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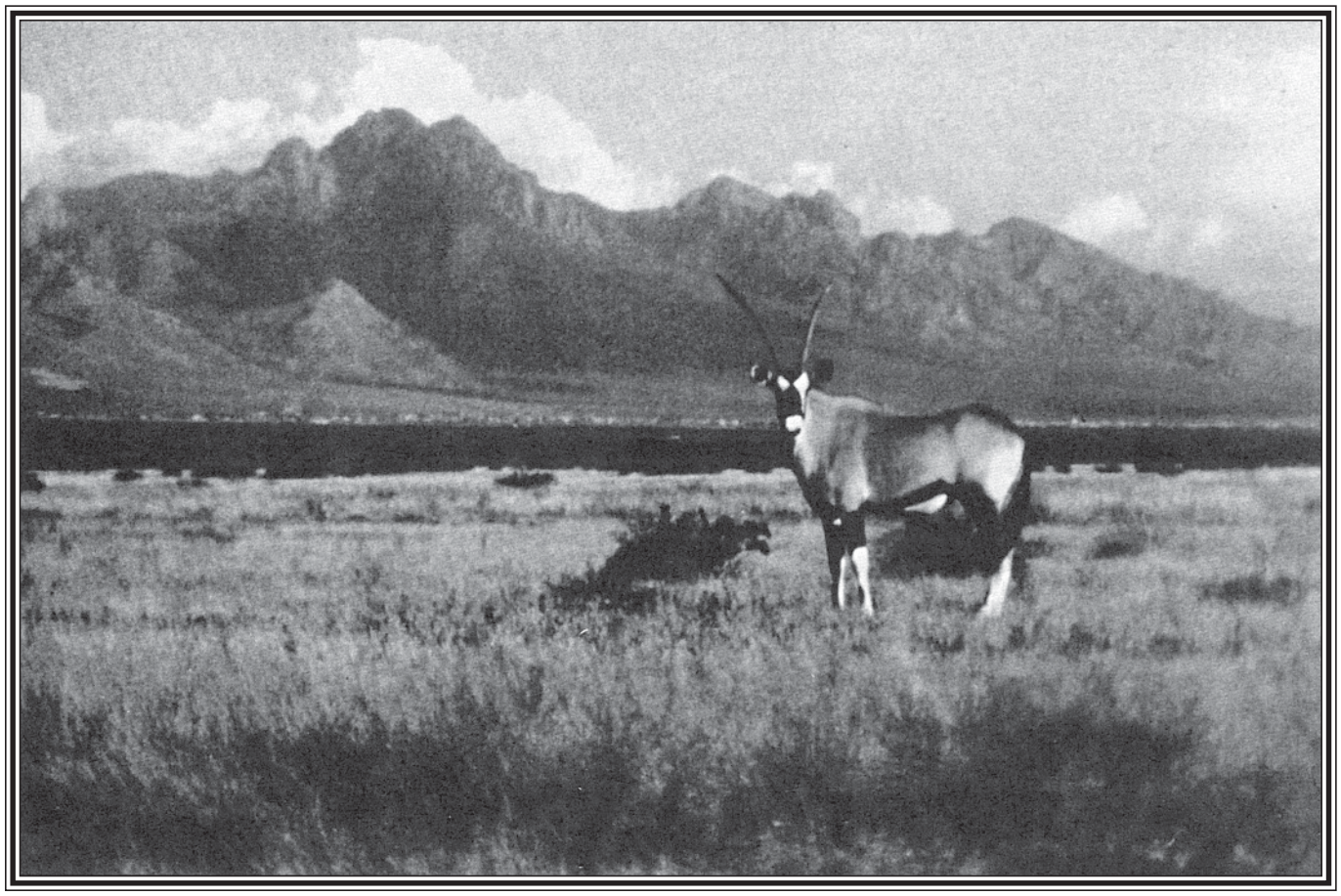
Proceedings: Shrubland Ecosystem Dynamics in a Changing Environment



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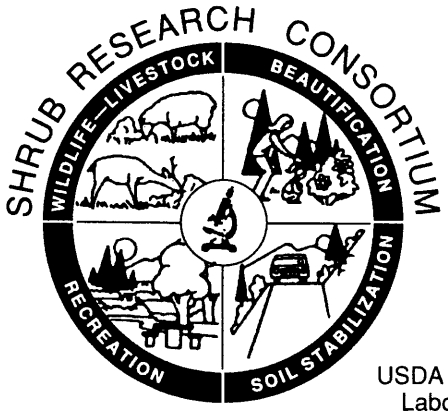

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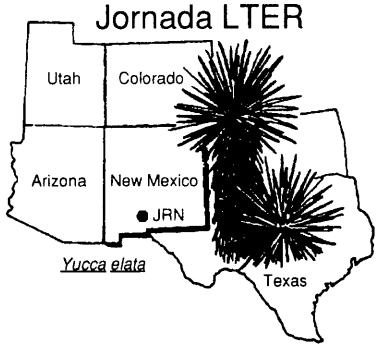

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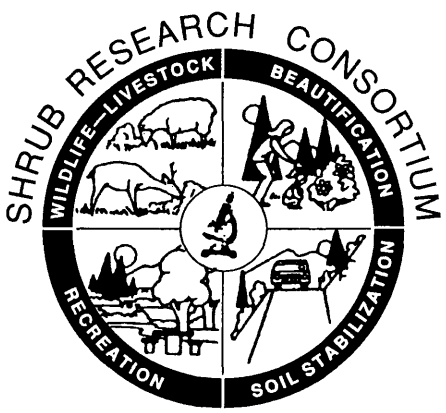

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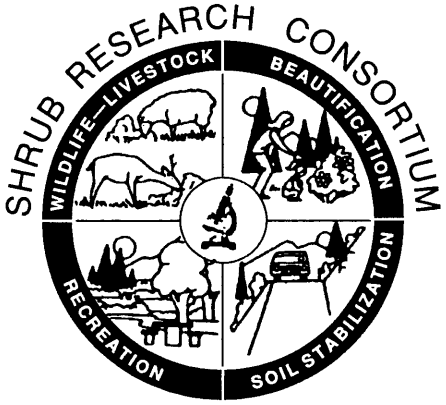

Introduction and Overview

Introduction: Shrubland Ecosystem Dynamics in a Changing Environment

E. Durant McArthur

This symposium proceedings is the ninth in a series 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. The principal co-sponsors, all members of the Consortium, were the Shrub Sciences Laboratory of the Intermountain Research Station, New Mexico State University, and the Jornada Experimental Range/Long-Term Ecological Site (USDA Agricultural Research Service and National Science Foundation). Contributions emphasize the impact of changing environmental conditions on vegetative composition especially in the Jornada Basin and Chihuahuan Desert but also in other parts of western North America and the world.

The symposium consisted of oral presentations, posters, and a field trip. For convenience, we have divided the proceedings into five sections: Overview, Vegetation Dynamics, Management, Ecophysiology, and Field Trip. This volume includes 47 of the 68 papers and posters presented at the symposium, an account of the field trip, and one paper (Jabbes and others) presented in an earlier meeting, the Wildland Shrub and Arid Land Restoration Symposium (Shrub Research Consortium 1993), but not published in the earlier proceedings (Roundy and others 1995).

Our symposium and these proceedings were intended to report results, cultivate interest, and stimulate research and management activities and options in shrubland ecosystems in response to changing environmental conditions. One constant about environmental conditions is that they change (Johnson and Mayeaux 1992; Pickett and White 1985; Tausch and others 1993; Wondzell and Ludwig 1995; Worster 1993; Wu and Loucks 1995). Driving forces for environmental change include natural climatic cycles, pest irruptions, catastrophic fires, herbivore population management and dynamics, and soil development, maturation, and erosion. Human activities throughout history, but especially during the past few centuries and accelerating to the present time, are driving environmental changes both on local and global scales (Cottam 1947; Gates 1993).

Environmental changes, especially climatic changes, for western North America have been well documented (Betancourt 1984; Hughes and Diaz 1994; Miller and Wigand 1994; Neilson 1986; Nowak and others 1994; Spaulding and others 1983). Adaptation of life to past and projected future environments is a rich and fascinating area of study, (for example, Johnson and others 1993; Lande and Shannon 1996; McArthur and Tausch 1995; Smith and others 1995; Tausch and others 1995). Our symposium and two recent Interior West workshops (Tinus 1995; Waugh 1994) are evidence of the continuing need to network environmental change information to assist in ongoing management and research plans and decisions.

