough. However, as a general rule, it is clear that self-pollinated species are likely to show more inter-population differentiation than primarily outcrossed ones.

Exceptions—Although most land plants studied show a significant amount of genetic heterogeneity, both on a large and a small scale, in association with environmental heterogeneity, there are some notable exceptions to this pattern. The exceptions typically involve species that tend to possess little genetic variability to begin with. For this reason, it is not too surprising that there is little observable differentiation. For example, *Pinus resinosa*, although it occupies an extensive geographic range in eastern North America, has remarkably little morphological or electrophoretic variation (Fowler and Morris 1977). The same is true for *Pinus torreyana*, a California endemic (Ledig and Conkle 1983). Both species are thought to have undergone significant reductions in population size and associated genetic bottlenecks in the past. Despite this low genetic variability, however, there is evidence of some geographic variation in morphological characters in both species.

Aquatic species present especially intriguing exceptions. Most aquatic angiosperms have remarkably little genetic variability compared to land plants. They also have much less pronounced geographic differentiation, and what there is of it, is on a very large scale: populations form northern Europe are differentiated from those of southern Europe and the Middle East, for example (Triest 1991). The same is true for at least certain marsh plants such as *Spartina maritima*, *S. alterniflora*, and their presumed hybrid *S. angelica* (Thompson and others 1991). Reasons for these low amounts of variation are debated. The relatively more environmentally buffered conditions available to water-dwelling species are involved, as are the large amounts of phenotypic plasticity that are commonly found in these species. This plasticity is itself a trait, or more precisely a suite of traits, open to selection and evolutionary change (Bradshaw 1965; Thompson 1991).

One other class of exceptions involves studies that failed to find differentiation under conditions where it might be expected, such as in strongly contrasting habitats. These studies, very few in number, involve situations where sampling was inadequate and therefore differences between sub-populations were not statistically significant. For example, if sampling involves 3 to 5 individuals per location, differentiation is unlikely to be detected.

Management Applications

Biological Synthesis

Most plant species have a good deal of genetic variation. This variability is shaped, reasonably predictably, primarily by the interplay of gene flow, selection and random effects. The first two of these factors are most predictable: gene flow is a homogenizing force, and "dilutes" the effects of selection. In specific cases, however, especially those involving restricted seed dispersal, groups of seeds will lead to the simultaneous establishment of groups of genetically related individuals, i.e., family groups. A population will then consist of patches of family groups.

Selection is predictable in that, whenever a population, or stand, of a species spans some environmental gradient (a mountain side) or is exposed to severe biological interactions (competition or herbivory), adaptation to the conditions observed is likely to have occurred. Adaptive differentiation is evident in most species studied. Microgeographic differentiation has been documented in at least 50 species (table 1) and this is probably a very conservative figure. The list includes species which, by virtue of extensive cloning, can theoretically cover many square meter or hectares of area. In clonal species, there are often 10 or more clones per square meter, also allowing for differentiation. Random events, in the form of establishment following long distance dispersal of one or a few popagules, or large-scale mortality of all but a few individuals, are unpredictable, but their general effect is also likely to contribute to the highly patchy nature of genetic structure.

Considering all the factors together, there emerges the following perspective: In any ecosystem (or whatever other term is deemed suitable) the individuals of a single species are often grouped into assemblages that differ from one another very strongly. Some of the differences, usually due to selection, are predictable. For example, individuals on north-facing slopes will be characterized by certain features, those on south-facing slopes, by other features. At the local population level (a single hillside or a small valley) there may also be significant genetic differentiation if a strong environmental gradient is crossed. For example, plants along a streamside are likely to be genetically differentiated from their conspecifics on a nearby hillside. Superimposed on this selection-maintained heterogeneity is the patchiness produced by localized gene flow, especially seed dispersal. The end result is an extremely small-scale mosaic of genetic variation. This has been recognized for some time as being one of the important "consequences of being a plant" (Bradshaw 1972; Harper 1977; Levin 1978).

Selection-induced genetic differentiation is not only evident at the morphological and physiological levels. It also concerns other crucially important components of the life cycle. These include the mating system, the propensity to decrease or increase outcrossing and therefore gene exchange among individuals and populations. Such flexibility in the mating system in response to selection is common and indicates that plants can adjust some very basic features of their life history to a given environment. Even more fundamental a feature of life history is life span: in *Poa annua*, certain populations are annual, while other nearby ones are perennial (Law and others 1977). We tend to think of life spans as species characteristics, but they can also reflect adaptations to specific local conditions.

Adaptation to local conditions can involve varying amounts of the genome, depending, presumably, on the complexity of the environmental conditions generating selection. At one extreme, tolerance of heavy metals or herbicides can involve one or a few loci. However, even under these conditions, other loci seem to be affected, through epistatic interactions or modifier effects. That is a logical conclusion drawn from observations that plants tolerant of toxic levels of metals in soils are also poor competitors against non-tolerant plants in normal soils (Antonovics and others 1971; Kruckeberg 1954; Shaw 1990). At the other extreme, plants adapted, both morphologically and by a modified mating system, to specific situations including specific nursery conditions, have probably undergone changes at dozens of loci, or more.

If local adaptation is so precise, and so important, one may expect that disruption of such adaptation would have seriously negative effects. Such disruption can occur by mating between plants that are from very different environments. That is because such mating may be expected to break up the integrated gene complexes that allowed adaptation to a specific locale. That prediction is, in fact, being borne out, and "outbreeding depression" as it is now called is known in several herbaceous species (*Ipomopsis aggregata*, *Delphinium nelsonii*, *Impatiens capensis*) where there is evidence that progeny of plants produced by wide outcrossing between parents separated by about 100 to 200 m in some cases, and as little as 15 to 20 m in others, are poorly adapted to the environment of either parent: they either die off in higher frequencies, or grow more slowly than progeny of crosses between parents 1 to 5 m apart (Schmitt and Gamble 1990) and may be more susceptible to insects and diseases (Whitham 1988).

In conclusion, there appears to be genetic variability where you look for it. Environmental heterogeneity is a good predictor of local genetic variability. Marked differences in exposure, soil conditions, or community structure will be associated with local genetic differentiation in most plants spanning such environmental patchiness. Exceptions seem to involve mostly species that have little variation, such as most aquatic species, those that underwent serious population bottlenecks in the past, or those species which, for a variety of reasons have high levels of phenotypic plasticity.

Practical Applications

Individuals and populations tend to be highly adapted to local environmental conditions. If sampling of a species' gene pool is to be representative of a specific area, such as a National Park, seeds from a few (or many) individuals from one population only will be inadequate. Actual sampling schemes will depend on how the samples are to be used. If severe disturbance occurs, and revegetation must be done, the very best option is to use seeds or plant parts adjacent to the disturbance, and to encourage natural regrowth and regeneration.

If there is revegetation to be done, the very worst option is to use seeds from very far away, even if the seeds come from a "similar" environment because if the non-native plants grow to reproduce, they will introduce new alleles and therefore new features (growth form, flowering phenology, breeding system) into the local populations of the same species. These alleles can have negative effects:

- Local adaptedness of the native populations may be diluted by this gene flow, creating possible problems of diebacks or unexpected poor health in local populations (Schmitt and Gamble 1990). This is difficult to document. However, some European forest biologists think that the large-scale diebacks observed in many native European forests are in part due to the large-scale unplanned and unrecorded moving about of seed sources of many species in the 18th and early 19th centuries. Pollution is undoubtedly a major contributing factor, but poorly adapted offspring of hybrids between very different parental stock may be important as well.
- A related problem is that hybrids between very dissimilar parents may actually be poorly adapted to local herbivores and parasites. As a result, zones of contact between local and non-local plants may become foci of herbivore, parasite and disease activity. This is somewhat speculative, but it is based on studies demonstrating that hybrids between species are indeed more heavily parasitized than is either parent in zones of overlap (Whitham 1989). This has been demonstrated in oaks (*Quercus* spp.), poplars (*Populus* spp.), and in intervarietal hybrids of mice (*Mus*).
- A breakdown of adaptedness at the level of life history (spring-flowering annual versus fall-flowering biennial) is also possible as a result of hybridization. The Mountain Ibex of the Tatra Mountains in Czechoslovakia (*Capra ibex ibex*) was killed off by overhunting. It was successfully reintroduced from nearby Austria. Some years later, to enlarge the herd, *Capra ibex aegarus* from Turkey and *C. ibex nubiana* from Sinai were also brought in. The hybrids were fertile; unfortunately, they rutted in early fall rather than winter, as *C. ibex ibex* do. The kids of the hybrids were born in February, died of exposure, and the whole population went extinct shortly thereafter (Greig 1979).

Seeds or other plant materials for revegetation are often needed in large numbers, and for that reason are likely to come from nurseries. Nursery-grown stock are often exposed, perhaps for several generations, to nursery environments which include regular watering, fertilization and perhaps soil modifications, superimposed on local conditions. Given the heterogeneity of the landscapes of western North America, nursery grown stock from maritime West Coast environments, or even western, mesic Colorado may not be suitable for arid Utah, Nevada or eastern Colorado sites.

Species with small geographic ranges, endemics, which are often rare, tend to have less genetic variability than widespread species and are therefore somewhat vulnerable to abrupt environmental changes. They are worthy of special nurturing and protection in the contexts discussed here.

Different agencies will need to adapt the findings reported to their own specific missions and goals. For example, the National Park Service should be among the most "conservative" of the agencies, because one of its stated goals is to protect the genetic integrity of plants and animals within our National Parks. For this reason, a genetic and evolutionary perspective is needed to recognize that one of the attributes of every species is its genetic heritage, shaped by the local environments. This genetic heritage needs protection as well. Conversely, revegetation of seriously disturbed sites outside of parks, such as the Nevada Test Site and other sites where all native biota was essentially eradicated, need not be as conservative. At least some native plants should be started to prepare a base for the new biological communities that will, one hopes, get established there in the future.

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Genetic Variation and Revegetation Strategies for Desert Rangeland Ecosystems

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Abstract—Emphasis in rangeland revegetation has been placed on the selection of suitable species and on the development of techniques to increase establishment success. While the ecological consequences of deliberate revegetation have been examined extensively, relatively little attention has been paid to the genetic consequences of revegetation. Current interest among revegetation researchers has concentrated primarily on species composition within communities and not on genetic constitution of populations of individual species. Proper formulation of revegetation populations involves consideration of existing variation and accurate sampling of that variation. Improper sampling can lead to inbreeding, reduced genetic variation, poor adaptability, and a decrease in the overall stability of the revegetated ecosystem. Efficient plant breeding systems developed for use with crop plants can be adapted to produce more genetically appropriate populations for use in rangeland revegetation. Modification of one of these systems, Convergent-Divergent Improvement, may be especially effective for constructing genetically variable populations for use in revegetation of the highly diverse environments of arid rangelands.

There have been numerous, largely unsuccessful attempts to revegetate degraded desert rangelands in the southwestern U.S. (reviewed by Cox and others 1982; Cox and Jordan 1983; Roundy and Call 1988). A variety of reasons have been given to explain failures; however, genetic factors associated with the plants used in revegetation have not been implicated. There has been very little formal genetic improvement of plants for use in the revegetation of hot desert ecosystems (Wright 1975; Shiflet and McLauchlan 1986; Voigt and others 1987). Propagules (almost always seed) actually used in revegetation in these environments have been from a variety of sources including local populations of native species, nonlocal populations of native species, and introduced species (Cox and others 1982; Bainbridge and Virginia 1990; Jackson and others 1991).

Researchers have expended tremendous energy evaluating different plant species for use in rangeland revegetation (Cox and others 1982; Call and Roundy 1991; James 1992). In a few cases, individual populations within preferred species have been evaluated for their revegetation potential (Hull and others 1978; McArthur and others 1983; Petersen and others 1987; Cox and others 1990). This evaluation and selection process necessarily involves at least indirect consideration of genetic factors since the differences between species and populations are largely genetically based. However, after species and place of origin, relatively little attention has been paid to the genetic composition of individual accessions of species selected for use in rangeland revegetation. Current interest among revegetation researchers in “biodiversity” (BLM 1990) also concentrates primarily on species composition within communities and not on genetic constitution of populations of individual species.

The methods in which propagules are initially collected and increased for use in revegetation may have significant effects on both success in establishment and long-term persistence of revegetated rangelands. There is some evidence that basic genetic considerations have been ignored during collection and increase of plant materials for revegetation (Millar and Libby 1989). Many of the species used in rangeland revegetation in the United States are developed within public programs, such as the USDA-SCS Plant Materials Program (Shiflet and McLauchlan 1986). The Plant Materials Program has been evaluating plant materials and plant establishment techniques for rangeland or cropland revegetation and critical area stabilization since 1933 (USDA-SCS 1990). In these programs, selected plant materials are produced in adequate quantities to allow for their use in revegetation trials, simulating actual use conditions. Concentrating on the improvement of SCS plant selection and propagation procedures may therefore have a significant direct effect on the genetic health of revegetated rangelands.

We have two main goals in this paper. First we will describe the fundamental genetic principles that should underlie the basic assembly of plant populations for use in revegetation. The possible negative consequences of not observing these principles will be briefly described. We will then present simple plant improvement strategies that may yield broadly adapted, genetically robust populations of self or cross-pollinated plants for use in rangeland revegetation. Throughout, our emphasis is on the use of native plants where genotypes in existing stands (“reference populations” from Aronson and others 1993) can be sampled.

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Genetic Foundations

Evolutionary adaptation to a harsh and variable environment requires populations of organisms with sufficient supplies of genetic variation. This genetic variation represents the building blocks that permit organisms to evolve unique adaptations to the environment. We believe that understanding how genetic variation is organized within natural plant populations will help in developing populations for revegetation use. This should increase revegetation success and the population's long-term ecological vitality.

Genetic variation within plant species is organized hierarchically: among members of a family, among families within a population, among populations within a region, and among regions. The distribution of particular forms of genes (alleles) or genotypes describes the "genetic structure" of a species or population within a particular range of its distribution. Genetic structure of plant populations is largely determined by their mating system—the degree to which plants are self or cross-pollinated (Brown 1990). Effective collection and use of plants in revegetation demands some knowledge of their genetic structure in natural stands. Variation from complete cross-pollination to complete self-pollination (or apomixis) may occur within individual species. However, it is generally possible to roughly place most species within the cross to self-pollinated spectrum using floral, life history, or ecological factors (Loveless and Hamrick 1984). Species that are self-pollinated (or apomictic) tend to grow as disjunct populations. Generally there is very little variation within these populations since most individuals descend from self-pollination of a single individual. Most genetic variation in these species exists between populations. Alternatively, plants that are cross-pollinated tend to exhibit significant genetic variation both among individuals within individual populations as well as between populations (Millar and Libby 1989).

Most self-pollinated species do not exhibit reduced fitness when related individuals are mated ("inbreeding depression") while cross-pollinated species are likely to display inbreeding depression. Because of their sensitivity to inbreeding, much more care must be taken in collecting and propagating populations of cross-pollinated species for use in revegetation. Sampling at least 50 to 100 genotypes that are widely dispersed in the reference population is crucial to avoid inbreeding in succeeding generations (Frankel and Soulé 1981). Similar attention to plant population size is crucial during seed multiplication in cross-pollinated species.

In addition to concerns about inbreeding, adequate sampling strategies are important in both cross and self-pollinated species in order to capture and maintain significant amounts of the genetic variation present in reference populations. Sampling too few individuals causes the population to experience a "bottleneck" and to lose genetic variation simply as a result of sampling error. In cross-pollinated species, loss of genetic variation is proportional to the number of plants sampled (Table 1). When population sizes are routinely low, bottlenecks are faced every generation and the effects are cumulative. This loss of genetic variation reduces long-term evolutionary potential (Frankel and Soulé 1981). With plants used in revegetation, drastic changes in genetic structure will be most deleterious when they occur during initial seed collection. Nothing done during subsequent seed production, short of introduction of additional genetic variation, will overcome initial sampling errors. These changes, referred to as genetic drift, would be associated with unpredictable performance and inability to adapt to changing environmental conditions. Sampling as many plants as possible (>100 individuals) is critical in constructing populations for use in native ecosystem revegetation regardless of mating system, growth habit, or site conditions. This practice minimizes problems associated with inbreeding, loss of genetic variation, or genetic drift.

Maintaining Genetic Variation

It is unclear how frequently genetic structure factors have been considered when plant populations have been constructed for use in revegetation. In the SCS Plant Materials Program, which represents the most organized of such efforts, plant materials are initially collected from a wide range of environments and grown at a common location. Accessions (individual collections) are evaluated for establishment and production characteristics at a single location. The accessions that exhibit superior qualities are placed in advanced tests where adequate amounts of propagules are produced for use in revegetation trials (Shiflet and MacLauchlan 1986). Since 1935 this program has released over 360 accessions for conservation use and greater than 53% of these have been native to the United States (Peterson and Sharp 1992). Traditionally, the SCS Plant Materials Program has compared and selected

Table 1—Retention of genetic variation in small populations (Frankel and Soulé 1981).

	Percentage genetic variation remaining			
Population Size	1 Generation	5 Generations	10 Generations	100 Generations
2	75	24	6	<1
6	91.7	65	42	<1
10	95	77	60	<1
20	97.5	88	78	8
50	99	95	90	36
100	99.5	97.5	95	60

single source populations that exhibited a desired or superior trait. But, it is unclear what portion of SCS releases are from single source populations. For example, 'Vaughn' sideoats grama (*Bouteloua curtipendula*), a widely used native grass, was originally collected from native stands near Vaughn, New Mexico in 1935 and then bulk-increased for commercial use (Hanson 1972). However, records do not state the number of individuals or sample size that comprised this release.

Underlying much of the plant selection in revegetation with native species is the assumption that adaptation to a revegetation site will be greatest in populations native to or adjoining the site (Vallentine 1989; Guinon 1993). Unfortunately, little solid research supports this assumption for highly disturbed desert sites. Limited research indicates that it may not always be true (McArthur and others 1983). While it is not possible to draw firm conclusions, there is some doubt whether single-source or local populations are necessarily optimum for use in rangeland revegetation. Moreover, the range of environments for potential use and the cost of collection and increase of propagules are both likely to be great for populations of plants for use in large-scale (>0.25 ha) rangeland revegetation. Together, these observations may suggest that such populations should have as wide a range of adaptability as possible. Ideally, these populations should contain genotypes adapted to essentially all of the typical native environments of the species. In self-pollinated or apomictic species, such genetically broad-based populations can be created by bulking equal numbers of propagules from representative populations from throughout the range (or a selected portion of the range) of the species. Because intermating between populations would be very infrequent, increase and maintenance of such bulk populations (or their components) would be relatively straightforward. However, because genetic recombination between different populations would be limited, the range of adaptation of the bulk population may be confined to environments very similar to those originally sampled. Genotypes able to successfully exploit intermediate environments may be infrequent. Nevertheless, because the total genetic variation that bulk populations contain will be greater than individual component populations, bulk populations of self-pollinated species should offer increased chances for successful establishment and persistence than populations derived from a single site (Marshall and Brown 1973).

The bulk population concept can be extended to cross-pollinated species with the potential that genotypes with adaptation to intermediate environments can be produced. We propose that this could be achieved by using a plant breeding strategy originally developed for corn (Convergent-Divergent Improvement, hereafter "CDI") (Lonnquist and others 1979). In its simplest form, this procedure is initiated with collection of propagules from populations of the desired species located throughout the targeted range (Fig. 1). This is followed by equal bulking of these propagules and planting at a single location (Convergence) where plants are allowed to randomly interpollinate. Equal amounts of seed (produced from interpollination) from each individual plant is then bulked. This bulk seed is then used at selected locations within the targeted area (Divergence). The "selected locations" are locations that best simulate where the plant is to be used. Equal amounts of propagules (plants or seed) of surviving plants at these selected locations are then collected, brought back to a single location, and planted in a crossing block to simulate and facilitate random cross-pollination (Convergence-cycle 2).

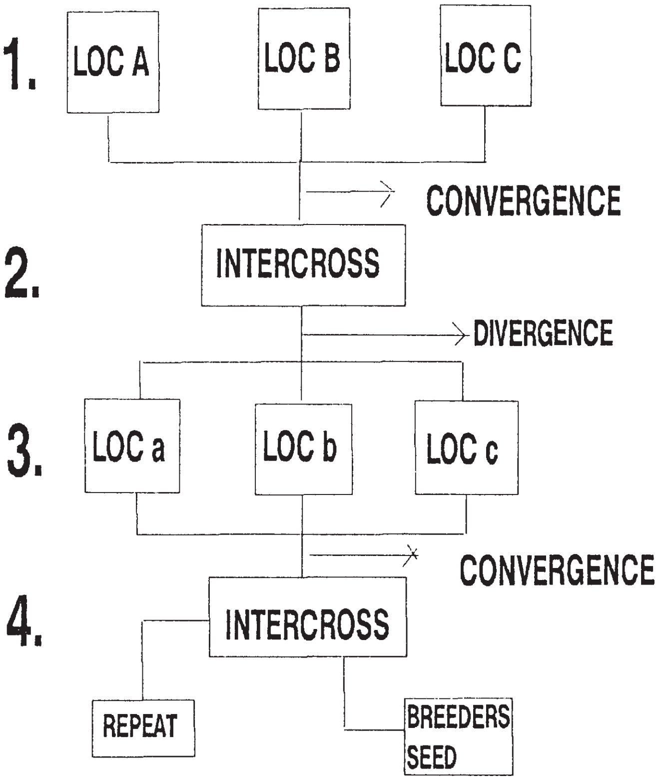

Figure 1—Flow diagram describing the four basic steps in Convergent-Divergent Improvement with populations from three environments. Step 1: Propagules are collected from separate locations within the natural range of the species. Step 2: Propagules are bulked with equal representation of locations, planted at a single location, and allowed to randomly intermate (Convergence). The resulting seed may be released directly for use in revegetation. Step 3: Samples of seed produced in Step 2 are sown/transplanted at locations representative of the environments the improved population would be used in (Divergence). Step 4: Propagules of plants persisting at field locations are collected, bulked, planted at a single location, and allowed to randomly intermate (Convergence). Seed may be released for use in revegetation or subjected to another cycle of divergence.

CDI should result in cross-pollinated populations that have:

- A wide range of genetic variation, including novel genotypes not present in any of the originally sampled populations
- Proven ability to establish at variable locations and environments

- The capability to be no more time consuming or expensive than the traditional SCS-Plant Materials Program methods of selection and increase of single-source populations.

Conclusions

In the SCS Plant Materials Program it may take 12 to 15 years to test, select, and release for commercial production a superior plant material. CDI could reduce this to less than 10 years. Furthermore, the use of bulk populations of self-pollinated species or CDI with cross-pollinated species has the potential to produce a product that has a better chance for successful establishment and persistence, potentially reducing the cost of revegetation projects.

Currently, the Tucson Plant Materials Center is implementing CDI and the production of bulk populations for three species: Spike dropseed (*Sporobolus contractus*); Mesa dropseed (*Sporobolus flexuosus*); and Slim tridens (*Tridens muticus*). By fall of 1995 we will have our initial bulk populations (Convergence) for the above species and will begin planting into their targeted areas (Divergence) by summer of 1996.

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Verification of Germplasm Origin and Genetic Status by Seed Certification Agencies

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Abstract—Federal, State, and private agencies engaged in acquisition, selection, and development of reclamation plant materials have been uncertain as to the degree of development a given germplasm acquisition should undergo, or under what circumstances or nomenclature it should be released to the public, given circumstances where it is needed for specific site restoration but otherwise has limited commercial potential.

The Association of Official Seed Certifying Agencies (AOSCA) has recently published standards which address this problem. These standards outline certification for germplasm of plant materials which have not been developed to variety/cultivar status, but for which there is an immediate need in the reclamation effort. A flow chart with footnotes is presented which summarizes these standards.

Successful reclamation of disturbed sites requires an adequate supply of appropriate plant materials. These may include cultivars of domestic or exotic origin, or may be limited to local native ecotypes.

The traditional approach of plant breeding has been to develop widely adapted cultivars processing outstanding and/or unique characteristics. Such cultivars take many years to test and release, and the projected market demand must compensate for the development costs. Reclamation industry clients now indicate an increasing need for local ecotypes where superior characteristics are secondary to the desire to maintain natural ecosystem integrity. Verification of genetic origin and purity of these germplasms is just as important as it is for traditional cultivars.

Federal, State, and private agencies engaged in acquisition, selection, and development of plant materials for restoration or revegetation have thus been uncertain as to the degree of development a given germplasm acquisition should undergo, or under what circumstances or nomenclature it should be released to the public. They agree that there is justification for a "fast track" alternative release procedure when:

(1) There are inadequate existing commercial sources for a species.

(2) Propagation material of specific ecotypes are needed for ecosystem restoration.

(3) There is high potential for immediate use.

(4) There is limited commercial potential beyond specific plant community sites.

The Association of Official Seed Certifying Agencies (AOSCA) is designated in the Federal Seed Act to certify seed and other propagative materials as to cultivar identity, genetic purity, and high quality standards. Recently, Pre-Variety Germplasm Standards (AOSCA, 1994) have been published for certification of plant germplasms which have not been developed to cultivar status, but for which there is an immediate need in the reclamation effort.

The flow chart (Figure 1, AOSCA, 1994) with accompanying footnotes demonstrates the genetic status, seed certification nomenclature, and tag identification for a germplasm accession as it is developed from a natural species population to either a genetically manipulated cultivar or a non-genetically manipulated "natural" variety.

Seed (or other propagative materials) may be marketed, with proper tag identification, at any of the development stages. "Source Identified Class" denotes germplasm for which no comparisons with other germplasm accessions of the same species have been made, but is verified as to geographic origin. "Selected Class" germplasm has been compared on a common site with other germplasm accessions of the same species and shows promise of superior and/or unique traits. "Tested Class" germplasm has been progeny tested to ensure that superior and/or unique traits are heritable and stable, which makes it equivalent genetically to a variety/cultivar. Projected market demand would determine whether it should be released as a tested germplasm or as a named variety/cultivar.

This seed certification scheme is a practical way for seed buyers to be assured of genetic identity and purity of plant materials which are designated for a "fast track" alternative release procedure and collected from wildland sites or produced in commercial seed fields.

Reference

Association of Official Seed Certifying Agencies, 1994. Certification Handbook, p. 1-10 to 1-12, and p. 2-66 to 2-70.

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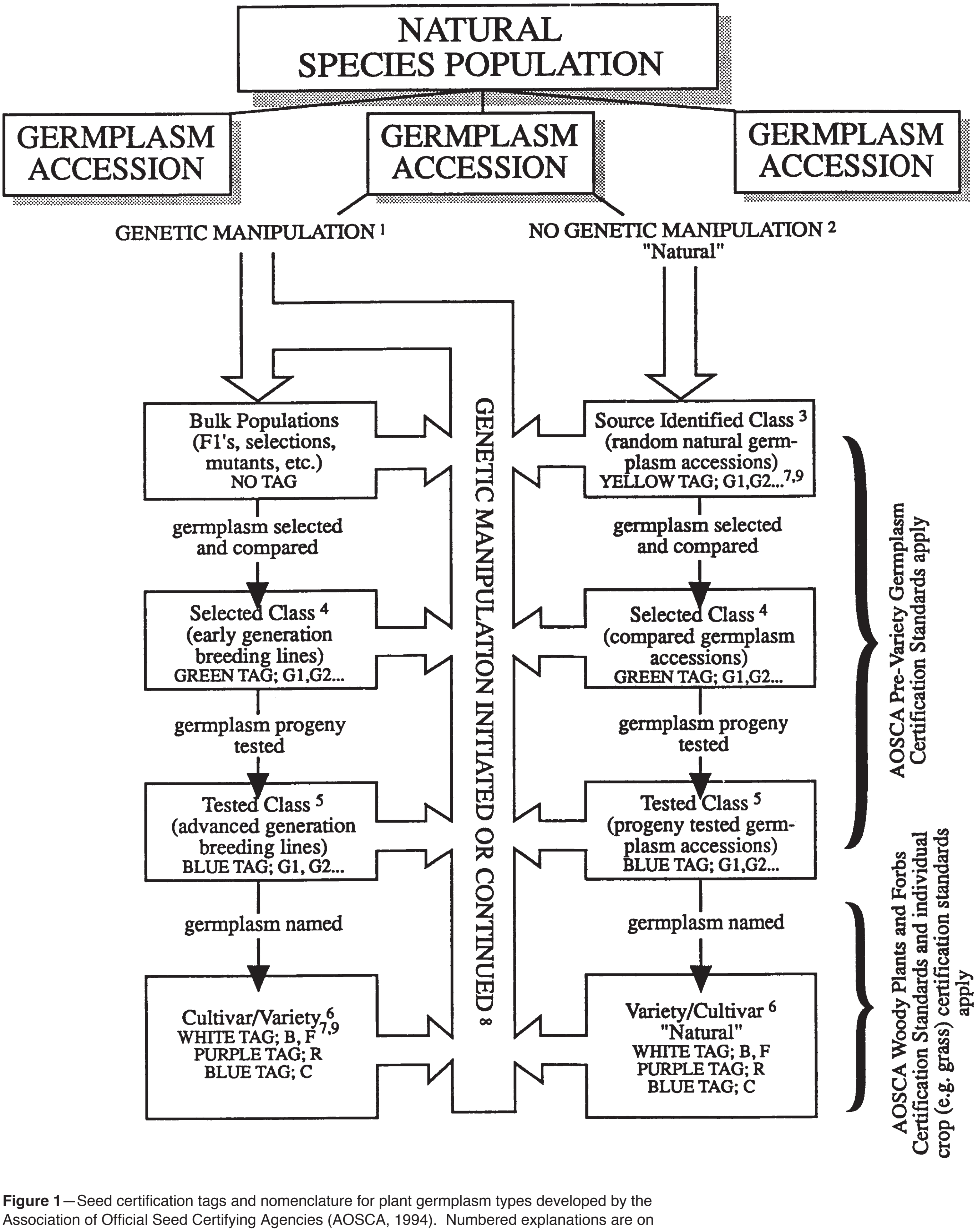

Figure 1—Seed certification tags and nomenclature for plant germplasm types developed by the Association of Official Seed Certifying Agencies (AOSCA, 1994). Numbered explanations are on the facing page.

Numbered Explanations for Figure 1

1. This involves "purposeful selection," such as recurrent selection, crosses within or between species, mutation inducement, biotechnology methods, etc.

2. Protocols should be established to minimize involuntary "non-purposeful" selection. If desired, the "Natural" designation may be printed on Source Identified, Selected, or Tested class or variety/cultivar Foundation, Registered, or Certified tags to indicate the "natural" non-manipulated genetic integrity of the germplasm collection, accession, or ecotype.

3. May be native or naturalized germplasm; wild collected or orchard produced. The Source Identified tag lists geographic location (minimum of elevation and county) of seed collection or production. Comparisons with other germplasm collections, accessions, or ecotypes of the same species not known.

4. Shows promise of superior and/or identifiable traits as contrasted with other germplasm accessions, breeding lines, or variety/cultivars of the species. Selection criteria and supporting comparative data is required. Seed of breeding lines at this stage would be rarely tagged; tagging and marketing wild collected or orchard produced seed of Selected class "Natural" germplasm may be commonly applicable in the reclamation seed industry.

5. Requires progeny testing to prove that traits of interest are heritable in succeeding generations. Testing procedures (number of sites, generations required, etc.) are as outlined for each species by individual seed certification agencies (AOSCA guidelines are being developed).

Tagging of Tested class advanced generation breeding lines may be accommodated, but is normally pre-empted by cultivar release or discarding of the line. Tested class "Natural" wild collected or orchard produced germplasm may be tagged (as is customary for individual forest trees). Named variety release should be considered if the germplasm has been tested in several locations and appears to have wide adaptation and usage demand.

6. Naming and recognition of a cultivar/variety must comply with Federal and State seed law definitions. Source Identified, Selected and Tested class germplasm may have a number or place designation associated with the species/kind listing on the tag (i.e., "ARS 2936 source" scarlet globemallow or "Maybelle origin" antelope bitterbrush), but it is not to be construed as a variety name in commerce.

7. Designation of generations through which germplasms may be multiplied. B = Breeder, F = Foundation, R = Registered, C = Certified. Source Identified, Selected and Tested Classes should use Generation 1 (G1) as equivalent to Foundation, and Generation 3 (G3) as equivalent to Certified. Number of generations allowed for seed production and length of stand for perennial plants varies by species.

8. When germplasm at any stage can be shown to have been significantly altered from the original collection or accession, it loses its non-manipulated "Natural" status and is routed to the bulk population (manipulated germplasm) track.

9. Tags are issued by individual seed certification agencies and clearly state the class of seed in block letters across the top of the tag. Tags also normally display agency insignia or logo along with other information that identifies and/or describes the variety or germplasm.

Management Options

Growing and Harvesting Fourwing Saltbush (*Atriplex canescens* [Pursh] Nutt.) Under Saline Conditions

Earl F. Aldon
J. Rafael Cavazos Doria

Abstract—Fourwing saltbush is an important species in arid and semiarid plant communities. It is palatable to domestic livestock, is drought resistant, and provides good soil protection and food for wildlife. In many areas of the world, lands once used for growing crops are now without any vegetation because of declining water tables, brackish groundwater, saline soil conditions, or combinations of these. Fourwing saltbush can grow in such areas and improve site productivity and stability.

This paper reports the results of studies that explored ways of germinating, growing, and harvesting this plant under varying saline conditions in Baja California. Management implications of these findings are discussed.

In order to determine ways to grow fourwing saltbush under saline conditions, the Rocky Mountain Forest and Range Experiment Station and the Instituto Nacional de Investigaciones Forestales y Agropecuarias have recently conducted three cooperative studies at the Todos Santos Experiment Station near La Paz, Baja California Sur, Mexico. This paper summarizes these studies and outlines management strategies that might be used to grow fourwing saltbush on degraded sites or on abandoned agricultural sites that are no longer able to grow crops due to saline soil conditions resulting from saline irrigation or saline groundwater encroachment.

Fourwing saltbush is a valuable and common shrub on western ranges in the United States and Mexico. It is widely distributed from North Dakota to Oregon and as far south in Mexico as the States of Zacatecas and Baja California (Vines 1960). It occurs in arid and semiarid habitats and is common in grassland and pinyon-juniper woodlands. Scattered individuals may be found in pine and fir forests. It is commonly associated with other *Atriplex* species (Wagner and Aldon 1978). This species and other species of this genus are grown throughout the world in sparsely vegetated areas where extreme conditions of high temperature, soil salinity, and drought persist. Without irrigation these lands often are marginal for anything but grazing (Hyder 1981, Richardson and McKell 1980).

Methods of establishing fourwing saltbush by direct seeding, vegetative propagation, and seedling planting have been determined (Springfield and Bell 1967, Nord and others 1970, Weisner and Wallace 1977, Aldon 1984). Under nonsaline water conditions, it exhibits high germination at 19-21 °C (Aldon 1970).

Direct seeding is less successful than transplants due to low seed germination, inadequate seed bed preparation, and depredation by rodents and lagomorphs (such as rabbits). Transplants can be grown under controlled conditions and planted when soil moisture is optimum and the probability of precipitation is greatest. Repellents can protect transplants from wildlife until the transplants become established (Aldon 1984).

These studies used distilled water or water low in naturally occurring salts. But many lands that were once used for growing crops now have little vegetation because of declining water tables, brackish groundwater, saline soil conditions, or combinations of these factors. In these areas of sparse vegetation, brackish water is sometimes more readily available than fresh water. If plants could tolerate brackish water, then fresh water supplies can be extended. Fourwing saltbush has been shown to be tolerant of highly saline conditions (Osmond and others 1980, Wilkins and Klopatek 1984).

As an example, Stewart (1967), using sprinkler and flood irrigation of saline water on well-drained observational plots in New Mexico found fourwing saltbush transplants grew up to 75 cm in the first growing season and were considered firmly established after $1\frac{1}{2}$ years.

The objectives of the studies reported here were:

Study 1. To test the effect of water salinity on fourwing saltbush seed germination at a temperature known to promote high germination (Agredano and Aldon 1993).
Study 2. To test saline irrigation methods and the survival of two ages of fourwing saltbush seedlings (Cavazos and Aldon 1993).
Study 3. To determine survival and growth of fourwing saltbush subjected to two levels of crown biomass removal using minimum amounts of supplemental saline and fresh water irrigation (Cavazos and Aldon, in press).

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Methods

Study Location

The experiments were conducted at the Todos Santos Experiment Station near La Paz, Baja California Sur, Mexico. Todos Santos, located about 111 km south of La Paz at 15 m above sea level, receives an average of 182 mm of precipitation per year. Average temperature is 22.1 °C with 1738 mm of evaporation per year. The topography is made up of small, gentle hills and crossed with irregular ridges with arroyos, which run after summer thunderstorms. Major associated native vegetation consists of *Pachycereus pringlei, Bursera microphylla, Fouqueria diguetii, Cytocarpa edulis, Lemaireocereus thurberi, Jatropha cinerea, Opuntia cholla, Yucca valida, Cercidium floridum, Simmondsia chinensis,* and *Turnera diffusa*. The dominant soil series is Sierosem, a dark-brown, sandy-textured soil about 2 m deep with a pH of 7.3 to 8.9, low in organic matter, nitrogen, and phosphorous, but rich in potassium.

Daily maximum and minimum temperatures and precipitation are measured at the weather station at the Todos Santos Experiment station yearlong.

Details of the methods used in each study can be found in the references. Only brief outlines of methods will be given here to familiarize the reader with general techniques used.

Study 1 (Agredano and Aldon 1993)

Dewinged seeds obtained from the USDA Soil Conservation Service Material Center in Los Lunas, New Mexico, were used. The seed (from SCS lot number 478837) had 98.95% pure live seed with 40% germination. This New Mexico ecotype was used because it is commercially available and was certified disease-free.

Tests were conducted in a germinator set at a constant 21 °C (Aldon 1970). Scarified and nonscarified seeds (50) were tested in petri dishes. Scarification was done manually with a knife by giving the seed coat a single cut about 1 mm in depth. Treatments consisted of mixtures of distilled water with 0, 10, 15, 25, 50, 75, or 100% by volume of Pacific Ocean seawater. Germinated seeds were counted every day for 30 days. Seeds were considered germinated, and then removed, when roots extended at least 4 mm.

Study 2 (Cavazos and Aldon 1993)

The same source of seeds used in study 1 was used here. Seeds were germinated in a sandy nursery soil having a texture of 97% sand, 0.44% silt, and 2.56% clay that had been fumigated with methyl bromide. The seed bed was saturated with fresh water every other day. All seedlings were transplanted into 800-cm plastic, well-drained containers containing the same soil. Seedlings were grown in nursery beds under plastic shade screens (33% shade). The containers were irrigated three times weekly with 100 ml of fresh water per plant. Two groups of seedlings were grown. One group (small plants) began receiving saline irrigation after 48 days of growth. Plant mean height for this group was 5.2 cm at 48 days. The other group (large plants) began receiving irrigation after 70 days of growth. Plant mean height was 18.6 cm at 70 days. Plant height was measured weekly during the course of the study from the basal stem at ground level to the apical leaf bud.

Plant survival and height were measured weekly. During the eighth week after saline irrigation started, plants were harvested from the containers, washed, dried at 60 °C, and measured for top and root weight.

Seventeen irrigation treatments were conducted on the two plant sizes (Table 1). Treatments consisted of variation in the salinity concentration of the irrigation water and variation in the length of time plants were subjected

Table 1—Irrigation schedules and saline concentrations

	Weeks							
Treatment	1	2	3	4	5	6	7	8
	Saline concentration %							
1	0[a]	0	0	0	0	0	0	0
2	75[b]	75	75	75	75	75	75	75
3	100[c]	100	100	100	100	100	100	100
4	75	75	75	75	75	75	75	0
5	100	100	100	100	100	100	100	0
6	75	75	75	75	75	75	0	0
7	100	100	100	100	100	100	0	0
8	75	75	75	75	75	0	0	0
9	100	100	100	100	100	0	0	0
10	75	75	75	75	0	0	0	0
11	100	100	100	100	0	0	0	0
12	75	75	75	0	0	0	0	0
13	100	100	100	0	0	0	0	0
14	75	75	0	0	0	0	0	0
15	100	100	0	0	0	0	0	0
16	75	0	0	0	0	0	0	0
17	100	0	0	0	0	0	0	0

[a] 0% seawater (fresh water)
[b] 75% seawater (by volume)
[c] 100% seawater

to these concentrations. The control plants received fresh water for 8 weeks from a well that was used for agricultural crops. The other treatments were designed to test two saline concentrations (75% and 100%) for a varying number of weeks, after which fresh water was used for varying number of weeks (1 to 8). The 75% seawater, by volume, was diluted with the same well water. The seawater was obtained from the Pacific Ocean near Todos Santos. Plants were watered three times per week with 100 ml of the designated treatment water.

Study 3 (Cavazos and Aldon, in press)

Seedlings were grown by the same method as in study 2. A 3 X 2 factorial experiment in a randomized block design was used in the field at the Todos Santos Experiment Station. A 1.0-ha area was cleared of all vegetation and leveled. Irrigation furrows 15 cm deep and 24 m long were constructed at 2.0-m intervals over the area. The furrowed area was divided into three blocks to evaluate irrigation water quality. Each block was further subdivided into two harvesting intensity sub-plots (144 m^2 each) replicated nine times. The irrigation water quality levels were:

- Saline well water (Electrical conductivity [E.C.] = 5160 mmoh cm^{-1} and NaCl = 2715 mg L^{-1}).
- Fresh water from the experiment station's water supply.
- No irrigation; natural precipitation only.

The harvesting intensities were:

- 50% of total plant height removed.
- 100% of total plant height removed (everything 10 cm above the soil surface).

Fourwing saltbush transplants averaging 28 cm high were planted 1.5 m apart and 15 cm deep on the ridges above the furrows in October 1990. The planted experiment covered 7776 m^2 and contained 2592 plants.

Gravimetric soil moisture samples (0-30 cm) were taken weekly at random locations along the furrows in each subplot. When moisture levels fell below 5% of field capacity, the plots were irrigated. Irrigation water (saline and fresh) was applied in the furrows at a rate of 1 L sec–1 for about 4-5 minutes to bring soil moisture up to field capacity. Three irrigations were required; in March and July 1991, and in July 1992. Plant crowns were harvested in October 1991 and again in July 1992. A more frequent plant harvesting schedule was planned, but was not possible due to slow growth and high mortality after cutting.

Plant height (from the soil surface to tallest part of the plant) and crown diameter (largest diameter plus smallest diameter/2) was measured monthly on eight randomly selected plants in each sub-plot and averaged. When harvested, the eight plants were divided into leaf/small-branch (<0.05 cm) and large stem portions. Green and air-dry weights of these portions were determined.

Statistical Analysis

An analysis of variance and Tukey's multiple comparisons were conducted in all studies to evaluate treatments. Regression analysis was conducted in study 1.