The Shrub Research Consortium Executive Committee has tentatively planned two additional Wildland Shrub Symposia in the next 4 years. Subjects will be Shrubland Ecotones and Shrubland Genetics. The eight previous symposia dealt with 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; Roundy and others 1995; Tiedemann and Johnson 1983; Tiedemann and others 1984; Wallace and others 1989).

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Acknowledgments

I thank my organizing committee colleagues, Jerry R. Barrow, Ronald E. Sosebee, and Robin J. Tausch, for their assistance with all aspects of the planning and conduct of the symposium. Jerry R. Barrow, Kris Havstad, and Valerie Gamboa were gracious and helpful in making the local arrangements. New Mexico State University Office of Conference Services personnel Katie Dunford and Carol Floren superbly publicized the symposium in its advance and facilitated its fruition in every way. Louise Kingsbury and staff of the Intermountain Research Station Research Information Group have been most helpful in preparation of the symposium proceedings volume. Various sessions of the symposium were moderated by Robin J. Tausch, Dean M. Anderson, Daniel J. Fairbanks, Jannelle L. Downs, W. Kent Ostler, and Ronald E. Sosebee. The field trip was lead by Kris Havstead and Reldon Beck with assistance from Jerry Barrow, Ed Fredrickson, Dale Gillete, Jeff Herrick, Laura Huenneke, Curtis Monger, Bill Schlesinger, and Walt Whitford.

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Long- and Short-Term Climate Influences on Southwestern Shrublands

Julio L. Betancourt

Abstract—New findings raise questions about long and short-term climatic effects on Southwestern shrublands. Millennial-scale climate variability during the last glacial may have quickened the pace of evolution for genetically variable shrub species. During the last deglaciation, greater plant water use efficiency due to 30 percent CO_2 enrichment was not enough to offset Holocene aridity, and desertscrub replaced woodlands over much of the Southwestern United States. Likewise, the degree to which present CO_2 enrichment is driving C_3 shrubs into C_4 grasslands is probably a function of interdecadal climate variability. Shrub encroachment accelerated during the 1950's drought, when both winters and summers went dry, and continues under the wet winter-summer dry regime since 1976. Climate is also modulating the spread of exotic annual grasses and introduction of a vigorous fire regime in native shrublands, where none existed before. A combination of biogeographic, historical, experimental, modeling, and monitoring approaches is proposed to predict the ecological outcomes of climate change and direct human impacts.

Interest in global change has produced new insights about the functioning of the Earth's climate system and its interaction with the biosphere. We have rescaled our view of the world to recognize that variability occurs along a continuum of spatiotemporal scales. We have developed and refined tools to measure and understand climate variability, from satellite observations to general circulation models. Our understanding of past climates has increased exponentially, in large part due to advances in geochemistry and generous support for highly collaborative ice core and ocean drilling programs.

In areas occupied by shrublands, aridity has hindered limnological/palynological approaches, yet has provided other unique opportunities to decipher the past. In the arid interior of North America, we have used noble gas concentrations in radiocarbon-dated groundwaters to reconstruct glacial temperatures (Stute and others 1995), fecal pellet diameter in fossil middens to study the evolutionary response of packrat body size to global warming during deglaciation (Smith and others 1995), and carbon isotopes from soil carbonates to discriminate changes in the dominance of C_3 versus C_4 plants (Cerling and others 1991; Cole and Monger 1994; Quade and others 1989). Our knowledge about the past distribution of key shrubs in the Southwestern United States comes almost wholly from packrat middens. The sequence of species departures and arrivals on the Holocene landscape indicate individualistic responses to changing climate (Betancourt and others 1990). At northern and upper limits, the arrivals are recent enough to confound the distinction between ongoing migration since the end of the Pleistocene and "invasion" driven by fire suppression and overgrazing.

In setting the stage for this symposium on "Shrubland Ecosystem Dynamics in a Changing Environment," I will focus my presentation on a selection of new findings that raise questions about both long and short-term climatic influences on southwestern shrublands. These include (1) the ecological consequences of unusually low atmospheric CO_2 levels (180 to 200 ppmv) during the last glacial, and implications for future CO_2 enrichment effects; (2) discovery that glacial conditions were more variable than previously thought, and how that might alter our thinking about the evolutionary history of key shrubs; (3) increasing recognition that modern climate varies on an interdecadal scale, and the conundrum of discriminating climatic from anthropogenic effects in recent vegetation trends, from shrub encroachment of grasslands to exotic grass invasion of native shrublands.

This brief synthesis updates other recent summaries of climatic effects on arid lands vegetation in the Western United States, including Betancourt and others (1993) and Tausch and others (1993). My intent here is to introduce this audience to the more recent literature, and perhaps inspire new thought about the role of climate in the evolutionary history, ecology and management of North American shrublands.

CO_2 Enrichment Effects: Lessons From the Fossil Record

Knowledge that atmospheric CO_2 increased 30 percent during the last deglaciation (from about 190 to 270 ppmv) (Raynaud and others 1993) and again since industrialization (from 270 to 360 ppmv) has stimulated research linking this greenhouse gas with past, present, and future climate change. The ice core record of atmospheric CO_2 has inspired laboratory experiments that simulate plant responses at subambient (about 180 to 200 ppmv) levels (Polley and others 1993; Polley and others 1994), as well as new paleoecological approaches (Marino and others 1992; Toolin and Eastoe 1993) and interpretations of the fossil record that consider direct CO_2 effects (Cole and Monger 1994; Van de Water and others 1993). Some of these interpretations bear directly on recent claims that modern CO_2 enrichment is at least partly driving encroachment of C_3 shrubs into C_4 grasslands (Idso 1992; Johnson and others 1993; Polley and others 1992; Polley and others, this volume; Tischler and others, this volume; for opposing view see Archer and others

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1995). During deglaciation, mean annual temperatures increased by 5 to 6 °C (Stute and others 1995) and winter precipitation decreased, possibly by more than half of glacial values (Phillips and others 1992). Apparently, the putative increase in water use efficiency due to the 30 percent CO_2 enrichment (Van de Water and others 1994) was not enough to offset increasing aridity, and glacial woodlands were replaced by Holocene desertscrub (Betancourt and others 1990). In water-limited ecosystems such as Southwestern shrublands, questions remain about the relative roles of climate variability, CO_2 fertilization, and overgrazing/fire suppression in shrub invasions and desertification.

Millennial-Scale Variability During the Last Deglaciation

For an evolutionary biologist, it is critical to know the degree, frequency, and rapidity of environmental change during evolutionary time scales. Redistribution of land masses and mountain uplift drives large-scale changes in global climate on scales of 10^6 years, while changes in the Earth's orbital parameters (Milankovitch) pace changes on scales of 10^4 and 10^5 years, including glacial-interglacial cycles. The most recent challenge to paleoclimatologists and paleoecologists stems from increasing recognition of global changes at higher frequencies (10^3 years) during the last glaciation.

At the scale of 10^3 years, the Greenland ice core record documents more than 20 abrupt, millennial-scale warming events during the last glaciation, referred to as "Dansgaard-Oeschger interstadials" (Dansgaard and others 1993). Warming apparently occurred within decades, followed by gradual return to glacial conditions over hundreds of years. These 2,000 to 3,000-year oscillations occur in series (referred to as Bond cycles), in which the amplitude increases until an unusually cold phase is succeeded by unusual warmth. The extreme cold swings are recorded as major ice-rafting events (coarse debris) in North Atlantic deep-sea sediments, so-called Heinrich events occurring 11,600, 14,500, 21,000, and 27,000 years ago, and two poorly dated events between 36,000 and 70,000 years (Bond and Lotti 1995). In addition, minor ice-rafting cycles synchronous with the cold phase of the Dansgaard-Oeschger temperature shifts have now been identified in glacial sediment from the North Atlantic.

Dansgaard-Oeschger events, Bond cycles, and Heinrich events are not well understood, but may result from transient changes in boundary conditions including surging of continental ice sheets, reversals in ocean thermohaline circulation, short-term increases in atmospheric CO_2, and solar variability (for popular accounts, see Broecker 1995; Kerr 1993, 1996; Lehman 1993). Originally thought to be restricted to Greenland and the North Atlantic, evidence for Dansgaard-Oeschger and Heinrich events now is proposed for key areas in North America, including offshore sediments along the Pacific margin (Behl and Kennett 1996; Kennett and Ingram 1995; Thunnell and Mortyn 1995), mountain glaciation (Clark and Bartlein 1995) and lake levels in the Western United States (Allen and Anderson 1993), and pollen variations in lake sediments from Florida (Grimm and others 1993), a region teleconnected to the tropical Pacific (and the Southwestern Unites States) via the subtropical jet stream.

Despite ample evidence for rapid global-scale changes during the last glaciation, involving the climatically important Pacific, the glacial vegetation record for the American Southwest appears relatively monotonous (Betancourt and others 1990; Thompson and others 1993; Van Devender and others 1987). Part of this has to do with the nature of the fossil record: temporally discontinuous packrat midden sequences not necessarily straddling Pleistocene ecotones, where the changes must have been registered, and lake muds with sedimentation rates too slow to log rapid changes in climate and vegetation.

In the near future, one of the greater challenges for Southwestern paleoecologists (and evolutionary biologists) will be consideration of the regional ecological and evolutionary consequences of Dansgaard-Oeschger/Heinrich events. For example, is the unexpected distribution of ploidy/flavonoid races and morphological forms of shadscale (*Atriplex confertifolia)* and four-wing saltbush (*A. canescens)* due to repeated introgression during the shorter and more recent Dansgaard-Oeschger cycles of the last glaciation, as lagging populations hybridized with immigrant genotypes, or is it a product of longer-term glacial-interglacial cycles (Sanderson and others 1990)? To what extent is the explosion of *Atriplex* (Stutz 1978) and other genetically rich genera a function of glacial/interglacial cycles, millennial-scale variability during the last glaciation and/or Holocene aridity? How did climate variability on these different time scales affect (drive) the immigration of creosote bush (*Larrea divaricata*) to North America and subsequent evolution and redistribution of three chromosomal races across the hot deserts of the Southwestern United States (contrast Wells and Hunziker 1976 with Van Devender 1990).

Notwithstanding spectacular advances in climatology past and present, many key questions about past global change remain unresolved. For example, climatologists are polarized over whether or not tropical sea surface temperatures (SST's) are somehow "thermostated" to below 28 °C, or can increase enough to fuel higher atmospheric water vapor concentrations and "global warming" (ICC 1995). The most recent thinking is that the thermostat is maintained by the dynamic ocean-atmosphere coupling that gives rise to east-west SST gradients and the Walker atmospheric circulation in the tropical Pacific (Sun and Liu 1996). Not surprisingly, GCM's used by different groups to simulate global warming from increases in atmospheric CO_2 vary by a factor of two in estimates of tropical warming (Rind 1990).

Conventional wisdom that SST's were the same during the last glacial maximum as the modern ocean (Crowley and North 1991; Rind and Peteet 1985) is now challenged. Strontium/calcium and oxygen isotopes of drowned coral reefs offshore Barbados show that tropical SST's were 5 °C cooler during the last glacial maximum (Guilderson and others 1994). Coral records also show that tropical SST's have varied by 1 to 3 °C during the last few hundred years (Dunbar and others 1994).

Abrupt increases in tropical Pacific SST's have been related to increasing global temperatures since 1976. Linkage to "greenhouse warming" and an accelerated tropical hydrological cycle have been proposed (Graham 1994). Regardless

of their origin, the post-1976 changes bear directly on attempts to detect and explain recent vegetation trends in the Western United States, where regional climate is strongly teleconnected to SST variations in the tropical Pacific on both interannual and interdecadal scales.

Interdecadal Variability and 20th Century Vegetation Change

Evidence for climate behavior on interdecadal scales (15 to 30 years) has been demonstrated empirically from historical climate data sets (Ghil and Vautard 1994; Halpert and Ropelewski 1992; Latif and Barnett 1994; Mann and Park 1994; Mann and others 1995; Miller and others 1994; Rasmussen and others 1990; Trenberth 1990; Xu 1993) and high-resolution (annual) proxies including tree rings, corals, marine and lake sediment varves, and ice cores (Cole and others 1993; Diaz and Pulwarty 1994; Dunbar and others 1994; Ebbesmeyer and others 1991; Jones and others 1996; Linsley and others 1994; Meko and others 1993; Slowey and Crowley 1994; Stahle and others 1993; Stocker and Mysak 1992). These high-resolution proxies provide a context for evaluating the uniqueness of twentieth century climate and thus, for identifying possible anthropogenic influences on recent climate (Diaz and Bradley 1994). Particularly relevant are long-term changes evident in the Southern Oscillation, the flip flop in sea surface pressure patterns across the equatorial Pacific that marks alternation between El Niño (warm Pacific) and La Niña (cold Pacific) States.

The importance of interdecadal variability is underscored by the unusual frequency of El Niños during the last 20 years (since 1976), when the Southern Oscillation locked into the negative, warm (El Niño) phase, and the length of the most recent El Niño (1991 to 1995), which topped the prolonged 1911 to 1915 and the 1939 to 1942 events. Based on time series modeling, Trenberth and Hoar (1996) suggest that the unusual string of El Niños since 1976 and the protracted 1991 to 1995 event should occur only once every thousand years. This begs the question of whether greenhouse warming or natural climate variability shoulders the blame.

Global average tropospheric temperatures have been rising during the past century, with the most recent portion of record showing a sharp rise since the mid-1970's. Empirical evidence suggests that this sharp rise, roughly half of the 0.6 °C long-term global warming attributed to the Greenhouse Effect, may be due to an enhancement of the tropical hydrologic cycle driven by increasing tropical SST's. Graham (1994) has reproduced the global temperature record since 1976 with an atmospheric model forced with observed SST's (see also Kumars and others 1994). He suggests that the tropical Pacific is now operating at a higher mean temperature, not simply experiencing more frequent El Niño events.

In the Southwest, El Niño conditions are associated with stormier winters and springs (Andrade and Sellers 1988) and drier summers (Harrington and others 1992), the opposite considered true for La Niña years. Using tree rings from Oklahoma, Texas and northern Mexico, Stahle and others (1993) have shown that the influence of the Southern Oscillation on North American winters also may be subject to changes in the frequency and amplitude of both warm and cold events on decadal to multidecadal timescales. Forest fire-Southern Oscillation relations in the Southwest inferred from fire scars show a similar interdecadal behavior (Swetnam and Betancourt 1990, 1992). Twentieth century climatic trends stemming from the interdecadal behavior of the tropical Pacific include wet winters in the early part of the century, a mid-century dry period, and wet winters and erratic summers since 1976. The 1950's drought is the most extreme event of recurrent widespread drought in the southern United States during the past 300 years (Betancourt and others 1993; Meko and others 1993; Stahle and Cleavaland 1988).

At issue is the degree to which recent vegetation changes, such as shrub invasions, can be attributed to climatic variability, compared to overgrazing and fire suppression (Bahre and Shelton 1993; Grover and Musik 1990; Neilson 1986). The debate is confounded by the fact that progressive range deterioration since 1870 has been inferred from historical data (Bahre and Shelton 1993), while long-term monitoring indicates substantial range improvement with wetter conditions following the 1950's drought (McCormick and Galt 1994). Such ambiguity will continue to plague ecosystem research and management, especially if the trend towards a warmer Pacific resumes after the 1996 La Niña (cold Pacific) event, which is producing extreme drought across northern Mexico, the southern High Plains, and the Southwestern United States.

For example, climate appears to be regulating the invasion of red brome (*Bromus rubens*) in the upper Sonoran Desert of central and southern Arizona, an alarming phenomenon. Wetter winters since 1976 have encouraged the spread of this winter annual, and the buildup of fine fuels in native shrublands. Consequently, large fires have become chronic in desert communities that burned rarely only 20 years ago (Harper and others, this volume; McLaughlin and Bowers 1982). Many desert plants, such as saguaros (*Carnegiea gigantea*), grow slowly and recruit episodically; on decadal timescales, desert fires have irreversible consequences. A shift to drier winters and wetter summers might slow the red brome invasion, while encouraging exotic summer annuals like African buffel grass (*Cenchrus ciliare*), which becomes flammable in the fall. It is unclear what remedy can be applied, if any. One could propose an aggressive program of fire suppression in the Sonoran Desert. This might be viewed as inconsistent by a ranching community that is increasingly accepting fire as an ecological process capable of holding shrub invasion of grasslands at bay.