Results

Study 1

Overall, germination percentages were highest in scarified seeds, regardless of saline concentration (Table 2). Scarified seed averaged 39.1% germination versus 16.4% for nonscarified seeds, for all treatments combined. Both nonscarified and scarified seeds showed primarily a linear decrease in germination percentage with increasing saline concentrations (R = –0.65 and R = –0.83, respectively). However, with scarification there is a general improvement in germination percentage. Mean germination percentages ranged from 16% to 54% in scarified seed, but only from 3% to 22% in nonscarified seed, depending on saline concentrations. These results indicate that it would be possible to germinate fourwing saltbush seeds in areas of high soil salinity concentrations treated with nonsaline water or to use brackish water in nonsaline soils.

Study 2

All large plants survived for the 8 weeks except one plant, regardless of watering regime. Survival showed the effects of salinity on small plants after the second week. Several treatments had zero survival after the second week. Survival of plants irrigated with 100% seawater was less (26% survival, overall) than those irrigated with 75% seawater or fresh water (56% and 100% survival). Little can be ascertained from the survival rates of these smaller plants to

Table 2—Mean germination of *Atriplex canescens* seed after 30 days of treatment with seawater solution at 21 °C constant temperature

		Saline concentrations		Mean % seed germination + se	
Treatments (% seawater)	pH of solution	PPM/L of dissolved salts	Molarity/L	Scarified	Nonscarified
0	6.53	19	0.0060	54.25 ± 3.67	21.80 ± 1.46
10	7.34	3,938	0.1314	46.85 ± 2.24	18.60 ± 2.46
15	7.64	5,901	0.2040	48.45 ± 4.06	19.80 ± 1.69
25	7.91	8,995	0.3099	41.33 ± 2.65	20.00 ± 1.90
50	8.12	15,575	0.5402	31.59 ± 2.86	10.80 ± 0.66
75	8.23	22,196	0.7400	36.78 ± 2.91	20.60 ± 1.86
100	8.29	25,212	0.8810	15.58 ± 1.62	3.00 ± 0.77

offer a recommended watering regime. Plants that survived to the end of 4 weeks made it to the end of the experiment. Therefore, if saline water is used to establish fourwing saltbush, older larger seedlings should be used.

Initially, there was no significant difference in plant height between treatments for large or small plants. After 8 weeks, there was no significant difference in plant height among large plants ($P > 0.05$) (Table 3). Final plant heights for large plants ranged from 24.9 cm to 37.6 cm, with a mean height of 32.4 cm. The small plants showed the effect of saline irrigation versus fresh water after 8 weeks. Those plants receiving saline irrigation grew significantly less than the fresh water control. Small plants continuously irrigated with 100% seawater only grew to 10.9 cm in height, while the control (fresh water only) grew to 36.6 cm.

After 8 weeks, total dry matter production (tops and roots) was significantly different in large plants ($P \leq 0.05$) and ranged from 1.02 ± .12 g (100% seawater only) to 2.95 ± .32 g (100% seawater for 1 week and fresh water irrigation for the remaining 7 weeks). Top weights increase as time and amounts of salinity irrigation decrease.

Total dry matter production of small plants was significantly different ($P \leq 0.05$) and ranged from a low of 0.30 ± .11 g to 2.42 ± .06 g in the control. Top weights accounted for 80% of the total dry matter overall.

Study 3

Transplant height increased slowly during the first 6 months after planting. Transplants averaged 28 cm at planting time and grew about 20 cm during the first winter and spring. Growth accelerated from June to September 1991 (Fig. 1). By the first harvest (October 1991), the plants irrigated with fresh water averaged 78.52 cm in height, and plants irrigated with saline water averaged 82.61 cm. These values were not significantly different, but the plants grown with natural precipitation only were significantly shorter (52.06 cm) ($P \leq 0.05$) (Fig. 1). This would be expected since two irrigations (March and July 1991) had been applied, and after December 1990, very little natural precipitation fell until 80 mm fell in September 1991.

Between the first harvest and just prior to the second harvest, treatment effects became evident. The 100%-cut plants started smaller and stayed significantly smaller than those cut 50% (21.07 versus 41.12 cm) ($P \leq 0.05$).

Plant crown responses were similar to those for plant heights. After a small growth increment in the month following transplanting, crowns remained stable until June of 1991 when branching began. Just prior to the first cutting, there were no differences in average crown diameter due to irrigation (saline water 101.08 cm and fresh water 93.80 cm), but these crowns were significantly larger than crowns on plants with natural rainfall only (69.01 cm) ($P \leq 0.05$).

After 9 months regrowth, crown means were significantly larger on plants cut 50% (59.47 cm) than those cut 100% (37.11 cm). There were no significant differences between the saline and fresh water irrigation treatments, but these crowns were larger than those receiving only natural rainfall (Fig. 2).

Plant mortality was measured at the end of the study (August 1992). Plants with crowns harvested at 50% experienced from 4% to 14% mortality. Plants with crowns harvested at 100% suffered 66% mortality. Mortality was not significantly different ($P > 0.05$) due to irrigation treatment. Termite activity was noted at the base of many of the plants harvested at 100%. It is not known how much these insects contributed to mortality.

As might be expected, soil salinity increased on plots irrigated with saline water. At the 0-30 cm soil depth, the three irrigations caused salinity to increase (E.C. = 698 to 4580 mmohs cm^{-1}). At the 30-60 cm depth, E.C. values from 2062 to 5320 mmohs cm^{-1} were measured at planting and after the third irrigation.

Management Implications

These studies have shown that it is possible to germinate, grow seedlings, and harvest this plant under saline conditions. If possible, these sites should be managed to reduce or eliminate saline soil and water conditions. Where this is difficult, it is possible to germinate scarified seeds at 21 °C and expect more than 40% germination with 25% saline water.

Table 3—Average plant height of small (5.2 cm) and large (18.5 cm) fourwing saltbush seedlings after 8 weeks under different irrigation schedules

Small plants						Large plants					
100% seawater		75% seawater		0% seawater		100% seawater		75% seawater		0% seawater	
Trt.	Plant Ht.	Trt.	Plant Ht.	Trt.	Plant Ht.	Trt.	Plant Ht.	Trt.	Plant Ht.	Trt.	Plant Ht.
#	*(cm)*	*#*	*(cm)*	*#*	*(cm)*	*#*	*(cm)*	*#*	*(cm)*	*#*	*(cm)*
3	10.9a[1]	2	18.8 a	1	36.6 b	3	24.9 a	2	33.2 a	1	34.6 a
5	—[2]	4	11.7 a			5	31.2 a	4	31.2 a		
7	—	6	19.4 a			7	28.3 a	6	29.5 a		
9	—	8	18.1 a			9	33.6 a	8	37.6 a		
11	16.9 a	10	19.8 a			11	31.4 a	10	31.8 a		
13	—	12	13.2 a			13	34.4 a	12	32.2 a		
15	22.8 a	14	—			15	35.1 a	14	32.1 a		
17	—	16	27.6 a			17	35.9 a	16	34.2 a		

[1] Numbers followed by the same letter in a column are not significantly different at the 5% level.
[2] Plant height was not measured due to low survival.

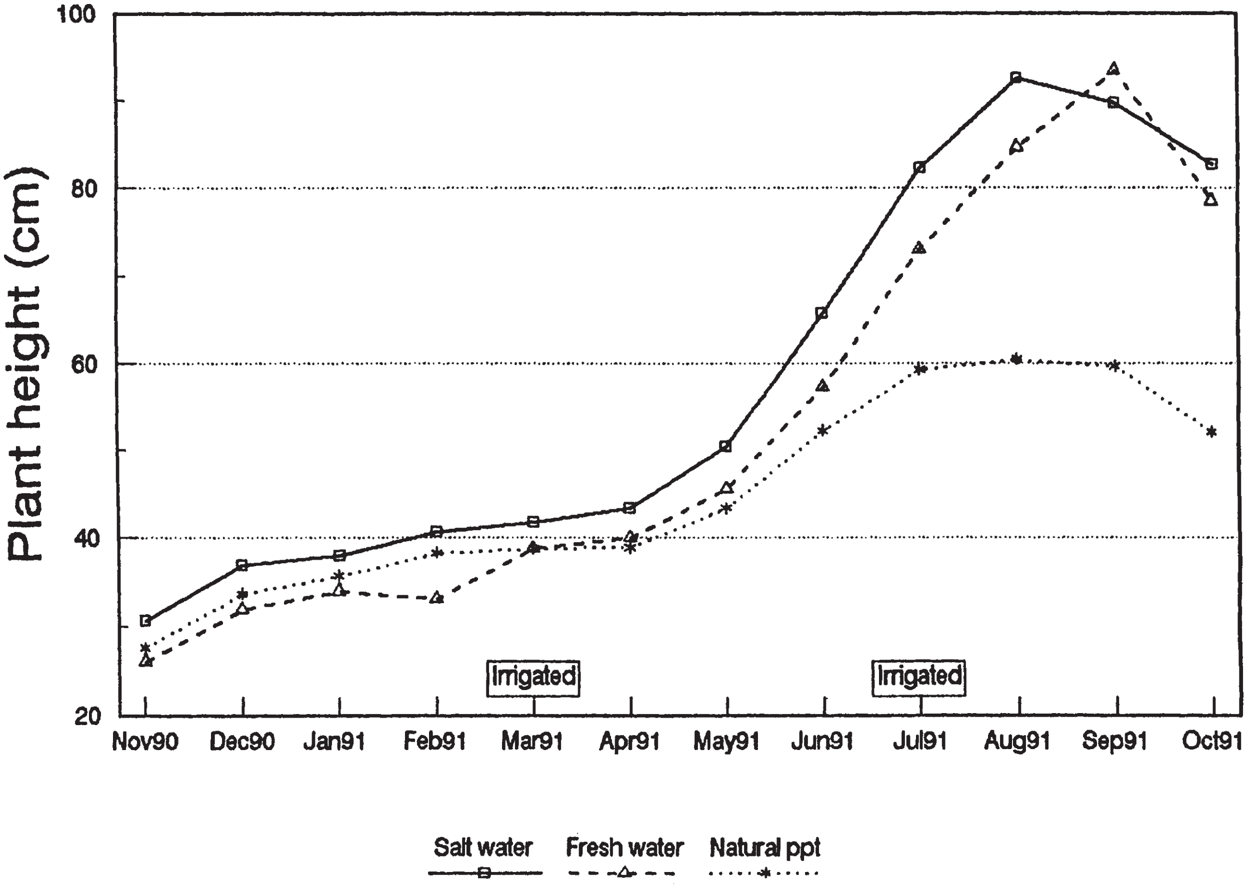

Figure 1—Plant height (cm) of fourwing saltbush grown under three water regimes from planting to the first cut.

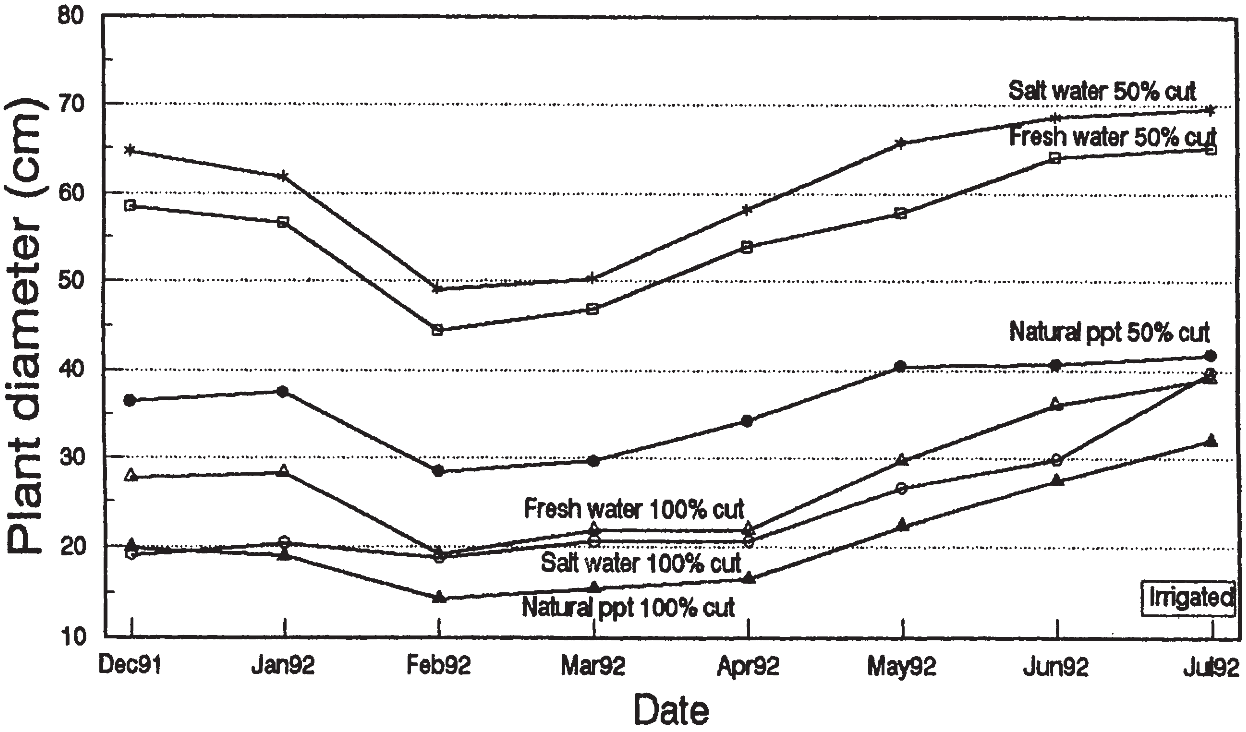

Figure 2—Average crown diameter of fourwing saltbush showing the effects of three water regimes and two harvesting intensities. Data taken after the first harvest to the end of the study.

A critical period then occurs when the seedling is between 30 and 70 days old. During this time, if transplanted seedlings are subject to saline irrigations, high mortality may result. Larger (and older) seedlings tolerate saline irrigations of various concentrations and durations far better than smaller seedlings.

Once plants have been established under saline irrigations, no more than 50% of their crown heights should be harvested yearly. Higher harvesting percentages will result in increased mortality of the plants when saline irrigations are done after soil moisture falls below 5% of field capacity. Plants survived when salt build-up in soils (0-30 cm) resulted in E.C. readings of 4580 mmhos cm^{-1} and (30-60 cm) 5320 mmhos cm^{-1} after 2 years.

Natural precipitation must be relied upon for sustaining these plants in the long run. Infrequent heavy rainfall will reduce saline build-up and maintain and perpetuate stands of fourwing saltbush. Use of saline water should be considered a temporary step to establish this plant on areas now devoid of productive vegetation.

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Is Netleaf Hackberry a Viable Rehabilitation Species for Idaho Rangelands?

Ann M. DeBolt
Bruce McCune

Abstract—Netleaf hackberry's (*Celtis reticulata*) fragmented distribution in Idaho appears to be controlled by a variety of factors. Hackberry is generally restricted to semi-arid portions of the state where temperatures are least severe during the winter months, such as in river canyons and at elevations below 1,500 m. Hackberry occurs in a variety of habitats; however, it is most abundant on sites with a southeast to southwesterly aspect and a rocky surface cover.

Although seeds have low germination rates and individuals are often slow growing, the variable site conditions which hackberry tolerates, in addition to its other positive attributes (landscape structure, wildlife food and cover, resprouting potential), are favorable qualities for rehabilitation species. While experimental study plots are needed to test the species' ultimate suitability for rangeland rehabilitation in Idaho, some general planting recommendations can be made based on the results of this research combined with field observations.

Netleaf hackberry (*Celtis reticulata*) is an irregularly shaped deciduous shrub or small tree in the elm family (Ulmaceae) with a wide but fragmented distribution. It occurs in semi-arid regions of the western United States, in portions of the Great Basin, western Great Plains, Pacific Northwest, and southwestern United States (Lanner 1983; Little 1976; Stephens 1973). However, its distribution becomes especially fragmented near its northern limit in Idaho, Oregon, and Washington.

Hackberry occurs in a variety of habitats, including mountain shrub, deciduous riparian woodlands, and live oak-mixed shrub communities, in rocky canyons, and as scattered individuals in semi-desert grasslands, Joshua tree and pinyon-juniper woodlands (Albee and others 1988; Glinski 1977; Plummer 1977). Populations are often small and highly localized (Daubenmire 1970; Dooley and Collins 1984), particularly near its northern limit (Eliot 1938). Little is known about its ecology, presumably due to its position as a minor component in many of its habitats and its fragmented distribution (Lanner 1983).

Hackberry is sparsely distributed in Idaho (fig. 1), but it exhibits wide ecological tolerances. It is a member of both riparian and upland communities between 250 m and 1,500 m, where it can be a locally abundant, overstory dominant (Huschle 1975; Johnson and Simon 1987). Along the Wiley Reach of the middle Snake River, it forms narrow but extensive gallery forests of nearly pure hackberry (Bowler 1981). On steep shoreline escarpments of the lower reaches of the Snake River, hackberry is characterized by a dense, nearly closed canopy (Huschle 1975). Where it grows on

Figure 1—Distribution of netleaf hackberry in Idaho.

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the gentle shoreline slopes, alluvial fans, and colluvial cones of the lower Snake River, it forms an open savanna (Daubenmire 1970; Huschle 1975).

Hackberry produces a fleshy, orange-red drupe containing a single seed. Fruits ripen in late fall and are dispersed by birds, rodents and other small mammals, and by gravity (Dayton 1931; Lanner 1983; Martin and others 1951). Leaves and twigs are browsed by a variety of wildlife, including bighorn sheep (Rosentreter 1990), elk, mule deer, and wild turkey (Johnson 1990), in addition to domestic livestock (cattle, sheep, horses). Following the removal of aboveground portions by herbivory or other disturbance, plants readily resprout from the root crown or stem base (Carter 1964). Hackberry also commonly resprouts after fire (Armstrong 1980; Carmichael and others 1978; DeBolt 1992).

In addition to food, hackberry provides cover and nesting habitat for wildlife and game species, often on sites where other shrub or tree species are scarce or absent. In the Snake River canyon, Asherin and Claar (1976) documented the importance of hackberry communities for at least 41 species of birds.

Hackberry can persist in the presence of many anthropogenic perturbations and natural disturbances, and it is sometimes the only woody species of any height remaining on degraded rangelands (Daubenmire 1970; Johnson and Simon 1987). Due to hackberry's apparent tolerance of harsh growing conditions, its potential to resprout following disturbance, and its wildlife values, using this species to enhance disturbed habitats is of interest to public land managers. However, little research in this area has been done to date. This study sought to gain some basic knowledge on hackberry growth rates, longevity, and ecological tolerances to evaluate the species' utilization potential for rehabilitation projects in Idaho. This knowledge, in addition to field observations, can help us begin to formulate guidelines for planting netleaf hackberry in Idaho.

Methods

Two hundred forty-one hackberry stands spread over much of the species' range in Idaho, and adjacent Oregon and Washington were sampled ($N = 241$). Stands were selected based on within-site homogeneity of apparent history, topography, and parent material, and a minimum population size of six hackberry individuals (many more individuals were usually present). Sampling areas were typically irregularly shaped and small, usually less than 0.25 ha.

Stands were assigned to the following topographic positions or physiographic classes: river/stream terrace, high water line, rocky draw, bench, toe slope, lower slope, broken lower slope, mid slope, upper slope, talus, and draw. Stand-level data recorded in addition to topographic position included: elevation; latitude; longitude; aspect (converted to a heat load index with values ranging from 0 [NE slopes] to 1 [SW slopes]); slope; percent surface rock cover; parent material; surface soil texture; an assessment of total stand density; an assessment of density within four reproductive classes, including seedling, juvenile, mature, and decadent individuals; topographic shelter; number of cohort modes; grazing intensity; and associated dominant plant species.

Within each stand, a minimum of three individuals, chosen to represent the modal size in the stand, were sampled ($N = 939$). The modal size is defined as the typical size of individuals in the dominant (most abundant) cohort. Measurements recorded for each tree included height, age, diameter at core height (typically 20 cm above ground level), number of live and dead stems, and percent rock cover below the canopy as centered over the main trunk. When two or three modal sizes were present, all modes were sampled, for a minimum total of either six or nine individuals. When stands were all-aged with no apparent modal tree size, at least six individuals of the dominant canopy cohort were sampled. The number of modes present, from 1 to 4, with 4 equivalent to an all-aged stand, was recorded as a stand-level variable. Sampling methodology was identical in overgrazed stands for all variables, although a greater number of trees were typically sampled.

To compare hackberry growth rate differences under various environmental conditions, a 50-year site index was developed as a measure of growth potential (site quality), as outlined in Husch and others (1972). Site index is the most widely used method of evaluating site quality for tree growth (Daubenmire 1976; Husch and others 1972). Utilizing regression analysis, the relationship of tree height to age formed the basis for the index (DeBolt 1992).

A separate stand-level data set was constructed from stand-level variables and averages of tree-level variables. Thus, site index values were averaged for each stand to obtain one variable as the single numerical expression of site quality for a given stand. The original tree level variables were also averaged and included in this data set.

Statistical techniques included one-way analysis of variance (ANOVA), simple linear regression, cross tabulation, and analysis of covariance. All differences were accepted as statistically significant at $p \le 0.05$, unless otherwise noted.

Results and Discussion

Fifty-year old hackberry trees in Idaho averaged 3.9 m tall, while the mean height of dominant and codominant hackberry, regardless of age, was 4.9 m. Site quality, as expressed by the height-based site index, differed among the eleven topographic positions identified ($p = 0.0001, F = 4.4$). However, variation within topographic positions was large so that only draws differed from any other specific topographic position. A general pattern of faster growth where plants were in sheltered and mesic habitats to slower growth on more xeric and exposed sites was identified (highest site index values in draws, lowest values on talus slopes).

An examination of 241 stands and 939 individual trees demonstrated that hackberry is most prevalent on southeast to westerly aspects. Twenty-five percent (60) of the stands were found on SW slopes, with a heat load between 0.95 and 1.00, the hottest values of the heat load index. Only 32 stands (13 percent) were located on the coolest sites between 0.00 and 0.20, or between 350° and 98° east of north. The mean heat load index was 0.69. However,

Table 1—Cross tabulation of the number of hackberry stands by the number of modes and grazing intensity. The hypothesis of independence of mode number and grazing intensity is rejected with $p = 0.0008$.

	Modes			Row total
Grazing intensity	**1 mode**	**2 modes**	**All-aged**	**Row percent**
Low to moderate				
observed	143	23	37	203
expected	149.5	22.1	31.4	85
Severe				
observed	33	3	0	36
expected	26.5	3.9	5.6	15
Column total	176	26	37	239
Column percent	74	11	15	100

aspect was not a good predictor of growth rate, as topographic features appeared to override the influence of aspect, creating growing conditions that are probably not as harsh as they first appear. Under arid and semi-arid conditions, local topography becomes of considerable importance for plant growth, as even the slightest depression can collect run-off and lower temperatures (Heth 1981). Of 241 hackberry stands, 168 (70 percent) had an intermediate or better topographic shelter, although variability within each class of shelter was large ($r^2 = 0.13$).

While hackberry occurs in a variety of habitats, the ground surface is nearly always rocky ($\bar{x} = 39$ percent). Field observations suggest that sites may be even rockier below the surface, with rock possibly serving as a reservoir of subterranean moisture. The presence of rock, particularly bedrock, may in fact be critical for hackberry's existence on certain sites, and at least partially explains its fragmented distribution in Idaho. Other rock-associated species have been observed in semi-arid regions as well.

In the shrub-steppe region of eastern Montana, Rumble (1987) found that scoria rock outcrops provided a unique habitat for several relatively mesic species. Skunkbush sumac (*Rhus trilobata*), chokecherry (*Prunus virginiana*), currant (*Ribes* spp.), and juniper (*Juniperus* spp.) were found only in association with rock outcrops in that ecosystem. He concluded that their occurrence was probably related to protection from wind, snow drift accumulation, shading, and the mulch effects of the rocks. Oppenheimer (1964) and Potter and Green (1964) suggested that the association of mesic species with rocky substrates was due to the temporary water reservoirs that rock fissures provide. In Arizona, Johnsen (1962) reported that one-seed juniper (*Juniperus monosperma*) was largely limited to rock outcrops, where he recorded 2 to 2.5 times as much available moisture. The theory of extra moisture availability in rock fissures could also hold true for the deeply rooted hackberry, helping explain its frequent presence on southerly aspects. Although rock may be important for recruitment, trees show a weak tendency to grow more slowly with a higher surface rock cover ($r^2 = -0.28$, $p = 0.0001$).

In Idaho, hackberry is typically slow-growing and long lived (to 374 years, $\bar{x} = 66$ years). Trees grow best where maximum topographic shelter is present, such as in draws, and where soils are loamy ($p = 0.017$), although variability was high among soil and shelter classes. Site potential was higher on the finer textured soils (clay or loam) than on coarse textured soils (sand), probably because of their greater water-holding capacity and nutrient content (Brady 1974). However, 80 percent of the stands occurred on soils with some sand component, and 30 percent were on sand or coarse sand. The presence of good drainage may be an important limiting factor for hackberry, as the finer textured soils of the uplands were nearly always skeletal.

Hackberry grows on a variety of parent materials in Idaho, including sandstone, granite, alluvium, and basalt. Although no growth rate differences were found among parent materials ($p = 0.43$), individuals growing on sandstone were often shrubbier (greater number of stems) than those on other substrates. The multiple stems probably result not so much from the sandstone as from anthropogenic and geographical factors confounded with sandstone. All sandstone-associated stands were near Boise, where fire frequencies are higher. This resulted in more live and dead stems per individual. Sandstone sites were typically dry uplands away from perennial water sources and draws that act as natural fire breaks.

Few newly established hackberry stands were observed during the study. Within these stands, surface cover was typically rocky, suggesting that rock may provide "safe sites" for establishment. Despite the fact that only six new stands were recorded, populations seem to be maintaining themselves, with juveniles present in the majority of stands. Stands under heavy livestock grazing pressure may be an exception, however, as recruitment was often lower and a single cohort was dominant (Chi-square, $p = 0.0008$) (table 1). Of 239 stands, 36 (15 percent) were on sites classified as severely overgrazed. Overgrazed sites lacked all-aged stands, tending almost completely towards demographic unimodality (92 percent). In contrast, 70 percent of the light to moderately grazed stands had only one mode, 11 percent were bimodal, and 18 percent were all-aged.

Hackberry has a remarkable combination of life history characteristics that make it a promising species for rehabilitation of damaged sites. It is resilient to fire and resistant to grazing pressure once established. While hackberry does not readily colonize new sites, it is quite persistent on the sites where it does occur. This suggests that plantings, with several years of protection, have a high probability of long-term persistence. The wide range of conditions in which hackberry is found imply that rehabilitation will be successful in many different habitats; however, an evaluation of outplanted seedlings across site conditions is needed.

The potential longevity of hackberry, its fruit production for wildlife, tolerance of sites that appear harsh, and the structure and cover it provides are positive qualities for a rehabilitation species in arid landscapes. Until additional studies are conducted, the planting recommendations that follow will provide some guidance for interested land managers.

Recommendations

1. Because of hackberry's low germination rate and generally slow growth rate, introducing the species to a site is best accomplished with seedlings (rather than by direct seeding. An optimum size or age for container seedlings has not been determined, but one full year of growth is probably a minimum.
2. Seedlings should be grown from local seed sources, as the range of adaptability for most hackberry populations is unknown.
3. Seed should be subjected to a cold stratification (with pulp retained) treatment to increase percent germination. Seed less than two years old is probably preferable, as viability declines with age (Bonner 1974).
4. Plant seedlings in the spring on sites with a high percentage of surface rock cover (greater than 25 percent), adjacent to or within portions of rock outcrops with soil, and place rocks around newly planted seedlings. This will increase moisture availability to seedlings and reduce competition with adjacent vegetation. Rock or gravel mulches have been used successfully in Montana (Richardson 1977) and Arizona (Heidman and others 1977) to establish shrub and conifer seedlings.
5. Seedlings should be planted on well-drained soils with an east, south, or west aspect.
6. Seedlings should be planted where surface rock or the surrounding topography provide some shelter from the environment (draws, stabilized gullies, rock outcrops).
7. Seedlings can be planted adjacent to perennial water, but they should be above the zone of extended root saturation.
8. Create small water catchment basins around each seedling when planting. These will capture extra moisture for the seedling.
9. For nursery-grown seedlings, innoculation of soil with local mycorrhizal fungi and other soil microorganisms should be considered.
10. Seedlings and young juveniles are often eaten by rodents, rabbits, and probably livestock. Protecting seedlings from herbivores with mesh "cages" or other such structures should increase the survival rate of hackberry seedlings.

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Browsing by Native Ungulates: Effects on Shrub and Seed Production in the Greater Yellowstone Ecosystem

Charles E. Kay

Abstract—Long-term grazing exclosures were used to compare browsed versus unbrowsed shrubs in the Greater Yellowstone Ecosystem. Deciduous shrubs protected from wild ungulates exhibited significantly greater canopy-cover, height, size, and volume than unprotected plants. Browsed shrub populations were dominated by significantly smaller plants than were unbrowsed populations. Protected shrubs increased in canopy-coverage and size while browsed plants remained static or declined. Ungulate browsing in recent times has virtually eliminated shrub seed production in areas frequented by wintering elk. Shrubs measured inside exclosures produced up to 20,000 times more berries than unprotected plants. Individual unprotected shrubs with a few stems beyond the reach of ungulates displayed a similar pattern. Stems above the browse height (2.5 m) produced an abundance of berries while none were produced on that portion of the plants exposed to browsing. Old photographs and historical journals indicate that tall shrubs and berries were common prior to park establishment, so the present lack of berries and the browsing-stunted shrub growth form were not the conditions prevailing in pre-European times. The virtual elimination of shrub seed production over much of the ecosystem suggests that ungulate populations are not in equilibrium with their food resources, as required under the "natural regulation" paradigm. These circumstances are not unique to Yellowstone. Similar situations exist in other Western States where wild ungulate numbers are at historical highs. At many locations, large populations of native ungulates are having dramatic impacts on shrub growth and seed production. Without adequate seed production and recruitment, existing plants are not replaced when they die, and plant populations cannot be in long-term equilibrium with herbivores or the environment. By reducing or eliminating seed production, native ungulates may render long-term shrub restoration ineffective. The impact of native ungulates should be carefully considered in the planning and implementation of all shrub revegetation projects.

The relationship between vegetation and native ungulates in the Yellowstone National Park—Jackson Hole region has long been a subject of conflicting opinions and intense debate (Chase 1986, Kay 1990). Until 1968, the National Park Service contended that an "unnaturally" large elk (*Cervus elaphus*) population, which had built up in Yellowstone during the early 1900s, had severely "damaged" the park's northern winter range, including deciduous shrub communities. (Terms such as "overgrazing," "range damage," and "unnatural" elk populations are common in all early government reports on the elk herds in the Greater Yellowstone Ecosystem. Since these terms are value-laden, they are used throughout this paper only in their historical context.)

Agency biologists now hypothesize, however, that elk and other animals in Yellowstone are "naturally regulated," being resource (food) limited (Houston 1982). "Natural regulation" was initially formulated using the logistic-growth equation (Cole 1974), but more recently, agency biologists have also cited Caughley's (1976) plant-herbivore model to support their paradigm (Houston 1982). Under "natural regulation": (1) Predation is an assisting but non-essential adjunct to the regulation of ungulate populations. If wolves (*Canis lupus*) were reintroduced into the ecosystem, they would only kill the ungulates slated to die from other causes, primarily starvation, and hence predation would not lower ungulate numbers. (2) If ungulates and vegetation have co-evolved for a long period of time and if they occupy an ecologically complete habitat, the ungulates cannot cause retrogressive plant succession or range damage. The ungulates and vegetation will reach an equilibrium, termed "ecologic carrying capacity," where continued grazing will not change plant species composition. (3) At equilibrium, competitive exclusion of sympatric herbivores due to interspecific competition will not occur. In Yellowstone, this means elk have not reduced the numbers of smaller-bodied ungulates or other animals such as beaver (*Castor canadensis*).

Park Service biologists now believe that elk, vegetation, and other herbivores in Yellowstone have been in equilibrium for the last several thousand years (Despain and others 1986). Any changes in plant species composition since the park was established in 1872 are believed to be due primarily to suppression of lightning fires, normal plant succession, or climatic change, not ungulate grazing. If deciduous shrub communities have actually declined on the northern range because of ungulate browsing, this would be a basis for rejecting the "natural regulation" hypothesis (Houston 1976). Because "natural regulation" is a global equilibrium model, grazing-induced changes in vegetation height or seed production since park establishment would also indicate that the herbivores have not been in equilibrium with their food resources. Therefore, if ungulate browsing on the northern range has changed what were once tall shrub communities into diminutive shrub types or if ungulate browsing has drastically reduced what was once abundant seed

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production, these would be additional grounds for rejecting "natural regulation."

Historically, the Jackson Hole region of the Greater Yellowstone Ecosystem has had an elk situation similar to that on Yellowstone's northern range (Boyce 1989, Kay 1992). At first, it was thought: (1) Jackson Hole was not a historical elk winter range, (2) European settlement forced elk to winter in the valley, (3) supplemental feeding permitted the growth of an abnormally large elk herd which, (4) caused substantial damage to the winter range. But agency biologists now believe: (1) large numbers of elk have wintered in Jackson Hole for the last several thousand years; (2) feedlots have only replaced winter range lost to human developments; (3) therefore, today's elk populations are not unnaturally high, though the distribution of wintering animals may have changed; (4) elk-induced range damage has not occurred; and (5) elk populations would "naturally regulate" if hunting ceased.

This paper explores the impact that native ungulates — elk, moose (*Alces alces*), mule deer (*Odocoileus hemionus*), pronghorn antelope (*Antilocapra americana*), bighorn sheep (*Ovis canadensis*), bison (*Bison bison*)—in and around Yellowstone National Park exert on the growth and sexual reproduction of four deciduous shrubs; serviceberry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*), buffaloberry (*Shepherdia canadensis*), and bitterbrush (*Purshia tridentata*). Long-term grazing exclosures were used to compare unbrowsed versus browsed shrub communities.

Study Areas

The Greater Yellowstone Ecosystem encompasses portions of northwest Wyoming, southern Montana, and northeastern Idaho (Clark and Zaunbrecher 1987). Study sites were located on the winter ranges of both the northern Yellowstone and Jackson Hole elk herds. Elk presently number around 50,000, comprising approximately 80% of all ungulates in the Greater Yellowstone Ecosystem (Kay 1990). Houston (1982) provides a description of the climate, physiography, and vegetation of Yellowstone's northern range while Boyce (1989) provides similar information for Jackson Hole. Location, dates of establishment, and size of the five exclosures used in this study have been summarized by Kay (1990).

Methods

Shrub Growth and Canopy-Cover

Agency files were searched for existing information on each exclosure. Care was taken to locate (1) all prior vegetation data, (2) any written description of permanent vegetation sampling schemes, and (3) any old photographs. Whenever possible, previously established permanent plots were resampled. Unfortunately, only one exclosure (East Elk Refuge) contained permanent transects to measure shrub canopy-cover. Those transects were remeasured during 1987.

Shrub canopy-cover was measured by multiple 30-m line-intercepts (Hanley 1978) inside and outside each exclosure. The height, crown length, and crown width of individual shrubs inside and outside each exclosure were also recorded. All serviceberry, chokecherry, and bitterbrush plants within the Camp Creek (constructed in 1932), Uhl Hill (1963), and East Elk Refuge (1952) exclosures were measured. Outside these exclosures, an adjacent comparable area was delineated on which all shrubs of these species were measured. Because the Mammoth (1957) exclosure contained a large number of buffaloberry plants, random samples of 120 shrubs both inside and outside the exclosure were measured. At the Lamar-West (1962) exclosure, random samples of serviceberry and chokecherry plants were measured inside the exclosure, as were all individuals of those species on an adjacent, outside area.

Berry Production

Except for bitterbrush, berry production data were recorded for all plants measured inside and outside the exclosures. For plants appearing to have fewer than 400 berries, all berries were counted. Plants appearing to have more than 400 berries, but less than 2,000, were divided into quarters and a quarter on each plant was randomly selected. All the berries within that quarter were counted and multiplied by four to estimate total numbers on each plant. Plants appearing to have more than 2,000 berries were divided into eighths, an eighth was randomly chosen on which all the berries were counted, and then multiplied by eight to estimate total berries. Berries were counted while green to minimize removal by birds or other animals. The Lamar-West exclosure was sampled in 1989, while the others were sampled during 1987.

Some unprotected shrubs on Yellowstone's northern range have branches beyond the reach of elk, although such shrubs are rare (Chadde and Kay 1991). On those plants, a few tall central stems are surrounded by a large number of lower, repeatedly browsed stems. Several of these "mushroom" chokecherry plants exist along the park highway east of Slough Creek Junction. To evaluate the effect of browsing on berry production of individual shrubs, the number of berries on all stems above and below the browse height (2.5 m) was recorded for each plant in 1989.

Repeat Photographs

Archival photographic collections at Yellowstone National Park, the Montana Historical Society, the University of Montana, Montana State University, the University of Wyoming, the Colorado Historical Society, the Library of Congress, the National Archives, and the U.S. Geological Survey's Denver Photographic Library were searched for historical photos of the Greater Yellowstone Ecosystem. Approximately 50,000 images were reviewed, but only a small number contained views of deciduous shrub communities. During 1986-1989, the locations in those historic pictures were rephotographed to form sets of comparative photos, a process called repeat photography (Rogers and others 1984). Under magnification, the photo sets were visually evaluated to determine changes in abundance, distribution, and growth form of deciduous shrubs.

Old photographs of the exclosures were obtained from the National Park Service, U.S. Department of Agriculture, Forest Service, and the Montana Department of Fish, Wildlife, and Parks. The locations in those pictures were rephotographed during 1986-1988 to form additional sets of comparative photos. The resulting, multiple-image photo sets were used to evaluate changes inside and outside the exclosures over time.

Results

Shrub Growth and Abundance

Serviceberry, chokecherry, buffaloberry, and bitterbrush inside exclosures had greater canopy-cover, grew significantly taller, and were significantly larger than browsed plants outside exclosures (Table 1). Browsing also affected the height-class frequency distributions of the shrub populations (Figures 1-3). Plant populations outside the exclosures were dominated by significantly shorter height classes than those protected from browsing (all $p < .001$; x^2 test of inside-outside comparisons). The same was true for size and volume-class frequency distributions (all $p < .001$; x^2 test of inside-outside comparisons).

Shrub canopy-cover inside the East Elk Refuge exclosure increased over a 35-year period (Table 2). Highly palatable species such as serviceberry and chokecherry increased from 0.5% to 39.5% average canopy-cover. Repeat photographs of this exclosure taken in 1952, 1957, 1967, and 1987 show that shrubs increased inside while remaining relatively static outside. Repeat photographs taken at the other exclosures show an identical trend. Protected shrubs increased in canopy-cover, height, size, and volume while those outside remained the same or declined. Repeated browsing by native ungulates clearly has had a major impact on Yellowstone's shrub communities and these data support the conclusion of Major and Rejmanek (1992: 149) that the Camp Creek exclosure "illustrates degradation of vegetation ... caused by excessively heavy winter use by large game animals."

Berry Production

Repeatedly browsed shrubs produced practically no berries (Table 1) whereas inside Yellowstone exclosures, there was a positive correlation between the size of individual plants and the number of berries (Table 3). Serviceberry plants outside the Camp Creek exclosure produced an average of 0.07 berries per plant, while protected individuals produced an average of 1,333 berries, a 20,000-fold difference. In most situations, buffaloberry is not eaten by elk (Nelson and Leege 1982), but in Yellowstone this shrub is heavily browsed, as indicated by the plants' severely hedged growth form, as well as their greater canopy-cover and height inside the Mammoth exclosure (Table 1). Buffaloberry plants inside the exclosure produced an average of 1,191 berries per female plant while individuals on the outside produced an average of 2.5 berries, a 476-fold difference. Chokecherry plants outside Yellowstone Park's Lamar-West exclosure produce no berries, while protected individuals produced an average of 2,121 berries (Table 1).

Individual plants with a few stems beyond the reach of ungulates on Yellowstone's northern range showed a similar pattern. Chokecherry stems above the browse height (2.5 m) produced an abundance of berries, while none were produced on that portion of the plant exposed to browsing (Table 4).

Table 1—Effect of ungulate browsing on shrub canopy-cover, height, size (length + width + height), volume (length x width x height), and berry production inside and outside exclosures in the Greater Yellowstone Ecosystem.

Exclosure	Mean percent canopy-cover		Mean height (cm)		Mean size(cm)		Mean volume (m^3)		Mean number of berries per plant	
and species	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside	Outside	Inside
Mammoth										
Buffaloberry	1.0	15.0*	48	133**	278	524***	1.08	6.34**	2.50	1191.46**
East Elk Refuge										
Serviceberry	0.4	13.0*	124***	276**	440***	820**	5.54***	30.22**	13.20***	1300.20**
Chokecherry	0.9	11.9*	121***	282**	341***	730**	3.17***	17.27**	33.40***	1517.00**
Uhl Hill										
Serviceberry	0.7	14.0*	60	143**	192	414**	0.42	3.75**	0.00	104.68**
Chokecherry	2.0	6.5	52	130**	126	376**	0.08	2.34**	0.00	65.08**
Camp Creek										
Serviceberry	0.5	18.5*	32	181**	106	528**	0.09	13.15**	0.07	1333.07**
Bitterbrush	1.3	13.0*	36	86**	221	443**	0.46	3.66**	——	———
Lamar-West										
Serviceberry	0.1	7.7*	20	87**	63	246**	0.01	1.48**	0.00	1110.47**
Chokecherry	0.1	9.8*	25	121**	77	545**	0.02	17.28**	0.00	2121.78**

* Outside-inside comparisons $p < .05$; percentages were arcsine transformed; Student's *t* test.

** Outside-inside comparisons $p < .001$; Student's *t* test.

*** Snowbank site; these plants were partially protected from ungulate browsing by drifted snow.

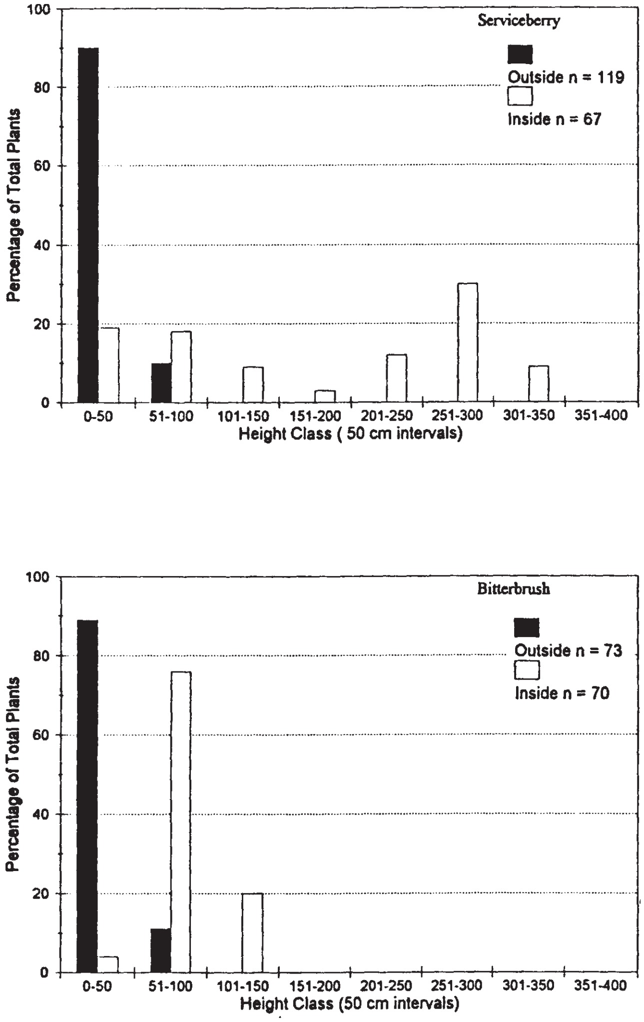

Figure 1—Height-class frequency distributions for shrubs inside and outside the Camp Creek Exclosure in Jackson Hole, Wyoming.