Conclusions

In assessing ecosystem dynamics in a changing environment, there is always the temptation to develop massive simulation models that couple many physical and biological processes. Such models require a detailed understanding of all the feedbacks and constraints that limit the range of the output, including external forcing such as climate variability. Alternatively, we can study interactions between selected properties of ecosystems during extreme events or conditions, and look for predictable behavior (Mann 1995). Such phenomological studies include investigation of processes along climatic (and land use) gradients; century to millennial scale reconstructions of plant migration and

ecotonal shifts; reconstruction of demographic trends (Parker 1993) and changes in community composition using repeat photography and remote sensing (Eve and Peters, this volume; Lancaster and others, this volume; Sanders and Sharp 1995; Walker and others, this volume); monitoring efforts persistent enough to capture extreme events (Goldberg and Turner 1984; Havstad and Schlesinger, this volume; Huenneke, this volume); simulation of extreme conditions in experimental research (de Soyza and others, this volume; Heydari and others, this volume; Polley and others, this volume; Tischler and others, this volume; Virginia and Reynolds 1995; Weltzin and McPherson 1995); and modeling approaches that simulate the appropriate spatiotemporal scales of disturbance (Ludwig and others, this volume; Reynolds and Virginia 1995; Wiegand and others 1995; Wiegand and Milton, this volume). In addition, one could also promote biogeographic approaches that compare areas with opposing interdecadal climatic trends, such as the Southwestern United States and the Pacific Northwest, or areas where the same species (or similar genera) have experienced different climatic and land use histories. For example, why do mesquite (*Prosopis* spp.) and creosote bush (*Larrea* spp.) tend to be so widespread, dominant, and invasive wherever they occur in both North and South America? Clearly, some of our questions about ecosystem dynamics in a changing environment may find answers in comparative studies that employ similar approaches in shrublands worldwide.

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Reflections on a Century of Rangeland Research in the Jornada Basin of New Mexico

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Abstract—A historical analysis can generally take one of three formats: 1) narrative, 2) context, or 3) analog. As narrative, the analysis is limited to a description detailing events. As context, historical analysis explains the present state based on interpretations of its varied history. As analog, the analysis attempts to support predictions regarding future conditions. The narrative format is the safest in that it typically involves the least interpretation and assumption, especially if the historical record is well-documented. The context format can be the most enlightening. The analog, though, is the most useful, and the most precarious, and shares the central premise of scientific experimentation, the desire to make predictions about the future. The Jornada Experimental Range's history overlaps that of the discipline of rangeland management. Reviewing the history of the range should not be a parochial exercise, but should have a wider generic application to the history of the discipline. The history of research at Jornada has six often overlapping and evolving themes: classic range management, animal husbandry, ecology, range improvement, interdisciplinary sciences, and ecosystem science.

Inception of the Experimental Range

Elmer Otis (E.O.) Wooton was appointed in 1890 as the plant taxonomist for the New Mexico College of Agriculture and Mechanical Arts. Though Wooton specialized in taxonomy, his scientific interests were highly diverse (see Allred 1990). His botanical excursions throughout the New Mexico territory at the turn of the century helped form a well-based assessment of rangeland conditions in the region.

Wooton, in 1908, published a New Mexico Agricultural Experiment Station Bulletin that detailed his assessment of these range conditions. Based on his observations and surveys of ranchers' opinions throughout the region, his assessment was bleak. He reported greatly diminished carrying capacities for rangelands throughout the Southwest. Surprisingly, 67% of the surveyed stockmen attributed their deteriorated conditions to overstocking. Wooton estimated that a 20% increase in carrying capacities could be realized with implementation of grazing controls and good management practices. These practices included fencing, stock water development, livestock rotation, weed control, and erosion control.

Wooton also stated that proper stocking rates would have to be determined through research and that many of these practices and research results would have to be demonstrated to stockmen throughout the region. It was this conclusion that prompted Wooton to later propose the formation of the Jornada Range Reserve. Wooton had initiated research with cooperative ranchers in the Southern New Mexico Territory by 1904, but desired a more fixed and permanent location for his studies.

Established in 1912, the Jornada Range Reserve was formed within the USDA's Bureau of Plant Industry. Wooton, who had left New Mexico in 1911 to join the USDA was appointed the first director of the Reserve.

In 1915, the Reserve (later named the Jornada Experimental Range) was transferred to the Forest Service, which quickly developed long-term research objectives and implemented scientific investigations under the direction of C.E. Fleming. The initial objectives as detailed in the 1915 Memorandum of Understanding between the Forest Service and Charles T. Turney, the cooperating rancher who stocked the reserve, were to:

1. Develop a range management plan to minimize stock loss during drought.
2. Establish a system of forage utilization consistent with growth requirements of forage species and which will build up depleted range and minimize non-use losses.
3. Identify advantages of controlling stock and the range for improving stock performance.
4. Quantify carrying capacity of native range under control and comparative capacity of these lands without control.
5. Identify costs of handling stock under controlled conditions compared to uncontrolled conditions.
6. Quantify loss of stock under controlled conditions compared to uncontrolled conditions.
7. Identify number and distribution of stock watering places necessary to secure proper use.
8. Examine the possibility of range improvements by introduction of new plants, seed planting, conservation of runoff, etc.

Obviously, implicit in the original goals of the Range Reserve was to demonstrate the advantages for both stock and the land of controlling the grazing use of the open range.

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Historical Narrative

Range Management

A key problem for range management was quickly identified as inaccurate judgement of carrying capacity (Wooton 1915). The Jornada Experimental Range's (JER) research program focused on quantifying proper utilization levels of the principle species. Jardine and Forsling (1922) established early guidelines for carrying capacities of black grama (Bouteloua eriopoda) rangelands. Subsequent research during ensuing decades has reinforced the accuracy of these guidelines, as Campbell and Crafts (1938), Paulsen and Ares (1962) and Holechek and others (1994) have reached strikingly similar conclusions. These authors all concluded that proper utilization of black grama should be less than 40% of current year's growth.

The original philosophy was that proper utilization of the leaves and stems of the main forage plants was the basic principle of range management (Canfield 1939). General management guidelines published in the 1910's and 1920's are very similar to those promoted today. For example, nearly 80 years ago Jardine and Forsling (1922) recommended the following drought strategies: 1) limit breeding stock to carrying capacities during drought, 2) utilize surplus stock during good forage years depending upon market conditions, 3) adjust range use seasonally depending upon growth characteristics of key species, 4) establish permanent watering points no more than five miles apart, and 5) establish both herding and salting practices that achieve optimal stock distribution. Similar recommendations for drought conditions are outlined in one of the most current textbooks on range management (see Holechek and others 1995).

Husbandry

Initial research on livestock production also emphasized strategies for drought. Most of the original efforts focused on supplemental feeding programs, especially those that used locally available foodstuffs such as cottonseed products. For example, general recommendations were for 1 to 2 pounds of supplemental protein to augment range forage for maintenance (Forsling 1924), with slightly higher quantities suggested for growth of stockers (Jardine and Hurtt 1917). These general recommendations have persisted during ensuing decades. However, more recent research focuses on the use of protein and energy supplements for specific animal production stages to trigger specific physiological activities (see Gambill and others 1994).

More novel research has emphasized specialized practices for emergency feed conditions and management of poisonous plants. Soapweed (*Yucca elata*) was found to be a palatable emergency feed when fed chopped and fresh (Forsling 1919). Ensiling was not determined to be necessary. Other plant species were either deemed not suitable as emergency feeds (i.e., *Dasylirion wheeleri* and *Yucca macrocarpa*) or required spine removal (*Opuntia* spp.). Interestingly, burning spines from prickly pear cactus (in 1924 Forsling estimated that one person could prepare cactus feed for 200 to 400 hd of cattle in a day) was employed during the 1994-95 drought in the Southwestern U.S. However, even in the 1910's and 1920's the use of emergency feed practices was not viewed as responsible management for properly stocked rangelands.

As in other western rangeland regions, studies on poisonous plants provided both initial guidelines for livestock management and insight into the difficulties of plant control in a desert environment. For southern New Mexico drymaria (*Drymaria pachyphylla*) became a problem in response to overgrazing (Little 1937). For clay soils, drymaria was viewed as an early seral species (Campbell 1931). Avoidance of grazing in drymaria infested areas was the recommended management strategy. Various measures of control (fencing, burning, spraying, revegetation) were examined and determined to be either too expensive or ineffective. The recommended control practice was hoeing, but eradication was not viewed as a viable possibility. These general characteristics relative to management and control recommendations for poisonous plants persist today (see James and others 1993).

Development of techniques (such as esophageal fistulation) for animal nutrition research led to investigations of the interactions between plants and livestock. Early work identified foraging behaviors of different cattle breeds (Herbel and Nelson 1966), but irrespective of breed, cattle are generalists in this environment. A current research emphasis is identification of animal production capabilities most suitable to forage characteristics of desert rangelands (Walker and Winder 1993). Cattle genotypes with relatively modest performance traits, such as milk production, would be more successful in this nutrient sparse environment. It is possible that some desired characteristics will mirror those inherent to the original cattle breeds introduced to North America in the 16th century.