Repeat Photographs

Despite an extensive archival search, few historical photos of Yellowstone's deciduous shrub communities were located. The vast majority of early photographs were of scenic attractions such as hot springs or other thermal features. Relatively few early photographs were taken on low-elevation ungulate wintering areas because hot springs or other scenic attractions, with very few exceptions, are not found there. It also was impossible to identify the species of deciduous shrubs in a number of distant-view photographs taken during the late 1800's. None of the earliest photographers specifically took photographs of vegetation, except when, by chance, their human subjects were posed in front of plant communities (Figure 4).

Nevertheless, I was able to make four repeat photo sets of deciduous shrub communities on Yellowstone's northern range, with the earliest dating from 1872. All the photo sets show that previous tall shrub communities have now been completely eliminated or are presently represented by only a few browsing-stunted stems (Figure 4).

This decline is comparable to that reported for riparian shrub and aspen communities in the park (Chadde and Kay 1991; Kay 1990). Repeated browsing by wild ungulates has virtually eliminated palatable woody plants throughout much of the Greater Yellowstone Ecosystem.

Discussion

Comparison With Other Studies

Numerous authors have demonstrated that browsing by native ungulates can impair the growth of trees and shrubs which may lead to elimination of those species from their natural habitats (Risenhoover and Maass 1987, Putman and others 1989). In particular, elk can have a major impact on plant communities by reducing woody vegetation and promoting grasses through a combination of grazing

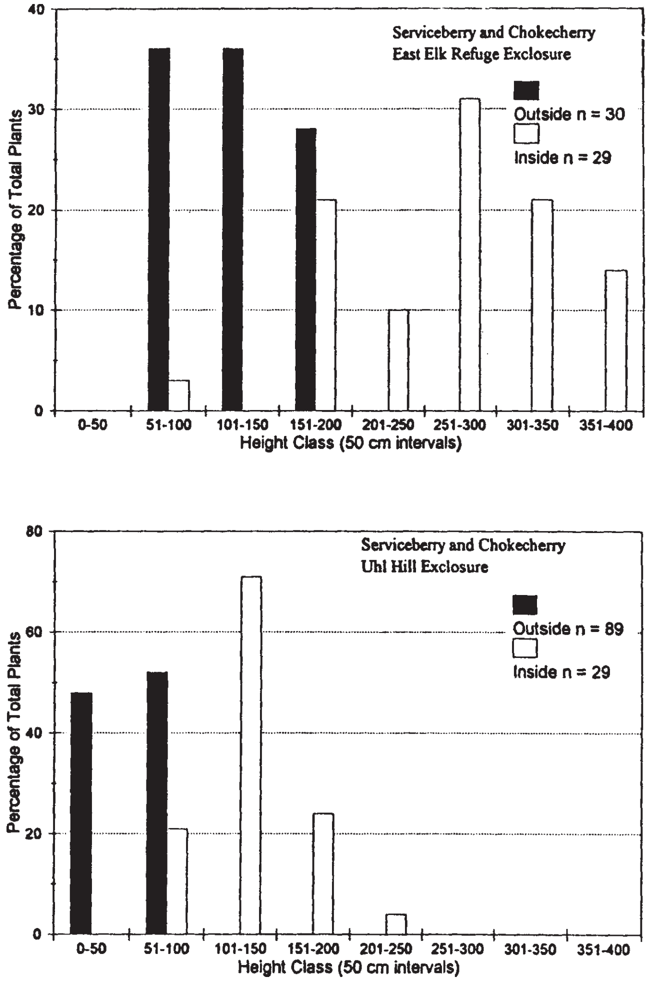

Figure 2—Height-class frequency distributions for serviceberry and chokecherry plants inside and outside two exclosures in Jackson Hole, WY. Plants outside the East Elk Refuge exclosure were taller than shrubs outside other exclosures because they are partially protected from ungulate browsing by drifted snow.

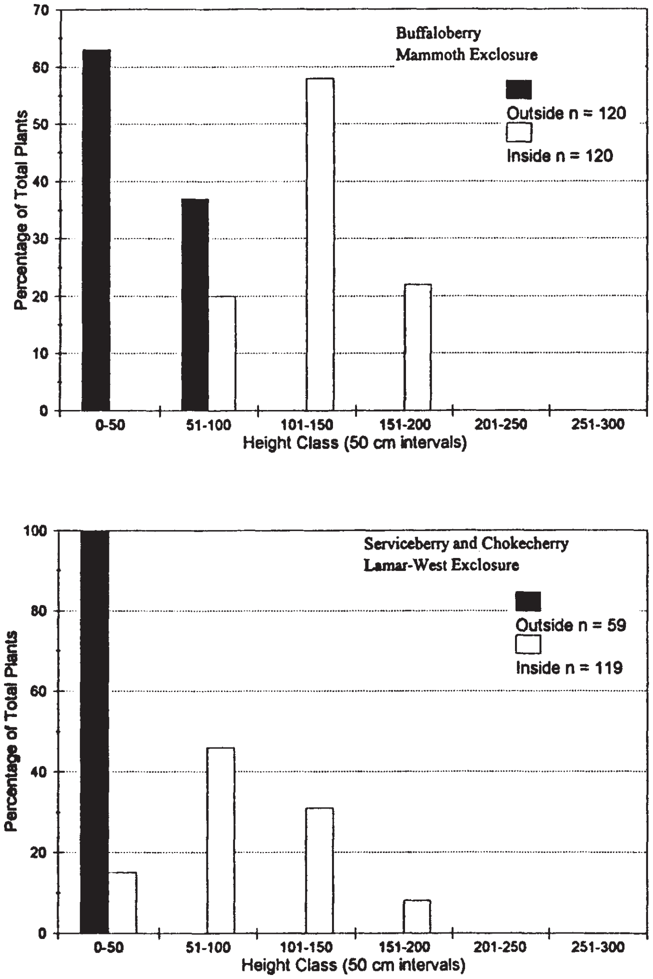

Figure 3—Height-class frequency distributions for shrubs inside and outside two exclosures in Yellowstone National Park.

Table 2—Shrub canopy-cover inside the East Elk Refuge exclosure 1952-1987.

	Percent canopy-cover by year			
Transect and species	1952	1959	1967	1987
G-9				
Artemisia tripartita	2	4	2	0
Symphoricarpos oreophilus	9	7	6	5
Rosa woodsii	8	10	17	43
Chrysothamnus nauseosus	3	2	0	1
Chrysothamnus viscidiflorus	0	0	4	0
Prunus virginiana	1	3	8	35
Ribes spp.	0	3	8	22
Amelanchier alnifolia	0	0	2	16
Subtotals	23	29	47	122
G - 10				
Artemisia tripartita	0	0	3	2
Symphoricarpos oreophilus	18	19	20	22
Rosa woodsii	6	8	16	49
Chrysothamnus nauseosus	11	5	0	10
Chrysothamnus viscidiflorus	0	2	15	0
Prunus virginiana	0	0	2	11
Tetradymia canescens	1	1	1	0
Amelanchier alnifolia	0	2	2	17
Subtotals	36	37	64	111

and trampling (Edgerton 1987; Hanley and Taber 1980; Tiedmann and Berndt 1972).

In response to this concern, wildlife biologists have conducted numerous clipping experiments to determine "proper use" levels for many shrubs because those plants are often key foods for big game during critical winter periods (Aldous 1952; Julander 1937; Lay 1965). In general, they found that most shrubs increase vegetative production under light to moderate clipping. Based on these experiments and field observations, ungulate browsing is thought to stimulate above-ground shrub production. This has been seen as a positive influence by most game managers who often overlook long-term community relationships.

A few researchers, however, have cautioned that browsing may depress seed production and thereby negatively impact plant populations over several generations (Verkaar 1987). Clipping suppressed flowering in many common browse species and most plants produced flowers only on their upper, unclipped branches (Garrison 1953). Simulated winter browsing reduced female ament production in birch (*Betula pendula* and *B. pubescens*) (Bergstrom and Danell 1987), as well as seed production in rabbitbrush (*Chrysothamnus viscidiflorus*) and snowberry (*Symphoricarpos oreophilus*) (Willard and McKell 1978). Hemmer (1975) noted that browsing reduced berry production in serviceberry, while Shepherd (1971) observed that heavy clipping reduced seed production in serviceberry, mountain mahogany (*Cercocarpus montanus*), Gambel's oak (*Quercus gambelii*), bitterbrush, and big sagebrush (*Artemisia tridentata*).

Rodriguez and Welch (1989) reported that ungrazed big sagebrush "produced not only significantly longer seed stalks, but greater numbers of seed stalks per plant than grazed plants." Ungrazed big sagebrush also produced significantly more seeds than grazed plants (Wagstaff and Welch 1991). The shrubby legume engordacabra (*Dalea bicolor*) responded to "moderate browsing by shifting its resources from reproduction to vegetative growth.... Heavily browsed populations sacrifice[d] the ability to increase population size through seedling recruitment in order to tolerate excessive browsing" (Romero-Manzanares and Garcia-Moya 1990).

Katsma and Rusch (1980) reported that simulated winter deer browsing reduced apple production the following year. Ungulate browsing caused a 61-86% reproductive depression in *Rosa canina* (Herrera 1984). Allison (1990a,b) concluded that winter browsing by white-tailed deer (*O. virginianus*) affected Canada yew (*Taxus canadensis*) sexual reproduction by reducing pollen and seed production. On Isle Royale, repeated moose browsing prevented recruitment by balsam fir (*Abies balsamea*) and "no cone production was observed on any browse stunted sapling" (Brander and others 1990). Native ungulates reduced willow seed production from an average of 307,000 seeds per

Table 3—Effect of plant size on berry production inside Yellowstone area exclosures.

Species and size class*	n	Mean (SE) number of berries per plant	
Camp Creek Exclosure			
Serviceberry			
< 254cm	26	0.0	(0)
255 - 635cm	7	299.4	(114.2)
636 - 889cm	19	1285.6	(169.1)
> 889cm	13	2573.5	(183.1)
Lamar-West Exclosure			
Serviceberry			
< 127cm	18	40.7	(15.1)
128 - 254cm	30	455.8	(78.5)
255 - 381cm	21	1583.2	(130.3)
382 - 508cm	5	2883.6	(373.0)
> 508cm	4	6135.8	(1001.0)
Chokecherry			
< 254cm	9	341.1	(109.3)
255 - 508cm	16	769.7	(288.0)
509 - 762cm	9	3277.3	(762.3)
> 762cm	7	6016.7	(861.0)
Uhl Hill Exclosure			
Serviceberry			
< 254cm	3	0.0	(0)
255 - 508cm	10	52.9	(16.8)
> 508cm	5	166.4	(39.1)
East Elk Refuge Exclosure			
Serviceberry			
< 508cm	2	0.0	(0)
509 - 1016cm	7	841.3	(150.1)
> 1016cm	4	2750.0	(603.5)
Chokecherry			
< 508cm	2	80.0	(16.0)
509 - 762cm	7	656.0	(162.5)
763 - 1016cm	5	1652.8	(504.9)
> 1016cm	2	5228.0	(755.9)

*Size class = crown length + crown width + plant height (cm).

Table 4—Number of berries produced above and below browse height (2.5 m) on individual chokecherry plants in Yellowstone National Park.

Plant	Plant size canopy-cover (m^2)	Number of stems above browse height	Number of berries on plant: Within the browse zone	Number of berries on plant: Above browse height
1	6	1	0	50
2	9	4	0	278
3	4	1	0	67
4	12	1	0	96
5	2	1	0	42
6	2	1	0	217
7	12	4	0	461
8	50	5	0	519
9	50	2	0	162
10	70	5	0	329
Mean			0*	222*

*t = 3.88, p < .01

m^2 of female willow canopy-cover to zero in Yellowstone Park (Kay and Chadde 1992).

To the best of my knowledge, no studies of native ungulates have reported the level of reproductive depression in plants encountered in Yellowstone. Even studies of small mammals, birds, and insects have seldom documented the magnitude of seed loss observed in Yellowstone. For instance, Elmquist and others (1987) reported stem girdling by mice reduced willow seed production a maximum of 94%. In Yellowstone, however, ungulate browsing reduced berry and willow seed production by nearly 100%, and based on photographic evidence, few willows on the park's northern range appear to have produced seeds for the last 50 or so years (Kay and Chadde 1992). Similarly, serviceberry and chokecherry plants apparently have produced few berries since the early 1900's (see below).

Mechanisms Limiting Seed Production

Winter browsing limits seed production in at least three ways. First, browsing removes flower buds which developed the previous fall (Garrison 1953: 315-316, Mosseler and Papadopol 1989: 2569). When those plants begin growth the following spring, few flowering buds remain. Lateral buds propagate new leader growth, but they do not produce flowering buds that spring (Childers 1975: 128). Flowering buds most commonly develop on the previous year's growth. If that woody material is consumed by ungulates, those plants cannot flower the following spring and berries or seeds are not produced. Winter browsing removes virtually all of the previous summer's growth on serviceberry, chokecherry, and other deciduous shrubs throughout much of the Greater Yellowstone Ecosystem (Boyce 1989, Houston 1982).

Second, as Harper (1977: Chapter 21) noted, plants allocate resources between vegetal growth and reproduction. Plants which must allocate resources to herbivore-induced vegetative growth are unlikely to bear many berries or seeds (Watson 1984, Watson and Casper 1984). Further, woody plants pass through a juvenile or vegetative phase during which they cannot be induced to flower (Krugman and others 1974; Zimmerman 1972). On Yellowstone's northern range, repeatedly browsed shrubs often exhibit juvenile characteristics (Despain 1989).

Finally, since there is a positive correlation between size of individual plants and size of the fruit crop (Herrera 1984: 390, Peters and others 1988, Table 3), grazing-induced size limitation also reduces the number of berries produced. Because plants outside exclosures in Yellowstone were significantly smaller (Figures 1 - 3), this factor also works to limit berry production. These three mechanisms operate to curtail seed production when plants are exposed to frequent ungulate browsing, as occurs in the Yellowstone Ecosystem.

While this study only measured berry production, there is a correlation between chokecherry, buffaloberry, and serviceberry fruits and seed production. Since chokecherry fruits are a one-seeded drupe and buffaloberry bear drupelike ovoid fruits (achenes enveloped in fleshy perianth), fruit and seed production are equivalent in these

Figure 4—Repeat photo set of aspen and chokecherry on Yellowstone's northern range. (a) In 1893, aspen and chokecherry (solid arrow) showed no evidence of ungulate browsing. Shown are soldiers in Company D of the Minnesota National Guard on patrol. Yellowstone was under military administration from 1866 until 1916 when the National Park Service was established. Photograph by F. Jay Haynes (H-3069), courtesy Haynes Foundation Collection, Montana Historical Society, Helena, MT. (b) That same area 95 years later in 1988. Only a few aspen trees remain and the chokecherry plant depicted in the earlier photo is now represented by a handful of browse-stunted stems. In the absence of fire, conifers have increased markedly and show the effect of repeated ungulate browsing or high-lining. Charles Kay photo No. 3,049-27.

species (Schopmeyer 1974). Serviceberry fruits each contain from 4 to 10 small seeds (Robinson 1986; St. Pierre and Steeves 1990).

Despite a consistent yearly bloom in most shrubs, fruit production is highly variable due to weather and especially late frosts during flowering (Kendall 1986). "In any given locality, heavy crop years are often interspersed by years in which few fruit can be found" (St. Pierre 1989). Thus, seed production probably varies inside the exclosures, but since the shrubs' current annual growth is annually consumed outside the exclosures, few if any seeds could ever be produced by those plants. So, although seed production was only measured in 1 year, the pattern of virtually no seed production outside the exclosures, but seed production within, probably reflects what happens every year. Observations of shrubs at these exclosures in other years and at other exclosures not reported here support this conclusion (Kay 1990). Even after 3 years' protection from browsing, willows in Yellowstone produced few seeds, and it apparently takes newly protected shrubs 10 to 15 years, or longer, to regain their full reproductive potential (Kay and Chadde 1992).

"Natural Regulation"

As has been shown, some serviceberry and chokecherry plants persist on the northern range, but nearly all are less than 0.5 m tall and bear almost no fruit (Table 1). According to the "natural regulation" hypothesis, conditions which exist today are thought to reflect the pristine or pre-European condition of the Yellowstone Ecosystem and, by inference, other ungulate wintering areas throughout the Western United States. Gruell (1979: 67, 1980: 8) contended that a "suppressed growth form from persistent browsing was the historical norm" for serviceberry and other shrubs in Jackson Hole; implying that berries were always rare. Contrary to this claim, however, the Reverend Samuel Parker (1967: 85-86), who traveled through Jackson Hole in 1835, found an abundance of serviceberries and other shrub fruits along the Hoback River near where the Camp Creek exclosure is now located.

In September 1869, the Cook-Folsom-Peterson Expedition encountered Native Americans who were gathering and drying large quantities of chokecherries at the mouth of Tom Miner Creek a few kilometers north of Yellowstone Park. "Here we found a wickiup inhabited by two old squaws who were engaged in gathering and drying chokecherries . . . they had two or three bushels drying in the sun" (Haines 1965: 16). The Washburn Expedition of 1870 reported that near Yellowstone Park "we crossed a small stream bordered with black cherry trees [chokecherries], many of the smaller ones broken down by bears, of which animal we found many signs" (Langford 1972:13). Since shrubs have to be at least 2 m tall before branches are commonly broken down by feeding bears, chokecherry plants in 1870 not only produced abundant berries, but were also much taller than today's plants. Thus, early records suggest that berries were once common in the Greater Yellowstone Ecosystem, and that the present lack of berries was not the condition prevailing in presettlement times. Moreover, all ethnohistoric accounts indicate that Native Americans once gathered large quantities of berries throughout the West, especially serviceberries and chokecherries (Chamberlin 1911; Franzen 1978; Janetski 1987; Lowie 1909, 1924; Murphy and Murphy 1960).

Resource-limited ungulate populations and large quantities of berries are mutually exclusive on most western ranges. Even moderate numbers of ungulates curtail berry production because these plants provide highly preferred forage, especially in winter (Nelson and Leege 1982). Ungulate-induced berry reduction is even reflected in grizzly bear (*Ursus arctos*) food habits. While grizzlies throughout western North America commonly consume large quantities of berries (Dood and others 1986; LeFranc and others 1987), bears in the Yellowstone Ecosystem eat few berries. From 1977 to 1989, over 6,500 grizzly bear scats were collected and analyzed in Yellowstone, yet chokecherries were only reported in one scat, serviceberries in two, and buffaloberries in 51 (Kay 1989).

Without seed production and recruitment, plants cannot be in long-term equilibrium with their ungulate herbivores (Crawley 1992). Repeat photographs dating back to the 1880's of deciduous shrubs in the Greater Yellowstone Ecosystem show that tall shrubs were common when Yellowstone Park was established, but that they have now virtually disappeared. Those photos also demonstrate that shrubs inside today's exclosures have the same height and physical structure as that of shrubs on the open range during the 1870's-1890's. So, present conditions inside the exclosures more closely approximate the level of ungulate use existing when Yellowstone Park was established than do contemporary conditions.

Based on 48 repeat photographs of tall willows (Chadde and Kay 1991) and 81 of aspen (*Populus tremuloides*) (Kay 1990; Figure 4), aspen and tall willow communities decreased approximately 95% since Yellowstone Park was established, due, primarily, to repeated ungulate browsing, not succession, climatic change, or fire suppression. Furthermore, aspen, willows, conifers, and deciduous shrubs depicted in early (1870-1890) photographs show no evidence of ungulate browsing and suggest that large numbers of resource-limited elk did not winter there during the late 1700's up until after park establishment (Kay and Wagner, in press, Figure 4).

Agency biologists have postulated that 12,000-15,000 elk wintered on the northern range for the last several thousand years (Despain and others 1986; Houston 1982), while Boyce (1989) contends that another 15,000 or so elk wintered in Jackson Hole. Some objective measure of pre-European ungulate populations and relative species abundance is needed, however, to determine the level of grazing pressure under which deciduous shrubs have persisted in the Yellowstone Ecosystem. Based on extensive archeological research into aboriginal subsistence patterns in western Wyoming, Wright (1984) concluded that large herds of elk did not inhabit Jackson Hole until the late 1800's.

The available archeological evidence suggests that elk were actually quite rare in the Yellowstone area over the last several thousand years (Frison 1978; Frison and Walker 1984; Harris 1978; Hoefer 1986; Lahren 1976; Walker 1987). Of more than 52,000 ungulate bones identified from over 200 archeological sites in the Intermountain West, only 3% were elk (Kay 1990, 1992). Few elk bones have ever been identified from any of the archeological sites excavated in Jackson Hole (Wright 1984) and only 1% of the ungulate bones found in Yellowstone-area archeological sites have been identified as elk (Kay 1990). Furthermore, aboriginal subsistence patterns indicate that all ungulates were rare throughout this area for the last 9,000-10,000 years (Wright 1984).

This may explain how deciduous shrubs and other woody plants were able to maintain viable populations over the past millennia. These data do not support the "natural regulation" paradigm and would also suggest that some factor besides resource competition was the primary determinant of ungulate abundance and distribution prior to European influence. Elsewhere, I have developed an "Aboriginal overkill" hypothesis to explain the absence of large, pre-Columbian ungulate populations in the Intermountain West (Kay, in press a, b).

Implications for Revegetation and Restoration

Although I measured the impact of native ungulates on shrub growth and seed production only in Yellowstone, those circumstances are not unique to that ecosystem. Similar situations exist in other Western States where big game numbers are at historic highs (Cundy 1989; Davis and Brotherson 1991; Duncan 1975; Schultz and others 1990). At many locations, large populations of native ungulates are having dramatic impacts on shrub growth and seed production (Kay, unpublished photos). Without adequate seed production and recruitment, existing plants are not replaced when they die, and plant populations cannot be in long-term equilibrium with herbivores or the environment. Even where seedlings become established, repeated ungulate browsing can prevent those plants from being recruited into their sexually reproducing populations. Unless corrective measures are taken, I predict that many shrub species will be eliminated from these ranges in the years to come.

Native ungulates may also render long-term shrub revegetation or restoration ineffective by repeated browsing and by reducing or eliminating seed production. The impact of native ungulates should be carefully considered in the planning and implementation of all shrub revegetation projects. In this regard, excessive grazing by native ungulates can be just as damaging as heavy grazing by domestic livestock (Crisp 1978; Crisp and Lange 1976; Roundy and Ruyle 1989; Silander 1983).

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Return of the Native: a Look at Select Accessions of North American Lewis Flax

Stanley G. Kitchen

Abstract—Lewis flax (*Linum lewisii*) is a widely distributed perennial forb in the Western United States. I compared the performance of native Lewis flax accessions with that of the European cultivar 'Appar'. In common garden studies, significant differences in survival, vigor, rust resistance, and seed production were observed among 'Appar' and 14 Lewis flax accessions. Some native Lewis flax accessions compared favorably to 'Appar' for each of these traits. Greenhouse seedling emergence percentages for 12 of 18 Lewis flax accessions were not significantly different than that of 'Appar'. Early seedling growth for six Lewis flax accessions at three field locations was also comparable to that of 'Appar'. Hybridization among accessions possessing desired traits may enhance selection for high performance Lewis flax releases.

Restoration efforts on disturbed lands in the Intermountain West require appropriate seed mixes to obtain the desired community composition. Adapted forb species are an important component of most of these communities, providing diversity and stability. Familiarity with the traits of adapted forb species and their potential is essential in developing expectations for restoration efforts (Kitchen 1994).

Few native forbs have been developed to the point that seed is grown commercially. Cultivars exist for only a few species, including Palmer penstemon (*Penstemon palmeri*), Rocky Mountain penstemon (*P. strictus*), northern sweetvetch (*Hedysarum boreale*), and Louisiana sagewort (*Artemisia ludoviciana*) (McArthur 1988). 'Appar' was released as a broadly adapted cultivar of Lewis flax (*Linum lewisii*). Favorable traits include good seedling vigor, excellent seed production, and a showy inflorescence (Howard and Jorgensen 1980; Shaw and Monsen 1983). However, recent work (Pendleton and others 1993) has clearly demonstrated that 'Appar' belongs to the European species, perennial blue flax (*L. perenne*), and that it is a distinct species from North American Lewis flax. As such, 'Appar' should not be used as a native.

My objective in this study was to compare the performance of populations of native Lewis flax to that of 'Appar' perennial blue flax for traits associated with stand persistence, commercial seed production, and seedling establishment. Results will be used to develop native flax releases for commercial seed production and for restoration plantings.

Materials and Methods

Study Sites

Three field sites were selected to evaluate the growth of Lewis flax in field conditions. Low-elevation sites were selected to test drought tolerance. Brief descriptions of the sites follow.

The Orchard site is 32 km southeast of Boise, ID, and 6.5 km south of the Orchard exit on Interstate 84. Elevation is 970 m. The soil is a deep (rooting depth greater than 1.5 m) sandy loam with good to fair drainage and 0 to 2 percent slope. Seventy-eight percent of the 28 cm mean annual precipitation occurs during winter and spring (November to May). Mean annual temperature is 10.1 °C. Principal perennial species of adjacent, somewhat intact communities include Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), Sandberg bluegrass (*Poa secunda*), and bottlebrush squirreltail (*Elymus elymoides*).

The Nephi site is 13 km southwest of Nephi, UT, on the Utah State University Agricultural Experiment Station's Nephi farm. Elevation is 1,580 m. The soil is a deep loamy clay on a 0 to 2 percent slope. Mean annual precipitation is 34 cm, with 67 percent of the precipitation occurring from November to May. Mean annual temperature is 9.7 °C. This typical basin big sagebrush (*A. tridentata* ssp. *tridentata*) site has been used for testing small grains, alfalfa (*Medicago sativa*), and numerous forage grasses, forbs, and shrubs.

The Skull Valley site is 13 km north of Dugway, UT. Elevation is 1,450 m. The soil is a deep, well-drained sandy loam with a 0 to 5 percent slope. Mean annual precipitation is 18 cm, with 57 percent of the precipitation occurring in winter and spring. Mean annual temperature is 11.5 °C. Few perennials remain on this site due to a history of repeated wildfires and past overgrazing. Before disturbance, vegetation was likely dominated by bottlebrush squirreltail, shadscale (*Atriplex confertifolia*), Indian ricegrass (*Oryzopsis hymenoides*), budsage (*Artemisia spinescens*), and winterfat (*Ceratoides lanata*).

Common Gardens

Common gardens were established with transplants in the spring of 1989 at the Orchard and Nephi sites. Transplants were grown using seed collected from 14 native

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populations and from 'Appar' seed (table 1). Replicated plots of 24 plants each were randomly arranged within three blocks at each site. Each plot consisted of four rows (120 cm spacing between rows) of six plants each (60 cm spacing within rows). Spacing between plots was 150 cm. Individual plants were rated yearly from 1989 to 1991 at the Orchard site and from 1989 to 1992 at the Nephi site. All living plants were scored for vigor on a scale from 1 (low) to 5 (high). The abundance of leaves and stems and their color, flower production, and overall succulence were considered in determining individual plant vigor scores. In 1990 plants at the Nephi site were also scored for rust infection on a scale from 0 (no visible evidence of rust) to 5 (rust infection on more than 90 percent of the plant). All plants at the Nephi site were treated with the systemic fungicide, Plantvax, in May 1990.

Seed Production

Seed production was determined for eight plants of 13 Lewis flax accessions (table 1) and for 'Appar' at the Nephi site during 1990 and 1991. Vigorous, nonborder plants were selected 2 weeks before flowering began. Reproductive stems were counted on each plant after flowering had ceased. Mean numbers of flowers and fruits per stem were estimated by counting aborted flowers and fruits on a subsample of 20 (1990) or 10 (1991) stems from each study plant. Seeds from 20 fruits from each plant were harvested just before capsules were fully ripe. Seeds were counted and divided by 200 to determine percent fruit fill (maximum possible seeds per fruit is 10). After seeds (fruits) had matured and capsules had begun opening, bulk samples were collected from more than 20 plants of each accession. Seed weight was determined with four replications of 100 seeds. Estimates of the total number of seeds and the weight of seeds per plant were extrapolated from these data.

Greenhouse Seedling Emergence

In November 1991, I evaluated seedling emergence in controlled greenhouse conditions (25 °C during day, 15 °C during night) for 19 Lewis flax accessions and 'Appar' (table 1). Fifty seeds of each accession were planted in three replicated rows at a depth of 3.2 cm in well-drained planter boxes. The planting medium was a loamy sand. Row length was 70 cm; spacing between rows was 6 cm. Boxes were watered periodically so soil moisture would not be limiting. Emerged seedlings were counted weekly for 42 days after planting. In addition, germination trials were conducted on each seedlot to determine total germinable seed percentages. Four replications of 25 seeds were placed in Petri dishes on top of two germination blotters moistened to saturation with tap water. Petri dishes were placed in a cardboard box enclosed in a plastic bag and stored in the greenhouse for 21 days. Germinated seeds were counted and removed weekly. Ungerminated seeds were classified as dormant or dead using a simple cut test. Emergence percentages were adjusted by dividing raw emergence percentages by percent germinable for each accession.

Table 1—Site information for 19 Lewis flax seed collections. 'Appar' perennial blue flax seeds were from a commercial lot. Accessions were used in a combination of studies including common garden (1), seed production (2), greenhouse emergence (3), and field seedings (4).

Collection name	County	State	Elevation	Mean annual precipitation	Vegetation type	Studies
			m	*cm*		
Confusion Range	Millard	UT	1,870	22	Saltbush-grass	1,2,3,4
Potosi	Clark	NV	1,850	25	Pinyon-juniper	1,2,3
Burr Trail	Garfield	UT	2,030	25	Pinyon-juniper	1,2,3,4
Yuba Dam	Juab	UT	1,630	33	Sagebrush-grass	1,3,4
Mona	Juab	UT	1,540	34	Sagebrush-grass	1,2,3
Cove Fort	Millard	UT	1,760	34	Sagebrush-grass	1,2,3
Maple Grove	Millard	UT	2,000	36	Sagebrush-grass	1,2,3
Lava Hot Springs	Bannock	ID	1,460	36	Sagebrush-grass	1,2,3,4
Little Antelope Summit	White Pine	NV	2,270	36	Pinyon-juniper-Mountain brush	3
Black Hills	Custer	SD	1,340	36	Ponderosa-mahogany	3
Fort Collins	Larimer	CO	1,760	38	Ponderosa-mahogany	3
Asotin	Asotin	WA	320	38	Palouse grassland	1,2,3,4
Provo Overlook	Utah	UT	1,970	43	Sagebrush-grass	1,2,3,4
Blue Springs Hill	Box Elder	UT	1,570	43	Sagebrush-grass	1,2,3
Hyde Park	Cache	UT	1,540	44	Sagebrush-grass	1,2,3
Richmond	Cache	UT	1,710	47	Sagebrush-grass	1,2,3
Parley's Summit	Summit	UT	2,060	58	Mountain brush	1,2,3
Panguitch Lake	Garfield	UT	2,580	58	Ponderosa-bitterbrush	3
Elk Knoll	Sanpete	UT	3,160	71	Alpine meadow	3
'Appar'	—	—	—	—	—	1,2,3,4

Field Seedling Emergence

Small plots at the Orchard, Nephi, and Skull Valley sites were seeded in October 1991 using seed from six Lewis flax accessions and 'Appar' (table 1). Sites were fallowed to reduce competition from weeds.

On each site, sets of four parallel furrows 5 to 10 cm deep and 45 cm apart were made perpendicular to the prevailing winter wind direction using common farm equipment. Seeds of each accession were planted in three 8-foot plots (four furrows each) arranged in a randomized complete block design. Seeding depth was 1 to 2 cm. Seeding rate was 67 seeds per meter of row. Seedling density was determined in late spring using eight 60-cm subplots randomly located along the seeded rows of each plot. Emergence percentages were calculated from seeding rate and seedling densities. Subjective observations for plant size, stand survival and vigor, and flowering intensity were made in the summer of 1993.

Transplant survival and seedling emergence percentage data were arcsine transformed before statistical analysis. Results of all experiments were subjected to analysis of variance procedures appropriate to the experimental design used. Within a treatment, significant differences among accessions were determined using the Student-Newman-Keuls (SNK) multiple range test. Regression analysis was used to examine the relationship of mortality and vigor to rust resistance at the Nephi garden and the relationship between emergence percentages in the greenhouse and in the field.

Results

Common Gardens

Initial transplant survival (5 months after transplanting) at the Orchard common garden was 19.2 percent. Survival percentages for eight Lewis flax accessions were not significantly different than for 'Appar' (table 2). Mean survival 1 year after planting was 15.7 percent. Most mortality between years occurred among accessions collected from more mesic sites (see mean annual precipitation, table 1). At this time, survival for five Lewis flax collections was not significantly different than that of 'Appar'. Survival after 2 years was less than 5 percent for all accessions, including 'Appar' (data not shown).

Mean vigor of surviving plants at the Orchard common garden in August 1989 ranged from 1.0 to 2.0, with no significant differences among collections (data not shown). In 1990, mean vigor for all accessions was 2.9; mean vigor for 12 Lewis flax accessions was not significantly different from that for 'Appar' (table 2). Lower vigor tended to be associated with collections that experienced the highest mortality between August 1989 and April 1990. At the Orchard site, 'Appar' and Confusion Range were the only accessions that flowered to any significant extent (Kitchen, field notes).

Table 2—Survival and vigor of 'Appar' perennial blue flax and 14 Lewis flax collections at the Orchard common garden (planted March 1989). For all collections, 1991 survival was less than 5 percent. Plant vigor is on a scale of 1 (low) to 5 (high). Within columns, means followed by the same letter are not significantly different at the $P < 0.05$ level (Student-Newman-Keuls multiple range test).

Collection	Transplant survival 1989	1990	Vigor 1990
	- - - - - - -*Percent* - - - - - -		
'Appar'	35a	35a	3.8ab
Confusion Range	33a	31ab	4.1a
Potosi	31ab	28abc	3.4ab
Burr Trail	31ab	26abcd	3.4ab
Yuba Dam	10bcde	10cdef	3.0abc
Mona	26abc	24abcd	3.4ab
Cove Fort	2e	2f	4.0a
Maple Grove	10bcde	8def	3.6ab
Lava Hot Springs	13bcde	10cdef	2.6abcd
Asotin	8cde	7def	2.9abcd
Provo Overlook	25abc	22abcde	3.3ab
Blue Springs Hill	19abcd	15bcdef	1.5cd
Hyde Park	21abcd	9cdef	1.6cd
Richmond	17abcd	7def	1.3d
Parley's Summit	7de	2f	2.0bcd

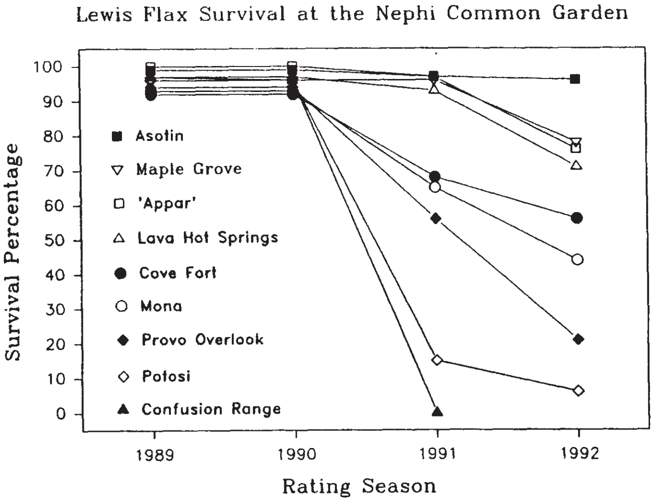

Figure 1—Survival of eight representative Lewis flax accessions and 'Appar' in a common garden near Nephi, UT. Greenhouse-reared seedlings were transplanted in April 1989. Mortality from 1990 to 1992 was significantly correlated with severity of 1990 rust infection ($P < 0.05$, $r^2 = 0.52$). All plants were treated for rust in 1991, minimizing infection.

Transplant survival for all collections at the Nephi common garden 1 year after planting was 95.3 percent. Survival varied greatly among accessions from the summer of 1990 to 1992 (fig. 1). Visible evidence of rust infection was first noted in April 1990; by mid-May rust infection was apparent throughout the garden. Blocks of 'Appar' remained free of any visible evidence of infection, while rust resistance in Lewis flax accessions varied considerably among accessions (table 3). Mortality from 1990 to 1992 was significantly correlated with mean rust index ($r^2 = 0.52$, d.f. = 13) even though fungicide application effectively controlled rust in 1991. All plants of the Confusion Range accession died by 1991. This accession showed the greatest susceptibility to rust.

Significant differences in the vigor of surviving plants were observed each year among accessions at the Nephi site (table 3). In 1989, nine accessions of Lewis flax had mean vigor values that were not significantly different than that of 'Appar'. In 1990, five accessions of Lewis flax had significantly higher mean vigor values than 'Appar' and one had a significantly lower value. Vigor in 1991 was significantly correlated with rust infection of the previous year ($r^2 = 0.61$, d.f. = 12). In 1991, mean vigor for the Maple Grove, Asotin, Hyde Park, and Parley's Summit accessions was not significantly different from that of 'Appar'. These accessions all had low rust indices. 'Appar' remained rust free. Vigor of surviving plants in 1992 was similar for 11 accessions, including 'Appar'. While several accessions had relatively high mean vigor values in 2 or 3 of the 4 years, only Maple Grove scored among the highest in each of the 4 years. 'Appar' scored among the highest during 3 years.

Seed Production

Seed production for 'Appar' was clearly higher than for all other accessions (table 4). However, 'Appar' seeds are smaller than those of all collections of Lewis flax. The gap in seed production between 'Appar' and the Lewis flax accessions is reduced when comparing grams of seeds per plant. Though mean first-year (1990) production was 37 g per plant for the eight most productive accessions of Lewis flax (compared to 53 g for 'Appar'), second year (1991) production was relatively poor or nonexistent for five of those accessions. Data were not taken for four accessions in 1991 because the study plants died. All accessions, including 'Appar', experienced reduced flowering and fruit set percentages in 1991 (data not shown). Two-year per-plant seed production among Lewis flax accessions was highest for the Mona, Maple Grove, Hyde Park, Cove Fort, and Lava Hot Springs accessions.

Seedling Emergence and Growth

Seedling emergence under greenhouse conditions ranged from 18 to 89 percent (table 5). Emergence percentages for 12 accessions of Lewis flax were not significantly different than that of 'Appar'. Seedling emergence in the field varied by site. Mean emergence percentage for the seven accessions at the Orchard site was 18 percent. There were no significant differences among accessions. Mean emergence at the Nephi site was 23 percent. Emergence percentages for the Lava Hot Springs (51 percent) and Provo Overlook (33 percent) accessions were significantly higher than those of the other five collections, including 'Appar'. Mean seedling emergence at the Skull Valley site was 63 percent, significantly higher than at the other two sites. At that site, only the Burr Trail accession had an emergence percentage significantly lower than that of 'Appar'. Combined field emergence percentages ranged from 42 percent for 'Appar' to 22 percent for Burr Trail and were not significantly correlated with greenhouse emergence percentages.

No seedlings at the Orchard and Whiterocks sites survived to the summer of 1993. Observations at the Nephi site revealed vigorous plants of each accession, all of which flowered and produced seed.

Discussion

Factors other than species adaptability affected successful establishment of transplants. Such factors include

Table 3—Mean vigor and rust index of surviving transplants of 'Appar' perennial blue flax and 14 collections of Lewis flax at the Nephi common garden. Plant vigor is on a scale from 1 (low) to 5 (high). Rust index values were scored from 0 (no infection) to 5 (more than 90 percent of plant infected). Within columns, means followed by the same letter are not significantly different at the $P < 0.05$ level (Student-Newman-Keuls multiple range test).

Collection	Mean vigor 1989	1990	1991	1992	Mean rust index (1990)
'Appar'	2.9a	2.1cd	3.9a	2.5abc	0.0g
Confusion Range	2.9a	2.3b	—	—	4.6a
Potosi	2.6abcd	2.2bc	1.4c	2.5abc	1.0d
Burr Trail	2.7abcd	2.0cd	1.6e	2.2abc	1.4c
Yuba Dam	2.9a	2.1cd	1.8e	2.2abc	1.8b
Mona	2.4dce	2.4ab	2.9bcd	2.5abc	1.2c
Cove Fort	2.7abc	2.0cd	2.8cd	2.4abc	1.0d
Maple Grove	2.9a	2.6a	3.4abc	2.6abc	0.4f
Lava Hot Springs	2.5bcde	2.4ab	2.9cd	2.1abc	0.6e
Asotin	2.2e	1.9de	3.3abc	2.9a	0.3f
Provo Overlook	2.8ab	2.1cd	2.4d	2.3abc	1.7b
Blue Springs Hill	2.6abcd	2.0cd	3.1bc	1.8bc	1.0d
Hyde Park	2.4de	2.1cd	3.5abc	2.0bc	0.6e
Richmond	2.9a	1.9de	2.9bcd	1.7c	1.0d
Parley's Summit	2.1e	1.7e	3.6ab	2.2abc	0.1g

Table 4—Seed production per plant for 'Appar' perennial blue flax and 13 collections of Lewis flax at the Nephi common garden. Within columns, means followed by the same letter are not significantly different at the $P < 0.05$ level (Student-Newman-Keuls multiple range test).

Collection	Mean seeds per plant		Seeds per gram	Mean grams per plant	
	1990	1991		1990	1991
				g	
'Appar'	34,012a	23,126a	641	53a	36a
Confusion Range	15,114b	—	465	33abc	—
Potosi	9,548b	—	343	28bc	—
Burr Trail	14,784b	—	428	35abc	—
Mona	14,466b	7,122b	360	40ab	20b
Cove Fort	18,820b	5,626b	474	40ab	12b
Maple Grove	17,323b	8,418b	452	38ab	19b
Lava Hot Springs	13,788b	5,266b	392	35abc	13b
Asotin	7,544b	4,031b	513	15c	8b
Provo Overlook	14,781b	—	365	40ab	—
Blue Springs Hill	16,865b	8,046b	481	35abc	17b
Hyde Park	10,375b	9,871b	362	29bc	27ab
Richmond	10,582b	5,939b	381	28bc	16b
Parley's Summit	8,988b	5,805b	527	17bc	11b

Table 5—Seedling emergence percentages of 'Appar' perennial blue flax and 19 Lewis flax collections in greenhouse and field seeding trials. Within columns, means followed by the same letter are not significantly different at the $P < 0.05$ level (Student-Newman-Keuls multiple range test).

Collection	Seedling emergence			
		Field sites		
	Greenhouse	Orchard	Nephi	Skull Valley
	Percent			
'Appar'	63abcd	21a	18c	88a
Confusion Range	43bcde	19a	14c	66ab
Potosi	89a	—	—	—
Burr Trail	60abcd	8a	14c	43b
Yuba Dam	41bcde	13a	12c	59ab
Mona	67abc	—	—	—
Cove Fort	88a	—	—	—
Maple Grove	68abc	—	—	—
Lava Hot Springs	58abcd	17a	51a	55ab
Little Antelope Summit	59abcd	—	—	—
Black Hills	19e	—	—	—
Fort Collins	18e	—	—	—
Asotin	22de	24a	21c	79ab
Provo Overlook	75ab	24a	33b	52ab
Blue Springs Hill	61abcd	—	—	—
Hyde Park	56abcd	—	—	—
Richmond	52abcde	—	—	—
Parley's Summit	67abc	—	—	—
Panguitch Lake	38bcde	—	—	—
Elk Knoll	24cde	—	—	—

differences in the condition of seedlings when they were transplanted, variability in transplant method among planters, and variability in conditions (such as air temperature) during transplanting. For this reason, caution is required in evaluating differences in 1989 survival data among accessions at the Orchard site. Changes in survival from 1989 to 1990 combined with 1990 vigor scores provide a truer indication of adaptation to xeric conditions, such as those encountered there (table 2). Based on these data, the drought tolerance of several accessions of Lewis flax may equal that of 'Appar'.

Interpreting data from the more mesic Nephi site requires similar caution. In general, accessions from drier collection sites were more susceptible to rust infection and shorter lived than those from more mesic sites. The role of rust in among-accession differences in plant longevity is unknown. However, rapid development and early reproductive maturity would be a great adaptive advantage for accessions from sites where drought is more frequent and more severe. Investment of resources into rust resistance or reserves necessary for long life would be less advantageous at such sites (Fenner 1985). Slower maturing accessions (those with low 1990 vigor or lower seed production) had greater rust resistance and were longer lived. Some of these accessions were from sites that receive up to 50 percent more annual precipitation than the Nephi site.

Because vigor is a qualitative measure subject to considerable bias, comparisons between sites or years should not be made. For example, the overall mean vigor in 1990 was 2.9 at Orchard and 2.2 at Nephi, even though the Nephi plants were undoubtedly larger and more productive than those at Orchard. However, comparisons for the same year and same site are valid because they were made by a single team and completed within 1 day.

Vigor, as we measured it, was affected by several intrinsic factors including resource allocation patterns and resulting growth rate, resource depletion in connection with reproduction, and susceptibility to rust. On the Orchard and Nephi study sites, vigor for most Lewis flax accessions was comparable to that of 'Appar', both when the accessions were grown as transplants and when they were seeded, suggesting that they may have the ability to perform as well as 'Appar'.

Accessions from collection sites receiving 34 to 44 cm mean annual precipitation (the middle of the range for collection sites) had the highest 2-year seed production, although the production was considerably lower than that of 'Appar' (tables 1 and 4). Further work is needed to determine how seed yield might improve if rust were controlled or other culture conditions were improved. Though seed yields for Lewis flax accessions did not equal those of 'Appar', they were probably high enough for profitable commercial production.

Successful seedling emergence in the field is affected by factors that vary among sites and years. None of the seven accessions tested was superior to the rest when all three sites are considered. In addition, there is no correlation between the emergence means for all three study sites and greenhouse emergence success. Greenhouse emergence from deep planting is not likely to be a useful test or selection technique for this species.

These studies suggest that several accessions of Lewis flax have seedling growth capabilities equal to those of 'Appar'. However, single-year emergence percentages for Lewis flax accessions are reduced by the portion of viable seed that remains in the soil seed bank. In controlled germination studies, all Lewis flax accessions expressed some combination of traits that would enable them to maintain a seed bank (Meyer and Kitchen 1994). In this study, 'Appar' lacked this adaptive feature; virtually all seeds germinated at the first occurrence of favorable temperatures. Field retrieval studies at three contrasting sites confirmed the laboratory results. Care should be taken not to lose the capacity for seed banking in Lewis flax releases through intentional or inadvertent selection in an agronomic setting.

It appears that obstacles to the production and use of Lewis flax seed are largely those associated with field cultivation. Some accessions with otherwise favorable traits are quite short lived and susceptible to rust. Other accessions show relatively good rust resistance and longevity but may mature more slowly and produce less seed. The impacts of rust control on seed production are not yet known. There will also be additional costs associated with chemical control of rusts.

Hybridization could be used to pool favorable traits found in Lewis flax as a species. Hybrids that combine high levels of seed production, rust resistance, and drought tolerance are possible. We can only speculate concerning possible compromises to be encountered in such an effort. Broadly adapted collections or hybrids that pose minimal difficulty in seed production need to be identified. This work represents a first step.

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Propagating Bitterbrush Twigs for Restoring Shrublands

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Abstract—There was no significant difference in rooting success between bitterbrush (*Purshia tridentata* Pursh) plants from 7 different locations in southcentral Wyoming. Over 60% of all plants had roots at least 2 cm in length 45 to 60 days following propagation. Transplantation from propagation media to containers had no major negative impact on the plants, based on the 85% survival of all transplanted plants. When plants were subjected to artificial winter conditions of –25 °C, 2 hrs/day for 2 weeks, about 50% survived and resumed growth in the spring. The morphological development that followed exposure to winter conditions suggests propagation by cutting and outplanting prior to winter is a feasible method of preparing containerized bitterbrush plants for field planting.

The increasing demands on rangelands for forage necessitate development of cost-effective and efficient methods of increasing forage productivity. Bitterbrush possesses most of the qualities of a desirable browse plant, and diminishing quantities of bitterbrush within its range has prompted substantial restoration efforts (Nord 1965, Nord et al. 1967). However, increasing bitterbrush production through seeding has been only minimally successful.

For example, Nord (1959) states, "seed production in bitterbrush, an ice cream plant on western ranges, is erratic and unpredictable. Even well-filled seed may be worthless or at best produce seedlings unable to survive under natural conditions." Hubbard (1964) amplified the dilemma by noting that "successful seeding isn't cheap." However, when justifying the economics of a bitterbrush seeding project, he posed the question of what is more expensive: to let deteriorated ranges alone or to restore them.

Failure or minimal success in bitterbrush restoration has been associated with rodents, jackrabbits, grazing ungulates, and insects (Hubbard 1964). Because of the limited success in reseeding bitterbrush, a more viable alternative for bitterbrush establishment may be propagation from stem cuttings (Nord 1959).

However, no study has reported success of propagated stems upon transplantation and survival once plants are subjected to winter conditions. Guidelines on soil chemical composition necessary for continuous growth of the transplanted plants is also missing. Therefore, the objective of this study was to determine methods of enhancing bitterbrush stem propagation, winter survival, and transplantation success.

Methods

During the spring of 1989, bitterbrush populations representative of distinct geographical ranges, elevations, vegetation types, plant morphology, and soil factors were selected in 7 areas within southcentral Wyoming. From each population, 10 mature, vigorously growing plants were selected, and 10 current growth, unbrowsed twigs (total of 100/population), at least 10 cm long, were cut with a heel of last growth in late June 1989. Heels from older wood facilitate leader growth (Nord 1959). At this time, the twigs were capable of withstanding water and nutrient shortage and propagating under a conducive environment. The twigs were put in a cooler containing ice to avoid excessive loss of water.

Propagation procedures followed those recommended by Nord (1959). Heels were moistened with water, and dipped in a common rooting hormone preparation containing 0.3% indol-3-butyric (IBA) acid in talc. Stem origin was labeled on a plastic board. Cuttings were randomly planted 2 to 4 cm deep in propagating flats at a greenhouse in Laramie.

The rooting medium had equal amounts of sand, sponge rock and vermiculite with a pH of 7.0. To avoid or minimize root disease, a fungicide was applied to the soil. The chemical composition of the soil used is shown in Table 1. Temperature was maintained at 20 to 25 °C, and plants were watered daily until roots developed after 45 to 60 days. Cuttings were transplanted to labeled containers in mid-August and grown for 5 months with 3 watering days/week before they were gradually introduced to winter conditions.

In February, the plants were subjected to 8 hours of daylight at 2.2 °C, and watered once a week for 30 days. Plants were put in a freezer at –25 °C, 2 hours/day for 2 weeks before returning them to 2.2 °C, 8 hours of daylight for 2 weeks. From April to June, plants were grown at 20-25 °C, watered twice a week, and kept in weed free conditions.

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Table 1—Characteristics of the soil used after propagation.

Chemical Composition	
Total nitrogen (NO_3N; ppm)	18.5
Avail. phosphorus (PO_4P; ppm)	12.0
Potassium (K; ppm)	331.0
Iron (Fe; ppm)	4.1
Zinc (Zn; ppm)	4.6
Organic matter (OM; %)	2.6
pH	7.5
Electrical conductivity (ds/m)	1.5
Texture	
Sand (85%); silt (10%); clay (5%)	
Soluble Cations	
Sodium (Na; meq/l)	2.1
Calcium (Ca; meq/l)	19.1
Potassium (K; meq/l)	1.2
Magnesium (Mg; meq/l)	2.1
Extractable Cations	
Sodium (Na; meq/100g)	0.5
Calcium (Ca; meq/100g)	20.7
Potassium (K; meq/100g)	<0.1
Magnesium (Mg; meq/100g)	0.7
Cation Exch. Cap. (meq/100g)	7.4

Results and Discussion

There was no significant difference in rooting success between plants from different locations. Over 60% of all plants had roots at least 2 cm in length 45 to 60 days following propagation. This rooting success was about twice that achieved by Nord (1959) using 9 cuttings as opposed to the 700 used in this study. Nord (1959) reported better rooting success with 0.1% of indol-3-butyric acid compared to 0.3%. Transplantation from propagation media to containers had no major negative impact on the plants, based on the 85% survival of all transplanted plants.

By February, when bitterbrush plants would have lost their leaves in the field, about 40% of the plants had green leaves. Also a living plant could not be differentiated from a dead one easily in those plants with no leaves. Thus, no estimate on the actual number of living plants was obtained before artificial wintering. However, all plants were subjected to artificial winter condition. About 50% survived and resumed growth in the spring. Higher survival may be possible with a less rigorous wintering process. Two months after the wintering process (June), the regrowth height ranged from 20 to 26 cm with a mean of 23.1 ± 6.1 cm; overall leaf length ranged from 13.6 to 19.7 mm with a mean of 16.2 ± 2.0 mm; leaf width (based on widest part) ranged from 7.0 to 9.6 mm with a mean of 8.3 ± 1.6 mm. The morphological development that followed exposure to winter conditions suggests propagation by cutting and outplanting prior to winter is a feasible method of preparing containerized bitterbrush plants for field planting.

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Restoring Shrub Quality in a Sagebrush-Bitterbrush Vegetation Type of South-Central Wyoming

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Abstract—This study was conducted in south-central Wyoming over a four-year period to determine N, P, ash, and in vitro dry matter digestibility in bitterbrush (*Purshia tridentata* Pursh.) following 2,4-D and mowing treatments to reduce sagebrush density. Nitrogen and phosphorus contents of untreated bitterbrush varied among years in the summer, but not the winter; ash and in vitro digestible dry matter contents varied among years in the winter, but not during the summer. Forage quality of treated bitterbrush increased significantly during the first growing season following treatment, decreased to untreated plant levels in the dry, second growing season, and increased again with higher precipitation in the third and fourth year following treatment. Small scale improvements systematically located on a rotational basis over a large area each year will provide continuous high quality forage for range herbivores.

In Wyoming, and throughout most of the western rangelands, winter range is usually the most critical habitat for big game. Generally, these rangelands are dominated by monotypic stands of sagebrush (*Artemisia* spp.), a relatively less palatable species than those associated with it. Livestock ranges often are managed by employing sagebrush eradication to delay its inevitable reinvasion. However, this is detrimental to the winter range of big game species since sagebrush provides browse during periods of deep snow and cover for hiding and thermal protection.

Given these important contributions of sagebrush to winter wildlife ranges, a management approach is needed that focuses on reduction rather than eradication. By manipulating sagebrush density to obtain the optimum "mix" (Hobbs et al. 1981) of browse species, rangeland stewards may achieve the highest quality of habitat on a nutritional basis (Wallmo et al. 1977). Wildlife habitat that provides nutritious forage improves the winter survival chances of game animals, since their survival depends on the conditions under which they begin the winter season (Wallmo et al. 1977). Therefore, the objective of this study was to investigate the response of nutritional values of bitterbrush (*Purshia tridentata*) for several seasons (winter 1985-86 through summer 1989) after the application of 2,4-D and treatment by mowing.

Herbicide application on old-growth stands rejuvenates shrubs for big game and stimulates new growth from sprouts (Valentine 1989). When applied at optimum environmental and plant physiological conditions (i.e., minimal drift and before maximum translocation, respectively) 2,4-D reduces sagebrush considerably, with a slight reduction in bitterbrush (Kituku 1988). In addition, bitterbrush twigs from plants sprayed with 2,4-D contained a higher nutrient content than twigs from untreated plants (Kituku and Powell 1990).

Improvement of range forage value follows mechanical treatment (Everitt 1983, Powell and Box 1979). Mowing also rejuvenates shrub plants (Hiehle 1961). An earlier study (Schneegas and Zufelt 1965) reported that mechanical manipulation of bitterbrush in early spring produced a 47% increase in current twigs during the first growing season. However, long-term results were not evaluated.

Methods

Study Area

This investigation was conducted on Cedar Creek Ranch, south-central Wyoming, an area used by big game in the fall, winter, and spring, and by cattle in summer. The elevation ranges between 2,100 and 2,600 meters. Most of the precipitation in this region falls as snow, ranging between 380 and 480 mm annually. Soils are North Park Formation brown sandy loams developed on loess, limestone, sandstone, and tuff (Dunnewald 1957). Dominant plant species include bitterbrush, mountain big sagebrush (*A. tridentata* subsp. *vaseyana*), Idaho fescue (*Festuca idahoensis*), sandberg bluegrass (*Poa secunda*), canby bluegrass (*P. canbyi*), western wheatgrass (*Agropyron smithii*), bluebunch wheatgrass (*A. spicatum*) and thickspike wheatgrass (*A. dasystachyum*).

Experimental and Sampling Design

Four different sites were selected within the study area to serve as replications. Three treatments, untreated, 2,4-D, and mowing, were applied to areas of 3 to 6 hectares on each site, providing 12 experimental units in a randomized block design (Steel and Torrie 1980). In the summer of 1985, preliminary soil and vegetation surveys were conducted to describe the 12 relatively homogeneous units.

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Three permanent belt transects, each measuring 100 m x 1 m, were established in each of the 12 units. Each unit was surveyed to provide detailed soil and vegetation descriptions along the same belt transects.

The chemical treatment was applied in mid-May 1986 when the environmental and plant physiological conditions were most suitable for minimal drift and maximum translocation following recommendations set forth by Alley (1965). This procedure achieved the project objective, in that it maintained bitterbrush in the mixed shrub vegetation type and minimized forb kill while reducing sagebrush cover to a maximum of 15 to 20%.

Mowing was done with a rotary blade shredder in late May as soil moisture conditions permitted. The stubble height was 2 to 3 cm above the ground. This enhanced rapid regrowth during the year of treatment, minimized rock damage to the mower, and decreased treatment time. A 265 Massey Ferguson Model 1538 tractor with power take-off provided power.

Samples of bitterbrush twig parts similar to those consumed by browsing animals were collected in late winter and late summer (1986 to 1989) for laboratory analyses. Each sample collected was put into a labeled paper bag and taken to the laboratory where it was dried until no change in weight at 65 degrees C., ground through a Wiley Mill with a 40 mesh screen, and stored in labeled airtight papers until analyses could be done. Analyses were conducted in duplicate samples and the values were averaged. Ash, nitrogen, phosphorus, and in vitro digestibility were determined following the Association of Agricultural Chemists (1980). In vitro dry matter digestibility was determined using the technique described by Tilley and Terry (1963).

Long-term (i.e., 1961-89) and study period (i.e., 1986-89) data on precipitation and temperature were obtained from the Saratoga Weather Station 25 km west of the study area.

Statistical Analysis

The response variables in this study were nitrogen, phosphorus, ash and in vitro digestible dry matter contents in bitterbrush twig tips and leaves. Analysis of variance was conducted using sites (replications, 4), treatments (3), years (4), and seasons (2) as the independent factors.

Results

All differences discussed are significant at the 5% level of confidence unless otherwise indicated. The following abbreviations and terms are used: site = replication and "sprayed" = application of 2,4-D. Means ± standard errors are shown.

Untreated Plants

The mean nitrogen content of untreated bitterbrush current growth (i.e., twigs and leaves) for all sites, years, and seasons in the study area was 1.42 ± 0.026 % (Table 1).

Table 1—Mean (± SE) chemical composition (%) of untreated bitterbrush twig tips and leaves for different years and seasons. Those means for different years or for different seasons followed by a different letter are significantly different at the 5% level.

Year	Summer	Winter	Mean
		-------------------------%-------------------------	
		Nitrogen	
1986	1.49 ± 0.015 b	1.35 ± 0.017 a	1.41 ± 0.29 ab
1987	1.43 ± 0.019 b	1.35 ± 0.019 a	1.39 ± 0.019 b
1988	1.53 ± 0.014 ab	1.21 ± 0.027 a	1.37 ± 0.062 b
1989	1.66 ± 0.074 a	1.32 ± 0.037 a	1.49 ± 0.075 a
Mean	1.53 ± 0.029 a	1.31 ± 0.018 b	1.42 ± 0.026
		Phosphorus	
1986	0.123 ± 0.005 b	0.115 ± 0.003 a	0.119 ± 0.003 b
1987	0.103 ± 0.003 b	0.110 ± 0.007 a	0.106 ± 0.004 b
1988	0.203 ± 0.013 a	0.120 ± 0.004 a	0.161 ± 0.017 a
1989	0.200 ± 0.012 a	0.120 ± 0.007 a	0.160 ± 0.016 a
Mean	0.157 ± 0.012 a	0.116 ± 0.003 b	0.137 ± 0.007
		Ash	
1986	3.53 ± 0.075 a	3.00 ± 0.000 a	3.26 ± 0.105 a
1987	3.75 ± 0.250 a	2.25 ± 0.250 b	3.00 ± 0.327 a
1988	3.39 ± 0.129 a	2.44 ± 0.058 ab	2.91 ± 0.190 a
1989	3.88 ± 0.194 a	2.66 ± 0.077 ab	3.27 ± 0.250 a
Mean	3.63 ± 0.093 a	2.59 ± 0.094 b	3.11 ± 0.114
		In Vitro Digestible Dry Matter	
1986	44.08 ± 1.00 a	39.81 ± 0.46 a	41.94 ± 0.95 a
1987	47.19 ± 0.67 a	35.36 ± 1.80 ab	41.27 ± 2.41 a
1988	45.05 ± 0.44 a	34.70 ± 0.22 b	39.88 ± 2.05 ab
1989	44.94 ± 0.91 a	32.35 ± 0.40 b	37.89 ± 2.15 b
Mean	44.94 ± 0.51 a	35.55 ± 0.86 b	40.25 ± 0.98

Nitrogen contents ranged from 1.21 ± 0.027% in the winter of 1988 to 1.66 ± 0.074% in the summer of 1989. The annual mean of both seasons was highest in 1989 and lowest in 1988. Nitrogen contents were only slightly lower in winter (1.31 ± 0.018%) than in summer (1.53 ± 0.029%) indicating the persistence of relatively high forage value of bitterbrush browse into winter.

The mean phosphorus content of untreated bitterbrush current growth for all sites, years, and seasons was 0.137 ± 0.007% and ranged from 0.103 ± 0.003% in the summer of 1987 to 2.03 ± 0.013% the following summer. Differences among phosphorus contents in different years and seasons were relatively greater than those of nitrogen.

Unlike the nitrogen and phosphorus contents, ash contents varied among years for the winter season, but not for the summer season. Ash contents for all sites, years, and seasons averaged 3.11 ± 0.114% and ranged from 2.25 ± 0.250% in the winter of 1987 to 3.88 ± 0.194% in the summer of 1989.

The mean in vitro digestible dry matter (DDM) contents of bitterbrush current growth for all sites, years, and seasons was 40.25 ± 0.98% and ranged from 32.35 ± 0.40% in the winter of 1989 to 47.19 ± 0.67% in the summer of 1987. Year X season interaction was significant because DDM contents varied among years in the winter, but not during the summer. DDM contents were about 10% greater in the summer than in the winter.

Using the annual mean of each forage quality factor as a basis for comparison between seasons, the difference in nitrogen, phosphorus, ash, and DDM contents between summer and winter seasons was 15%, 30%, 33%, and 23% of their annual mean values, respectively. Compared to other browse plants in the Intermountain area, bitterbrush appears to be of medium forage value.

Treated Plants

Nitrogen Content—Bitterbrush nitrogen contents varied among sites in the winter, but not in the summer, although the difference in nitrogen contents on site 1 and on site 4 in the winter was relatively small (Table 2). Mean values for all sites, treatments, and years for different seasons were similar to those for untreated plants.

Nitrogen contents in bitterbrush plants sprayed with 2,4-D were higher than those in either mowed or untreated plants the year of treatment. There were no differences among treatments the following two relatively dry years, but nitrogen contents in mowed plants were lower than those in untreated plants in 1989, a relatively wet year. In general, treatments had relatively little effect on nitrogen contents in any year.

The greatest differences in nitrogen contents were among years in the summer season, with no significant differences occurring among years in the winter. The year of treatment, 1986, was much wetter than the following year.

Phosphorus Contents— Phosphorus contents in the regrowth of mowed bitterbrush plants was greater on site 4 than on site 1; however, there were no significant differences in phosphorus contents among sites for untreated or sprayed bitterbrush plants (Table 3). Site 4 was relatively more productive with deeper soils than site 1 whose soil profile contained between 30 and 60% stones.

Differences among phosphorus contents for different sites were also significant during the summer, but not during the winter season. Bitterbrush plants on site 4 contained more phosphorus in the summer than did those bitterbrush plants on site 1.

A significant treatment X season interaction occurred because untreated plants had the lowest phosphorus contents in the summer and the highest in the winter, whereas regrowth on mowed plants had the highest phosphorus contents in the summer and the lowest contents in the winter. The year X season interaction for bitterbrush plant phosphorus contents, including treated as well as untreated plants, was similar to that for untreated plants.

Ash Contents—The year X season interaction for bitterbrush plant ash contents for treated and untreated plants was significant at the 15% level and generally similar to that for untreated plants (Table 4). However, the effects of differences in site productivity on ash contents were more pronounced when both treated and untreated plants were analyzed together. A treatment X year X season interaction was significant at the 15% level. Ash contents were different among years on site 1 and site 4, but not on site 2 or site 3.

Table 2—Mean (± SE) nitrogen content (%) of bitterbrush twig tips and leaves for different sites, treatments, years, and seasons. Those means for each different main effect followed by a different letter are significantly different at the 5% level.

Season	Site	Site 2	Site 3	Site 4	Mean
			%		
Summer	1.55 ± 0.036 a	1.53 ± 0.034 a	1.56 ± 0.035 a	1.60 ± 0.052 a	1.56 ± 0.020 a
Winter	1.31 ± 0.020	1.29 ± 0.023 ab	1.29 ± 0.023 ab	1.27 ± 0.017 b	1.29 ± 0.010 b
Mean	1.43 ± 0.032	1.41 ± 0.031 a	1.43 ± 0.035 a	1.43 ± 0.044 a	1.43 ± 0.018
Year	**Control**	**2,4-D**	**Mowing**	**Mean**	
1986	1.41 ± 0.029 c	1.59 ± 0.099 a	1.51 ± 0.066 b	1.51 ± 0.042 a	
1987	1.39 ± 0.019	1.39 ± 0.030 a	1.42 ± 0.041 a	1.40 ± 0.018 bc	
1988	1.37 ± 0.062	1.37 ± 0.052 a	1.34 ± 0.063 a	1.36 ± 0.033 c	
1989	1.49 ± 0.075	1.45 ± 0.067 ab	1.36 ± 0.066 b	1.43 ± 0.040 b	
Mean	1.42 ± 0.026 ab	1.45 ± 0.035 a	1.41 ± 0.031 b		
Season	**1986**	**1987**	**1988**	**1989**	
Summer	1.67 ± 0.045	1.46 ± 0.024 c	1.51 ± 0.011 bc	1.60 ± 0.036 ab	
Winter	1.34 ± 0.008	1.34 ± 0.010 a	1.21 ± 0.013 a	1.27 ± 0.022 a	

Table 3—Mean (±SE) phosphorus content (%) of bitterbrush twig tips and leaves for sites, treatments, years, and seasons. Those means of main effects followed by a different letter are significantly different at the 5% level.

Site	Control	2,4-D	Mowing	Mean
	- - - - - - - - - - - - - - - -	- - - - - - - - -%-	- - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - -
1 0.141	±0.016 a	0.137 ± 0.013 a	0.126 ± 0.012 b	0.135 ± 0.008 a
2 0.133	±0.010 a	0.139 ± 0.013 a	0.145 ± 0.018 ab	0.139 ± 0.008 a
3 0.137	±0.018 a	0.129 ± 0.013 a	0.140 ± 0.013 ab	0.135 ± 0.008 a
4 0.135	±0.016 a	0.144 ± 0.013 a	0.149 ± 0.019 a	0.143 ± 0.009 a
Mean	0.137 ± 0.007 a	0.137 ± 0.006 a	0.140 ± 0.008 a	0.138 ± 0.004
Season	**Site 1**	**Site 2**	**Site 3**	**Site 4**
Summer	0.153 ± 0.013 b	0.163 ± 0.011 ab	0.162 ± 0.012 ab	0.173 ± 0.012 a
Winter	0.117 ± 0.004 a	0.114 ± 0.004 a	0.109 ± 0.002 a	0.112 ± 0.003 a
Season	**Control**	**2,4-D**	**Mowing**	**Mean**
Summer	0.157 ± 0.012 a	0.161 ± 0.009 a	0.171 ± 0.010 a	0.163 ± 0.006 a
Winter	0.116 ± 0.003 a	0.114 ± 0.003 a	0.109 ± 0.002 a	0.113 ± 0.002 b
Season	**1986**	**1987**	**1988**	**1989**
Summer	0.143 ± 0.006 b	0.113 ± 0.004 c	0.194 ± 0.005 a	0.202 ± 0.008 a
Winter	0.113 ± 0.002 ab	0.105 ± 0.003 b	0.117 ± 0.003 a	0.116 ± 0.003 a
Mean	0.128 ± 0.004 a	0.109 ± 0.003 c	0.156 ± 0.008 a	0.159 ± 0.010 a

Ash contents were generally highest on site 1 and lowest on site 4. This trend was opposite of that for phosphorus contents on site 1 and site 4.

In Vitro Digestible Dry Matter Contents (DDM)—In vitro digestible dry matter contents were also higher in bitterbrush plants on site 1 than in bitterbrush plants on the other three sites (Table 5), although differences were relatively small (i.e., < 2%). In 1986, the year of treatment, DDM contents were lower in untreated plants than in sprayed growth or mowed regrowth; however, differences among treatments were not significant at the 5% level in any following year of the study. When DDM contents of both treated and untreated plants were averaged across sites and treatments, the differences among years were accentuated. This was primarily because of a greater number of degrees of freedom in the analysis of variance. Digestibility declined over time for both treated and untreated plants.

This decline over the four-year study was more pronounced in the winter than in the summer. In the summer, DDM contents declined only about three percentage points, whereas in the winter DDM contents declined about 7.5 percentage points.

Discussion

Both nutrient content and digestibility of bitterbrush twigs declined significantly after the first growth season following manipulations. The later (1989) increase in nutrients may reflect the increase in precipitation, rather than being an effect of treatment. Bitterbrush nitrogen content values in this study generally are similar to those reported by other researchers. Bitterbrush nitrogen contents on similar sites in Colorado ranged from 1.70% to 1.23% during early to late winter (Dietz, et al. 1962). During summer, values were reported as high as 1.86% on one site and 2.14% on another. All of these values indicate the importance of bitterbrush's contribution to the 1.42% nitrogen requirement recommended for wintering sheep (NAS-NRC 1975), especially if sheep select twig tips and leaves.

Table 4—Mean (±SE) ash content (%) of bitterbrush twig tips and leaves for sites, treatments, years, and seasons. Means for different main effects followed by a different letter are significantly different at the 5% level.

Year	Summer	Winter	Mean	
	- - - - - - - - - - - - - - - -	- - - - - - - - -%-	- - - - - - - - - - - - - - - -	- - - - - - - - - - - - - - - -
1986	3.84 ± 0.07	3.00 ± 0.00	3.42 ± 0.09 a	
1987	3.58 ± 0.15	2.42 ± 0.15	3.00 ± 0.16 bc	
1988	3.45 ± 0.05	2.34 ± 0.04	2.89 ± 0.12 c	
1989	3 .72 ± 0.11	2.54 ± 0.05	3.13 ± 0.14 b	
Mean	3.65 ± 0.05 a	2.57 ± 0.05 b	3.11 ± 0.07	
Year	**Site 1**	**Site 2**	**Site 3**	**Site 4**
1986	3.43 ± 0.20 a	3.43 ± 0.20 a	3.43 ± 0.20 a	3.38 ± 0.20 a
1987	3.33 ± 0.33 a	3.17 ± 0.31 a	2.83 ± 0.31 a	2.67 ± 0.33 b
1988	2.89 ± 0.26 b	2.93 ± 0.27 a	2.91 ± 0.27 a	2.85 ± 0.23 b
1989	3.07 ± 0.22 ab	3.07 ± 0.17 a	3.07 ± 0.32 a	3.32 ± 0.40 a
Mean	3.18 ± 0.13 a	3.15 ± 0.12 a	3.06 ± 0.14 a	3.05 ± 0.15 a

Table 5—Mean (±SE) in vitro digestible dry matter contents (%) of bitterbrush twig tips and leaves for sites, treatments, years, and seasons. Those means of main effects followed by a different letter are significantly different at the 5% level.

Site	Mean			
	%			
1	41.43 ± 1.09 a			
2	40.30 ± 1.26 b			
3	40.16 ± 1.11 b			
4	40.23 ± 1.20 b			
Mean	40.53 ± 0.58			
Year	**Control**	**2,4-D**	**Mowing**	**Mean**
1986	41.94 ± 0.95 b	44.87 ± 1.40 a	43.75 ± 0.98 a	43.52 ± 0.67 a
1987	41.77 ± 2.41 a	41.70 ± 1.71 a	40.68 ± 2.24 a	41.22 ± 1.18 b
1988	39.88 ± 2.05 a	39.43 ± 2.19 a	39.60 ± 2.42 a	39.63 ± 1.23 c
1989	37.89 ± 2.15 a	37.11 ± 2.31 a	38.25 ± 1.84 a	37.75 ± 1.17
Mean	40.25 ± 0.98 a	40.76 ± 1.05 a	40.57 ± 1.00 a	
Year	**Summer**	**Winter**		
1986	46.19 ± 0.64 a	40.84 ± 0.42 a		
1987	46.44 ± 0.51 a	36.00 ± 0.80 b		
1988	45.36 ± 0.34 a	33.91 ± 0.48 bc		
1989	43.03 ± 0.47 b	32.47 ± 0.65 c		
Mean	45.25 ± 0.31 a	35.81 ± 0.55 b		

Bitterbrush twigs in sprayed areas appeared to have more leaves per stem than did twigs from mowed areas, which had fewer leaves per stem, but much larger stems. The greater leaf:stem ratio on sprayed areas would have increased the nitrogen content in samples of leaves and twigs similar in extent to those browsed.

Excessive stem growth resulting from a high level of precipitation in June 1986 may have caused a dilution effect of the nitrogen absorbed by roots of mowed bitterbrush plants. Rapid elongation of sprouts during the first growing season after top removal is not uncommon for many shrub species, especially during years of adequate soil water (Box and Powell 1965, Powell, et al. 1972).

In addition, herbicide kill of shrubs appears to produce a fertilization effect on plants not affected by the herbicide (Powell and Box 1979). The decrease in bitterbrush nitrogen content on sprayed areas from 1.59% in 1986 to 1.39% in 1987 indicates that any fertilization effect had dissipated by the second growing season. However, a significant increase in nitrogen content in bitterbrush occurred in 1989 compared to the previous two years. However, this could be due to relatively high precipitation received in 1989.

After the season of growth following treatments, treated bitterbrush twigs showed little difference in nutrient contents compared to untreated bitterbrush twigs. The same trend was reported by Everitt (1983) and by Powell and Box (1965) on browse species in south Texas. Shredded plant regrowth increased nutrient contents soon after shredding, but after 6 to 9 months there was little or no difference in nutrient content when compared to untreated plants.

In the present study, ash contents in bitterbrush twigs were not affected by range manipulations. The mean value of 3.11% ash is relatively low compared to ash values in herbaceous plants, and the 2.29% range in values is considered to be relatively unimportant.

Ash content can vary with water content (Nord 1965). In Nevada, bitterbrush ash contents ranged from 2.11% to 2.48% in March, and from 3.31% to 4.04% in September (Tueller 1979). In this study, ash values were lowest when plant water content was lowest during the relatively dry winter seasons of 1987-89. Ash contents in bitterbrush twigs during the growing seasons showed the same trend of ash/plant water relationships. The summer seasons of 1986 and 1989 had higher precipitation and, as such, ash contents in bitterbrush twigs were significantly higher than levels in 1987 and 1988.

Ash content often varies with season (Dietz 1972, Tueller 1979) and plant part (Dietz 1972). Bitterbrush ash contents have been reported at 3.3% (Dietz, et al. 1962, Dietz, et al. 1968), 4.2% in natural stands with ponderosa pine (Dealy 1966), and from 2.1 to 2.5% in March and from 3.3 to 4.0% in September (Tueller 1979). The present study agrees with other studies on the seasonal variation of ash contents in bitterbrush twigs.

Although soil phosphorus contents were not determined, phosphorus uptake during the first growing season was apparently related to greater phosphorus availability in soils with thicker A horizons. Additional research should be conducted to determine the interrelationships between treatment responses and soil fertility.

Interpretations of the results of this study are confounded by differences in soil water content and age of treatment. The decline in both nitrogen and phosphorus contents between the first and second growing seasons after treatment may have resulted from treatment age differences. However, precipitation and soil water were also much lower during the second growing season than during the first season. Phosphorus uptake may have been decreased by low soil water availability during the second growing season. Therefore, the interrelationships among soil water availability, plant water stress, soil fertility, and plant chemical composition merit additional research.

Whereas bitterbrush nutrient contents declined significantly after the first growth season following manipulations and increased later, in vitro dry matter digestibility showed a progressive decline throughout the study period. Ward (1971) found that in vitro dry matter digestibility of dried bitterbrush samples collected from November through March was 22.2 to 24.7%, and was highest in the March samples. In this study, samples were collected in April and August. Average digestibility values ranged from 27.5 to 40.84%, and from 43.03 to 49.2%, respectively. The lowest values in both winter and summer seasons occurred during the fourth year after treatment.

Nutrient content variations between and within years in the present study seemed to correlate well with moisture availability. Years or seasons with higher precipitation resulted in significantly higher nutrient contents in bitterbrush. This pattern leads one to the conclusion that range manipulations played an insignificant role in increasing nutrient levels. However, other studies (Everitt 1983, Powell and Box 1979) found significant nutrient increases in browse plants a few months following manipulations. The increase was short-lived, and nutrient contents fell to the levels of untreated plants.

However, the later (1989) increase in nutrients observed in this study, following a significant decline, raises the speculation that after manipulations soil nutrients are rapidly taken up by plants and are probably tied up in the aboveground biomass. Those nutrients may not be available for plant uptake until later. The validity of this speculation may be tested by measuring the nutritional status of previous years' current growth and correlating that status to the current year's leader growth. The speculation is valid if those old twigs on long-term bases show a decline of nutrient contents while the current twigs show a proportional nutrient increase, assuming insignificant environmental variations occur.

Kituku and Powell (1990) indicated that small areas, when subjected to range improvement practices under a yearly management plan, could result in a continuously high quality of forage for range animals. The present long-term study on the effects of manipulation on bitterbrush nutritive value further confirms their findings and conclusion.

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Applications of the Water Balance Approach for Estimating Plant Productivity in Arid Areas

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Abstract—Plant productivity is often estimated using precipitation, evapotranspiration, or transpiration as a predictor for plant water use. Hydrologic models are used to calculate a water balance and to estimate evapotranspiration and transpiration. The water balance approach accounts for first order environmental effects in plant productivity and is adequate for many applications. The water balance approach can be used for screening, experimental design including determining the length of records needed to sample climatic variability, and analysis of soil properties affecting plant productivity. However, it does have limitations. Stresses due to nutrients, competition, herbivory, disease, and so forth are not directly considered. The approach is process-based in terms of climate, hydrology, and soil water dynamics, but is empirically based in terms of biological activities.

Arid and semiarid areas are widespread, generally along two wide belts centered at approximately 30 degrees latitude north and south of the equator, and comprise more than one-third of the world's land surface. Approximately 80% of the world's rangelands are within these arid and semiarid areas where precipitation is generally less than potential evapotranspiration (Branson and others 1981). Under these conditions, water availability is the most important factor controlling plant survival and production (Brown 1974).

The importance of water availability is the basis of the water balance approach in predicting plant water use and annual above-ground net primary productivity (ANPP). The purpose of this paper is to describe applications and limitations of the water balance model-water use efficiency approach for estimating plant productivity in arid areas. Emphasis is on first order environmental effects represented by the CREAMS Simulation Model and the example application emphasizes hydrologic modeling and estimation of ANPP for perennial shrubs at the Rock Valley Site in Nevada.

Methods and Procedures

A Discrete Form of the Water Balance Equation

Over a discrete time period (day, month or year) and on a unit area (square meter or ha), if we assume no runon, no net subsurface water movement in the horizontal direction, and a plant rooting depth significantly above the permanent water table, a discrete form of the water balance equation can be written as follows:

$$\Delta S/\Delta t = P - Q - ET - L \qquad (1)$$

where:

ΔS = change in soil water content to the plant rooting depth (mm, representing units of volume per unit area),
Δt = time period for calculations (usually days summed to monthly or annual values),
P = precipitation depth for the time period (mm),
Q = runoff from the area for the time period (mm),
ET = combined evaporation and plant transpiration for the time period (mm), and
L = percolation or seepage below the root zone for the time period (mm).

All terms in Eq. 1 depend on the amount of precipitation, P; the other terms (Q, ET, and L) are strongly related to soil water content. Therefore, feedback is an essential feature of water balance equations. For example, ET depletes soil moisture, and soil moisture status often limits the rate of ET.

Potential Evapotranspiration, Soil Moisture, and Actual Evapotranspiration

Potential evapotranspiration (PET) is the rate of ET when water is not limiting; PET represents a maximum from atmospheric demand under a complete plant canopy. Actual evapotranspiration (AET) is always less than or equal to PET and depends on soil moisture and atmospheric demand, as well as on soil and vegetation characteristics when water is limiting. Soil moisture (SM) is often expressed as the soil water content, S in Eq. 1, normalized by the soil water content when the soil is saturated.

Values of AET can be estimated if the ratio of AET to PET is known. Most of our knowledge of the ratio of AET to PET comes from cropland research. Veihmeyer and Hendrickson (1955) suggested that the ratio of AET to PET

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remains nearly constant as soil moisture decreases from field capacity to near the plant wilting point. Thornthwaite and Mather (1955) suggested a linear relationship between AET/PET and soil moisture; other investigators have proposed a variety of nonlinear relationships (Hanson 1973; Fig. 3, P. 16).

The general relationship among soil moisture, AET, and PET can be summarized in equation form as follows:

$$AET = \begin{cases} PET & SM \geq SM_1 \\ f(SM,PET) & SM_0 < SM < SM_1 \\ 0 & SM \leq SM_0 \end{cases} \quad (2)$$

where SM_1 is a limiting soil moisture above which SM does not influence AET, SM_0 is a limiting soil moisture below which soil water is not available to plants, and f is a function expressing AET/PET when soil moisture is between SM_0 and SM_1. On croplands, SM_1 is often assumed equal to soil moisture at field capacity (usually –1/10 to –1/3 bar) and SM_0 is often assumed equal to soil moisture at the permanent plant wilting point (usually –15 bars).

In contrast with crops, plants in arid and semiarid areas appear to be more efficient in extracting soil moisture under relatively dry soil conditions with soil water potentials below –15 bars (see Ackerman and others 1980). The volume of water stored in soils at potentials less than –15 bars is small compared with the volume stored between –15 bars and –1/3 bar, but that water is important to plant growth and survival in arid and semiarid areas. Plant growth and water balance models applied to arid and semiarid conditions usually assume a wilting point at soil water potentials below –15 bars (Hanson and others 1987), but wilting point values (SM_0 in Eq. 2) under these conditions are not well quantified. However, simple water balance models may not be sensitive to assumed wilting point values (Williams and others 1980; table II-5, p. 173).

Simple Soil-Water-Plant Relationships for Arid and Semiarid Areas

Relationships, models, and applications presented here are intended to illustrate a range of complexity in approaches in estimating ANPP using selected examples. No attempt has been made to represent all approaches, nor are the citations intended to be complete. The general progression of complexity in predicting ANPP varies from using 1) annual or seasonal precipitation, 2) annual or seasonal AET, and 3) annual or seasonal actual plant transpiration.

Models to predict net primary productivity using mean annual precipitation were summarized by Lieth (1975) based on earlier work by Lieth (1962) and by Walter (1939; 1964). The "Walter's Ratio" for arid areas is a linear equation through the origin as follows:

$$Y = 2.0\ P \quad (3)$$

where Y is net productivity ($g/m^2/y$) and P is mean annual precipitation (mm). Equation 3 is limited to application in dry climates, does not consider temperature or life form, and predicts net productivity to be positive even as mean annual precipitation approaches zero. Lieth (1975) solved the problem of extending the precipitation-based predictions to wetter climates by assuming an upper limit on net productivity and a saturation-curve model which approaches the upper limit asymptotically. Lieth's saturation-curve model retains the other limitations of Walter's Ratio.

Rosenzweig (1968) used estimates of AET to predict ANPP as follows:

$$ANPP = 0.0219(AET)^{1.66} \quad (4)$$

where ANPP is in $g/m^2/y$ and AET is annual actual evapotranspiration in mm/y. This is an improvement over Eq. 3 in that AET is a better predictor of plant water use than annual precipitation because temperature is reflected in the AET estimates. However, AET includes water lost from evaporation from plants and litter, as well as from soil evaporation. Finally, like Eq. 3, Eq. 4 predicts productivity to increase without bounds as AET increases, and because 1.66 is an exponent in Eq. 4, ANPP increases even faster than AET increases. Webb and others (1978) proposed an equation of the form:

$$ANPP = 496 - 666(e^{-0.0025\ AET}) \quad (5)$$

where ANPP and AET are as defined above. Notice that Eq. 5 predicts zero ANPP for values of AET below about 118 mm and that ANPP approaches an upper limit of 496. For these reasons it is an improvement over Eq. 4, but like Eqs. 3 and 4 it does not consider soil or vegetation characteristics.