Research on plant-animal interactions now reflects the widespread distribution of shrubs in the Chihuahuan Desert. Foraging behaviors are strongly mediated by secondary plant chemistry (Estell and others 1994), and chronic ingestion may have post-ingestive consequences that further shape preferences (Fredrickson and others 1994). Remediation of shrub-dominated rangelands will require cost effective technologies. The use of livestock as bio-control agents for remediation will require detailed knowledge of this chemically mediated interaction in order to be an effective technology.

Ecology

One of the early objectives of the JER was to understand the role of management in natural revegetation of rangelands (Jardine and Hurtt 1917). By the late 1920's, patterns of succession were described (Campbell 1929; Campbell 1931). These observations were generally in areas where livestock numbers had been substantially reduced (or eliminated) and yearlong grazing had been adjusted to seasonal use. For example, on sandy soils five successional stages were described in the natural revegetation of sand dunes: 1) mat stage of low prostrate annuals, 2) inderal stage of large annual and perennial forbs, 3) snakeweed (*Gutierrezia sarothrae*) stage (viewed as critical), 4) dropseed (*Sporobolus* spp.) stage (regeneration of perennial grasslands), and 5) grama grass stage. These observations reflected the succession-and-climax paradigm of the period.

However, these early observations did not portend larger scale transformations that were documented over ensuing decades. Probably the defining publication from the first half-century of research in the Jornada basin was Buffington and Herbel's (1965) reconstruction of vegetative changes in the area between 1858 and 1963. The broad scale encroachment of shrubs was attributed to seed dispersal, heavy grazing and periodic droughts (Buffington and Herbel 1965).

Concomitant with the vegetation dynamics has been substantial change in surface soils. Gibbens and others (1983) documented effects of wind erosion of soil fractions as an ungrazed landscape changed from perennial grassland to coppice dunes dominated by mesquite. Both soil movement and the redistribution of sand, silt and clay factions were substantial.

Emerging from this reconstruction and associated research has been a key postulate regarding changes in ecosystem properties that accompany grassland conversion to shrubland (desertification). This central hypothesis is that the distribution of soil resources is altered from spatially homogenous, as seen in semiarid grasslands, to heterogeneous, as seen in shrublands, with desertification (Schlesinger and others 1990). Further, these emerging resource islands act as positive feedback to further the invasion and persistence of shrubs. This hypothesis has formed the basis for the research efforts of scientists affiliated with the Long-Term Ecological Research (LTER) program at the Jornada (fig. 1).

This hypothesis counters the earlier observations regarding the potential for disturbed lands in arid environments to naturally revegetate to semiarid grassland conditions. Current research in other arid regions would also support a hypotheses of nonlinear vegetation dynamics in these environments (for example, see Milton and others 1994).

Improvements

The first articles on classical techniques for improving forage production on desert rangelands were published in the 1940's (Cassady and Glendening 1940; Parker 1943). These research efforts primarily focused on reseeding practices and a variety of brush control methods. With the development of appropriate machinery (i.e., the rangeland drill) and herbicides, examinations of intensive improvement practices were a significant part of the research program for the next 45 years (Parker 1949; Herbel and Ares 1961; Herbel and Gould 1970; Herbel and others 1985). The principles of these intensive improvements have been well articulated (Herbel 1983), however, more recent economic assessments of these practices have not been wholly favorable. For example, Sherwood (1994) concluded that over 95% of the possible reseeding practices suitable for the Jornada basin would result in a negative economic return. Similar doubts have been raised regarding the cost effectiveness of chemical methods for brush control (Herbel and Gould 1995).

One of the original objectives of the Experimental Range was to identify a management system that brings about natural reseeding of desired species (Jardine and Hurtt

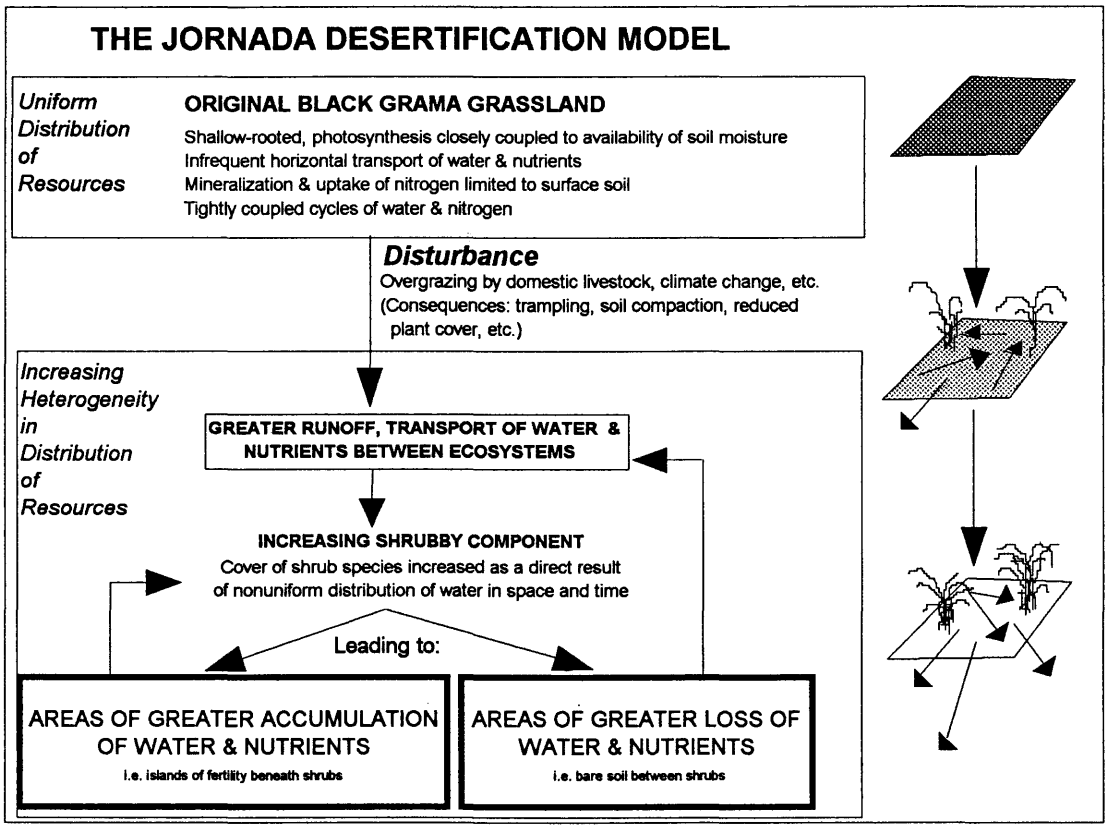

Figure 1

1917). With our emphasis on developing specialized intensive technologies we have not accomplished this original objective. Low-input techniques that are economical and effective are still required. Four premises need to be advanced: 1) biological integrity of both above- and belowground systems in addition to the short-term establishment of desired species, is necessary to buffer against future disturbances, 2) resource redistribution over time at the community and landscape levels plays an important role in both desertification and restoration processes, 3) restoration efforts should focus on fertile sites best suited for reestablishment of native species, and 4) planting technologies should be based on readily available "natural" dispersal systems (Herrick and others 1995).

Interdisciplinary Sciences

Interdisciplinary research began in earnest in the 1960's. Rangeland science has typically been presented as an applied, interdisciplinary field, but involvement of related sciences (other than animal science and other directly related agricultural fields associated with range livestock production) was slow to develop. The interactions with this new group of scientists occurred in conjunction with an expanding appreciation for the multiple uses and values of desert rangelands.

In the Jornada basin these interactions involved both biological and soil sciences. Gile (1966) provided new insights into soil horizon development processes in arid environments. In particular, descriptions of clay illuviation in high carbonate sediments greatly revised our understanding of argillic horizons in arid soils (Gile and Grossman 1968; Gile and Hawley 1972). These clay horizons develop slowly in deserts, and can be masked by subsequent accumulations of carbonate.

Whitford and others (1983) provided initial insights into the role of decomposers and herbivores on nutrient cycling in the desert. For example, cleverly designed field studies identified the mass of subterranean termites (*Gnathamitermes tubiformans*) in the Jornada at 30 kg/ha (MacKay and others 1989). Termites were estimated to recycle 11% of litter N and 13% of annual and grass standing crops (Schaefer and Whitford 1981).

Hundreds of studies in the past 25 years have expanded our knowledge on a range of topics, including soil biota (Virginia and others 1992), biogeochemical processes (Schlesinger and Peterjohn 1991), nitrogen fixation (Herman and others 1993), surface hydrology (Tromble 1988), primary production controls (Cunningham and others 1979), effects of lagomorphs (Gibbens and others 1993), and distributions of rodent populations (Hoover and others 1977).