Wight and Hanks (1981) used a simple hydrologic model to solve Eq. 1 and then used the ratio of actual to potential transpiration (AT/PT) to predict site forage yield. Their equation for the growing season forage yield is:

$$Y = Yp(AT/PT) \quad (6)$$

where Y is actual site yield (kg/ha), Yp is potential site yield (kg/ha), AT is actual transpiration (mm) during the growing season, and PT is site potential transpiration (mm) during the growing season. This model represented several conceptual (and complexity) advances over Eqs. 1-5. First, the model solved a daily water balance that accounted for climate, soils, changes in soil moisture, runoff, and percolation. Second, results of the water balance calculations and knowledge of life form seasonal growth patterns and site specific herbage yield data were used to estimate Yp and AT/PT. Third, the Wight-Hanks model used actual transpiration, not actual evapotranspiration, to estimate plant water use and thus avoided the conceptual problem of including evaporation not involved in plant growth in plant growth predictions.

Lane and others (1984) used the CREAMS Model (Knisel 1980) to solve Eq. 1 (daily time step) and estimate AET. The ET component of the CREAMS Model uses a seasonal leaf area index (LAI) to separate AET into actual transpiration and actual evaporation. Estimates calculated on a daily basis were used on monthly, seasonal, and annual bases. The CREAMS Model was applied to lysimeter data from Los Alamos, NM, to field data from the southern Tunisian steppe (Floret and others 1982), and to field data from Rock Valley, NV (Romney and others 1973; Turner 1973; Ackerman and others 1980). The equation used to estimate ANPP is:

$$ANPP = Ke\ AT \quad (7)$$

where Ke is a water use efficiency factor (g dry matter production per m^2 per year per mm of transpiration).

The advantages of this approach over that of Wight and Hanks (1981) include 1) values of Ke can be estimated from greenhouse and field plot studies and can vary through the growing season to reflect phenology, 2) the CREAMS Model is operated on a daily time step throughout the year, has a more detailed description of the soil profile, and thus can better reflect soil moisture status at the beginning of the growing season, and 3) daily variations in rooting development, LAI-AET feedback, and soil moisture status by soil layer make the water balance calculations more responsive to changing weather inputs. Disadvantages include 1) it is not known how well water use efficiency factors derived under controlled conditions apply to field conditions, 2) the use of site specific values of Yp from field measurements may result in improved forage yield predictions, and 3) the CREAMS Model is more complex and requires more input data.

The approaches represented by Eqs. 2 through 7 and the accompanying narrative illustrate increasing sophistication and incorporation of more physically based models at the expense of increasing complexity. Equation 2 represents the influence of annual precipitation only, while Eq. 7 and the water balance model used to calculate AT represent a more process-based approach in terms of climate, hydrology, and soil water dynamics, but remain empirical in representing the biological processes such as root development, leaf area index, and water use efficiency.

Example Application at Rock Valley

Rock Valley is on the Nevada Test Site near Mercury, NV, in the northern Mojave Desert. The experimental site is at latitude 36°40' N and longitude 116°05' W. Elevation at the site is approximately 1,020 m MSL. Based on 9 years of data, mean annual precipitation is 161 mm and mean annual temperature is 17 °C. The climate is classified as hot desert.

Soils were sampled at 72 profiles representing sites with shrub cover and sites with bare soil (with 45 to 60% surface rock cover or desert pavement). Most of the soils are underlain by calcrete at an average depth of 64 cm. Texture under the shrubs ranged from sand to loamy sand and texture in the bare areas ranged from loamy sand to gravelly sandy loam. Average soil properties over the entire area (under the shrubs and in the bare areas) were: depth to calcrete 64 cm, porosity 34%, –1/3 bar soil moisture 16% by volume, and –15 bar soil moisture 7% by volume (Romney and others 1973).

Data from 7 years of measurements on 8 vegetation quadrats (2 x 50 m) were used to estimate percent canopy cover for all species (25.2%) and standing crop for all species (2,440 kg/ha). Four dominant species (*Ambrosia dumosa, Grayia spinosa, Larrea tridentata,* and *Lycium andersonii*) make up 74% of the vegetative cover and 82% of the standing crop.

Daily precipitation and mean daily temperature data for 5 years, the above cited soil and vegetation characteristics, phenology, and seasonal LAI estimates were used as input to the hydrologic component of the CREAMS Model. No observed runoff or ET data were available; however, 60 observed monthly values of average soil moisture at 15 and 35 cm were used to calibrate the hydrologic component of the CREAMS Model by fitting observed and computed mean monthly soil moisture (Lane and others 1984). With n = 60, the regression equation between fitted (y) and observed (x) mean monthly soil moisture is $y = 1.3 + 0.85\ x$, with $R^2 = 0.93$.

Simulated daily water balance data were summed to obtain annual values of AT for the simulation period 1968 through 1976. Annual AT values were then multiplied by an estimated water use efficiency of Ke = 0.75 g d.m./mm to predict ANPP. Observed values of ANPP were available for 1968 and 1971 through 1976. With n = 7, the regression equation between predicted (y) and observed (x) ANPP is $y = 25.0 + 0.90\ x$, with $R^2 = 0.84$.

To interpret these results, we examine reduction in the width of the 95% confidence intervals (95% CI) on ANPP. Observed mean ANPP was 301 kg/ha and the 95% CI was (±154). Using mean annual precipitation in a regression equation ($R^2 = 0.51$), the mean of 301 kg/ha was preserved and the width of the 95% CI was reduced to (±124) or 19%. Using the CREAMS Model and the estimated water use efficiency factor the mean of 301 kg/ha was preserved and the width of the 95% CI was reduced to (±72) or 53%.

Although 7 years of data represents a small sample of weather and ANPP, the results suggest that the water balance-water use efficiency procedure explains more than 80% of the variation in mean ANPP and is a significant improvement over using annual precipitation as a regression predictor.

To illustrate the uncertainty in ANPP estimates further, Turner and Randall (1989) corrected and revised the 7 years of ANPP data from Rock Valley and added two additional years of data not available to Lane and others (1984). The most significant result of their reanalysis was that to fit the corrected and additional data (n = 9), the Lane and others estimates of ANPP would have to be increased by about 21%. This bias of 21% is significant, but not unexpected when basing model predictions on only 7 years of data. Plant productivity studies in arid areas should be of sufficient duration to accurately predict ANPP (surely >7 years in this case) and should be based on experimental designs that incorporate our knowledge of water balance simulations and the affects of climatic variation on ANPP in arid areas such as Rock Valley.

Discussion of Applications and Limitations

Based on the example and the previous discussion, it is possible to suggest potential applications of the water balance-water use efficiency approach related to prediction of ANPP. These applications include:

1) Screening experimental designs for field studies of abiotic-biotic interactions affecting ANPP. In particular, estimating annual variability in ANPP to determine sampling protocols and sizes.

2) Assessing the influence of climatic variability on ANPP.

3) Determining the influence of soil properties (depth, texture, water holding capacity, hydraulic conductivity, and so forth) on ANPP.

4) Predicting expected productivity for mapping and inventory assessment of vegetation resources. A specific application might be to estimate ANPP for a spatially referenced data base (GIS) in the presence of limited, and point,

measurements of ANPP but more extensive and spatially referenced soil and climate data.

The main weakness of the water balance-water use efficiency approach is that it poorly represents plant physiology and is weak in reflecting feedback and the impacts of land use and management on plant productivity. Specific limitations include:

1) The procedure is weaker in more humid climates where water is less often the limiting factor for plant growth and survival.
2) The procedure accounts for water and temperature stresses, but ignores plant stresses such as nutrient deficiency, toxicity, competition, fire, and herbivory.
3) Land use and management practices that are not strongly reflected in their impacts on LAI (leaf area index) and soil properties are not well represented.

Summary and Discussion

Plant productivity is often estimated using precipitation, evapotranspiration, or transpiration as a predictor for plant water use. Improving estimates of plant productivity by using transpiration as a predictor instead of precipitation represents increasing sophistication at the expense of increasing complexity. Plant transpiration-based calculations represent a more process-based approach in terms of climate, hydrology, and soil water dynamics.

Hydrologic models are used to calculate a water balance and estimate evapotranspiration, which can be separated into evaporation and transpiration components. The water balance approach accounts for first order environmental effects in plant productivity and is adequate for many applications. The water balance approach can be used for screening, experimental design including determining the length of records needed to sample climatic variability, and analysis of soil properties affecting plant productivity. However, it does have limitations. Stresses from nutrient deficiency, competition, herbivory, disease, and so forth are not directly considered. The approach is process-based in terms of climate, hydrology, and soil water dynamics, but is empirically based in terms of biological activities.

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Visual Perceptions of Management on Arid Lands

Arthur W. Magill

Abstract—A study determined people's perceptions of many types of managed and unmanaged landscapes as represented on slides. In scenes of arid lands in the western United States, most respondents liked natural features such as deserts and mountains. In scenes of mining operations, respondents perceived "roads" as the most prevalent evidence of management activity. Areas reported as having an "arid look" were disliked by the respondents, and areas having "no trees" or "no vegetation" were disliked even more. Nonetheless, arid lands that were reported as "deserts," "sand dunes," "prairies," and "open range," were liked by more than twice as many respondents; thus, people tended to have a positive perception of arid lands. People may have liked arid landscapes, despite not liking arid-looking lands, because landscapes such as deserts and prairies project an image of "openness," which was liked by most respondents.

Visitors to wildland areas of the United States see an untold variety of natural and manmade features that comprise our national landscape. But what do they really see, and do they express their feelings about their perceptions in a meaningful way? People endow meaning to landscapes (Lynch 1960; Lee 1976), as landscape architect Garrett Eckbo (1969) said: "The physical landscape is visual; the social landscape is verbal." Thus, it is through words that people express what landscapes mean to them and their concern for what is seen. Verbal expressions of what people see in landscapes provide clues not only to the meanings they assign to landscapes, but also to their concern for management and its influence on visual quality. Verbal expression, then, can indicate to managers the public's reaction to natural resource management, and these expressions can suggest management alternatives that are sensitive to the desires of the viewing public.

Efforts to assess public concerns about the landscape and its management led to the development of sensitivity levels in the Visual Management System used by the U.S. Department of Agriculture, Forest Service to plan management within visual constraints. Presumably, sensitivity levels measure viewer interest in the scenic quality of landscapes by determining the frequency of visitor travel along highways. However, actual concern of the public has not been measured; it is assumed on the basis of the public's presence along the highways coupled to a value judgment that they have a concern for aesthetics.

Objectives and Methods

In 1989 a study was completed to determine if indicators of concern, or peoples' feelings, about the visual quality of landscapes could be developed based upon whether people liked or disliked objects and management actions they reported seeing in scenes of various landscapes (Magill 1990, 1992). Forty-one different groups of respondents were shown sets of color slides that illustrated various landscape components, structures, and management actions throughout the western United States. Slide sets represented objects photographed from fixed positions using lenses of different focal lengths to simulate their appearance at different distances. Slides were randomly distributed into 8 slide shows of 30 slides each. During shows, respondents completed a questionnaire providing brief descriptions of two objects, in order of importance to them, that attracted their attention in the slides. Because the questions were open-ended, all of the objects were described in respondents' own words. Also, they indicated whether they liked, disliked, or were indifferent to the objects seen. All objects reported by respondents were either natural objects, manmade objects, or indicators of management actions including forests, mountains, deserts, timber cutting, grazing, electronic sites, and mining.

This paper describes peoples' perceptions and opinions about natural and managed arid landscapes.

Results and Discussion

Despite efforts to obtain a heterogeneous sample, the results showed that 41 percent of the respondents were professionally trained persons and another 29 percent were retirees. Eight percent had attended college, and 73 percent had annual gross family incomes of $25,000 or more. Two-thirds of the respondents were male, and most recreated on wildland areas 3 to 10 times per year. The majority of the 788 respondents were primarily long-term suburban residents of California.

The respondents reported seeing 154 objects as most important to them in the slides of managed and unmanaged areas. Among the objects perceived that might be associated with shrub lands or arid lands were landscape vegetation, conditions, and forms variously described as brush, vegetation, deserts, open range, desolate, openness, and arid look. Also included were perceptions such as roads, mines, ranches, grazing, and overgrazing, which indicated management activities.

According to Vernon (1968), people tend to focus attention on objects which are most important to them, while things of lesser interest are seen only peripherally. People also tend to be more interested in and assign more importance

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Table 1—Respondent opinions about some vegetative objects on all sites.

Vegetative object	Number of responses	Opinions reported Like	Dislike	Indiff.
		- - - - - - - *percent* - - - - - - -		
No trees	(180)	7	79	10
No vegetation	(85)	9	71	18
Sparse vegetation	(131)	15	53	25
Sparse forests	(227)	23	42	27
Brush	(1,047)	47	17	30
Vegetation	(675)	74	8	13

to natural landscape elements, such as forest stands and mountain ranges and peaks, in contrast with various indicators of management, like roads and mining. And, 79 percent of the responses described various combinations of trees, hills, valleys, mountains, vegetation, and other objects descriptive of natural landscape conditions. Thus, most people, in this study, were attracted by natural landscape objects seen in slides, regardless of management or lack of it.

Perceptions of Natural Resources

The most frequently reported object and one of the most liked landscape elements in the study was "forest stands." The stands accounted for nearly 13 percent of the responses for scenes of managed and unmanaged landscapes. The next most frequently reported vegetative object was "brush" (2.7 percent) followed by "vegetation" (1.8 percent), and they were liked, respectively, by 47 and 74 percent of those reporting them (Table 1). (Small frequency percents are the consequence of the large number of objects reported.)

Apparently respondents preferred seeing landscapes that were well covered by trees or vegetation, rather than arid lands with little or no vegetation. For example, 42 percent of the respondents disliked "sparse forests" and 53 percent disliked "sparse vegetation" (Table 1). Negative opinions were greater for perceptions of barren or arid landscapes. Thus, landscapes reported as having "no trees" were disliked by 79 percent of the viewers, and those having "no vegetation" were disliked by 71 percent (Table 1).

"Bare areas" rated among the 10 most frequently reported natural landscape elements for all scenes in the study, and they were disliked by 61 percent of those who reported them for arid land scenes (Table 2). As might be expected, "barren valleys," "bare hills," "bare mountains," and "bare peaks" were also disliked. Yet, if valleys, hills, mountains, or peaks were described as forested, grassy, or green, they were liked. In fact, all predominantly green landscapes were liked by more than 80 percent of those that reported them. Respondents were more favorably disposed toward vegetated landscapes, especially well-forested and "lush" appearing landscapes rather than those perceived as barren or arid.

Only "bare areas," "deserts," "openness," and "prairies" were reported among the 23 most frequently reported objects or landscape conditions for scenes of all landscapes (Table 2). "Openness," while also descriptive of panoramic views of well-vegetated landscapes, is used commonly to describe arid lands, and 82 percent of the respondents liked scenes of arid lands that they perceived as having "openness" (Table 2). Additionally, 61 percent of the viewers liked "open range," 55 percent liked "deserts," and 46 percent liked "prairies" (Table 2). All are landscapes that may be characterized as "wide-open spaces." The "liking" of deserts may be enhanced if sand dunes are seen, because 76 percent of the respondents liked the "sand dunes" they reported (Table 2).

Some readers may be confused by the apparent inconsistency of respondents who like deserts and prairies, while others do not like areas that are bare, barren, desolate, or have an arid look. While deserts and prairies may be said to have all of these characteristics, nothing in the study clearly distinguishes why the dilemma exists. It has been shown that many respondents also like landscapes having traits suggestive of openness. Possibly, the wide-open appearance of deserts and prairies may override perceptions of desolation, barenness, or aridness. If so, those who see deserts and prairies as wide-open spaces may view them favorably, while those who do not see them as open spaces may perceive only the negative traits.

Another perspective suggests that while most of the present study's respondents liked scenes of "deserts" and background "mountain ranges" (76 percent), a study in the eastern United States rated a scene of sand dunes and arid mountains as the last choice of respondents (Shafer and others 1969). In the current study, respondents were overwhelmingly from California where desert and other arid landscapes are common. The eastern study's respondents were predominantly Easterners who may not have experienced arid landscapes. Thus, it seems likely that persons raised or living in the Southwest may perceive openness, deserts, and prairies more favorably than those living in locations without such landscape features.

Not all objects that are components of arid lands were liked. Some respondents said that scenes had an "arid look" and others said scenes looked "desolate." Fifty-three percent of those who reported "arid look" did not like it, and 51 percent said they did not like scenes they perceived as "desolate" (Table 2). Bare or brown hills and mountains project the appearance of an arid environment, whereas green or forested hills and mountains do not appear as arid. Thus, an example of the respondents' dislike for arid lands was demonstrated by whether they liked or disliked arid

Table 2—Respondent opinions about conditions reported for arid lands.

Conditions	Number of arid land responses	Opinions reported Like	Dislike	Indiff.
		- - - - - - - *percent* - - - - - - -		
Openness	(248)	82	6	7
Sand dunes	(139)	76	3	15
Open range	(54)	61	9	20
Deserts	(460)	55	17	22
Prairies	(266)	46	16	31
Desolate	(49)	26	51	12
Arid look	(218)	14	53	24
Bare areas	(410)	13	61	20

and lush conditions. Arid hills and mountains were disliked by 46 percent of those who reported them, while only 22 percent liked such landscapes. By contrast, 81 percent of the respondents who reported lush-looking hills and mountains liked them while a mere 4 percent disliked them. These data support the conclusion that people may like deserts, sand dunes, prairies, and open range if they perceive them as wide-open, but if they perceive landscapes as arid, bare, or desolate they regard them with little favor.

Perceptions of Management

In the study, several objects associated with land management were reported frequently enough for scenes of arid lands to merit discussion. "Roads" were reported more frequently, whether on arid lands or elsewhere, than other evidence of land management. Even in scenes of timber harvesting, they were reported more frequently than forest clearcuts, though only minimally. In addition, respondents either disliked roads (41 percent) or were indifferent to them (31 percent) with one notable exception (Table 3): forty-one percent of the respondents liked a dirt road that faded from the lower right corner into the center of a range land scene. This finding, as well as a couple of examples from non-arid lands, suggests that certain types of roads may contribute aesthetic quality to some scenes, thereby drawing favorable responses.

"Roads" on arid lands were disliked most at two locations in eastern California: Death Valley Junction, near the California-Nevada border, (72 percent) and Poleta Creek, on the Inyo National Forest (75 percent). At these locations, dislike of "roads" may be attributed to different conditions, but study data did not permit determining why respondents' opinions differed for various landscape scenes.

Seventy-two percent of those who reported "roads" for Death Valley Junction disliked them. The objectionable "roads" were mining exploration roads located 4 miles from the photo point and oriented away from the viewers. Also, they were seen as parallel lines that were several miles apart, and the light color of the dirt roads made them stand out from the adjacent vegetation. The regularity of spacing, along with the color contrast with surrounding vegetation, possibly suggested human activity where none was expected by the respondents.

Table 3—Respondent opinions about objects reported for scenes of managed arid lands.

Object	Number of responses	Opinions reported Like	Dislike	Indiff.
		- - - - - - - *percent*	- - - - - - -	
Overgrazing	(37)	0	95	3
Powerlines	(145)	5	68	22
Microwave towers	(140)	8	58	29
Mines	(58)	22	50	9
Roads	(567)	21	41	31
Fences	(236)	28	29	38
Trails	(67)	49	28	18
Grazing	(49)	51	16	27

The "roads" at Poleta Creek were 3 miles from the photo point, and they were irregularly scattered over the landscape. However, soils at the location were white, so road cuts and fills, eroded soils, and unvegetated areas contrasted strongly with the short, sparse vegetation. The combination of naturally exposed soils and road exposures may have caused respondents to see more "roads" than actually existed, thus eliciting negative responses to perceptions of an excessive number of roads.

"Microwave towers" and "powerlines" may or may not be easily seen when they are located on arid lands; visibility depends upon their location, color, and the distance from the observer. Those located along skylines may be seen easily, while those with mountains for a background are less likely to be seen unless their color contrasts sharply with soils and vegetation. Of course, the greater the distance from the towers or powerlines to the observer, the less likely they will be seen. Whenever they were seen by respondents, "microwave towers" and "powerlines" were disliked by 58 and 68 percent, respectively (Table 3).

Electronic devices drew relatively large numbers of responses for only two of five scenes. In one scene, a satellite dish was consistently mistaken as a microwave tower and disliked by 59 percent of the viewers. Located on the crest of a hill, it seemed that more respondents should have seen and reported the object as a satellite dish. Though it drew the most responses for the scene, some attention was diverted by other objects such as roads, rocks, vegetation, brush, buildings, and hills.

Respondents were attracted by "powerlines" in another scene, and 68 percent did not like the lines (Table 3). Again, the powerlines drew the most responses, but attention also was drawn to brush, hills, and mountain ranges. In both cases, attention was diverted by objects probably of more interest to the respondents than either the satellite dish or the powerlines.

Commonly, mines may be seen on arid lands, and spoil overcasts and piles usually are easily detected. In general, mines seen on arid lands were disliked by 50 percent of the respondents while 22 percent liked them (Table 3). However, it may be necessary for people to be interested in mining before mines are actually seen as visual intrusions. Few reported seeing "mines" in the arid land scenes. Gold mining in Nevada resulted in the entire top of some low mountains being removed, and only flat tops and considerable overcast material were seen. Yet, less than 2 percent of the respondents reported "mines," and half of them did not like the mining. Most people reported "mountain ranges" (13 percent), "hills" (13 percent), "brush" (12 percent), and "deserts" (7 percent) for the scene. Low detection of the mining may be related to the color of the mining spoils. Spoils were similar in color to surrounding hills, thus contrast was very low. At other locations, mining spoils contrasted sharply with adjacent soils and vegetation making them easier to detect.

A few respondents reported "grazing" or "overgrazing" for scenes of managed lands, and many of the reports were for arid lands. Grassland scenes apparently stimulated perceptions of grazing or overgrazing, even when cattle were not present, but nothing in the data explained such responses. When reported, "grazing" was liked by 51 percent of those who had viewed scenes of arid landscapes, and only 17 percent disliked it, while some were indifferent (Table 3). On the other hand, not a single person liked "overgrazing." The percentage of people who disliked "overgrazing" was greater than those who disliked "roads" (41 percent) or "clearcuts" (76 percent), although the number of reports was much greater for "roads" and "clearcuts."

Management Implications

Study determined that most respondents were more interested in and assigned more importance to natural landscape elements in contrast with various management actions (Magill 1992). Examination of the study's arid landscape components revealed that respondents liked scenes of deserts, prairies, and range lands primarily for the openness or wide-open feeling they conveyed. Yet, whenever scenes were perceived as arid or desolate, they were disliked by the respondents. Thus, arid or desolate-appearing landscapes may be regarded unfavorably by people, whereas a sense of openness or a wide-open feeling may override their negative perceptions.

The openness that people like makes management difficult, because roads, electronic devices, buildings, and mining operations on arid lands cannot be easily concealed. Thus, evidence of management activities needs to be carefully located to avoid unfavorable public reaction, especially if it can be seen from places frequented by many people. In general, roads detract from the aesthetic quality of arid land scenes. Though one case suggested that meandering, unimproved roads might contribute aesthetic quality to arid land scenes, this potential was not verified and would require further study.

It may be advisable for managers to consider the color of soils and vegetation whenever they are making management plans. Mine spoils and road cuts and fills that blend with surrounding landscapes are less likely to be detected and arouse criticism. If they contrast sharply, then mitigating actions, such as employing site preparation and plantings, may be necessary. In the case of microwave and powerline towers, painting them colors compatible with the surroundings may be effective.

Overgrazing has long been a contentious issue between ranchers and land managers and the viewing public. The study did not determine when respondents ceased to be favorably impressed with grazing and commenced seeing range lands as overgrazed and disliked. Nevertheless, managers should be aware that many lay people will perceive some arid lands and range lands as overgrazed, whether they are or not.

In conclusion, a different approach has been described for evaluating public perceptions and opinions of arid landscapes. It documented what some people saw in color slides of managed and unmanaged landscapes and identified what they liked and disliked about the scenes. Hopefully, resource managers have been provided with a better understanding of public concerns for the visual impact of management practices on arid lands and have been made more visually sensitive to public desires.

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Plant Inventory, Succession, and Reclamation Alternatives on Disturbed Lands in Grand Teton National Park

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Abstract—Sixteen study areas ranging in size from 12 to 870 hectares were selected for inventory and analysis in sagebrush-grass, meadow, and lodgepole pine plant communities. All study areas had some human-induced disturbance, ranging from grazing to intensive agriculture, prior to incorporation into the National Park System. Vegetation data including density and cover were collected. Disturbance values (D) were determined for each study area and compared among the study areas by a method that considered frequency, density, and life form, in eight different significance classes. Soils were characterized for each study area. All study areas had good vegetative cover, but badly disturbed sites were virtually covered with exotic, aggressive grass species (mainly smooth brome and Kentucky bluegrass). Management options are suggested that could restore the disturbed sites to more natural conditions. Some of these options would require chemical or mechanical eradication of existing vegetation, followed by seeding or transplanting native stock. Natural succession to the pre-agricultural vegetative state could take centuries or may not occur at all without human intervention.

Grand Teton National Park is located in northwestern Wyoming (fig. 1). It is dominated by the magnificent Teton Mountain Range of the Rocky Mountain System. The Teton Range, an upthrown fault block, forms the western half of the Park (National Park Service 1984). The balance of the Park is a downthrown, sediment filled, fault block known as Jackson Hole. The Snake River flows through Jackson Hole where it is joined by several smaller tributaries. There are several lakes in Jackson Hole including Jackson Lake, which was enlarged by a dam constructed several decades ago to increase water storage for downstream irrigation purposes.

The lands disturbed by human agency in Grand Teton National Park are found in Jackson Hole. The Teton Range is so rugged it remains largely undisturbed except for ski, cabin, and road development. These developments are outside the Park.

The vegetation of Jackson Hole consists of a patchwork of communities. Clark (1981) listed several principal riparian (aquatic, shrub-swamp, willow) and valley (meadow, sagebrush) plant communities for Jackson Hole. Upland communities, those above the valley floor, include juniper, aspen, lodgepole pine, Douglas fir, spruce-fir, and alpine (Clark 1981). The upland types most prone to human disturbance are the lower elevation, open parks amid the sagebrush, juniper, aspen, and lodgepole pine communities. The main disturbance sites in the Park have resulted from livestock grazing, hayfield and pasture development, and small grain farming by private interests before the Park was established. Other disturbances resulted from Park management activities, such as the establishment of pastures for holding horses and buffalo (bison) and camp construction. The main disturbance areas are on the valley floor and lower slopes.

Grand Teton National Park, as presently constituted, derived from the original Grand Teton National Park of 1929 (the Teton Range) and incorporation of the Jackson Hole National Monument in the Park in 1950 (Stark 1984). The National Monument was established in 1943 and included the Jackson Hole Valley areas currently in the Park (Stark 1984). The John D. Rockefeller, Jr. Memorial Parkway is a land corridor connecting Grand Teton and Yellowstone National Parks that is administered by the National Park Service (fig. 1).

The National Park Service mandate is, in part, to preserve natural ecosystems for the education and enjoyment of future generations. To that end we obtained a competitive grant from the University of Wyoming/National Park Service Research Center to meet the objectives described in this report:

1) describe the composition and abundance of woody and herbaceous species on moderately and severely disturbed sites (study areas),
2) describe the soils of the study areas, and
3) make recommendations for restoration of native plant communities based on ecological principles and agronomic properties of existing and desired vegetation.

Methods

Field work was performed during the 1985 field season. Sixteen areas were selected for study after reconnaissance visits and consultation with National Park Service personnel. Seven of these areas had been farmed or ranched and

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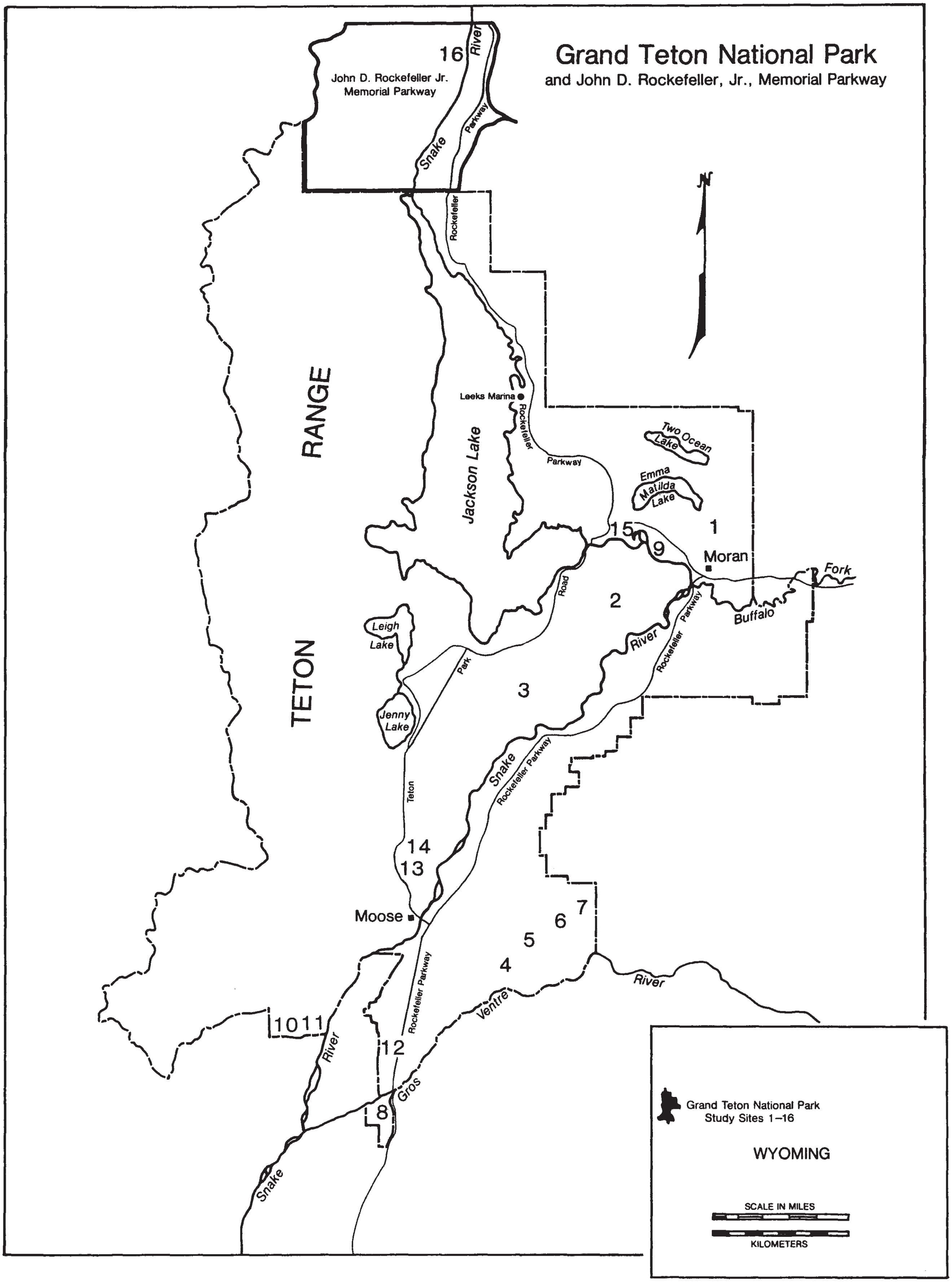

Figure 1—Grand Teton National Park Study Areas.

Table 1—Study areas used to assay disturbance of plant communities in Grand Teton National Park

Number	Name	Location	Size (hectares)	Year of last major disturbance	Approximate species Number	Approximate species Percent introduced
1	Three Rivers Ranch	T45N, R114W Sec. 13, 14	35	[1]1949	36	33.3
2	Cow Lake	T45N, R114W Sec. 28,29,32,33	180	1957	45	4.2
3	Pot Holes	T44N, R115W Sec. 1-3,10-15,22,23	870	1957	48	2.1
4	Mormon Row Hayfields	T42-43, R115W Sec. 3-5,32,33	445	1974	16	56.2
5	Mormon Row Sagebrush	T43N, R115W Sec. 34	145	1950	41	17.1
6	Clark Moulton Sagebrush	T43N, R115W Sec. 35	65	1930	41	4.9
7	Clark Moulton Dry Farm	T43N, R115W Sec. 26	65	1979	20	50.0
8	Abercrombie Warm Sprs. Ranch	T41-42N, R116W Sec. 2,35	95	1975	33	15.1
9	Buffalo Pasture	T45N, R114W Sec. 16,21	30	1970	64	9.4
10	Aspen Ranch Corp.	T42N, R116W Sec. 17,18	13	[1]1969	13	38.5
11	Rocky Mountain Energy Corp.	T42N, R116W Sec. 17	40	1970	49	12.2
12	Heim Hayfield	T42N, R116W Sec. 23	15	1949	8	50.0
13	Cottonwood Creek Hayfield	T43N, R116W Sec. 13,14	30	1930	35	22.9
14	Cottonwood Creek Sagebrush	T43N, R116W Sec. 13	[2]135	1950	38	7.9
15	Oxbow Bend Horse Pasture	T45N, R114W Sec. 17	15	1975	50	16.0
16	Huckleberry Hot Springs	T48N, R115W Sec. 20	12	1983	74	16.2

[1] Trespass grazing continues.
[2] Stand is much larger, extending into R115W and into sections 7, 12, 18, 24, but we sampled only from section 13.

had been disturbed by plowing and/or had sustained heavy grazing. One area was a former campground. Two areas were formerly fenced Park Service pastures for horses or buffalo, and six were formerly grazed by livestock but in recent years had received only occasional trespass grazing (table 1). Twelve of the study areas were sagebrush-grass sites or had been sagebrush grass sites before disturbance; three were meadow sites, and one was a lodgepole pine site. These study areas ranged in size from 12 to 870 hectares.

Each study area was subdivided into five or more equal parts. These site divisions were sections (section = 640 acres or 259.1 hectares) wherever possible (the large sites), quarter sections (64.8 hectares) on smaller sites, and five more or less equal subdivisions on the smallest sites. A 50-m line transect was established in each of five subdivisions at each site. Where there were more than five subdivisions, the five chosen were selected by random means. The starting points and compass directions for each transect were also determined by random means within the typical homogeneous vegetation matrix of each study area. Ditches and edges and other non-typical areas were avoided. Starting points on each transect were marked by iron rebar stakes and recorded on U.S. Geological Survey topographic maps (7.5 minute, 1: 24,000 scale) stored at the Shrub Sciences Laboratory and at the Rocky Mountain Regional Office of the National Park Service, Denver, Colorado. The vegetation along the transects was characterized by placing 1 m^2 quadrats on alternate sides of the transect every 5 m beginning at the transect starting point. Thus, data were collected from 10 quadrats from each subdivision and 50 from each study area.

The data collected included the number of individuals of each plant species within the quadrat (density); the cover class of each species and litter, rock, bare ground, and cryptogams; and the aspect, slope, and direction of each transect. For dense intermixed stands of rhizomatous or clonal species the number of ramets or stems was estimated by converting the mean cover values to stem numbers obtained from 10 closed stand values (table 2). Species were identified and classed as annuals, biennials, or perennials and whether they were native to the Park, native to North America, or alien following Cronquist and others (1972, 1977, 1984), Hitchcock and Cronquist (1973), and Shaw (1976) (table 3, McArthur and others 1986). Species cover

Table 2—Number of stems for rhizomatous species. Means are based on ten 625 cm^2 (96.9 in^2) samples per species in pure stand sample sites

Species	Number of stems per m^2		Sample sites
	mean + se	range	
Bromus inermis	635.6 + 21.2	552- 736	Heim Hayfield (3), Mormon Row Hayfield (7)
Poa pratensis	980.0 + 53.7	728-1,172	Heim Hayfeld (3), Mormon Row Hayfield (7)
Aster chilensis ssp. *adscendens*	249.6 + 17.6	176- 332	Aspen Ranch (10)
Smilicina stellata	223.6 + 28.8	116- 392	Huckleberry Hot Springs (4), Cow Lake (6)

Table 3—Master species list. Numbers in Table header: 1-16 are the sites (table 1) with x = taxon present, 17, Longevity; 1 = Annual, 2 = Biennial, 3 = Biennial-perennial, 4 = Perennial; 18, Distribution; 1 = Native, 2 = Exotic (from NA), 3 = Exotic (extra-NA). References: Anderson 1986; Cronquist and others 1972, 1977, 1984; Hitchcock and Cronquist 1973; Shaw 1976

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
GRASSES:																		
Agropyron trachycalum (*A. caninum* var. var, *majus*)				x	x	x	x	x	x		x	x	x	x	x	x	4	1
Agropyron caninum var. *unilaterale*																x	4	1
Agropyron cristatum								x		x							4	3
Agropyron repens					x												4	3
Agropyron smithii					x			x	x		x		x				4	1
Agropyron spicatum		x	x		x	x		x			x			x			4	1
Agrostis alba var. *alba* (*A. stolonifera*)																x	4	3
Agrostis scabra var. *geminata*																x	4	1
Agrostis scabra var. *scabra*									x								4	1
Bromus carinatus var. *carinatus*				x												x	4	1
Bromus carinatus var. *linearis*													x	x	x		4	1
Bromus inermis	x			x	x		x	x	x	x	x	x	x	x	x	x	4	3
Calamagrostis stricta									x								4	1
Calamagrostis rubescens						x	x										4	1
Dactylis glomerata	x			x									x				4	3
Danthonia intermedia		x	x													x	4	1
Danthonia unispicata														x			4	1
Deschampsia caespitosa									x							x	4	1
Deschampsia sp.									x								4	1
Elymus glaucus																x	4	1
Festuca idahoensis		x	x			x			x		x					x	4	1
Festuca ovina var. *rydbergii*		x	x														4	1
Hordeum brachyantherum	x								x								4	1
Koeleria macrantha (*K. nitida*)	x	x	x		x			x	x		x		x	x		x	4	1
Melica bulbosa		x														x	4	1
Melica spectabilis											x			x			4	1
Phleum pratense	x				x				x						x	x	4	3
Poa cusickii var. *cusickii*			x											x			4	1
Poa compressa															x		4	3
Poa juncifolia						x		x									4	1
Poa nevadensis								x									4	1
Poa pratensis	x	x		x	x	x	x	x	x	x	x	x		x	x	x	4	3
Poa palustris					x				x								4	1
Poa secunda		x															4	1
Poa sp.			x														4	?
Sitanion hystrix var. *hystrix*			x											x			4	1
Stipa columbiana		x	x		x	x		x	x					x		x	4	1
Stipa comata			x		x			x									4	1
Stipa lettermanii		x	x								x			x		x	4	1
Stipa occidentalis															x		4	1
Trisetum spicatum																x	4	1
Trisetum wolfii									x								4	1

(con.)

Table 3 (Con.)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
GRASS-LIKE SPECIES:																		
Carex athrostachya	x								x							x	4	1
Carex douglasii	x																4	1
Carex geyeri																x	4	1
Carex hoodii							x										4	1
Carex lanuginosa									x						x	x	4	1
Carex petasata															x		4	1
Carex praegracilis									x						x		4	1
Carex rossii		x	x		x	x		x	x					x	x		4	1
Carex vallicola		x					x		x		x			x		x	4	1
Juncus balticus									x								4	1
Luzula campestris	x																4	1
FORBS:																		
Achillea millefolium ssp. *lanulosa*	x	x			x	x		x	x	x	x		x		x	x	4	1
Agoseris glauca		x	x			x			x						x	x	4	1
Allium geyeri var. *tenerum*									x								4	1
Androsace septentrionalis	x										x						4	1
Antennaria microphylla (*A. rosea*)	x	x	x		x	x	x	x			x		x	x	x	x	4	1
Arabis cobrensis											x		x	x			4	1
Arabis drummondii		x	x		x						x			x	x	x	4	1
Arabis holboellii var. *retrofacta*		x	x		x	x		x			x		x		x	x	3	1
Arabis sp.			x														?	?
Arenaria congesta		x	x										x	x		x	4	1
Arnica chamissonis ssp. *foliosa*	x								x								4	1
Artemisia ludoviciana var. *ludoviciana*										x					x		4	1
Aster campestris									x						x		4	1
Aster chilensis ssp. *adscendens*				x	x	x	x	x		x	x	x	x				4	1
Aster hesperius var. *laetevirens*									x						x	x	4	1
Aster integrifolius									x		x		x			x	4	1
Aster perelegans						x											4	1
Astragalus agrestis (*A. dasyglottis*)															x		4	1
Astragalus convallarius						x											4	1
Astragalus miser						x					x						4	1
Astragalus miser var. *hylophilus*					x												4	1
Balsamorhiza sagittata			x		x						x			x			4	1
Camissonia subacaulis									x								4	1
Campanula rotundifolia		x	x												x	x	4	1
Capsella bursa-pastoris																x	1	3
Carduus nutans							x										2	3
Castilleja flava						x								x			4	1
Castilleja pilosa (*C. longispica*)		x	x												x		4	1
Cerastium arvense			x						x					x		x	4	1
Cerastium vulgatum	x																3	3
Chenopodium album	x			x			x				x		x				1	3
Cirsium arvense				x			x			x						x	4	3
Cirsium scariosum (*C. foliosum*)									x						x	x	4	1
Collinsia parviflora	x																1	1
Collomia linearis	x	x	x	x					x				x	x	x	x	1	1
Comandra umbellata var. *pallida*		x	x		x	x					x			x			4	1
Cordylanthus ramosus					x	x											1	1
Crepis acuminata		x	x								x				x	x	4	1
Delphinium nuttallianum		x			x				x								4	1
Delphinium occidentale									x								4	1
Draba crassifolia																x	3	1
Dracocephalum parviflorum (*D. nuttallii*)				x													4	1
Epilobium angustifolium																x	4	1
Epilobium glandulosum																x	4	1
Epilobium minutum													x				1	1
Epilobium paniculatum													x		x	x	1	1
Epilobium watsonii									x								4	1

(con.)