Although many of these topics require further research, we still have two particular, and different, research needs. First, this body of work lacks effective synthesis. Without complete and detailed synthesis, the application of this information to the management of these desert rangelands is seriously curtailed. Second, there is an overwhelming need for research on the roles of soil biological systems in the recovery of degraded lands (Whitford and Herrick 1995).

Ecosystem Science

The creation of the International Biological Program (IBP) provided the impetus for an ecosystem framework for research. The Jornada basin was the location for the desert grassland site within the IBP. By the early 1970's scientists had assessed system variables as a foundation for model development and expanded insight into ecosystem processes. For example, Pieper and others (1972) quantified that 4% of captured energy was transferred from plants to herbivores in the desert.

As the IBP dissolved in the late 1970's, the LTER program emerged in the 1980's as its evolved successor. The LTER, now in its second decade, has five core research efforts: 1) pattern and control of primary production, 2) spatial and temporal distribution of populations selected to represent trophic structure, 3) pattern and control of organic matter accumulation in surface layers and sediments, 4) pattern of inorganic inputs and movements of nutrients through soils, groundwater and surface waters, and 5) pattern and frequency of disturbances. Research in these core areas has provided a basis for modeling efforts. In particular, modeling has linked transport processes to the spatial and temporal dynamics of soil resources, a key premise of the Jornada model. Based on these efforts the regional stability of desert ecosystems has been described as a function of resource distributions among smaller scale (patch) mosaics within the larger landscape (Reynolds and others 1995). Understanding the cascading effects (both positive and negative) of both management and remediation practices in the desert will require the continued development of larger scale ecosystem models.

Context of Research History

Two prevailing themes arise from an analysis of the history of research conducted in the Jornada basin. These themes are degradation and utilitarian environmentalism. The JER has its roots in the deteriorated range conditions of the region during the later decades of the 19th century. Much of its research effort throughout the 20th century was devoted to developing range management practices suitable for degraded lands or intensive technologies for their improvement. Even today a central postulate of our research is based upon a hypothesis of degradation processes (the "Jornada model"). Yet, if there is one key deficit to these research accomplishments, it is the failure to identify usable technologies for remediation of degraded conditions.

This failure is probably more a function of the dynamics of our environment, our economy, our attitudes, and our expectations than from an inefficient use of the scientific method. We now believe that remediation has to be accomplished in a more extensive fashion and based on a more complete knowledge of the basic ecological processes that occur in desert rangelands.

Since its establishment, the JER research program has included a significant element devoted to ecological studies. Livestock production and an understanding of the principles

for managing the forage on which the range livestock industry is based was the initial emphasis. However, the emerging principles have an ecological basis. Though an increasing emphasis is now placed on the study of ecological principles, livestock grazing as a viable use and tool for landscape management is still central to the research. This can best be labeled as a utilitarian environmentalism, a concern for the long-term capacity to harvest food and fiber from a highly variable (transient) environment. Our terms for this goal, such as "proper use" and "sustainability", have not withstood rigorous examinations. The theme, though, has been and will continue to be how to use this resource based on a thorough understanding of our surroundings and our interactions with those surroundings.

History as Analog

The history of research results from the JER supports three emerging postulates from the broader body of rangeland science in recent years. These postulates are: 1) many ecological processes have thresholds below and above which they become discontinuous, chaotic or suspended, 2) ecological character is reflected by dominant species, and 3) species are interdependent and many of these interdependencies form highly specialized interactions.

Many of the observations in the Jornada basin during this century have documented surprisingly rapid changes across the landscape. Yet, our frustrations in effecting change, even with intense inputs, supports the second postulate. Remediation within this ecosystem will require specific knowledge of species interactions, which may have to be regenerated before corrective management actions will be effective. Needless to say, we can predict from our observations that simply abandoning the landscape will not promote recovery, or prevent further deterioration.

Within this context, livestock grazing must be managed so as to neither disrupt species interactions nor drive impacted processes beyond the thresholds. The average annual carrying capacity for this hot desert is 9.5 AU/section. This would require the annual harvest of approximately 10-20g of forage per m^2 with even distribution of grazing use. We have the basic management techniques for controlling grazing for this level of defoliation. However, we still need the ability to effectively monitor that use over large areas, detect impacts of use on key processes, more rapidly recognize seasonal forage dynamics and develop methodologies for using the animal to effect desired changes.

Conclusions

Much of the research conducted during the early 20th century is still applicable to today's management issues. Though the experimental designs employed in the 1910's, 1920's and 1930's might not entail the sophistication serviceable by current statistical analyses, the thoroughness and detail of the early field research more than compensates. In addition, the length of the research record itself becomes a powerful tool for insight and scientific speculation.

One perception that surfaces from a review of the research record of the Jornada basin is the complexity of this arid ecosystem. This complexity cannot be easily communicated. Yet, these desert rangelands will continue to provide critical resources to a significant portion of the human population. It is important that we not oversimplify our understanding of this system in our attempts to communicate our knowledge to interested segments of our society. Solutions to today's management problems are generally not simple, and we should not create false expectations. We need to use the full scientific history of experimental stations like the Jornada to create more complete understanding. This should be a prominent objective within our research programs. In fact, using the Jornada Experimental Range as a demonstration for our knowledge of desert rangelands was an original objective of the U.S. Forest Service in 1915 and it is still valid today.

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Potential Natural Vegetation in the 17 Conterminous Western United States

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Abstract—Küchler and Bailey constructed continental scale maps of the vegetation of the United States. These maps are compared for the 17 Western United States. The vegetation categories (vegetation types for Küchler and ecoregions for Bailey) are quantified by category and by state with particular emphasis on shrub vegetation categories. The Küchler map has 30 shrub vegetation types (including pinyon-juniper shrub mosaics) that account for about 40 percent (1.8×10^6 km^2) of the area in the 17 states. In the Bailey map, 15 ecoregions account for about 34 percent (1.6×10^6 km^2) of the area in shrublands.

In our previous work with Küchler's (1964) classic map and manual, "Potential Natural Vegetation of the Conterminous United States," we have been unable to locate summary area totals of his vegetation types in a single source. West (1983) provides summaries for some community types. We undertook this study to put area data with Küchler's map for the conterminous 17 Western United States and to compare that with Bailey's map (1976) and manual (1978) that provide a more generalized vegetative map than does Küchler. We were particularly interested in the extent of dominant shrublands. Our Shrub Sciences Laboratory of the Intermountain Research Station, since the lab's 1975 beginning, has had research responsibilities in western shrublands.

The extent of shrublands is not as clearly understood as one might think. For example, Plummer (1974) listed the area for cold desert shrubs in the Western United States (his northern desert shrubs, pinyon-juniper, mountain brush, and salt desert shrubs) as 1.7 million km^2; West's (1983) equivalent cold desert shrubland figure based on Küchler's map was 814,000 km^2; and McKell and Garcia-Moya (1989) gave an approximate figure of 886,000 km^2 based on Bailey's map. To illustrate this point further, we present some figures on sagebrush (subgenus *Tridentatae* of *Artemisia* or big sagebrush and its close relatives—see McArthur and others 1981) areas. We present some information from Utah and Wyoming. Beetle (1960) gave a sagebrush area for Utah of 106,580 km^2, West (1974) an area of 25,130 km^2, McArthur (1983) 28,570 km^2, and Johnson (1989) 43,770 km^2. Beetle's high value undoubtedly reflect his inclusion of areas where sagebrush is present but not dominant. Beetle's sagebrush area for Wyoming was 150,800 km^2 but McArthur (1981) listed 105,000 km^2.

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In this report we quantify Küchler's (1964) areas and compare those with Bailey's (1976, 1978) areas by vegetative community type and by state. Küchler's map was at a scale of 1:3,168,000; Bailey's at a scale of 1:7,500,000. Bailey's map and manual is intended to describe ecoregions of continuous geographical areas characterized by distinctive flora, fauna, climate, land form, soil, vegetation, and ecological climax. Bailey's map and manual was compiled from many references but especially gave weight to Köppen's climatic regions (Thornthwaite 1931) and Küchler's (1964) vegetation communities. However, the Bailey map is generalized relative to the detailed and mosaic patterns presented by Küchler (fig. 1). For the conterminous United States, Küchler (1964) listed 116 vegetative communities whereas Bailey (1976, 1978) recognized only 53. Larger scale maps provide even more detail for vegetational mosaics. For example, Foster (1968) mapped 117 separate areas as sagebrush communities on a 1:500,000 map. By comparison, Küchler mapped 34 for the same area. Küchler's map was developed through consultation with academic and agency personnel well acquainted with vegetative communities throughout the United States (Küchler 1964). Küchler (1964) defines potential natural vegetation as "...vegetation that would exist today [1964] if man were removed from the scene and if the resulting plant succession were telescoped into a single moment...[which]...eliminates the effects of future climatic fluctuations while the effects of man's earlier activities are permitted to stand. [Potential natural vegetation] is a term that applies to a specific period."