Table 3 (Con.)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
FORBS:																		
Equisetum laevigatum	x								x						x	x	4	1
Erigeron divergens											x						3	1
Erigeron eatonii		x	x												x		4	1
Erigeron glabellus	x																3	1
Erigeron pumilus ssp. *intermedius*			x														4	1
Erigeron pumilus		x			x		x	x			x						4	1
Erigeron speciosus var. *macranthus*															x		4	1
Eriogonum caespitosum								x									4	1
Eriogonum umbellatum		x	x		x	x		x		x	x		x	x	x	x	4	1
Eriophyllum lanatum var. *integrifolium*		x	x						x								4	1
Erysimum cheiranthoides									x								1	1
Fragaria vesca var. *bracteata*											x						4	1
Fragaria virginiana var. *glauca*									x							x	4	1
Frasera speciosa						x											2	1
Fritillaria pudica		x											x	x			4	1
Galium boreale											x						4	1
Galium trifidum									x						x		4	1
Galium triflorum																x	4	1
Gayophytum nuttallii													x	x	x	x	1	1
Geranium richardsonii						x											4	1
Geranium viscosissimum var. *viscosissimum*						x			x						x	x	4	1
Geum macrophyllum var. *perincisum*									x							x	4	1
Geum triflorum		x				x											4	1
Geum triflorum var. *ciliatum*			x														4	1
Gilia aggregata var. *aggregata*											x						3	1
Helianthella quinquenervis									x								4	1
Lactuca pulchella						x									x		4	1
Lactuca serriola							x										2	3
Lappula redowskii								x									1	2
Lepidium campestre	x														x		1	3
Lepidium densiflorum var. *densiflorum*											x		x				1	1
Lepidium densiflorum var. *pubicarpum*	x												x			x	1	1
Lepidium virginicum var. *pubescens*																x	1	1
Linanthus harknessii	x	x	x					x	x	x	x		x	x	x	x	1	1
Linaria vulgaris													x				4	3
Linum perenne var. *lewisii*		x			x						x						4	1
Lithospermum ruderale					x	x											4	1
Lomatium ambiguum			x														4	1
Lupinus polyphyllus															x	x	4	1
Lupinus sericeus var. *sericeus*		x	x		x	x		x			x	x	x	x		x	4	1
Lychnis alba													x				3	3
Machaeranthera canescens			x											x	x		3	1
Madia glomerata													x				1	1
Medicago lupulina											x					x	1	3
Medicago sativa	x			x			x					x					4	3
Melilotus officinalis						x											2	3
Mertensia oblongifolia								x									4	1
Microseris nutans		x	x											x			4	1
Orobanche fasciculata														x			4	1
Orthocarpus luteus		x															4	1
Penstemon procerus								x	x								4	1
Perideridia bolanderi													x	x			4	1
Perideridia gairdneri		x	x						x						x	x	4	1
Phlox hoodii			x		x			x			x						4	1
Phlox longifolia				x	x	x					x		x				4	1
Phlox multiflora																x	4	1
Polygonum aviculare																x	1	3
Polygonum bistortoides									x								4	1
Polygonum douglasii	x	x	x		x	x			x	x	x		x	x	x	x	1	1
Potentilla arguta var. *convallaria*					x	x	x		x						x		4	1
Potentilla gracilis var. *elmeri*	x								x						x		4	1

(con.)

Table 3 (Con.)

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
FORBS:																		
Potentilla gracilis var. *glabrata*									x	x	x				x	x	4	1
Ranunculus inamoenus	x																4	1
Rorippa curvisiliqua	x								x								2	1
Rorippa palustris (*R. islandica*)									x								2	1
Rumex salicifolius	x																4	1
Rumex acetosella	x												x				4	3
Rumex occidentalis									x								4	1
Rumex venosus		x															4	1
Sedum lanceolatum			x		x						x			x			4	1
Sedum stenopetalum			x														4	1
Selaginella densa		x	x														4	1
Senecio integerrimus		x															4	1
Senecio sphaerocephalus																x	4	1
Senecio streptanthifolius (*S. cymbalariodies*)						x											4	1
Smilicina stellata																x	4	1
Solidago canadensis var. *salebrosa*																x	4	1
Solidago spathulata								x								x	4	1
Spergularia rubra																x	1	3
Stellaria calycantha									x								4	1
Stellaria crassifolia																x	4	1
Stellaria sp.		x	x														?	?
Taraxacum officinale	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	4	3
Thalictrum occidentale									x								4	1
Thlaspi arvense	x			x			x		x						x		1	3
Tragopogon dubius	x			x	x		x				x		x		x	x	2	3
Trifolium hybridum	x								x								4	3
Trifolium longipes var. *reflexum*									x						x	x	4	1
Trifolium praetense	x																4	3
Trifolium repens	x															x	4	3
Valeriana edulis									x								4	1
Valeriana occidentalis									x							x	4	1
Veronica serpyllifolia var. *huifusca*	x															x	4	1
Vicia americana				x													4	1
Viguiera multiflora var. *multiflora*					x	x					x		x				4	1
Viola adunca																x	4	1
Viola nuttallii var. *praemorsa*		x															4	1
Zigadenus paniculatus			x														4	1
Unidentified annuals and seedlings	x	x	x		x	x	x		x		x	x	x	x	x		?	?
Avascular cryptogams	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	?	?
SHRUBS:																		
Artemisia arbuscula ssp. *arbuscula*														x			4	1
Artemisia cana ssp. *viscidula*									x						x		4	1
Artemisia frigida								x									4	1
Artemisia tridentata ssp. *vaseyana*		x	x		x	x	x	x		x	x			x	x		4	1
Artemisia tripartita			x			x		x									4	1
Berberis repens					x						x					x	4	1
Chrysothamnus nauseosus ssp. *graveolens*[2]						x		x									4	1
Chrysothamnus viscidiflorus						x											4	1
Chrysothamnus viscidiflorus ssp.*puberulus*			x		x			x			x						4	1
Pachystima myrsinites																x	4	1
Prunus virginiana var. *melanocarpa*											x						4	1
Purshia tridentata					x						x						4	1
Rosa woodsii						x											4	1
Symphoricarpos oreophilus var. *utahensis*					x	x					x						4	1
Tetradymia canescens								x									4	1
TREES:																		
Pinus contorta																x	4	1

[1] Cronquist and others, 1972, 1977, 1984.

[2] Anderson (1986) lists *C. n.* ssp. *glabratus* as a synonym of ssp. *graveolens*.

was estimated visually into the following cover classes: 1 = 1 - 5 percent, 2 = >5 - 25 percent, 3 = >25 - 50 percent, 4 = >50 - 75 percent, 5 = >75 - 95 percent, and 6 >95 percent, modified from Daubenmire (1959). Photographs were also taken of each transect (fig. 2).

Soils at the sites were characterized by bulked soil samples that were analyzed for pH, cation exchange capacity (CEC), percent organic matter, electrical conductivity (EC), sodium adsorption ratio (SAR), nitrate nitrogen, phosphorus, potassium, zinc, iron, manganese, copper, calcium, magnesium, and sodium (Black 1968; Page 1982) and by reference to Young (1982).

Plant specimens collected in the Park were identified and curated. Specimens were deposited in the herbaria of Snow College, the Shrub Sciences Laboratory (SSLP), and Grand Teton National Park.

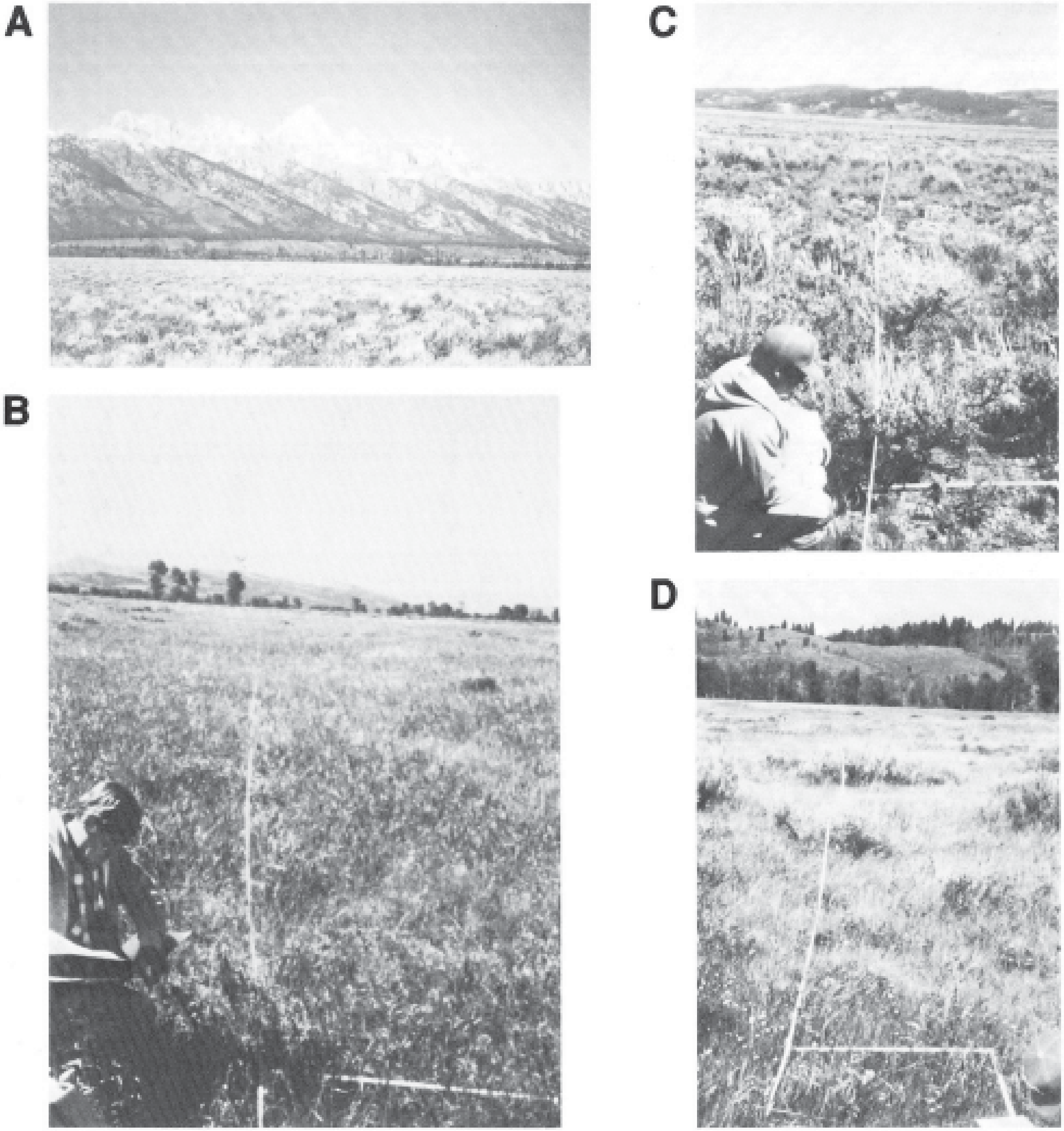

Figure 2—Photographs of Grand Teton National Park Study Areas.

A. Jackson Hole with Teton Range in the background. Note mountain big sagebrush in the immediate foreground, the Snake River channel in the mid foreground, and lodgepole pine on the terraces at the base of the Teton uplift.
B. Transect on Study Area 12, Heim Hayfield.
C. Transect on Study Area 14, Cottonwood Creek Sagebrush.
D. Transect on Study Area 15, Oxbow Bend Horse Pasture.

A site disturbance value was determined by the formula:

$$\text{Disturbance Value (D)} = \frac{\text{Sum [Cover} * \text{(Longevity - Origin Scores)]}}{\text{Number of Species}}$$

Where longevity scores are 1 = annual, 2 = biennial, 3 = biennial to perennial, and 4 = perennial. Origin scores are 1 = native to Grand Teton National Park, 2 = exotic to the Park but native to North America, and 3 = exotic to North America (see table 3). Disturbance values were arcsine transformed and subjected to one way analysis of variance (SAS 1988). Differences between mean values of study areas were determined by the SNK multiple means comparison test.

Under this formulation, original with us, disturbance values rise with increasing frequency of short-lived and exotic plants and with declining cover values and fewer species.

Possible rehabilitation options for each site were determined by reconnaissance visits to the sites and consideration of actions based on our previous experience (McArthur 1988; McArthur and others 1987; Monsen and Shaw 1983; Monsen and Stevens in review; Plummer and others 1968).

Results and Discussion

Our results and discussion focus on: 1) the vascular plants and their distribution in relation to plant community composition, disturbance, and soil factors, and 2) options for restoration to more natural plant communities on the disturbed sites.

Community Types, Disturbance, and Succession

The principal community types of the Jackson Hole valley floor are sagebrush-grass, meadow, and riparian. We did not work in the riparian communities and did only minimal work in upland communities above the valley floor. Our charge was to characterize larger areas, disturbed by human activities; these were in sagebrush-grass, meadow, and lodgepole pine communities. Twelve of our study areas were in sagebrush-grass (study areas 2 - 8, 10 - 14 of table 1), three in meadows (1, 9, 15), and one in lodgepole pine (16). The type of disturbances, years of natural recovery, and disturbance values are given in table 4. The disturbance values

Table 4—Study area disturbance history with disturbance values

Site		Species[1]			Cover[2]		Disturbance value[3]	Recovery years to 1985	Disturbance type
No.	Name	No.	Ave.	Intro.	Sum	Sum/spp.			
2	Cow Lake	45	17.5	2	31.3	1.76	0.10 A	28	Grazing
3	Pot Holes	48	11.6	1	22.5	1.93	0.21 A,B	28	Grazing
14	Cottonwood Creek Sagebrush	38	11.1	3	20.7	1.87	0.30 A,B,C	35	Grazing
11	Rocky Mountain Energy	49	12.4	6	25.5	2.05	0.34 A,B,C	15	Grazing
9	Buffalo Pasture	64	12.5	6	28.5	2.27	0.53 B,C,D	15	Grazing, fencing
5	Mormon Row Sagebrush	41	7.6	7	19.9	2.62	0.57 B,C,D	35	Grazing
6	Clark Moulton Sagebrush	41	7.4	2	19.6	2.65	0.71 C,D	55	Grazing
15	Oxbow Bend Horse Pasture	50	6.6	8	15.2	2.31	0.93 D	11	Grazing, fencing
16	Huckleberry Hot Springs	74	9.5	12	19.1	2.00	0.94 D	2	Campground
8	Abercrombie Warm Springs	33	5.6	5	14.1	2.52	1.53 E	10	Hayfield, pasture
13	Cottonwood Creek Hayfield	35	5.5	8	11.0	2.02	1.66 E,F	55	Hayfield
1	Three Rivers Ranch	36	6.4	12	13.4	2.09	1.98 F	36	Cleared, grazing
10	Aspen Ranch	13	3.8	5	10.2	2.68	2.00 F	16	Pasture, grazing
4	Mormon Row Hayfield	16	3.2	9	10.1	3.16	2.64 G	11	Hayfield
12	Heim Hayfield	8	2.2	4	7.9	3.58	3.54 H	36	Hayfield
7	Clark Moulton Dry Farm	20	3.3	10	9.3	2.82	3.60 H	6	Hayfield, dry farm

[1] No. = total number of species on the study area quadrats. Ave. = the average number of species per quadrat. Intro. = number of introduced species on the study area quadrats.

[2] Sum = total average cover class value per quadrat summed for all species. Both high cover class values and number of species contribute to this number, which therefore is not meaningful by itself. Sum/spp. = total average cover class per quadrat summed for all species divided by average number of species per quadrat. This number reflects relative cover per quadrat.

[3] Different letters in this column among study areas indicate significant differences ($P < 0.05$) in disturbance values by the SNK means comparison test.

were highest where the land had been cleared and hayfields and pastures were established. Values were much lower where grazing was the principal disturbance. Length of natural recovery time (= secondary succession) did not provide apparent compensation for the severity of the type of disturbance in all cases, for example, study areas 1, 12, 13, but did appear to be important in study areas 2, 3, 14 (table 4). Disturbance values ranged from 0.10 for Cow Lakes (grazing disturbance only and protected since 1950 to 3.60 for Clark Moulton Dry Farm (converted to a hayfield and dry farm and protected from disturbance since 1979).

The 16 study sites included eight classes of significant difference in disturbance values. Study areas that were grazed only, grazed and fenced, or grazed, fenced, and seeded without being completely cleared of preexisting vegetation composed the first four disturbance classes (A-D of table 4). The campground disturbance (Huckleberry Hot Springs, study area 16) was also in this group (disturbance class D). This area was mechanically disturbed during construction and maintenance of roadways, ditches, and camp spaces but was not artificially planted. Disturbance values A-D were all lower than 1 (0.10 - 0.94). The study areas with more interventive disturbances (land clearing and planting) had disturbance values above 1.5 (1.53 - 3.60, disturbance value classes E-H).

Plant Species Distribution—Table 3 lists the 215 species that we encountered in our study plots. These included 42 grasses (9 exotics, 0 annuals), 11 grass-likes (0 exotics, 0 annuals), 146 forbs (23 exotics, 23 annuals), 15 shrubs (0 exotics), and one tree (0 exotics). We documented the presence of 7 taxa that had not been previously recorded in Grand Teton National Park or the Rockefeller Parkway (table 5). Two of these were of European origin [mountain bluet (*Centaurea montana*) and sow thistle (*Sonchus uliginosus*)]. The other five [water plantain (*Alisma graminium* var. *angustissimum*), timber poisonvetch (*Astragalus convallarius*), hairy low rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *publerulus*), western dock (*Rumex occidentalis*), and Virginia pepperweed (*Lepidium virginicum* var. *pubescens*)] are widely distributed in western North American and therefore were not unexpected in the Park area.

Thirty-six species occurred on at least five of the 16 study sites (table 6). Ten of these were grasses, including the introduced forage grasses, Kentucky bluegrass (*Poa pratensis*) (14 sites), smooth brome (*Bromus inermis*) (13 sites), and Timothy (*Phleum pratense*) (5 sites). Slender wheatgrass (*Agropyron trachycaulum*) (12 sites) and June grass (*Koeleria macrantha*) (10 sites) were the most widely distributed native grasses. Two native, grass-like plants, Ross sedge (*Carex rossii*) (8 sites) and valley sedge (*C. vallicola*) (5 sites), were common. Twenty-two forbs occurred on at least five sites (table 6). The most common forbs were common dandelion (*Taraxacum officinale*) (all 16 sites), Douglas knotweed (*Polygonum douglasii*) and rosy pussytoes (*Antennaria microphylla*) (12 sites each), western yarrow (*Achillea millefolium*), sulphur buckwheat (*Eriogonum umbellatum*), and three seeded linanthus (*Linanthus harknessii*) (11 sites each), and silky lupine (*Lupinus sericeus*) (10 sites). All of these common forbs are native except dandelion. Plant densities reflect the commonality of the species (table 7). It should be kept in mind, however, that rhizomatous plant density was determined on a per stem rather than a per plant basis.

Sagebrush-Grass Communities—Our study areas in the large sagebrush-grass communities were conveniently divided into six areas that have been drastically disturbed (study areas 4, 7, 8, 10, 12, 13) and six areas disturbed mainly by livestock grazing (study areas 2, 3, 5, 6, 11, 14) (table 4). The species richness and relative abundance of native plants were dramatically lower in the more highly disturbed study areas than in the less disturbed study areas. Common plants in the less disturbed area included sulphur buckwheat (present in 81.7 percent of quadrats), mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) (70 percent of quadrats), June grass (58.5 percent of quadrats), silky lupine (55.6 percent of quadrats), and bluebunch wheatgrass (*Agropyron spicatum*) (49.3 percent of quadrats).

The more drastically disturbed study areas that had been sagebrush-grass prior to disturbance were dominated by smooth brome and Kentucky bluegrass. These grasses occurred in 80 and 65 percent of the quadrats, respectively, mostly as the dominant vegetation. Other common plants

Table 5—Species recently found at Grand Teton National Park (not listed in Shaw 1976)

Blauer, Sanderson & McArthur collection #	Species, location, and date
GTNP-138	*Centaurea montana* L. (mountain bluet). Alien from Europe growing in old ditch near disturbed lodgepole area, 3-Rivers Ranch. 13 July 1985.
GTNP-155	*Alisma graminium* Gmel. var. *angustissimum* (D. C.) Hendricks (water-plantain). Growing on exposed bed of Jackson Lake in mud. North of Leek's Marina. 15 July 1985.
GTNP-174	*Sonchus uliginosus* Bieb. (sow thistle). Roadside weed along Gros Ventre Rd. in south end of Mormon Row. Alien from Europe. 25 July 1985.
GTNP-212	*Astragalus convallarius* Greene (timber poisonvetch). Former dry farm now reverted to sagebrush. North side of section 35 next to Clark Moulton Dry Farm. 26 July 1985.
GTNP-228	*Chrysothamnus viscidiflorus* (Hook.) Nutt. ssp. *puberulus* Hall and Clements (hairy low rabbitbrush). Sagebrush flat in section 34 of Mormon Row. 29 July 1985.
GTNP-280	*Rumex occidentalis* Wats. (western dock). Grass/sedge meadow of Buffalo Pasture in Jackson Wildlife Park, National Environmental Study Area. 29 July 1985.
GTNP-362	*Lepidium virginicum* L. var. *pubescens* (Greene) C. L. Hitchcock (Virginia pepperweed). Lodgepole pine forest Huckleberry Hot Springs, Rockefeller Parkway. 16 August 1985.

Table 6—Common plants with number of study areas of occurrence listed by life form (minimum of 5 study areas)

Plant name	No. of study areas
Grasses	
Agropyron trachycaulum— slender wheatgrass (*A. caninum* var. *majus*)	12
Agropyron smithii—western wheatgrass	5
Agropyron spicatum—bluebuch wheatgrass	7
Bromus inermis—smooth brome	13
Koeleria macrantha—June grass	10
Phleum pratense—Timothy	5
Poa pratensis—Kentucky bluegrass	14
Stipa columbiana—Columbia needlegrass	8
Stipa lettermanii—Letterman needlegrass	5
Grass-like plants	
Carex rossii—Ross sedge	8
Carex vallicola—valley sedge	5
Forbs	
Achillea millefolium—yarrow	11
Agoseris glaca—mountain dandelion	6
Antennaria microphylla—rosy pussytoes	12
Arabis drummondii—Drummond rockcress	7
Arabis holboellii—Holboell rockcress	9
Aster chilensis—Pacific aster	9
Chenopodium album—lambsquarter	5
Collomia linearis—collomia	9
Comandra umbellata—bastard toadflax	6
Crepis acuminata—tapertip hawksbeard	5
Erigeron pumilis—low fleabane daisy	6
Eriogonum umbellatum—sulphur buckwheat	11
Linanthus harknessii—three seeded linanthus	11
Lupinus sericeus—silky lupine	10
Perideridia gairdneri—common yampah or false yarrow	5
Phlox longifolia—longleaf phlox	5
Polygonum douglasii—Douglas knotweed	12
Potentilla arguta—sharptoothed cinquefoil	5
Potentilla gracilis—slender cinquefoil	6
Taraxacum officinale—common dandelion	16
Thlaspi arvense—field pennycress	5
Tragopogon dubius—yellow salsify or goatsbeard	8
Shrubs	
Artemisia tridentata ssp. *vaseyana*—mountain big sagebrush	10
Chrysothamnus viscidiflorus—low rabbitbrush	5

Table 7—Density of common plants in each type of study area. There were 300 quadrats each for sagebrush-grass and sagebrush-grass treated study areas, 150 quadrats for the meadow study areas, and 50 quadrats for the lodgepole pine study area

COMMON SAGEBRUSH-GRASS PLANTS

Species	Percent of quadrats	Plants/m²
Eriogonum umbellatum sulphur buckwheat	81.7	3
Artemisia tridentata big sagebrush	70.0	3
Koeleria macrantha June grass	58.7	4
Lupinus sericeus silky lupine	55.6	3
Agropyron spicatum bluebunch wheatgrass	49.3	2
Poa pratensis Kentucky bluegrass	43.7	140
Linanthus harknessii three seeded linanthus	36.7	6
Polygonum douglasii Douglas knotweed	36.7	4
Festuca idahoensis Idaho fescue	29.3	2
Antennaria microphylla rosy pussytoes	28.0	1

Others[1]: *Arenaria congesta*—ballhead sandwart
Selaginella densa—Rydberg spikemoss
Aster chilensis—Pacific aster
Collomia linearis—collomia
Carex rossii—Ross sedge

COMMON SAGEBRUSH-GRASS TREATED AREA PLANTS

Species	Percent of quadrats	Plants/m²
Bromus inermis smooth brome	80.0	194
Poa pratensis Kentucky bluegrass	65.3	162
Taraxacum officinale dandelion	25.0	12
Aster chilensis Pacific aster	19.0	2
Medicago sativa alfalfa	17.0	1
Artemisia tridentata big sagebrush	13.0	1
Tragopogon dubius salsify	9.3	1

Others[1]: *Collomia linearis*—annual collomia
Agropyron trachycaulum—slender wheatgrass
Antennaria microphylla—rosy pussytoes

COMMON MEADOW PLANTS

Species	Percent of quadrats	Plants/m²
Poa pratensis Kentucky bluegrass	94.0	382
Phleum pratense Timothy	44.7	4
Taraxacum officinale common dandelion	40.7	6

(con.)

included alfalfa (*Medicago sativia*) (17 percent), common dandelion (25 percent), Pacific aster (*Aster chilensis*) (19 percent), and salsify (*Tragopogon dubius*) (9.3 percent). The characteristic dominant plant of the pre-disturbance community, mountain big sagebrush, was present in only 13 percent of the quadrats, despite a recovery period of up to 55 years for some of the disturbed sites (table 3). The drastically disturbed sites were dominated by healthy stands of sward-forming grasses with over 1,000 stems per m^2 (table 2) and with no mountain big sagebrush present (Mormon Row, Heim, and Cottonwood Creek hayfields). Each of these study areas was near healthy mountain big sagebrush populations (fig. 1).

The areas that had been disturbed only by grazing probably have denser stands of mountain big sagebrush than they had historically because of two primary factors.

Table 7 (Con.)

COMMON MEADOW PLANTS

Species	Percent of quadrats	Plants/m^2
Potentilla gracilis cinquefoil	38.0	4
Equisetum laevigatum horsetail	36.0	11
Achillea millefolium yarrow	33.3	9
Trifolium hybridum alsike clover	28.0	3
Polygonum douglasii Douglas knotweed	25.3	2
Bromus inermis smooth brome	24.7	17
Collomia linearis collomia	17.3	1

Others[1]: *Aster hesperius*—Siskiyou aster
Trifolium longipes—longstalk clover
Cirsium scopulorum—mountain thistle
Carex praegracilis—blackcreeper sedge
Lepidium campestre—field pepperweed

COMMON LODGEPOLE PINE PLANTS

Species	Percent of quadrats	Plants/m^2
Taraxacum officinale common dandelion	72.0	10
Poa pratensis Kentucky bluegrass	37.5	72
Achillea millefolium yarrow	37.5	3
Polygonum douglasii Douglas knotweed	48.0	26
Phleum pratense Timothy	40.0	2
Aster integrifolius thickstem aster	34.0	3
Elymus glaucus blue wildrye	30.0	2
Carex geyeri elk sedge	28.0	2
Bromus carinatus mountain brome	28.0	4

Others[1]: *Spergularia rubra*—red sandspurry
Collomia linearis—collomia
Agrostis alba—redtop
Geranium viscosissimum—sticky geranium
Fragaria virginiana—woodland strawberry
Arabis drummondii—Drummond rockcress
Pinus contorta—lodgepole pine

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[1] Plants listed in this table were those most common across study areas within community types with average densities ≥1. The other plants listed were also relatively common. For a complete species list for each study area see table 3.

One, preferential grazing of grasses by domestic livestock provided the sagebrush with a competitive advantage that has been subsequently maintained. Two, fire suppression since Caucasian settlement has also led to more dense sagebrush stands and to the exclusion of grasses (Clark 1981).

Meadow Communities—The meadow study areas were Three Rivers Ranch (study area 1), Buffalo Pasture (study area 9), and Oxbow Bend Horse Pasture (study area 15) (tables 1, 4, fig. 1). Three Rivers Ranch was more drastically disturbed than the other two areas (tables 1, 4); land there had been cleared and planted. The two pasture sites had some forage pasture plants added but the native meadow was not completely cleared. The Buffalo Pasture, which has had 4 years longer for recovery, appears to be in a more natural condition than the Oxbow Bend Horse Pasture. The seeded forage plants Kentucky bluegrass, Timothy, alsike clover (*Trifolium hybridum*), and smooth brome, and the weedy plants common dandelion and Douglas knotweed were among the most common plants in the meadow communities (table 7). However, especially in the two pasture sites, natural healing seems to be taking place with a rich array of native plants intermixed with the seeded forage plants.

Lodgepole Pine Community—The only lodgepole pine community was Huckleberry Hot Springs (study area 16) in the John D. Rockefeller Memorial Parkway. This area is a former campground that was closed in 1983 when the protozoan *Giardia lamblia*, the causative agent for giardiasis, was discovered in the hot springs. It was the smallest of our study areas, yet included the most species (tables 1, 3). Even though it had been abandoned for only 2 years, its disturbance value was intermediate and was significantly lower than that of study areas that had been cleared and seeded with recovery times of up to 55 years (table 4). The visually dominant plant at this site was, of course, lodgepole pine (*Pinus contorta*). However because of the large size of that tree in comparison to other species present and the clearings created for the establishment of the now abandoned campground, the density of lodgepole pine was 0.26 per m^2—less than several other plant species in the study area (table 7). Young lodgepole pine seedlings had established in the campground clearings. The most common plants in the study area included common dandelion, Kentucky bluegrass, yarrow, Douglas knotweed, and Timothy. These plants are all common in disturbed areas and are weedy (common dandelion, yarrow, Douglas knotweed) or had been commonly planted for forage or restoration purposes in the Jackson Hole area (Kentucky bluegrass, Timothy). Several of the common plants were native components of the lodgepole pine ecosystem (table 7), including thick stem aster (*Aster integrifolius*), blue wildrye (*Elymus glacus*), elk sedge (*Carex geyeri*), mountain brome (*Bromus carinatus*), sticky geranium (*Geranium viscossimum*), and woodland strawberry (*Fragaria virginiana*).

Soils—The soils of the study areas were soils of terraces and alluvial fans—Tieneman-Bearmouth-Greyback (study areas 2-7, 10-14), soils of the mountains and foothills—Buffork-Perceton-Tongue River (study area 1) and Hechtman-Rock outcrop (study area 16), soils of floodplains—Tetonville-Wilsonville-Tineman (study area 9) and Cryaquolis-Cryofibrists (study area 15) and soils of foothills, buttes, and glacial moraines—Turnerville-Tetonia-Greyback (study area 8) (Young 1982). These soils are deep and well drained except for the floodplain soils, which are poorly drained. The soils are gravelly and sandy loams. All of the soil profiles we examined were at least 0.5 m (table 8). Soil pH values were generally in the neutral range but varied from 4.9 to 7.7 (table 8). Values for soil organic matter were in the normal range for western rangeland soils (Webb 1994). Values for CEC and SAR were lower than is typical for western rangeland sites (McArthur and others 1994; Woodward and others 1984) except for the Huckleberry Hot Springs study area, which had higher than normal SAR values (table 8). Electrical conductivity (EC) values demonstrated that the soils are non-saline, less than 4×10^3. Values for the other soil minerals assayed were (all in ppm, N = 28, means ± standard deviation):

Nitrate nitrogen (NO_3-N)	5.56	±	5.21
Phosphorus (P)	22.22	±	14.85
Potassium (K)	262.03	±	166.07
Zinc (Zn)	1.87	±	1.96
Iron (Fe)	65.52	±	53.18
Manganese (Mn)	28.55	±	48.42
Copper (Cu)	0.96	±	0.44
Calcium (Ca)	65.74	±	34.04
Magnesium (Mg)	16.79	±	7.75
Sodium (Na)	21.28	±	45.60

These values are unremarkable except for the high variation in the sodium, manganese, and zinc values. This variation is attributable to Huckleberry Hot Springs study area. Sodium values there were as high as 145 ppm, manganese as high as 243 ppm, and zinc as high as 8 ppm (data on file at the Shrub Sciences Laboratory). The high mineral and SAR values for the Huckleberry Hot Springs study area are not unexpected; this is an area of geothermal venting. The values for phosphorus and iron are relatively high for western rangeland sites (Webb 1994). The values for the more drastically disturbed sites were not different in any systematic way than those for the less drastically disturbed sites.

Restoration Options

Treatment alternatives by general study area community type (drastically disturbed sagebrush-grass, meadow, lodgepole pine) were developed for those study areas with disturbance values above 0.9 (table 4). We believe those areas with disturbance values below 0.9 will naturally heal. Recommendations for each study area were discussed elsewhere (McArthur and others 1986).

The study areas were once grazing lands, pastures, farmland, and in one case, a campground (table 4). The sagebrush-grass and converted sagebrush-grass sites (study areas 2-8, 10-14) occur under somewhat similar conditions. The soils and potential natural plant communities are quite similar. The more drastically disturbed of these sites (onetime farms and ranches) have been seeded for production purposes and support more or less similar mixtures of native and exotic species (table 3). Many disturbance sites

Table 8—Summary of soil characteristics at study areas

Site name	Horizons	Depth (cm)	pH	CEC	%OM	ECx10^3	SAR
Sagebrush-Grass, Grazed							
Cow Lake	A	0-15	5.50	20.30	3.89	0.33	0.12
“	B	15-61	5.10	14.90	1.24	0.20	0.08
Pot Holes	A,B	0-33	5.70	31.60	5.29	0.31	0.02
“	C	33-71	6.12	22.87	4.60	0.28	0.04
Mormon Row Sagebrush	A	0-61	6.30	18.10	5.43	0.39	0.08
Clark Moulton Sagebrush	A	0-71	6.70	16.30	2.11	0.58	0.03
Rocky Mountain Energy	A	0-10	6.10	16.10	5.28	0.38	0.04
“	B	10-51	5.80	14.40	2.92	0.23	0.06
Cottonwood Creek Sagebrush	A	0-30	5.60	22.30	4.60	0.43	0.03
“	B	30-66	7.40	14.50	4.66	0.35	0.05
Sagebrush-Grass, Radically Disturbed							
Mormon Row Hayfields	A	0-61	6.50	24.40	2.68	0.87	0.04
Clark Moulton Dry Farm	A	0-71	7.10	18.60	2.53	0.68	0.02
Abercrombie Warm Springs Ranch	A	0-71	7.50	17.20	1.52	0.71	0.05
Aspen Ranch Corp.	A	0-8	7.00	20.40	5.20	0.63	0.02
“	A,B	8-20	7.30	19.20	3.53	0.57	0.03
“	B	20-61	7.70	16.00	2.06	0.68	0.02
Heim Hayfields	A	0-71	7.30	14.60	1.75	0.44	0.09
Cottonwood Creek Hayfield	A	0-15	6.20	13.70	4.40	0.96	0.08
“	B	15-76	4.90	9.78	3.17	0.40	0.09
Meadows							
Three Rivers Ranch	A,C	0-61	7.10	21.00	1.55	0.56	0.07
Buffalo Pasture	A	0-46	5.90	32.70	5.36	0.24	0.17
“	C	46-81	6.80	23.10	1.38	0.46	0.11
Oxbow Bend Horse Pasture	A	0-56	5.70	31.60	5.27	0.21	0.14
“	C	56-81	5.90	26.70	1.40	0.30	0.17
Lodgepole Pine							
Huckleberry Hot Springs	C	0-8	7.00	25.90	5.51	1.20	2.01
“	C	8-25	7.60	9.61	1.13	1.11	8.20
“	C	25-33	7.00	22.90	1.30	1.08	4.84
“	C	33-66	7.20	14.00	1.00	1.12	6.54

are dominated by smooth brome and Kentucky bluegrass. These species are well adapted to the sites they occupy. They are competitive and persistent and restrict the entry of native herbs and shrubs into their sward-like stands in a manner described by del Moral (1985) and Goldberg and Gross (1988). The meadow study areas (1,9,15), like the drastically disturbed sagebrush-grass sites, are dominated by persistent, competitive species, such as Kentucky bluegrass, Timothy, and smooth brome.

Cotts and others (1991) in their work on restoration of abandoned roads in the lower elevations of Grand Teton National Park concluded that natural succession to native plant communities without seeding will occur on these areas but that community development is accelerated best with seeding of site indigenous plant materials and almost as well with non-site indigenous, but native, plant materials purchased from commercial seed dealers. Our study differs from that of Cotts and others (1991) in that many of our study areas had been previously planted to and managed for aggressive, competitive agricultural pasture and hayfield plants.

In management and restoration of these sites some limitations or constraints can influence the reestablishment of native plants.

1. Smooth brome and Kentucky bluegrass are well suited to this region. If present, these grasses, especially smooth brome, will prevent the reestablishment of natives. These grasses are rhizomatous and increase to attain dominance of seeded areas. They may attain impressive stem densities (table 2). Seeds of these grasses are easily spread and consequently they are found throughout the major lowland Park plant communities (table 3). If their presence and abundance are not acceptable to Park management, the plants must be removed by physical or chemical treatments.

2. If smooth brome is to be removed from the disturbed sites, plowing, disking, and spraying with herbicides are the only available treatments. Each of these treatments has management drawbacks. Plowing or disking would have to be repeated over a 2- to 3-year period. Plowing would not be effective unless the plants were repeatedly uprooted. This treatment eventually weakens and ultimately kills the roots. Sites would require plowing or disking three to four times each year until success is obtained. Areas would need to be summer-fallowed similar to "dry farming" operation. If areas were not treated correctly, re-rooting would occur. Selective spraying could be used to remove the introduced grasses without complete elimination of associated plants. Several applications may be required. The grasses cannot be eliminated or significantly reduced through natural succession alone. These species are more competitive than most of the natives.

Partial restoration (= substantive residue of exotic grasses) could be achieved by interseeding or interplanting into existing cover. Small clearings within the existing cover must be created to reduce competition to the new transplants and especially to the new seedlings.

3. Seed and planting stock quantities of many native herbs and shrubs are limited. Planting stock should be grown from seed collected near the study areas. This would require planning and time to acquire seed or propagate transplant stock, thus limiting the ability to plant large areas at one time. Some species are difficult to establish by artificial plantings even if seed or transplant stock is available. Therefore, natural succession must be relied on to accomplish reestablishment of these species. Plantings must be designed to allow entry and spread of these species. Some species will be extremely slow to fully recover and time must be provided to attain a natural plant composition. Seed mixtures proposed for treatment include native species that are compatible, can be established together, and for which seed can be acquired in large enough quantities to complete reasonably scaled projects.

4. Areas occupied by exotic grasses can be interseeded or inter-transplanted with shrubs. Small clearings need to be created to allow the small shrub seedlings to become established. Once shrubs have reached maturity, the understory grasses can be removed by selective spraying or plowing. Native herbs could be seeded as the grasses are removed. This sequence and combined methods of treatment could be employed on sites naturally dominated by shrubs. Once shrubs are established, removal of the understory herbs could be accomplished without exposing obvious bare ground patches. Treatment could be confined to small areas, and conversion of the vegetation could be completed by natural plant succession.

Drastically Disturbed Sagebrush-Grass Communities (Study Areas 4, 7, 8, 10, 12, 13)—Each study area has its own peculiarities (McArthur and others 1986) so the following treatment alternatives will need to be considered in light of those differences:

1. Leave in present condition recognizing that smooth brome, Kentucky bluegrass, and other exotic species are well adapted and may remain in situ indefinitely. Some of the pasture and hayfield lands such as Heim Hayfield, are esthetically pleasing to many visitors; this factor needs to be considered in management decisions.

2. Close existing roads and ditches as individual study areas may require. As possible, recreate natural drainage ways. Spray, plow, or disk to remove noxious weeds. Reduce existing vegetation by these same methods on mosaics that include approximately 20 to 30 percent of the areas under consideration, and interseed or transplant native species. Allow treatments to create a natural mosaic of plant communities. Selectively treat areas to remove dominant stands or patches of smooth brome and Kentucky bluegrass. Plants to consider seeding or transplanting, depending on the particular study area (table 3, McArthur and others 1986), include mountain big sagebrush, antelope bitterbrush (*Purshia tridentata*), Woods rose (*Rosa woodsii*), three tip sagebrush (*Artemisia tripartita*), rubber rabbitbrush (*Chrysothamnus nauseosus*), low rabbitbrush (*C. viscidiflorus*), mountain snowberry (*Symphoricarpos oreophilous*), and Saskatoon serviceberry (*Amelanchier alnifolia*) as the shrub component. Antelope bitterbrush, the sagebrushes, and rabbitbrushes can be seeded but the other shrubs should be established as transplants. Interseed a mixture of native grasses and broadleaf herbs with the shrubs. Some possible species, depending on the study area, include western wheatgrass (*Agropyron smithii*), bluebunch wheatgrass (*A. spicatum*), alpine Timothy (*Phleum alpinum*), needle and thread grass (*Stipa comata*), green needlegrass (*S. viridula*), Pacific aster (*Aster chilensis*), sulfur buckwheat (*Eriogonum umbellatum*), Lewis flax (*Linum*

lewisii), silky lupine, and arrowleaf balsamroot (*Balsamorhiza sagittata*). As plantings attain maturity, interplant additional segments until entire study areas have been restored. Individual segments or plantings will require approximately 5 years to attain maturity. Treating small segments at various times will diminish aesthetic impacts, and yet allow for the initial establishment and natural invasion of native species.

3. Remove existing grasses by plowing or spraying entire study areas (sites) in one operation. Seed mixture of native herbs described in alternative 2. Interseed or inter-transplant mountain big sagebrush through areas in random patterns. Inter-transplanting 1- to 3-year-old nursery stock would produce an immediate woody cover. Shrubs will develop rapidly and reach a mature stature similar to surrounding area within 3 to 5 years.

4. Interseed or inter-transplant shrubs throughout the study areas by making small clearings in existing vegetation to reduce grass competition. Allow seeded exotic grass to remain as an understory.

Meadows (Study Areas 1, 15)—Three Rivers Ranch (study area 1) and Oxbow Bend Horse Pasture (study area 15) are quite different. The Oxbow Bend Horse Pasture (study area 15) and the Buffalo Pasture (study area 9), however, are quite similar. The Buffalo Pasture shows less quantitative evidence of disturbance than the Oxbow Bend Horse Pasture (table 4) but recommendations for restorative techniques for the two are similar. We omit more specific reference to the Buffalo Pasture because its disturbance value was < 0.9 (0.53, table 4).

Treatment alternatives for Three Rivers Ranch:

1. Control trespass livestock grazing; allow vegetation to recover by natural succession. Cover portions of irrigation system; close access road.

2. Plow or disk major portions of abandoned fields to remove principal exotics. Seed with a complement of native herbs including slender wheatgrass (*Agropyron trachycaulum*), mountain brome, Idaho fescue (*Festuca idahoensis*), and western yarrow. Define natural ephemeral stream routes and transplant willow (*Salix* spp.), currant (*Ribes* spp.), bush cinquefoil (*Potentilla fruticosa*), and mountain snowberry (*Symphoricarpos oreophilus*). Transplant or seed upper benches with mountain big sagebrush and lodgepole pine. Allow for natural recovery of the herbs.

3. Remove exotics by disking, plowing, or spraying entire fields. Treat as described in alternative 2, but include additional herbs—sticky geranium, cinquefoil (*Potentilla gracilis*), and Pacific aster (*Aster chilensis*)—in seed mixture.

Treatment alternatives for Oxbow Bend Horse Pasture:

1. Treat by spraying, plowing, or uprooting to remove noxious weeds. If selective herbicides are used and the existing mix of perennial grasses is acceptable to Park management, seeding is not required. If sites are plowed, seed with mountain brome and tufted hairgrass (*Deschampsia caespitosa*). Manage remaining areas to allow natural recovery.