Both Küchler and Bailey published later revisions of their maps (Bailey 1980; Bailey and Hogg 1986; Küchler 1970, 1993). We chose to stay with the large-scale originals because of the availability of those maps and the accuracy that a large scale affords.

Our approach in quantifying the vegetation, while not sophisticated, still accurately quantifies the information presented by Küchler (1964). Current vegetation characterization is becoming more sensitive and accurate as new ground and aerial techniques are developed (Burgan and Hartford 1993; Cost and others 1990; Green and Van Hooser 1983; Loveland and others 1991).

Methods

In the United States, areas of shrub dominance are confined to the Western States (Bailey 1976, 1978; Küchler 1964; McArthur 1984). This study included the 17 conterminous Western United States (Washington, Oregon, California, Nevada, Idaho, Utah, Arizona, Montana, Wyoming, Colorado, New Mexico, North Dakota, South Dakota, Nebraska, Kansas, Oklahoma, and Texas). These portions of

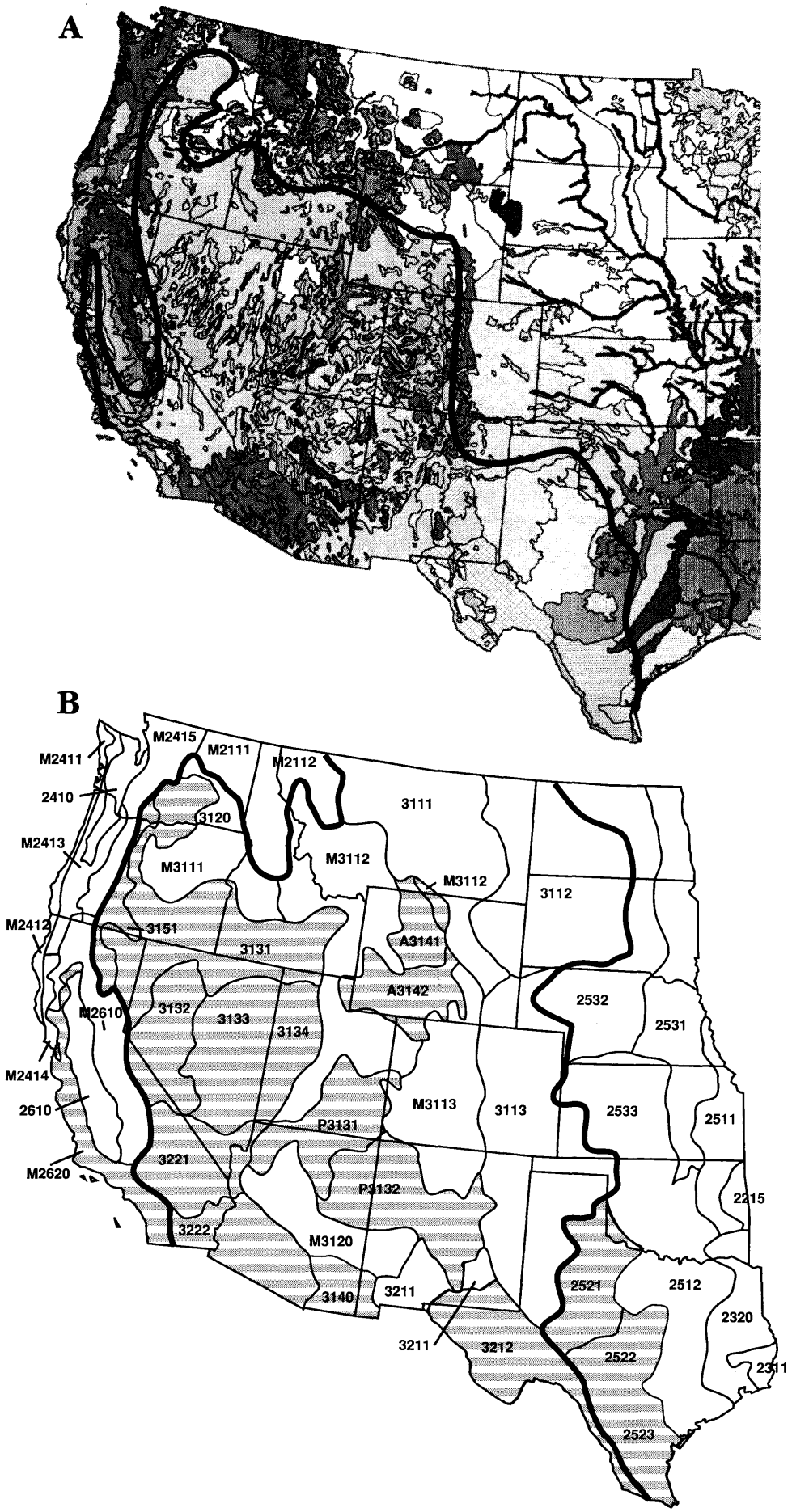

Figure 1—(A) The 1993 Küchler map showing mosaic vegetation patterns. Principal shrub-dominated areas are within the bold black lines but are not continuous within that area. (B) The 1976 Bailey map with the shrub dominated areas cross-hatched. The wide solid lines mark off domains with smaller solid lines marking off divisions, provinces, and sections.

both the Küchler (1964) and Bailey (1976) maps were photocopied on 27.94 cm (11 inch) by 43.18 (17 inch) paper of the same lot (each sheet of copy paper weighed about 8.89 g). The photocopied papers were then cut along state lines and at boundaries between vegetational communities. The resulting fragments were weighed to the nearest 0.1 mg. Weights were used to estimate the area of each type of vegetation by state and for the entire area covered by the 17 states of concern.

Using total surface area data (mi^2) from the World Almanac (Hoffman 1989), data were recorded in mi^2, km^2 (= 0.386 mi^2), and acres (640 per mi^2). These measures allow easy conversion to other commonly used units (ha = 2.47 acres or 0.01 km^2). Decimal fractions of area were not carried; our area data are shown to the nearest whole number, and percentages are reported to the nearest hundredth.

The large islands off the coasts of Washington, California, and Texas were included in the Küchler analysis but not the Bailey analysis. For the Küchler analysis, large lakes (those greater than 100 mi^2) were subtracted out and not considered in the vegetation totals. Surface areas of water reservoirs were not subtracted from land area totals. Bailey (1978) provided mi^2 data for some of his ecoregions; that information is compared with values we obtained using weight values for the same map fragments.

Results and Discussion

Our data are presented in the next three sections. The first section lists the Küchler (1964) vegetation types. The second section lists Bailey's (1976, 1978) ecoregions by state and area. The third section contains state summaries. We consolidated the Küchler vegetation types and Bailey ecoregions into eight summary categories (table 1). The finer detail of the Küchler map allowed the addition of categories (marshes, nonvegetated, and water), which nevertheless only accounted for 0.8 percent of the total.

The Küchler map was extrapolated to 28 shrub-dominated vegetative types including hardwood-shrub or juniper, shrublands, and shrub steppes that covered 33.1 percent of the area of the 17 conterminous Western United States (1,517,328 km^2). If the pinyon-juniper vegetative types are included (a case could be made for that because shrubs are an important component on most pinyon-juniper vegetative types), 30 vegetative types are included that account for 39.5 percent of the area (1,814,425 km^2). Corresponding extrapolation from the Bailey map gave 13 ecoregions dominated by shrubs. Shrubland would thus cover 28.1 percent of the area (1,316,379 km^2). If pinyon-juniper areas are included, 15 ecoregions are involved accounting for 33.8 percent of the area (1,583,602 km^2). The Küchler map with greater detail for mosaic patterns shows more shrubland than the Bailey map (table 1).

One test of our method was to compare the areas we obtained by cutting, weighing, and extrapolating the Bailey map to area values given by Bailey for the same mapping units. Our values are usually close to but consistently higher than those that Bailey reports. We suspect that the values given by Bailey may be estimates from larger scale maps that take into account the mosaic nature of vegetation patterns, whereas our data came directly from weighing map fragments.

In the introduction we cited some contrasting published information on the area occupied by cold desert shrublands and more specifically by sagebrush. Table 2 reviews, contrasts, and summarizes the cold desert shrubland data. Our conclusion is that there are about 80 million ha or 800,000 km^2 of cold desert shrublands and that much of the variation about that number has to do with different methods of dealing with mosaics of shrubs and pinyon-juniper woodland. Küchler and West (who used Küchler's map) have lower values for pinyon-juniper and shrublands, whereas Bailey and McKell and Garcia-Moya (who used Bailey's map) have higher values for pinyon-juniper woodlands and for shrublands.