2. This area is occupied by extensive and solid stands of smooth brome. Kentucky bluegrass is also abundant and widespread. Intermixed with both grasses are many native grasses and broadleaf herbs. The area consists of semi-wet and wet meadows. Many species native to these conditions are extremely difficult to reestablish. Treatments such as plowing or disking should not be conducted in areas where these native herbs occur. The large stands of smooth brome should be mapped and considered for treatment. These could be sprayed or plowed; spraying would be best over the areas of irregular terrain. The study area is highly visible. Artificial treatment will have a major impact on esthetics. The smooth brome areas could be treated segmentally over a number of years to reduce the visual impact. Seeding (after the spraying or plowing preparatory work) should consist of mountain brome, tufted hairgrass, Columbia needlegrass (*Stipa columbiana*), western yarrow, and slender cinquefoil. If sites are planted with this mixture, natural invasion of adapted natives will occur. Riparian sites should not be treated unless wilding transplants of sedge (*Carex*) and rush (*Junceus*) are available for use. Species of *Carex rossi*, *C. lanuginosa*, and *C. praegracilis* transplant well and can be used along streambanks. This is a very difficult area to restore. Where smooth brome is present natives will not establish. Artificial treatment will be required for rehabilitation where smooth brome is removed.

Lodgepole Pine (Study Area 16)—Only one study area was evaluated. We present a single treatment alternative.

1. Remove existing structures as determined necessary. Spray, plow, or uproot noxious weeds. Remove pathways and roads. Excavate asphalt surfaces and aggregates. Rip and plow compacted areas. Allow for recovery of native species throughout the small disturbances. Control further spread of weeds. Seed or transplant native herbs, shrubs, and lodgepole pine into larger disturbances (table 3). Natural invasion of native plants would be slow to develop in the larger disturbances. We recommend that lodgepole pine, bush cinquefoil, and mountain lover (*Pachystima myrsinites*) be amply transplanted to speed up the recovery time by providing larger plants early in the successional process. Transplant different ages and sizes of stock to provide a more natural appearance. Seed mountain brome and slender wheatgrass. Both of these grasses will provide initial cover, yet allow natural entry of adapted herbs.

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‘Rocker’ Tanglehead (*Heteropogon contortus* [L.] Beauv. ex Roem. and J.A. Schultes): An Improved Cultivar for Conservation

Mark J. Pater

Abstract—‘Rocker’ tanglehead (*Heteropogon contortus* [L.] Beauv. ex Roem. and J.A. Schultes) is a perennial, warm-season bunchgrass. It is recommended for use in critical area stabilization and rangeland revegetation as well as erosion control along roadways, construction sites and other disturbed areas within the desert Southwest. Its main use is intended for rill and gully erosion control where extra moisture is available. Rocker (9043377, P.I. 562143) was released on September 28, 1992 by the Soil Conservation Service (SCS) in cooperation with the U.S.D.A. Agricultural Research Service and the University of Arizona Agricultural Experiment Station. It was selected over other strains for its better overall vigor, ability to initiate spring growth, and capacity to produce an abundance of green herbage. Rocker also exhibits a later flowering date than the other strains it was evaluated with. Rocker is a “source identified” release, meaning that this material originated from a natural stand of known location and elevation. This release has not been subject to any genetic manipulation.

Rocker tanglehead (*Heteropogon contortus* [L.] Beauv. ex Roem. and J.A. Schultes) is a native, perennial bunchgrass; *Culms* tufted, 100 to 120 cm tall, usually branching well above the base; *Sheaths* compressed-keeled, glabrous with a few short hairs at the junction with the blade; *Ligule* short, truncate, fringed with short, stiff hairs; *Blades* mostly 5 to 8 mm wide, flat or folded, scabrous, 20 to 30, occasionally 36 cm long, usually ciliate on the margins with a few long, pappilose-hispid hairs; *Racemes* 3 to 7 cm long, produced on slender lateral culm branches as well as terminating the main culm; *Rachis* joints readily disarticulating at maturity; *Glumes of staminate spikelet* about 7 mm long, bright green, several-nerved, hirsute; *Fertile spikelet* about 1 cm long from the base of the long, stiffly-hispid callus to the glume apex, the first glume dark brown, correaceous, hispid, enclosing the second glume; *Awn of fertile lemma* stout, twisted, twice geniculate, pubescent below with spreading hairs mostly 0.5 to 1 mm long, readily deciduous at maturity, usually falling entangled with the awns of other spikelets (Taxonomic description for Rocker provided by Dr. John R. Reeder [ret.] at the University of Arizona Herbarium, Tucson). (Greek, *heteros*, different, and *pogon*, beard, referring to the awnless male and awned female spikelets [Munz and Keck 1973].)

Heteropogon contortus is an obligate apomict (Emery and Brown 1957). Normal chromosome numbers for this species are 2n=60 (Gould 1975). Tanglehead is a C4 plant and virtually all growth occurs after the onset of summer rains (in Arizona: late July to early August), unless warm spring temperatures coincide with adequate soil moisture (Novelly 1986).

Rocker tanglehead was comparatively evaluated with 26 accessions of *Heteropogon contortus* in the 1986 *Heteropogon contortus* Initial Evaluation Planting (IEP). In 1990, Rocker was one of four tanglehead accessions selected for best overall performance.

In 1991 all four accessions were transplanted into a spaced plant, mass selection block for evaluation and final selection. Rocker was the superior performer in this planting. It has shown vigorous growth, is a larger, more robust plant, and flowers at a later time. Throughout the whole evaluation process, Rocker tanglehead has consistently flowered 2 to 3 weeks later than all other accessions. Beginning in late September, it continues to flower and produce seed through early November.

Observations in the mass selection block have shown that Rocker averages a size of 120 cm by 120 cm versus an average size of all other plants of 70 cm by 90 cm.

Rocker tanglehead exhibited a greater tolerance to drought conditions than the other accessions within the IEP block. Following the summer of 1991, in which the Tucson Plant Materials Center received well below-average precipitation, Rocker produced an abundance of green herbage despite very low summer precipitation. All other accessions tended to remain mostly dormant throughout the rest of the summer.

The ability of Rocker tanglehead to initiate earlier spring growth than the other accessions will allow this selection to have a greater ability/advantage to compete for water and nutrients. In addition, the ability of this accession to stay green and initiate growth under extended drought-like conditions makes Rocker tanglehead a desirable conservation plant.

Rocker was primarily selected for use in controlling rill and gully erosion because it produces dense stands of seedlings in areas where extra moisture is available. Its low palatability permits it to mature and produce seed where more palatable species may be too closely grazed to do so (Ward and Martin 1972).

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According to Ward and Martin (1972), the value of tanglehead as an erosion control plant has been demonstrated on the Santa Rita Experimental Range, south of Tucson, Arizona. Before treatment (chaining), gullies and rills on the study area were raw and actively eroding. After chaining, dense stands of tanglehead filled most of the gullies and rills and erosion was greatly reduced.

Novelly (1986) states that the seed of *Heteropogon contortus* exhibits a dual inhibitory system to germination (Tothill 1977). Naked caryopses less than 4 months old exhibit dormancy akin to epicotyl dormancy, readily overcome by gibberelic acid, and also partly reduced by repeated wetting and drying. Dormancy declines with age with maximum germination occurring at 12 months of age. Seed remains viable for up to four years if adequately stored. Maximum germination was recorded at constant 30 °C (Tothill 1977), with little increase at 35 °C. Constant 25 °C reduced germination as did alternating temperatures if one temperature was below 30 °C.

Emery and Brown (1958) have stated that *Heteropogon contortus* consists of a relatively uniform series of populations with an extensive native range throughout most of the tropical and subtropical grassland regions of the world. The distribution of *Heteropogon contortus* is reported from every major land mass between 35° N latitude and 35° S latitude; it is endemic in the New World, and in the Old World from South Africa to Australia, and on numerous islands of the Pacific Ocean.

Rocker is best adapted to elevations ranging from 1,067 to 1,676 m with 305 to 406 mm of annual precipitation, and sandy loam surface soils with clay loam subsurface soils.

Other plants found growing in association with Rocker include: cane bluestem (*Bothriochloa barbinodes* [Lag.] Herter), sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), curly mesquite (*Hilaria belangeri* [Steud. Nash]), galleta grass (*Hilaria jamesii* [Torr.] Benth.) , fairy duster (*Calliandra eriophylla* Benth.), ocotillo (*Fouquieria splendens* Engelm.) and mesquite (*Prosopis juliflora* [Swartz]).

Rocker tanglehead seed can be drilled at a depth of 13 mm into a well prepared seedbed or broadcast seeded over a disturbed seedbed. Good seed-soil contact is required for optimum germination and establishment. The recommended seeding rate is 4 to 6 pure live seed (pls) pounds per acre for drill-seeding, and 8 to 12 pls pounds per acre for broadcast seeding. Plantings should be conducted after the onset of summer rains. Spring plantings could be conducted if spring rains appear to be above average in frequency, but they are not recommended. Plantings should be managed to prevent young seedlings from being grazed to insure establishment (normally 1 to 2 years of rest).

It is recommended that Rocker be utilized as part of a seeding mixture, comprising roughly 20 to 30% of the total mix. However, the percent composition can vary depending on the seeding objective. When seeding on sites subject to erosion, mulching is recommended to conserve soil moisture, prevent surface compaction or crusting, reduce surface runoff and erosion, control weeds, and help establish plant cover. If Rocker is to be drill-seeded, the material needs to be de-awned to prevent blockage in the drill tubes. If the seed cannot be de-awned, broadcasting or hydroseeding is required.

Foundation seed of Rocker for certified seed increase is available from the USDA-SCS Tucson Plant Materials Center, 3241 N. Romero Rd., Tucson, AZ 85705. Seed propagation of Rocker is restricted to two generations of increase from breeder seed and one of each from foundation and certified. Breeder and foundation seed will be maintained by the USDA-SCS Tucson Plant Materials Center.

For more information on availability and use of Rocker tanglehead, contact your local SCS office. All programs of the Soil Conservation Service are offered on a nondiscriminatory basis, without regard to race, color, national origin, religion, sex, age, marital status or handicap.

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Prescribed Burning on Upper Sonoran Rangelands

Dan Robinett

Abstract—Naturally occurring wildfires played an important role in shaping Sonoran grasslands in Arizona. Anglo settlement of the region caused a variety of impacts changing vegetation from grass to shrub. In an area transitional between semi-desert grassland and upper Sonoran desert, the reintroduction of fire in these ecosystems is resulting in a return to perennial grass dominance. Sandyloam range sites at elevations of 3,200 feet and with average annual precipitation of 12 inches have plant communities dominated by velvet mesquite, burroweed, cacti, annual and perennial grasses and forbs. Photographic evidence from the turn of the century shows these areas as open grassland. The use of prescribed fire in these plant communities has resulted in successful treatment of about 10,500 acres on one ranch in the Altar valley. Fires in May and June top killed mesquite and killed burroweed, allowing grasses to establish and thicken. A prescription and burning technique has been developed to safely burn these plant communities. Good management of grazing after the burns allows perennial grasses to flourish once again. The combination of prescribed fire and managed grazing in this area has resulted in many benefits including wildlife habitat, watershed values, reduced erosion and increased forage for livestock.

In Pima County, southern Arizona, an area transitional between semi-desert grassland and upper Sonoran desert occupies several hundred thousand acres of rangeland. Photographic evidence from the turn of the century shows much of this area to be open grassland (Humphrey 1987). Repeats of the same scenes today show plant communities dominated by shrubs, trees and cacti.

Anglo settlement of the region caused a variety of impacts that helped to bring about these changes (Bahre 1991, Hastings and Turner 1965). Cultural impacts like grazing, haying, farming and woodcutting interacted with natural factors like drought, flooding, fires, earthquakes and changing precipitation patterns to speed the change from grassland to shrubland in the last 100 years.

Climate in this region is dynamic with two distinct growing seasons and two sources of moisture for storms. Documentation of recent climate change has been made in flood records of major streams in the region (Webb and Betancourt 1992). On at least one site which has been fully protected from any cultural influences, mesquite has invaded a Sonoran desert plant community in the last 85 years (Turner 1990).

Naturally occurring wildfires played an important role in shaping desert grasslands in southern Arizona (Pase 1977, Leopold 1924). Lightning from summer thunderstorms, Indians using fire to hunt or clean up favorite campsites, or accidental starts from their campfires were common prior to the turn of the century (Bahre 1965, Leopold 1924). Natural fire frequencies for these grasslands are estimated at between 10 and 20 years (Pase 1977, Wright 1980). Periodic fire in these ecosystems would certainly favor perennial grass species over shrubs and cacti, helping to maintain their grassland aspect in the past (Wright and Bailey 1982, Wright 1988). A variety of human caused impacts since settlement has greatly reduced the frequency and spread of wildfires (Bahre 1991, Leopold 1924, Swetnam 1988). Over the last 100 years very little of Arizona's desert grassland has burned.

On one ranch in the Altar Valley near Tucson, prescribed fire has been used successfully since 1985 to reestablish grassland conditions. In this area elevations range from 2,900 to 3,400 feet. Average annual precipitation is 12 inches, equally distributed between the summer and winter seasons (NOAA 1992). Soils are in the aridic moisture regime and the thermic temperature regime. They are developing in light-colored sandy loam alluvium of moderate age. Hayhook soil series is typical of this area (USDA 1993).

Present day plant communities are dominated by velvet mesquite (*Prosopis*) with understories of burroweed (*Isocoma*), cacti (*Opuntia* spp.) and annual and perennial grasses and forbs. These communities now more closely resemble Sonoran desert vegetation of the Arizona upland subdivision than the grasslands they were once (Brown 1982). Technical range site descriptions for Deep sandyloam and Sandyloam upland range sites in a 10 to 13 inch precipitation zone show potential plant communities dominated by perennial grass (USDA 1988, 1991).

Prescribed fires in the hot, dry fore-summer (May-June) kill burroweed and top kill mesquite and cacti species. Management of grazing includes two years of deferment following the burn and rest-rotation thereafter. The combination of the fire and managed grazing allows native warm season perennial grasses to regain dominance of the understory. Repeat fires will be needed to actually kill mesquite trees on these sites. On the 54,000 acre Anvil ranch large pastures were fired in 1985, 1987, 1989, and 1991. About 10,500 acres of rangeland was actually burned out of a total of nearly 20,000 acres, leaving a mosaic of burned and unburned areas. The typical response of these plant communities is illustrated by plot readings of a trend monitoring transect installed in 1981 on Hayhook soils. The transect uses a pace-frequency format to record species composition and point sampling for cover. The area was burned in 1985.

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Species	Percent frequency			
	1981	1984	1989	1993
Burroweed	60	75	71	5
Mesquite	4	3	6	5
Opuntia	4	7	5	5
Santa Rita threeawn	5	17	38	67
Arizona cottontop	0	1	1	4
Annual grama	76	91	90	37
Basal cover	1	2	5	8
Production (lbs./ac. air dry)	20	100	200	400

Perennial grass production has quadrupled on this area and basal cover of perennial grass has increased from 2 to 8 percent in the 8 years since the burn. Research on similar soils on the Santa Rita Experimental Range has shown a decrease in soil erosion and water runoff on areas where shrubs have been controlled and grass cover has increased (Martin and Morton 1993).

Direct costs to the land owner for the burns average about $1.50 per acre. Deferment costs for the 24 month nonuse period after the fire is about $2.50 per acre in this area. The additional carrying capacity which has developed 8 years after burning is worth about $1.50 per acre. Depending upon the lifespan of this treatment, the practice appears to be a marginal to good investment for the land owner. The use of federal cost-share dollars (Agricultural Conservation Program) will help make it an attractive investment.

A safe technique and burn prescription has been developed over the years to minimize both the costs and the risks associated with this practice. Burn area perimeters are fired in the late afternoon to evening and allowed to carry several hundred feet into the interior. The burned edge is mopped up very early the next morning before dust devils become active. These small whirlwinds are the main reason for fire escapes in these flat areas. After the perimeter has been burned, the interior is burned in the daytime using headfires to get the hottest fires possible. These daytime burns also loft smoke columns to where high altitude winds can quickly disperse them. This is an important air quality consideration in an area close to a large city like Tucson.

Fine (one hour) fuel loads consist of annual grasses (95% dry) and burroweed (75% dry) and range from 3,000 to 4,000 pounds per acre. Ten to twenty mesquite trees per acre contribute to the fuel load. Prescription parameters call for the hottest fires possible to control shrubs. Burning is done in the hot dry season of May and June. Daytime temperatures range from 90 to 105 °F. Nighttime temperatures are from 65 to 90 °F. Relative humidities are usually less than 15 percent during the day and recover to 25 percent by evening. Dead fuel moisture values (10 hour) range from 2 to 6 percent. Burns are conducted with light prevailing winds of 2 to 8 miles per hour. Under these conditions daytime fires move at a rate of 20 to 30 chains (1,300-2,000 ft.) per hour with flame lengths of 10 to 15 feet. Backfires move at rates of 2 to 3 chains (130-200 ft.) per hour with 2 to 3 foot flame lengths.

Fire weather is monitored on site for two or three days prior to burning and each day while burning. Coordination is made with all the appropriate state, federal and county agencies to comply with all regulations, procedures and standards. Actual firing is done by ranch personnel with ranch equipment. Soil Conservation Service personnel act as fire managers, monitoring fire weather and behavior and advising the burn boss (rancher) to stay within prescription. Standby assistance from several agencies, including the Arizona State Land Department, the Buenos Aires National Wildlife Refuge, the Bureau of Indian Affairs and local volunteer fire departments, is almost always on hand. Large blocks (2,000 to 3,000 acres) usually take 5 to 6 days to burn.

The first summer rains arrive in this area in early July. In the first year the remnant perennial grasses on site recover and set seed. Annual grasses and forbs cover the burn areas. As the years go by, and with managed grazing, the perennial grasses expand and fill in the vacancies left by dead shrubs. Top killed mesquites take about 8 to 10 years to recover to their pre-burn canopies giving an additional advantage to grasses.

The reintroduction of fire in Sonoran desert grassland ecosystems appears to be a viable and needed undertaking. Safe techniques have been developed. The economics to the land owner appear to be good, especially when federal cost-share programs can be used. Not only is grass production increased, but also variability in forage production is reduced as the forage base changes from browse and annual plants to one of perennial grass. Burning also opens up shrubby areas, making livestock handling easier and more efficient. Public values improve in many ways and wildlife habitat is improved. A mosaic of burned and unburned areas greatly increases edge in treated pastures. Small herbivores increase tremendously as inedible shrubs are replaced by grasses and forbs. Birds increase in numbers and species in response to increased seed and insect production on burned areas. Improved covers of perennial grass reduce soil erosion, water runoff, and subsequent flooding and sedimentation downstream. The visual quality of these rangelands improves as the monotonous cover of mesquite and burroweed is broken up by open grassy areas.

Prescribed fire allows land managers to treat large areas at low cost in relatively short periods of time. Since 1985 nearly 20,000 acres of Sonoran rangeland has been improved by the combination of prescribed fire and managed grazing. Wildlife habitat, watershed values, recreational uses and grazing are all enhanced.

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‘Lassen’ Antelope Bitterbrush

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Abstract—‘Lassen’ antelope bitterbrush is recommended for restoring depleted rangelands, burned areas, mined lands, and other disturbed sites in the Intermountain West. Lassen was selected for its seedling vigor, upright growth habit, seed production, productivity, and retention of overwintering leaves. Selection trials indicate Lassen is adapted to antelope bitterbrush sites receiving 300 to 600 mm of precipitation at elevations ranging from 900 to 1,800 m. Best growth occurs on deep, coarse, well-drained, neutral to slightly acidic soils. Productive Lassen plantings have been established on such sites in northeastern California, eastern Oregon, and central and southern Idaho.

Antelope bitterbrush (*Purshia tridentata* [Pursh] DC.) is a widely distributed shrub of western rangelands, occurring from British Columbia to California and eastward from Montana to New Mexico. It grows at elevations from near sea level to 3,500 m on sites receiving 200 to 850 mm of annual precipitation (Giunta and others 1978; Nord 1965). Antelope bitterbrush, a member of the rose family, occurs as a community dominant and in other vegetation types ranging from blackbrush (*Coleogyne ramosissima* Torr.) to big sagebrush (*Artemisia tridentata* Nutt.), oak brush (*Quercus gambelii* Nutt.), mountain brush, pinyon-juniper (*Pinus* L.-*Juniperus* L.), lodgepole pine (*Pinus contorta* Dougl. ex Loudon), and ponderosa pine (*Pinus ponderosa* Lawson) and occasionally on exposed high-elevation ridges with limber pine (*Pinus flexilis* [James] Rydb.). It commonly occurs on deep, coarse-textured, well-drained, neutral to slightly acidic soils. Some stands, however, grow on shallow, fine-textured soils that may be quite alkaline (Giunta and others 1978).

Antelope bitterbrush populations differing in site requirements, seedling vigor, growth habit, and morphological characteristics have evolved as a result of intraspecific differentiation and recent and likely ongoing introgression with Stansbury cliffrose (*Cowania stansburiana* Torr.) (Jabbes and Brunsfeld 1993; McArthur and others 1983; Stutz and Thomas 1964). A number of extensive, productive, and easily accessible populations are regularly harvested by wildland seed collectors and sold to buyers throughout the Intermountain, Southwest, and Pacific Northwest regions. An understanding of the ecology and range of adaptability of these and other populations is needed to aid in prescribing seed sources for planting projects and to manage natural and seeded stands.

Over the last 50 years, characteristics of more than 200 populations of antelope bitterbrush, desert bitterbrush (*Purshia glandulosa* Curran), Stansbury cliffrose, and Apache-plume (*Fallugia paradoxa* [D.Don] Endl.) have been examined in ecological studies of native stands, range seeding studies, and species adaptation trials conducted in common garden settings in the Intermountain region, in northern California, and in the Pacific Northwest (Davis 1983). The importance of antelope bitterbrush in mule deer diets and stand depletion resulting from uncontrolled livestock grazing triggered early work with the species. More recent studies have examined species and population characteristics to provide clues to their evolutionary relationships. Use of the species in wildland plantings has expanded to include soil stabilization, low maintenance landscaping, and community restoration.

The collective results of this work, plus implementation of seed certification systems being developed or adapted for wildland species by State seed certification agencies, provide an opportunity to systematically begin (1) compiling descriptions and performance data for commonly collected antelope bitterbrush populations, (2) delimiting the range of adaptability for individual populations, and (3) providing land managers and revegetation specialists with procedures for verifying seed origin. One approach toward meeting these objectives is illustrated by the release of ‘Lassen’, a named variety of antelope bitterbrush.

Lassen Release

Released in 1984, Lassen is a distinctive antelope bitterbrush ecotype that has been extensively planted and studied over the last 40 years. Traits of interest in revegetation work are its seed production, seedling vigor, upright growth habit, productivity, winter leafiness, and palatability (Shaw and Monsen 1986; Shaw and others 1984a,b; Soil Conservation Service 1986). Lassen is recommended for planting in depleted rangelands, burned areas, mined lands, and other disturbed sites within its area of adaptation (Monsen 1987; Monsen and Davis 1986; Shaw and Monsen 1986).

Lassen is used by big game and livestock during all seasons and remains productive with moderate use. Mature, moderately grazed plants can provide more available forage than low, spreading forms of antelope bitterbrush, particularly when snow cover is present. The large plants provide hiding and thermal cover for many vertebrates and invertebrates. Birds, rodents, and insects consume its seeds. Lassen is an attractive shrub for low-maintenance landscaping in campgrounds, recreation areas, and along roadways. The root system contributes to soil stabilization, but mixed plantings with low-growing or spreading species may be more effective in stabilizing surface soils.

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Lassen's release resulted from cooperative efforts of the U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Soil Conservation Service, and the Utah Division of Wildlife Resources (Shaw and others 1984a,b). Seven State agencies in California, Idaho, Nevada, and Oregon cooperated. Characteristics of the variety and performance data were made available to potential users through release documents, a U.S. Department of Agriculture, Soil Conservation Service brochure, and a release announcement in Rangelands (Shaw and Monsen 1986; Shaw and others 1984a,b; Soil Conservation Service 1986).

Origin

Lassen originates from native stands in Lassen County, CA. The ecotype occurs in a narrow, 80-km strip along the eastern base of the Sierra Nevada Mountains extending from Susanville to drier sites near Doyle (fig. 1). Elevation at the Susanville airport is 1,250 m. Mean annual precipitation is 370 mm. The frost-free season averages 120 days with a range of 82 to 156 days. Average temperature is 9 °C. Temperature extremes normally range from highs near 43 °C to lows of -9 °C, although temperatures as low as -34 °C have been reported (Alderfer 1976; Nord 1963, 1965; National Oceanic and Atmospheric Administration 1982; Soil Conservation Service n.d.).

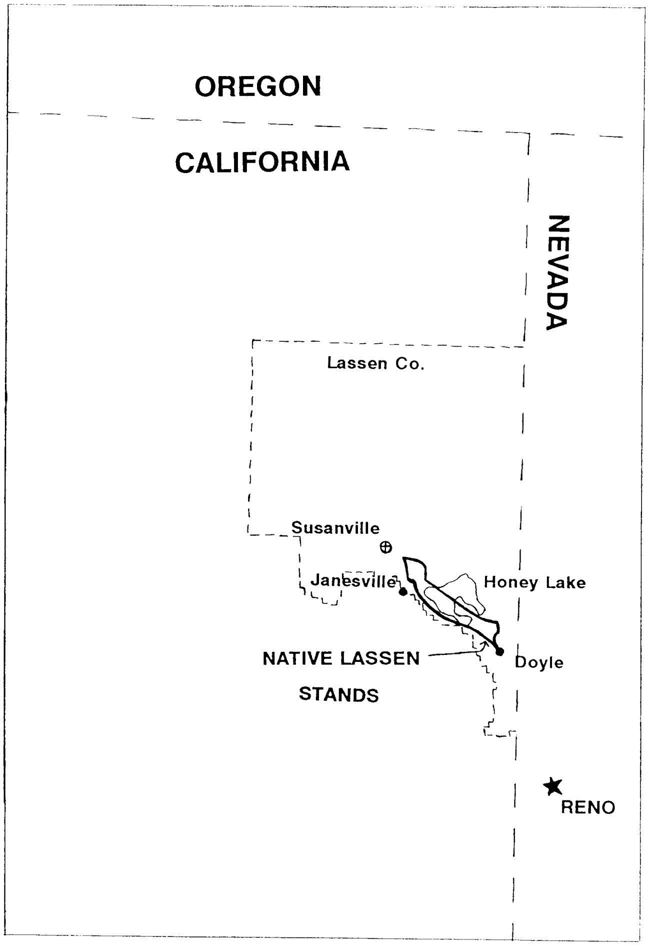

Figure 1—Native Lassen stands.

Native Lassen stands occupy dry lake beds, alluvial fans or terraces, and lower foothills of the Sierra Nevada Mountains. Soils are generally deep, slightly acid to neutral, gravelly to loamy sands derived from granite (Alderfer 1976; Nord 1965; Soil Conservation Service n.d.). Permeability is high. Vegetation is dominated by basin big sagebrush (*Artemisia tridentata* var. *tridentata*), antelope bitterbrush, and cheatgrass (*Bromus tectorum* L.) with ponderosa pine and Jeffrey pine (*Pinus jeffreyi* Balf. in Murray) in the foothills (Alderfer 1976; Nord 1965; Soil Conservation Service n.d.).

Since 1954, seed collected from this area has been planted in selection trials and field plantings in northeastern California (Shaw and others 1984a,b), western Nevada (Shaw and others 1984a,b), Utah (Davis 1983), Idaho (Shaw and Monsen 1983; Shaw and others 1984a,b; Welch and others 1983), and eastern Oregon (Edgerton and others 1983). Results of this work indicate Lassen has high potential for establishment on sites from 900 to 1,800 m that receive 300 to 600 mm of annual precipitation and that support, or once supported, antelope bitterbrush. It has performed well on sites with deep, coarse, well-drained, neutral to slightly acidic soils. It does not appear well adapted to basic, fine-textured, or poorly-drained soils.

Description

Mature Lassen plants are large, leafy, upright shrubs with few basal stems, heavy lateral spur production, and long, ascending to erect leaders (Alderfer 1976) (fig. 2). McArthur (1982) found plants growing near Janesville averaged 2.2 m in height with 3 m crowns. Nord (1962) reported a large shrub found near Janesville was 4 m tall with a crown spread of 6 m and a stem circumference of nearly 1 m, measured 0.2 m aboveground. Age of the shrub was estimated at 128 years based on a count of annual growth rings.

Figure 2—Lassen antelope bitterbrush growing near Janesville, CA.

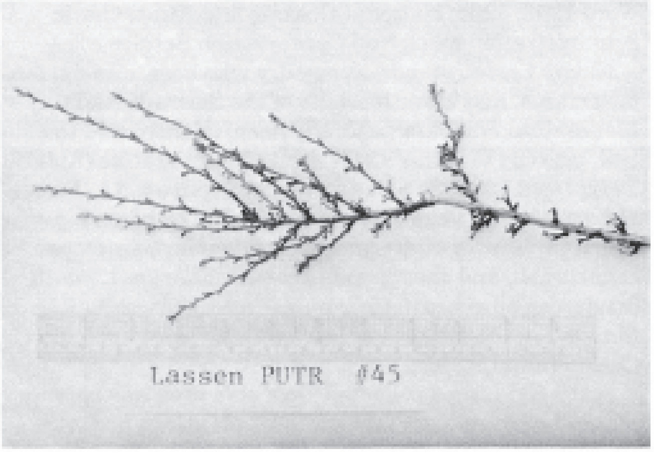

Figure 3—Overwintering leaves, Lassen antelope bitterbrush.

Lassen is an unusual ecotype; its vegetative and floral morphology is highly uniform and typical of pure antelope bitterbrush with little evidence of introgression with Stansbury cliffrose (Alderfer 1976). New leader growth is pubescent. Leaves are three-lobed, gray-green to gray, and tomentose beneath. Fascicles of small, gray-green pubescent leaves persist through the winter (Shaw and Monsen 1986; Welch and others 1983) (fig. 3). Glands on leaves are rare and their density on leaders is low (Alderfer 1976). Decumbent branches are uncommon; layering or root sprouting is rarely observed (Alderfer 1976; Nord 1965; Shaw and Monsen 1983). Gland density on the tomentulose hypanthium is variable (Alderfer 1976). Flowers have one or very rarely two pistils and a single series of approximately 25 stamens. Achenes are pubescent and obovate.

Chromosome number for Lassen and all other antelope bitterbrush populations tested to date is $2n = 18$ (Alderfer 1976; McArthur and others 1983). Alderfer's (1976) comparisons of 20 Oregon and northern California populations, including plants from the Janesville area, suggest a line of gene flow may have progressed from the Great Basin westward to the Cascade-Sierra Mountains in northern California and northward into Oregon and Washington. She suggested the Janesville population be assigned ecotypic status based on its high degree of uniformity in growth habit and morphological characteristics (Alderfer 1976; Winward and Findley 1983). The ecotype's growth habit and other attributes are retained in offsite plantings (Edgerton and others 1983; Monsen and Christensen 1975; Shaw and Monsen 1983; Shaw and others 1984a) (tables 1, 2).

Palatability and Nutrition

Lassen's palatability and response to use have not been examined in common garden settings with other antelope bitterbrush populations. Livestock are grazed on native Lassen stands in summer. Lassen and others (1952), studying the Doyle mule deer (*Odocoileus hemionus* Rafinesque) herd, found antelope bitterbrush constituted 48.8 percent of mule deer stomach contents in October, declining to 9.6 percent in January as diets shifted to big sagebrush. Hormay (1943) recommended that use of antelope bitterbrush in northeastern California be restricted to 60 percent of current annual growth to prevent stand degredation. To preclude excessive use on any portion of the range, the California Fish and Game Commission, Interstate Deer Herd Committee (1954) suggested that average stand use not exceed 34 percent.

Winter crude protein content of 8.9 percent is considered adequate for sheep and possibly mule deer (National Academy of Sciences 1975; Welch and others 1983).

Table 1—Growth habit, 1977-79 grasshopper damage, and 1981 growth characteristics for one *Cowania stansburiana*, one *Fallugia paradoxa*, and eight *Purshia tridentata* accessions planted at the Keating Uniform Garden, Baker County, OR, in April 1976. Elevation at the Keating Garden is 980 m, annual precipitation 300 mm, and frost-free season 145 days. Soils are fine montmorillonitic, mesic Calcic Argixerolls of the Brownscombe series (from Edgerton and others 1983)

Species and accession	Growth habit	1977-79 grasshopper damage		1981 growth characteristics			
		Leaf area	Bark area	Height	Crown	Biomass	Mortality
		Percent		*cm*		*g*	*Percent*
Cowania stansburiana							
American Fork, UT	Erect	32	12	80	91	452	3
Fallugia paradoxa							
Richfield, UT	Erect	37	8	103	141	497	7
Purshia tridentata							
Lassen, CA	Erect	34	5	88	127	824	0
Boise Basin, ID	Decumbent	30	2	76	138	851	0
Fort Hall, ID	Semierect	42	4	61	124	490	0
Garden Valley, ID	Erect	39	5	78	133	847	0
Hat Rock, OR	Erect	35	5	83	144	799	0
Keating, OR	Erect	38	6	78	137	867	0
Pringle Falls, OR	Decumbent	87	9	47	106	164	76
Warren Mt., OR	Decumbent	47	6	68	121	653	7

Table 2—Growth habit and 1980 growth characteristics of one *Cowania stansburiana*, one *Fullugia paradoxa*, and five *Purshia tridentata* accessions planted at the Boise Shrub Garden in March 1974. Elevation at the Boise Shrub Garden is 1,000 m, annual precipitation 430 mm, and frost-free season about 126 days. Soils are gravelly, sandy loams derived from granite (Shaw and Monsen 1983)

Species and accession	Growth habit	Height	Crown	Leader length	Shrub biomass	Survival
		cm	*cm*	*cm*	*g*	*Percent*
Cowania stansburiana						
American Fork, UT	Erect	115	153	6.4	43	94
Fallugia paradox						
Richfield, UT	Erect-diffuse	82	108	6.2	353	60
Purshia tridentata						
Lassen, CA	Erect	122	175	5.2	454	96
Maybell, CO	Diffuse	83	176	3.7	314	100
Lucky Peak, ID	Erect-diffuse	106	191	5.2	345	100
Starvation Canyon, UT	Diffuse	89	186	2.4	523	100
Eureka, UT	Diffuse	108	187	5.2	372	98

Bissell and others (1955) reported crude protein content of antelope bitterbrush near Honey Lake was approximately 8.8 percent in November and 9.4 percent in March. Welch and others (1983) found winter crude protein content of available browse was 15 to 34 percent greater for Lassen compared to four other antelope bitterbrush populations planted in a common garden near Boise, ID (table 3). Percent of winter leaves equaled or exceeded values for the other four populations by as much as 156 percent, and *in vitro* digestibility exceeded by other values by as much as 27 percent. Winter leafiness was 3.3 times greater for two desert bitterbrush and one Stansbury cliffrose accession planted at this site. Lassen's *in vitro* digestibility, however, was exceeded by only two accessions and its crude protein content was exceeded by only one of these evergreen accessions.

Table 3—Winter crude protein level, winter leafiness and *in vitro* digestibility of winter forage samples from one *Cowania stansburiana*, one *Fallugia paradoxa*, two *Purshia glandulosa*, and five *Purshia tridentata* accessions grown at the Boise Shrub garden. Data expressed on a dry matter basis (from Welch and others 1983). Within columns, means followed by the same letter are not significantly different at the 95 percent level

Species and accession	Crude protein	Winter leaves	Digested dry matter
	Percent	*Percent*	*Percent*
Cowania stansburiana			
American Fork, UT	8.8cd	47.5e	37.6d
Fallugia paradoxa			
Richfield, UT	4.8a	27.3d	29.8b
Purshia glandulosa			
Mono Co., CA	9.3d	50.5e	37.0d
Washington Co., UT	8.6cd	49.5e	34.6cd
Purshia tridentata			
Lassen, CA	7.9c	15.1c	30.6bc
Lucky Peak, ID	6.9b	5.9a	28.3ab
Starvation Canyon, UT	6.8b	9.0abc	26.4ab
Eureka, UT	6.6b	13.1bc	25.2a
Maybell, CO	5.9a	7.4ab	24.1a

Insects and Disease Relationships

Insects and microorganisms associated with Lassen have received little study; investigations have centered on those considered detrimental. Organisms studied and plant parts affected are listed in table 4; none are specific to this ecotype. Differential use of Lassen and other antelope bitterbrush populations by several grasshopper species in a northeastern Oregon common garden (Edgerton and others 1983) suggests increased knowledge of insect and microorganism relations may be essential to selecting appropriate seed sources for revegetation projects.

Seed and Planting Technology

Nord (1965) reported antelope bitterbrush plants near Doyle, CA, flowered in late April or early May and set seed in early July, with an average of 62 days from flowering to seed ripening. Shaw and Monsen (1983) monitored Lassen plants in a common garden at an elevation of 1,000 m in Ada County, ID. Floral buds appeared in April, reaching anthesis in early to mid-May; seeds ripened in early July. During the 2 years of study, time from appearance of floral buds to seed set averaged 80 days.

Nord (1965) reported seed production of northern California stands, including those near Janesville, was strongly influenced by the previous year's precipitation as seeds are produced on 1-year old leaders. Leader lengths and frequency of good crops were greater in areas receiving at least 250 mm of precipitation, in drainageways, in catchment basins, and where the water table was within 5 to 8 m of the surface.

Collection

Seed collection from native Lassen stands at Janesville is facilitated by high frequencies of good seed crops,

Table 4—Fungi and insects associated with Lassen antelope bitterbrush

Species	Common name	Plant part affected	Reference
Fungi			
Fusarium oxysporum Sahlecht	damping-off	seedlings	Nelson (1987)
Pithium ultimum Trow.	damping-off	seedlings	Nelson (1987)
Pithium irregulare Buisman	damping-off	seedlings	Nelson (1987)
Pithium catenulatum Matthews	damping-off	seedlings	Nelson (1987)
Insects			
Aulocara elliottii Thomas	grasshopper	leaves, twigs	Edgerton and others (1983)
Arphia pseudonietana Thomas	grasshopper	leaves, twigs	Edgerton and others (1983)
Melanoplus sanguinipes F.	grasshopper	leaves, twigs	Edgerton and others (1983)
Melanoplus foedus foedus Scudder or *M. f. fluviatilis* Bruner	grasshopper	leaves, twigs	Edgerton and others (1983)
Chlorochroa uhleri Stal	stink bug	seeds	Nord (1965)
Chlorochroa ligata Say	stink bug	seeds	Nord (1965)
Elatridae larvae	wireworm	seedling roots	Hubbard (1956)[1]
Lycophotia margaritosa Haworth	variegated cutworm	seedlings	Hubbard (1956)[1]
Malacosoma fragile Stretch	Great Basin tent caterpillar	leaves, twigs	Clark (1956) caterpillar

[1] Described from a seeded stand near Doyle, CA. Seed origin not specified.

extensive stands, high production per plant, and ease of collection from the large upright shrubs (Alderfer 1976; Nord 1962, 1965). Cleaned seeds from Lassen plants in California and Idaho average about 35,000/kg (Nord 1956; Shaw and others 1984a). Private seed dealers and State and Federal agencies have collected large quantities of seed from the Janesville site for use in revegetation projects in northern California and throughout the West, making it one of the major antelope bitterbrush seed collection centers in some years (Shaw and Monsen 1986). Seed availability has been reduced in recent years due to extensive wildfires and stand loss.

Certification

Release of Lassen permits verification of seed origin through cooperation with State seed certification agencies. Recognized classes of seed and plant materials for this release are foundation and certified (Shaw and others 1984a,b; Soil Conservation Service 1986). There is no registered seed or plant materials class.

- Foundation seed—Parent plants for the Lassen release are protected in a fenced exclosure near Janesville maintained by the California Department of Fish and Game. Foundation seed is harvested from this exclosure.
- Certified seed—Seed harvested from wildland stands in an area between Doyle and Susanville may be certified for commercial sales. Seed collectors should contact the California Crop Improvement Association, 231 Hunt Hall, University of California, Davis, CA 95616, for information regarding certification procedures and costs. Certified seed may also be harvested from certified seed orchards.
- Foundation seedlings—Seedlings are produced from foundation seed for establishment of certified seed orchards. Foundation seedlings are available from the Nevada Division of Forestry, 201 S. Fall Street, Carson City, NV 89710. Certified seed may not be used to produce seedlings for establishment of certified seed orchards.
- Certified seedlings—Seedlings produced from certified seed may be certified for commercial sales.

Native Lassen Stands

The recent history of the Doyle mule deer winter range parallels that of many other mule deer winter ranges dominated by antelope bitterbrush, but has been more thoroughly documented than most. The California Department of Fish and Game initiated a major study of this range in 1948 in response to concerns over the degredation of northeastern California mule deer winter ranges resulting from excessive browsing by livestock and mule deer, drought, and wildfires (Lassen and others 1952). They were later joined by the Nevada Fish and Game Commission, the U.S. Department of Interior, Bureau of Land Management, and the U.S. Department of Agriculture, Forest Service in forming the Lassen-Washoe Interstate Deer Study Committee. Documentation of overstocked deer populations, poor herd health, and decadent, heavily-browsed populations of major forage species with little regeneration led to recommendations for major changes in deer herd management and regulation (see, for example, Bissell and others 1955; Bissell and Strong 1955; Dasmann and Blaisdell 1954; Dasmann and Hjersman 1958; Lassen and others 1952; Leach 1956; Longhurst and others 1952).

Research conducted through a cooperative agreement between the California Department of Fish and Game and the U.S. Department of Agriculture, Forest Service, Southwest Forest and Range Experiment Station initiated in 1952 contributed to development of site preparation, planting, and stand management practices for the reestablishment of antelope bitterbrush in northeastern California and throughout its range (Hubbard 1962, 1964; Hubbard and McKeever 1961; Hubbard and others 1959; Neal and

Sanderson 1975; Sanderson and McIntosh 1961). Seeds for many of these studies were harvested near Janesville (Hubbard 1983; Neal 1983; Sanderson 1983), and several study sites were located in this area.

Factors contributing to the decline and loss of mature antelope bitterbrush stands on this range have also inhibited regeneration (Hormay 1943; Nord 1965; Updike and others 1990; Young and Evans 1981). Sanderson (1962) and Nord (1965) reported native seedlings established only infrequently. Sanderson (1962) found native seedlings on a site near Doyle established primarily from rodent caches, with survival greatest on sites with limited competition for moisture. Hubbard and Sanderson (1961) and Young and others (1972) noted one consequence of summer wildfires was the proliferation of cheatgrass and a reduction in natural antelope bitterbrush seedling recruitment.

During the 1980's, critically important antelope bitterbrush stands in the Doyle mule deer winter range were fragmented and fire suppression efforts were complicated by rural housing development (Hall 1992; Updike and others 1990). Substantial antelope bitterbrush stands were consumed by wildfires during this period. Remaining antelope bitterbrush stands have been mapped and digitized in a Geographic Information System to provide data needed by wildlife managers, land use planners, and fire suppression officials to aid in protecting the remaining stands (Hall 1992). Stand fragmentation was one factor leading to the decision to release Lassen as a named variety.

Future Use

The release of named varieties provides users with a comprehensive data summary, procedures for verification of seed origin, and regulations for maintaining the genetic identity of agriculturally produced seed. The variety release process, however, is rather costly, slow, and complex. It is not a viable approach for dealing with the many wildland populations of antelope bitterbrush and other species.

The accumulated literature on antelope bitterbrush (see, for example, Meyer 1989; Tiedemann and Johnson 1983 and bibliographies by Basile 1967; Clark and Britton 1979; and Hall 1964) plus unpublished data and reports provide a basis for describing additional commonly collected populations and their ranges of adaptability. There is a need to consolidate performance data for the most frequently harvested populations in publications or databases to aid in selecting seed sources and developing seed transfer guidelines.

The Association of Official Seed Certification Agencies has developed standards for four classes of wildland plant seeds representing increasing degrees of certainty of seed source origin (Association of Official Seed Certification Agencies 1991). These range from site-identified seed of nonselected populations for which certification involves field verification of origin to the seed categories (breeder, foundation, registered, and certified) developed for varietal releases. Most State seed certification agencies will now provide site-identified certification services for wildland seed collections. This program provides verification of seed origin if direct supervision of seed collection by the user is not possible. Additional information on procedures and costs can be obtained from State seed certification agencies. The development of additional antelope bitterbrush varietal releases or the intermediate categories of tested or selected seeds and plant material may depend on the level of demand for improved or agriculturally produced seed.

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Interaction Between Native and Seeded Introduced Grasses for 23 Years Following Chaining of Juniper-Pinyon Woodlands

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Abstract—Three juniper-pinyon woodland sites in central Utah were evaluated using density, cover, and production values over 23 years following chaining and seeding of introduced grasses. With the introduction of exotic grass species, results show that after 23 years the communities, though changing in density and percent cover, have not yet stabilized in plant dominance. The introduced exotic grasses are increasing in density, cover, and production at a greater rate than are the native grass species. Native grasses show less fluctuation in density, cover, and production than do the introduced species. The characteristics that allow introduced species to dominate native species are reduced somewhat with grazing pressure from livestock, big game, and rabbits.

A majority of the winter and spring-fall livestock and big game ranges in the Great Basin are located in the juniper-pinyon and sagebrush types (Plummer and others 1970a; Dwyer 1975). Forage and watershed resources within the juniper-pinyon woodlands have suffered from extensive depletion of understory vegetation. Reduction of species composition and cover has been attributed to a number of factors including overgrazing, fire suppression, and dominance by woody species (Arnold and others 1964; Tausch and others 1981).

Considerable effort has been directed toward increasing forage production for livestock and in restoring the plant communities and wildlife habitat on juniper-pinyon woodlands. Most pinyon-juniper modification projects have involved reduction of tree competition by mechanical means (chaining, cabling, or dozing), fire, or herbicides (Plummer and others 1968; Jordan 1982; Stevens 1987; Vallentine 1989). Seeding is often necessary where desirable understory species are absent or too sparse to respond to treatment.

Seed mixtures have included various introduced and native grasses, forbs, and shrubs (Stevens 1983). Establishment of seeded species has been inconsistent depending on site characteristics, species planted, and site preparation, and seeding techniques used (Jordan 1983; Plummer and others 1970a,b; Stevens 1986; Stevens and others 1977), with shrub establishment being the most erratic. Recovery of onsite indigenous species has been influenced by (1) plant density, condition, and age of the plants left on the site following treatment; (2) competition from seeded species; (3) grazing by wildlife and livestock; and (4) climatic conditions following treatment.

Over the past 30 to 40 years, introduced grass species have dominated most seed mixtures. Introduced grasses were selected for a number of reasons including availability of seed, ease of establishment, forage production potential, and soil stabilization characteristics. Research and development have resulted in considerable progress in improving availability of native grass seed, improving establishment of native grasses, identifying areas of adaptation, and determining secondary successional processes when native and introduced species are planted together. Research has promoted a shift away from revegetation and toward restoration seedings.

Study Sites

The study was conducted on three Utah juniper (*Juniperus osteosperma*)-pinyon pine (*Pinus edulis*) big-game range rehabilitation projects implemented between 1959 and 1961 in Central Utah's Sanpete County. The three study areas are known as Manti (located 1 mile south of Manti), Mayfield (1 mile southeast of Mayfield), and Fountain Green (8 miles east of Fountain Green). Sites vary in size from 242 to 400 ha and occur at elevations of 1,755 to 2,143 m. Long-term average annual precipitation ranges from 29 to 46 cm. Soils at Manti and Mayfield are limestone-derived cobbly loams in the Frontreen Series (USDA SCS and USDI BLM 1981). At Fountain Green, soils are formed in alluvium and colluvium derived from sandstone, limestone, quartzite, and mixed igneous rocks in the Deer Creek Series (USDA SCS and USDI BLM 1981).

Before the trees were removed, the sites supported juniper-pinyon with a scattered understory of basin big

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In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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sagebrush (*Artemisia tridentata* ssp. *tridentata*) and Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) and less abundantly, Indian ricegrass (*Oryzopsis hymenoides*), western wheatgrass (*Agropyron smithii*), bottlebrush squirreltail (*Sitanion hystrix*), black sagebrush (*A. nova*), white rubber rabbitbrush (*Chrysothamnus nauseosus* ssp. *hololeucus*), low rabbitbrush (*C. viscidiflorus*), broom snakeweed (*Xanthocephalum sarothrae*), and a number of annual forbs as well as considerable cheatgrass brome (*Bromus tectorum*). Species nomenclature follows Plummer and others (1977). All three sites were double-chained during October and November: Manti in 1959, and Mayfield and Fountain Green in 1961. Between chainings a seed mixture of native and introduced grasses, forbs, and shrubs was applied by fixed-wing aircraft (table 1).

Grazing by domestic livestock varied among the three sites after they were treated. The Fountain Green site was rested for 4 years; the Mayfield site was rested for 7 years; and the Manti site was rested for 12 years. The rest period was intended to enhance establishment of seeded species and recovery of native vegetation. Subsequent domestic grazing use was limited to spring (May and June) at stocking rates of 1 to 5 ha per animal unit month (AUM). However, trespass grazing occurred. Most livestock use has been by cattle. Blacktailed jackrabbit (*Lepus californicus*) populations were high, being near or at peak numbers the first 4 years after treatment.

Table 1—Seed mixtures and rates (kilograms per hectare) applied in three juniper-pinyon chaining studies

Sites in Central Utah			
	Seed rate		
Species seeded	**Manti**	**Mayfield**	**Fountain Green**
	- - - - -*Kilograms per hectare* - - - - -		
Fairway wheatgrass (*Agropyron cristatum*)	3.5	3.5	1.8
Standard wheatgrass (*Agropyron desertorum*)	—	—	1.8
Western wheatgrass (*Agropyron smithii*)	0.4	—	—
Intermediate wheatgrass (*Agropyron intermedium*)	0.9	1.8	4.9
Pubescent wheatgrass (*Agropyron tricophorum*)	0.4	1.8	—
Smooth brome (*Bromus inermis*)	1.8	0.9	2.4
Russian wildrye (*Elymus junceus*)	1.8	0.9	1.2
Orchardgrass (*Dactylis glomerata* 'Potomic')	0.4	0.4	0.6
Alfalfa {'Ladak' and 'Rambler'} (*Medicago sativa*)	2.2	0.9	1.2
Yellow sweetclover (*Melilotus officianalis*)	0.9	0.4	—
Small burnet (*Sanguisorba minor*)	0.4	—	—
Big sagebrush (*Artemisia tridentata*)	0.4	0.4	1.2
Rubber rabbitbrush (*Chrysothamnus nauseosus*)	—	0.4	1.2

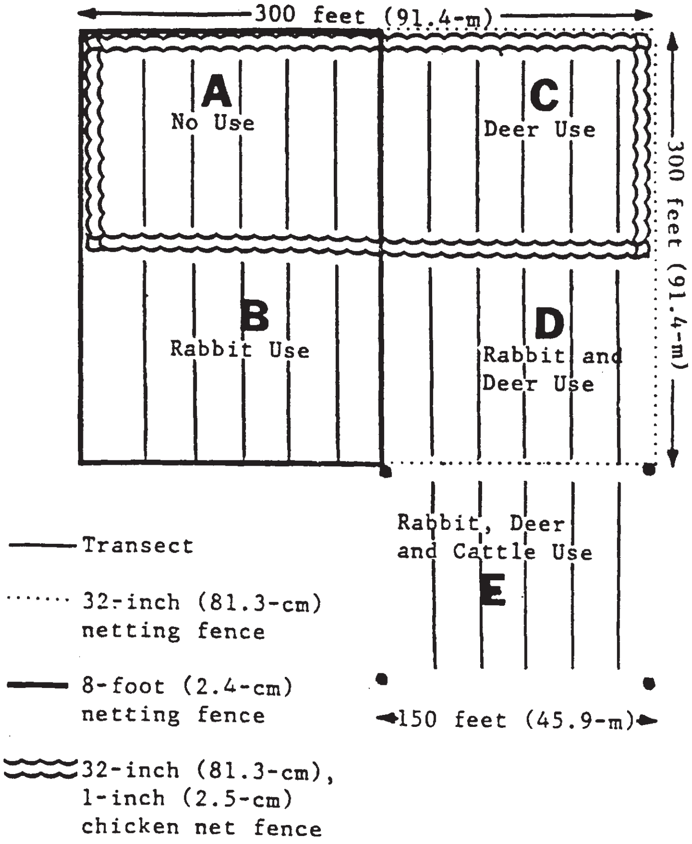

Figure 1—Five-way exclosure design used at three juniper-pinyon chaining study sites in central Utah.

During the summer of 1962, a 91.4 by 91.4 m five-way exclosure was constructed on each site (fig. 1). Five grazing treatments were provided with each exclosure; (a) control-rabbits, deer, and livestock excluded, (b) rabbit only access, (c) deer only access, (d) rabbit and deer access, and (e) accessible to rabbits, deer, and livestock. Monthly precipitation was recorded at each location beginning in 1962.

Methods

Data Collection

At each exclosure a set of five permanent 30.5-m long transects were randomly located within each of the five grazing treatments. Ten end-to-end plots, 3.0 m long by 0.3 m wide, were centered over each 30.5-m long permanent transect. Within each 3.0 m by 0.3 m subplot, the number of grasses and forb plants were tallied by species; in addition, an ocular estimate of above-ground herbage production was made. Percent cover was obtained by dropping a pointer at each 15.2-cm interval (200 points per transect) along the 30.5-m long transect, recording the first object encountered. Clipped samples of known weight were used to improve accuracy of biomass production estimates. The first ratings occurred 4 to 6 years after chaining and seeding. Transects were rated yearly for the first 3 years after treatments were established and at various intervals thereafter. Native and introduced grass (exclusive of cheatgrass brome) numbers, biomass production, and percent cover data from two treatments, the control treatment (ungrazed), and the fully accessible treatment (grazing by rabbit, deer, and livestock), are reported here. Data are for Mayfield, Manti, and Fountain Green in the years 1964, 1967, 1972, 1977, 1982, and 1987.

Statistical Analysis

Data from all three study sites were pooled for data analysis. Frequency was determined by the number of 3.0 m by 0.3 m subplots in each 30.5 m by 0.3 m transect in which a species occurred.

Percent cover, density of species, and biomass production were analyzed using a general linear model Analysis of Variance. Significant differences were determined at the $P < 0.05$ level. If differences were significant from the GLM-ANOVA, Fisher's LSD post-hoc test was used to determine where the differences occurred (Fisher 1966). Cover estimation was compared to production estimates and density data using Pearson's product moment correlation.

The effect of annual precipitation on change in plant communities at the three areas was determined with a simple linear regression. The mean annual precipitation was the independent variable and the mean production value was the dependent variable (Krebs 1989).

The introduced grass-to native grass-density ratio was determined by dividing the mean density of introduced grasses by the mean density of native grasses within a treatment. Likewise, the introduced grass-to native grass-production ratio was determined by dividing the mean production value of the combined introduced grasses by the mean production value of the combined native grasses within a treatment. As the ratios increase, the number of introduced grasses increases compared to the native grasses. An increasing trend line demonstrates that, within a given treatment, the introduced grasses are increasing in density or total production relative to the native grasses. A decreasing trend line shows that the native grasses are increasing faster than the introduced grasses.

Results

Data collected in 1964, 1967, 1972, 1977, 1982, and 1987 were compared to determine the interaction of introduced seeded grasses and native grasses following pinyon-juniper chaining. The results are based on the combined total of all seeded and endemic native species compared with the combined total of all introduced species, except cheatgrass brome.

Frequency and Density

The individual species composition for the introduced and native grasses within the grazed and ungrazed treatments for 1964 and 1987 are listed in tables 2 and 3. Species are ranked in order of highest frequency of occurrence, the number of 30.0 by 0.3 m transects where the species was found. The maximum number of transects was 15, except for the grazed treatment in 1987, where the maximum was 10. Species are also ranked by density per hectare.

Within ungrazed areas, introduced grass numbers (density) (fig. 2) increased significantly over the 23-year period. Numbers dropped from an average of 16.5 plants per square meter in 1964 to 8.7 plants/per square meter three years later, increasing to 27.1 per square meter by 1987. The total number of introduced plants in this treatment doubled from 9,066 to 18,084 plants per hectare during the period of the study (table 2). Fairway crested wheatgrass (*Agropyron cristatum*) changed little in density and frequency of occurrence from 1964 to 1987. Intermediate wheatgrass (*A. intermedium*) decreased in density from 1,990 plants per hectare in 1964 to 402 in 1987; its frequency declined from 15 to 11. Smooth brome (*Bromus inermis*) density increased significantly from 565 plants per hectare in 1964 to 11,745 in 1987. Its frequency of occurrence was unchanged. Russian wildrye (*Elymus junceus*) showed no change in density, however its frequency of occurrence doubled. Orchardgrass (*Dactylis glomerata*) and bulbous bluegrass (*Poa bulbosa*) occurred in 1964, but were absent in 1987.

The introduced grasses in the grazed treatment (fig. 3) decreased significantly during the first 3 years (1964-1967) from 18.3 plants per square meter to 6.6 plants per square meter. They increased significantly during the next 5 years (1967-1972) to 10.5 plants per square meter, showing no significant change in density for the next 15 years. Introduced species exposed to grazing (table 2) responded somewhat differently than those not grazed. Fairway wheatgrass density doubled from 5,360 plants per hectare to 10,635 between 1964 and 1987, and even though its frequency of occurrence decreased from 15 to 10. Intermediate wheatgrass density decreased from 1,918 plants per hectare in 1964 to 646 in 1987; its frequency of occurrence decreased from 14 to 7. Russian wildrye density increased sixfold from 29 plants per hectare in 1964 to 178 in 1987. Its frequency of occurrence also increased from 4 to 6 between 1964 and 1987. Smooth brome, bulbous bluegrass, and orchardgrass were present in 1964, but absent in 1987. The total number of introduced plants increased from 8,527 plants per hectare to 11,459 over the 23 years.

The density of native grasses in the ungrazed treatment (fig. 2) was significantly reduced in the first 13 years, declining from 3.0 plants per square meter in 1964 to .09 plants per square meter in 1977. The density of natives increased during the next 10 years to 5.8 plants per square meter in 1987. This increase was significant. Native grasses with no grazing (table 3) almost doubled in number, with 2,009 plants per hectare in 1964 to 3,856 in 1987. Bottlebrush squirreltail density in 1964 was 837 plants per hectare; by 1987 it had declined to 5. Frequency of occurrence dropped from 15 to 1 during the same period. Indian ricegrass density decreased substantially (598 to 24 plants per hectare), while frequency decreased from 11 to 3. Bluebunch wheatgrass (*A. spicatum*) frequency dropped from 9 to 2 and density decreased from 378 to 19 plants per hectare between 1964 and 1987.

Table 2—Rank of introduced grasses by frequency and by density for grazed and ungrazed treatments. The rank is based on the average of three study areas, in first data collection year (1964) and the last data collection year (1987), showing species composition changes

Species	Rank by frequency	Frequency of occurrence	Rank by density	Density*** (per ha)
Ungrazed				
1964				
Intermediate wheatgrass*	1	15	2	1,990
Fairway wheatgrass**	2	10	1	5,779
Smooth brome	3	5	4	565
Orchard grass	4	4	3	684
Russian wildrye	5	4	6	24
Bulbous bluegrass	6	3	5	24
Total				9,066
1987				
Fairway wheatgrass**	1	15	2	5,913
Intermediate wheatgrass*	2	11	3	402
Russian wildrye	3	8	4	24
Smooth brome	4	5	1	11,745
Total				18,084
Grazed				
1964				
Fairway wheatgrass**	1	15	1	5,360
Intermediate wheatgrass*	2	14	2	1,918
Smooth brome	3	10	3	1,091
Bulbous bluegrass	4	4	5	62
Russian wildrye	5	4	6	29
Orchard grass	6	3	4	67
Total				8,527
1987				
Fairway wheatgrass**	1	10	1	10,635
Intermediate wheatgrass*	2	7	2	646
Russian wildrye	3	6	3	178
Total				11,459

*Combination of intermediate and pubescent wheatgrass.

**Combination of fairway and standard wheatgrass.

***Number of individual culms with rhizomatous species. Number of individual plants with bunchgrasses.

Western wheatgrass density increased from 148 plants per hectare to 1,512; frequency increased from 4 to 9. Sandberg bluegrass (*Poa secunda*) increased in density from 29 plants per hectare to 2,296; frequency increased from 4 to 10. Needle-and-thread (*Stipa comata*) was present only in 1964.

In the grazed treatment, the density of native grasses (fig. 3) did not change significantly from 1964 to 1982. However, the density of native grasses significantly increased from 5.4 plants per square meter in 1982 to 13.8 in 1987. With grazing pressure individual native grass species performed somewhat differently than those exposed to grazing. Bottlebrush squirreltail and Indian ricegrass decreased in density and frequency of occurrence. Bluebunch wheatgrass density and frequency experienced little change. Sandberg bluegrass and western wheatgrass increased in density and frequency. Needle-and-thread showed a slight increase in numbers and no change in frequency (table 3).

Density Ratio

In the ungrazed treatment, the density ratio between introduced and native species (fig. 4) increased from 5.3 times more introduced grasses than native species in 1964 to 7.3 times more in 1987. In the grazed treatment, the density ratio (fig. 4) decreased from 4.8 times more introduced grasses than natives in 1964, to a ratio of 0.8 in 1987, indicating comparatively fewer introduced grasses than native grasses.

Production

The biomass production of the introduced grasses (fig. 5) in the ungrazed treatment fluctuated significantly over time. Beginning in 1964 average production per square meter was 62.8 grams. The lowest production, recorded in 1977 was 28.1 grams per square meter. The highest production, recorded in 1982, was 87 grams per square meter.

Table 3—Rank of native grasses by frequency and by density, for grazed and ungrazed treatments in the first data collection year (1964) and the last data collection year (1987), showing species composition changes

Species	Rank by frequency	Frequency of occurrence	Rank by density	Density* (per ha)
Ungrazed				
1964				
Bottlebrush squirreltail	1	15	1	837
Indian ricegrass	2	11	2	598
Bluebunch wheatgrass	3	9	3	378
Western wheatgrass	4	4	4	148
Sandberg bluegrass	5	4	5	29
Needle-and-thread	6	2	6	19
Total				2,009
1987				
Sandberg bluegrass	1	10	1	2,296
Western wheatgrass	2	9	2	1,512
Indian ricegrass	3	3	3	24
Bluebunch wheatgrass	4	2	4	19
Bottlebrush squirreltail	5	1	5	5
Total				3,856
Grazed				
1964				
Bottlebrush squirreltail	1	15	1	723
Indian ricegrass	2	13	2	698
Sandberg bluegrass	3	5	4	72
Bluebunch wheatgrass	4	5	5	48
Western wheatgrass	5	2	3	101
Needle-and-thread	6	1	6	5
Total				1,647
1987				
Sandberg bluegrass	1	10	1	9,989
Western wheatgrass	2	10	2	4,758
Indian ricegrass	3	5	3	75
Bluebunch wheatgrass	4	5	4	32
Needle-and-thread	5	1	5	22
Bottlebrush squirreltail	6	1	6	11
Total				14,887

*Number of individual culms with rhizomatous species. Number of individual plants with bunchgrasses.

The production of the native grasses in the ungrazed treatment (fig. 5) showed a slight increase from 21.3 grams per square meter, in 1964 to 33.6 in 1967, decreasing significantly in 1972 to 5.2 grams per square meter. Native grasses maintained a low level of production through 1987.

Yields of introduced grasses in the grazed treatment (fig. 6) decreased significantly from a high of 67.4 grams per square meter in 1964 to a low of 10.0 in 1977, increasing in 1982 to 39.2. Yields of native grasses (fig. 6) followed the same pattern in the grazed treatment as in the ungrazed treatment. In 1964 native grasses produced 13.3 grams per square meter, increasing significantly to 39.7 in 1967; production decreased to 4.4 in 1972 and did not change significantly through 1987 when production was 7.9 grams per meter squared, not significantly different from production in 1964.

Production of introduced grasses fluctuated more than native grasses in both treatments. Production of native grasses did fluctuate early in the study. Once introduced

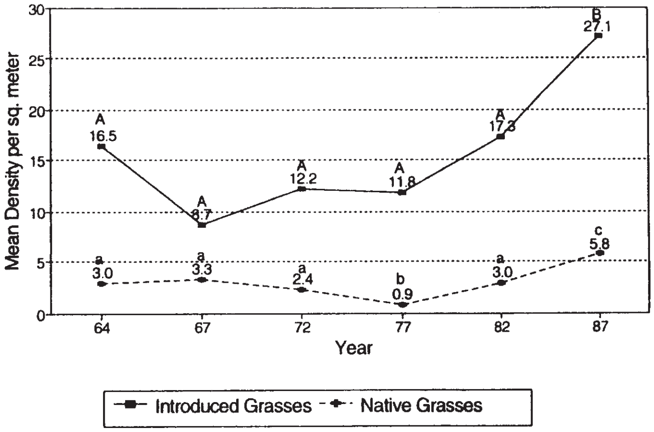

Figure 2—Average density of introduced and native grasses within the ungrazed treatment. Values with the same letter are not significantly different ($P < 0.05$).

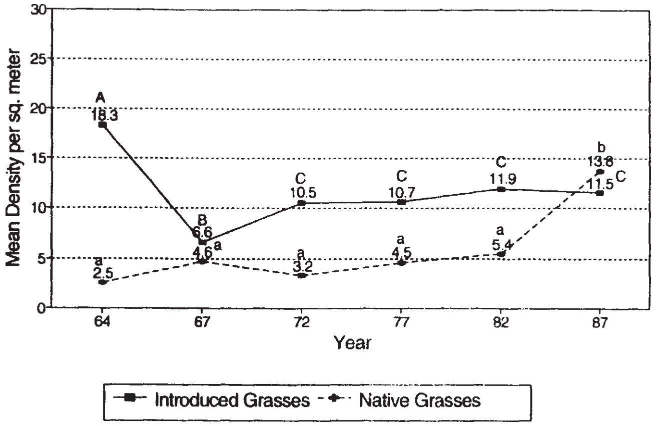

Figure 3—Average density of introduced and native grasses within the grazed treatment. Values with the same letter are not significantly different ($P < 0.05$).

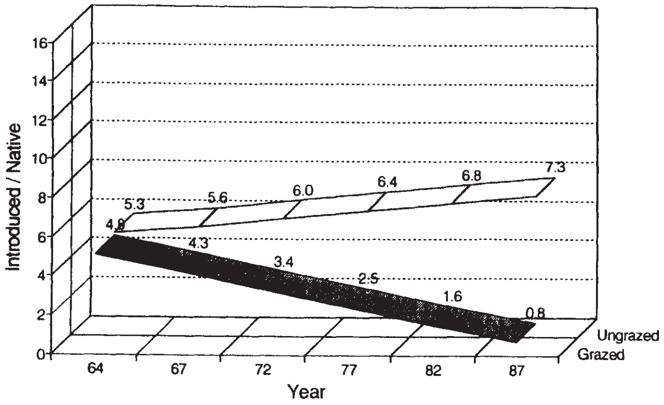

Figure 4—Average density ratio trend, of the introduced to native grasses within the grazed and ungrazed treatments.

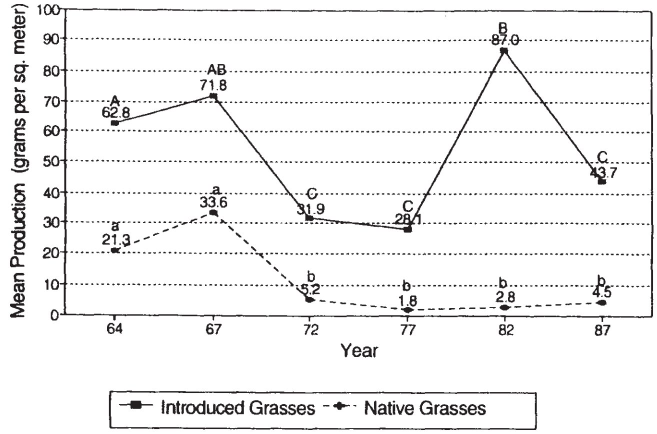

Figure 5—Mean forage production (g/m2) of introduced and natives grasses within the ungrazed treatment. Values with the same letter are not significantly different ($P < 0.05$).

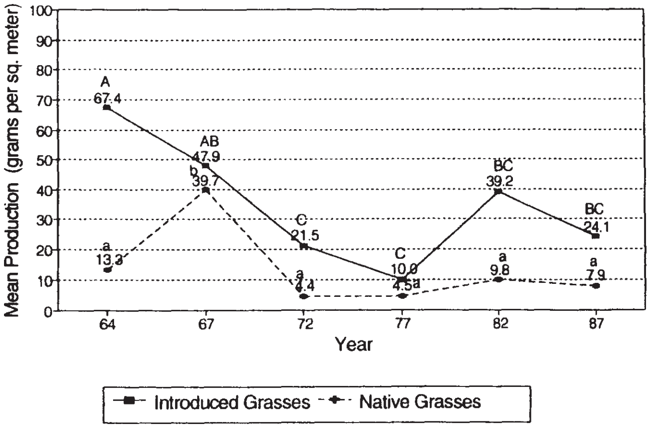

Figure 6—Mean forage production of introduced and natives grasses within the grazed treatment. Values with the same letter are not significantly different ($P < 0.05$).

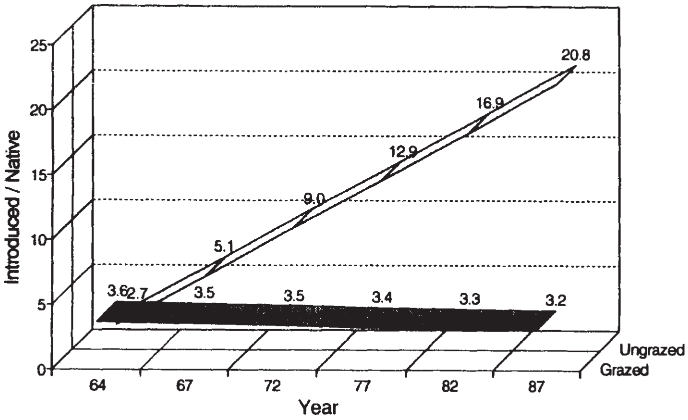

Figure 7—Average forage production ratio trend, of the introduced to native grasses within the grazed and ungrazed treatments.

grasses became established, native grass yields did not seem to respond to the precipitation cycles as did the introduced grasses.

Production Ratio

The production ratio trend between introduced and native grasses in the ungrazed areas (fig. 7) increased from 2.7 times more production from introduced grasses in 1964, to 20.8 times more in 1987. The production ratio within the grazed treatment decreased slightly from 3.6 times more introduced grass forage than native grass forage in 1964 to 3.2 times more in 1987.

Cover

Canopy cover changes and trends were more closely correlated with forage production values than with plant density (table 4). Correlation of cover with production

Table 4—Cover correlation values with production and density of ungrazed and grazed native and introduced grasses

Treatment		Correlations Cover with production	 Cover with density
Ungrazed	Native grasses	.832	.471
Ungrazed	Introduced grasses	.808	.439
Grazed	Native grasses	.823	.368
Grazed	Introduced grasses	.730	.656

was .832 for the ungrazed treatment compared to .471 for correlation of cover with density. Correlation data shows cover values follow similar patterns as forage production. Changes in cover were less dramatic with native grasses than with introduced grasses because density figures were much lower and smaller changes occurred.

Precipitation

The mean precipitation for the areas studied was compared with the production data for grazed and ungrazed treatments and with native and introduced grasses. The mean annual precipitation for the three areas is shown in figure 8. Results of the regression analysis of precipitation and the introduced grass forage production in the ungrazed treatment shows a significant relationship with a *P* value of 0.001. The regression fit shows a positive slope of 23.01 with an *R*-squared value of 0.96. The analysis of native grasses in the ungrazed treatment shows no correlation between production and precipitation (*P* value of 0.863, slope 0.97, and an *R*-squared value of 0.008).

In the grazed treatment the production of introduced grasses shows no significant relationship with precipitation (*P* value of 0.151, slope 10.59, and an *R*-squared value of 0.440). Likewise, the analysis of native grasses in the grazed treatment shows no relationship with precipitation (*P* value of 0.700, slope 2.49, and an *R*-squared value of 0.041).

Discussion

Competition for limited resources may determine the presence, absence, or abundance of species within a community as well as their spatial arrangement (Pyke and Archer 1991). After reviewing research investigating competition in arid and semiarid plant communities, Fowler (1986) concluded that competition does occur in these systems, involves different species, and is an important determinant of community structure.

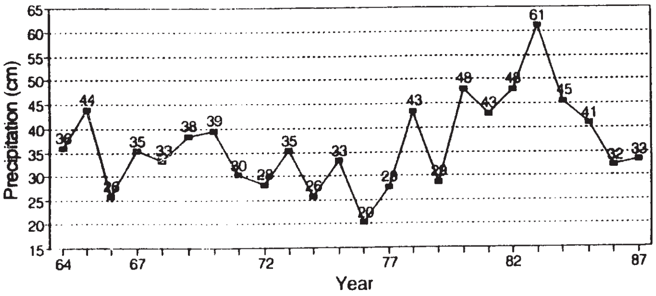

Figure 8—Mean annual precipitation for the three study sites in central Utah, from 1964 to 1987.

Rapid changes in plant communities occur on disturbed areas, such as chained and seeded pinyon-juniper sites (Stevens 1986, 1987). Community structure changes were recorded within the study areas. As seedlings of the seeded introduced species developed into mature plants, their density declined. This was no doubt due to competition for space, nutrients, and moisture. This decline occurred from the seedling years through 1967 in both the grazed and ungrazed treatments.

Data indicates that introduced species appear to be somewhat more competitive than native grasses, especially without grazing pressure from livestock, big game, or rabbits. With no grazing stress, the introduced species increased in density from 1967 to 1987. With grazing stress, the increase in density was significantly less. During the same period, native grasses responded similarly with and without grazing, but to a smaller degree.

Crested wheatgrass, with or without grazing, appears to be well adapted to and aggressive in juniper-pinyon sites with fair soil and average precipitation; intermediate wheatgrass, however, appears to be less adapted. Davis and Harper (1990) report that intermediate wheatgrass on shallow soils out-performed crested wheatgrass in the same county, even when intermediate wheatgrass received less precipitation. Smooth brome maintained and increased itself only in the absence of grazing. With grazing, smooth brome was eliminated. This would indicate that smooth brome is only marginally adapted to climatic and edaphic conditions on the study sites. Orchardgrass and bulbous bluegrass are even less adapted. They were eliminated with or without grazing.

Bottlebrush squirreltail and needle-and-thread responded favorably to removal of the juniper-pinyon, but succumbed to the more competitive species once they became established. Indian ricegrass and bluebunch wheatgrass are long-lived perennials that would be expected to respond favorably to tree removal. They did; however, as the introduced species became firmly established, these native species were not able to compete with the aggressive exotics, with or without grazing. Western wheatgrass was able to compete with the introduced species, with or without grazing. Sandberg bluegrass, an opportunist, did well growing in association with western wheatgrass and the introduced species.

Density data indicate that without grazing pressure, introduced grasses can dominate and suppress many native grasses. The density of introduced grasses fluctuated as annual precipitation varied. This indicates that the introduced species are somewhat less adapted to local climatic conditions than are the native species, which fluctuated less.

In the absence of grazing, vegetative cover data showed a somewhat different result than density. Between 1964 and 1967, the number of young introduced grasses decreased while cover increased, indicating that surviving plants attained larger crowns. Introduced grass cover decreased substantially between 1967 and 1977 during a drought period, increasing through the wet years of the early 1980's, and decreasing again with drought during the late 1980's. The total cover of native grasses responded less during drought periods than did the introduced species. Without grazing, the ratio of introduced to native grass cover from 1964 to 1987 inclined steeply going from 4.5 percent cover for introduced grasses in 1964 to 12.7 percent cover in 1987 for every percent cover of native grasses. The same trend in percent cover occurred in grazed areas, but the percentages were somewhat smaller.

Introduced grass production fluctuated with precipitation, with or without grazing. High yields occurred during wet periods in the mid-to-late 1960's and early 1980's; low production occurred during dry periods in the early to mid-1970's and late 1980's. Native grasses were less responsive to precipitation; their production, cover, and density were more stable. Native grass production responded positively to removal of competitive trees until 1967. Then, native grass production decreased, presumably because of competition from the introduced grasses.

Plant communities are continually changing in plant composition, density, and cover due to changing climate, precipitation cycles, and impacts from grazing or other disturbances. Changes in chained and seeded juniper-pinyon understory communities occurred over 23 years following chaining and seeding. Introduced grasses became more dominant in the communities, especially in the absence of grazing. Density, cover, and production data indicate that native grasses do not appear to compete well with the species that were introduced. These results are similar to those of Bock and others (1986) who reported that stands of exotic grasses support significantly lower variety and abundance of indigenous grasses.

The three chained juniper-pinyon woodland sites in this study exhibited community changes over time due to grazing, precipitation cycles, and competitive characteristics of the introduced exotic species. After 23 years, plant dominance has not yet stabilized in the communities. Our conclusions are similar to those of Davis and Harper (1990). They report that planting a mixture of introduced and native species may produce artificial plant associations in which species may or may not be fully compatible with each other; it is difficult to maintain a stand of specified composition because each species responds differently to natural and imposed environmental factors that affect competitiveness.

Acknowledgments

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Field Trip

Land Reclamation On the Nevada Test Site—A Field Tour

Von K. Winkel
W. Kent Ostler

Abstract—An all-day tour to observe arid land reclamation on the Nevada Test Site was conducted in conjunction with the Eighth Wildland Shrub and Arid Land Restoration Symposium. Tour participants were introduced to the U. S. Department of Energy reclamation programs for the Yucca Mountain Project and the Treatability Studies for Soil Media Project. The tour consisted of several stops that covered a variety of topics and studies including revegetation by seeding, topsoil stockpile stabilization, erosion control, shrub transplanting, shrub herbivory, irrigation, mulching, water harvesting, and weather monitoring.

According to the Nuclear Waste Policy Act of 1982 (as amended in 1987), the U.S. Department of Energy must study and characterize Yucca Mountain, Nevada, as a potential site for long-term underground storage of high-level nuclear waste.

Site characterization activities include a variety of geological, geochemical, geotechnical, and hydrologic studies that will disturb approximately 180 ha. of vegetation and soils. The Department of Energy is committed to reclaiming all lands disturbed by the project, and returning them to a stable ecological state, with a composition and productivity similar to pre-disturbance conditions.

The Reclamation Program of the Yucca Mountain Project

Since limited information exists pertaining to Mojave Desert reclamation, the Department of Energy has implemented a series of feasibility studies to investigate the success of various reclamation techniques for the Yucca Mountain area. The most successful techniques will be used for stabilizing and revegetating temporary topsoil stockpiles, and reclaiming sites released for final reclamation.

Yucca Mountain is at the northern edge of the Mojave Desert and the flora consists of a mixture of Mojave and Great Basin desert species. Dominant plant species include creosotebush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), Anderson wolfberry (*Lycium andersonii*), spiney hopsage (*Grayia spinosa*), and blackbrush (*Coleogyne ramosissima*). Elevations range from 944 to 1,789 m above sea level. The climate is characterized by hot summers and cool winters. Average annual precipitation is approximately 130 mm, falling sporadically throughout the year.

The first portion of the tour consisted of an overview of the reclamation program at Yucca Mountain. Several stops were made in this area to highlight some of the current reclamation research (fig. 1). The first stop was at a revegetation trial where participants listened to an overview of the Yucca Mountain reclamation program as well as a description of several revegetation trials being conducted in the Yucca Mountain area. Scientists are

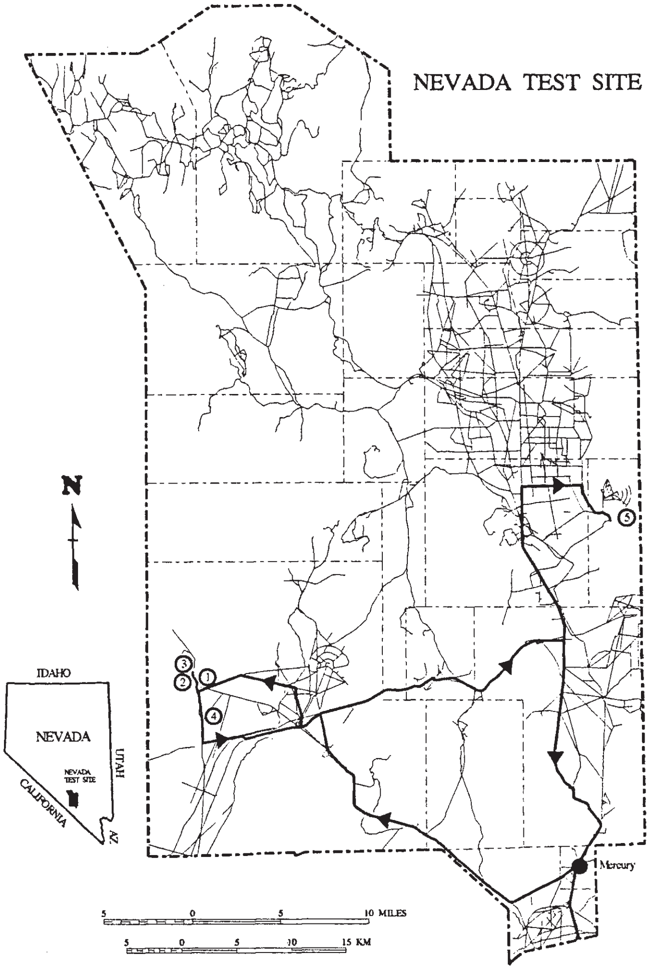

Figure 1—Map of the Nevada Test Site showing field tour stops.

In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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conducting a variety of trials utilizing various seed mixes, as well as testing seedbed modification and water management treatments such as ripping, imprinting, pitting, drill and broadcast seeding, irrigation and mulching.

The second stop was the site of a large topsoil stockpile recently established and stabilized with a vegetative cover. Studies are being conducted on the stockpile to determine the effects of time and stockpile depth on soil microbes. Various combinations of plant species are being evaluated to assess their effects on soil microbial and nutrient levels (particularly nitrogen) in the soil.

At the next stop (3), tour participants were shown a key element of the Yucca Mountain Project, the North Portal Facility. This is the site where a tunnel will be constructed that will drop over 300 meters to the geological formation that is being characterized for placement of high level nuclear waste. Participants observed the starter tunnel which was constructed using blasting techniques. The remainder of the tunnels used for site characterization will be dug with a tunnel boring machine.

The last stop (4) in the Yucca Mountain area was a reclaimed drill pad. Soils at this site are over 90% sand. This causes unique problems for vegetation establishment. The water holding capacity of the soil is low, it lacks structure and is very susceptible to erosion. To mitigate these conditions, scientists are studying the effects of mulches that cannot only conserve soil moisture but will protect the soil from erosion and provide organic matter and nutrients to the soil. Selected plots were also treated with polyacrylamide gel to assess the effects of this material under these conditions. Gels have been shown to be effective for holding and storing moisture for use by vegetation in the landscaping industry, and may have potential for aiding revegetation of disturbed lands in the Mojave Desert.

The Reclamation Program of the Treatability Studies for Soil Media Project

Tour participants traveled to Plutonium Valley (stop 5) on the Nevada Test Site to a site where a series of reclamation trials are currently being conducted for the Treatability Studies for Soil Media Project. During the 1950's and 1960's, a series of safety tests were conducted on and adjacent to the Nevada Test Site to determine the consequences of accidental detonation or destruction of a nuclear device. This led to the contamination of approximately 800 hectares with plutonium. The U.S. Department of Energy Nevada Operations Office has developed a feasibility study to examine methods for cleaning up these contaminated lands. The objectives of the program are to evaluate technologies to: 1) selectively excavate the contaminated soil, 2) remove the plutonium from the soil, and 3) stabilize and revegetate the disturbed sites.

Stabilization and revegetation of the disturbed sites are critical to control erosion and reestablish wildlife habitat. Several studies have been initiated to determine the most effective methods to provide short-term soil stabilization to mediate the human health risk from plutonium, and to establish a long-term self-perpetuating plant community to provide permanent soil stabilization and wildlife habitat.

The Plutonium Valley study site is situated on an alluvial fan of the northern slope of French Peak Mountain at an elevation of 1,271 m. The soil is a gravelly sandy loam. The slope at the site is 3-5 percent and the aspect is northwest. The site is in a transition zone between the Mojave and Great Basin deserts with major plant species consisting of shadscale (*Atriplex confertifolia*), winterfat (*Ceratoides lanata*), Anderson wolfberry (*Lycium andersonii*), and Indian ricegrass (*Oryzopsis hymenoides*). The climate is characterized by hot summers and cool winters. Average annual precipitation for the past 30 years, obtained 5 km from the site, is 168 mm, falling sporadically throughout the year.

At the Plutonium Valley site, studies are being conducted to assess the effects of seedbed preparation, irrigation, water harvesting and topsoil removal on plant establishment, as well as the effects of short-term soil stabilization treatments on wind and water erosion. Other studies are designed to determine effects of topsoil stockpiling on soil viability; and effects of irrigation, seed origin and herbivory on establishment of transplanted shrubs. Participants listened to an overview of the Treatability Studies for Soil Media Project and descriptions about the individual studies being conducted at the site. Participants were then allowed time to view the studies, as well as a variety of reclamation implements, an irrigation system, and weather monitoring systems.

Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer S.; Mann, David K., comps. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 384 p.

Includes 62 papers dealing with wildland shrubs and restoration of arid lands. The key topics include: overview, restoration and revegetation, ecology, genetic integrity, management options, and field trip.

Keywords: rehabilitation, revegetation, revegetation plants, restoration ecology, deserts, desert plants

Pesticide Precautionary Statement

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