Our bias is for the Küchler approach because it defines vegetational types on a finer scale. The Küchler map delimits more than twice as much sagebrush area as the Bailey map for Utah but not for Wyoming. For Utah the values are 35,315 km^2 for Küchler (vegetation types 38, 55) and 17,489 km^2 for Bailey (ecoregions 3131, 3133, A3142). Pinyon-juniper and mountain brush community types that also include sagebrush as a major component yield values of 73,832 km^2 and 62,065 km^2 from the Küchler and Bailey

Table 1—Summary of vegetation types in the conterminous Western United States (after Küchler 1964 and Bailey 1976).

General vegetative types	Küchler units			Bailey units		
	No.	*km²*	*Percent*	*No.*	*km²*	*Percent*
Coniferous forests	22	783,039	16.3	13	1,107,576	23.8
Pinyon-juniper	2	297,097	6.2	2	267,223	5.7
Hardwood forests	7	259,281	5.4	3	289,413	6.2
Hardwood-conifer forests	7	152,010	3.2	3	100,909	2.2
Hardwood-shrub or hardwood-juniper woodlands	4	102,101	2.1	2	142,068	3.0
Shrublands	11	631,876	13.2	7	743,428	15.9
Shrub steppe	13	875,531	18.2	4	430,881	9.2
Grasslands	21	1,607,373	34.6	9	1,581,223	33.9
Marshes	1	9,944	0.2	—		
Nonvegetated	—	19,928	0.4	—		
Water	—	9,237	0.2	—		

Table 2—Estimates of the extent of cold desert shrublands in the United States.

Source of estimate	Estimate in km²
Plummer 1974	1,700,000[a]
West 1983	814,000[b]
McKell and Garcia-Moya 1989	886,000[c]
Our data	
Küchler (1964)	794,000[d]
Bailey (1976, 1978)	937,000[e]

[a]His northern desert shrubs, juniper and pinyon, mountain brush, and salt desert shrubs.

[b]His Great Basin-Colorado Plateau sagebrush semi-desert, western Intermountain sagebrush steppe, Intermountain salt desert shrubland, Colorado Plateau-Mohavian blackbrush semi-desert, and southeastern Utah galleta-threeawn shrub steppe.

[c]His Intermountain sagebrush province (except the ponderosa shrub forest section), Colorado Plateau province, and Wyoming Basin province.

[d]Küchler (1964) vegetation types 23, 24, 38, 39, 40, 55, 56, and 57. With the omission of the pinyon-juniper types (23, 24) the value drops to 761,000 km². Vegetation types are characterized in Kücher's list beginning in the next column.

[e]Bailey (1986, 1978) ecoregions 3131, P3131, 3132, P3132, 3133, 3134, A3141, and A3142. With the omission of the pinyon-juniper ecoregions (P3131, P3132) the value drops to 700,000 km². Ecoregions are characterized in Bailey's list beginning on page 8.

maps, respectively. For Wyoming, the Küchler map (vegetation types 55, 56) gave 100,187 km² and the Bailey map (ecoregions A3141, A3142) gave 110,555 km² values for sagebrush dominated lands. The Küchler sagebrush values for Wyoming could be enlarged slightly by addition of the pinyon-juniper (23, 550 km²) and mountain brush (37, 1,435 km²) community types.

There are no Bailey ecoregions (other than A3141 and A3142) in Wyoming with a substantive sagebrush component. We believe that the differences between Utah and Wyoming are, again, derived at least in part from the pinyon-juniper and sagebrush mosaics that are common in Utah but only limited in Wyoming. Another reason for the low Bailey sagebrush value in Utah appears to be his large Douglas-fir ecoregion (M3112, fig. 1). Küchler has smaller more discrete forested areas mapped (fig. 1).

Large portions of the interior American West are shrublands because shrubs often dominate in habitats stressed by aridity, nutrient poor soils, poor soil aeration, cold winters, short growing seasons, and wind (McArthur 1984; McKell 1989; Stebbins 1972). In this paper we documented how extensive shrub dominance is by quantifying areas on Küchler's (1964) and Bailey's (1976) maps. There are differences inherent in the approaches taken by Küchler and Bailey, but both approaches show that there are indeed large expanses of shrubland in the area of concern. For the 17 Western States, the value for shrub-dominated land ranges from about 28 to 40 percent (1.3 to 1.8 x 106 km²) depending upon how one defines shrubland and how finely the vegetation mosaics are mapped. Our numerical values for vegetation types on Küchler's map are a contribution that, we believe, will be of value to others as vegetative mappers of increasing sophistication provide quantitative data for their maps.

Küchler (1964) Vegetation Types in the 17 Conterminous Western United States[1]

Type/state	Percent of state	mi²	Acres	km²
1. Spruce-cedar-hemlock forest (*Picea-Thuja-Tsuga*)				
Washington	5.47	3,729	2,386,593	9,662
Oregon	3.07	2,983	1,908,885	7,728
California	0.01	15	9,779	40
		6,727	**4,305,258**	**17,430**
2. Cedar-hemlock-Douglas-fir forest (*Thuja-Tsuga-Pseudotsuga*)				
Oregon	13.28	12,887	8,247,948	33,393
Washington	18.26	12,444	7,964,250	32,244
California	2.00	3,178	2,034,110	8,235
		28,510	**18,246,307**	**73,872**
3. Silver fir-Douglas-fir forest (*Abies-Pseudotsuga*)				
Oregon	5.94	5,767	3,690,728	14,942
Washington	6.95	4,735	3,030,169	12,268
		10,501	**6,720,898**	**27,210**
4. Fir-hemlock forest (*Abies-Tsuga*)				
Washington	6.58	4,483	2,869,275	11,617
Oregon	3.03	2,942	1,882,825	7,623
		7,425	**4,752,100**	**19,239**
5. Mixed conifer forest (*Abies-Pinus-Pseudotsuga*)				
California	12.97	20,588	13,176,077	53,344
Oregon	1.13	1,094	700,359	2,835
Nevada	0.29	316	202,141	818
		21,998	**14,078,576**	**56,998**
6. Redwood forest (*Sequoia-Pseudotsuga*)				
California	2.18	3,458	2,213,398	8,961
		3,458	**2,213,398**	**8,961**
7. Red fir forest (*Abies*)				
California	1.77	2,801	1,792,885	7,259
		2,801	**1,792,885**	**7,259**
8. Logepole pine-subalpine forest (*Pinus-Tsuga*)				
California	2.14	3,392	2,171,021	8,790
Nevada	0.14	153	97,810	396
		3,545	**2,268,831**	**9,186**
9. Pine-cypress forest (*Pinus-Cupressus*)				
California	0.14	224	143,431	581
		224	**143,431**	**581**
10. Ponderosa shrub forest (*Pinus*)				
Oregon	9.25	8,984	5,749,458	23,277
California	1.92	3,046	1,949,355	7,892
Washington	0.07	47	30,168	122
		12,077	**7,728,981**	**31,291**
11. Western ponderosa forest (*Pinus*)				
Idaho	10.40	8,691	5,562,071	22,519
Montana	4.04	5,940	3,801,355	15,390
Oregon	4.43	4,296	2,749,316	11,131
Washington	4.73	3,221	2,061,454	8,346
		22,147	**14,174,175**	**57,385**
12. Douglas-fir forest (*Pseudotsuga*)				
Montana	15.38	22,609	14,469,491	58,581
Wyoming	11.83	11,567	7,402,647	29,970
Washington	13.31	9,066	5,802,237	23,491
Utah	4.89	4,152	2,657,226	10,758
Idaho	4.17	3,484	2,229,985	9,028
Oregon	0.24	234	149,844	607

Type/state	Percent of state	Mile²	Acres	km²
Colorado	0.10	103	65,832	267
		51,215	**32,777,263**	**132,701**
13. Cedar-hemlock-pine forest (*Thuja-Tsuga-Pinus*)				
Idaho	7.68	6,415	4,105,492	16,621
Montana	0.44	644	412,471	1,670
Washington	0.55	372	237,989	964
		7,431	**4,755,952**	**19,255**
14. Grand fir-Douglas-fir (*Abies-Pseudotsuga*)				
Idaho	10.66	8,904	5,698,712	23,072
Oregon	7.86	7,630	4,882,967	19,769
		16,534	**10,581,679**	**42,841**
15. Western spruce-fir forest (*Picea-Abies*)				
Colorado	10.37	10,790	6,905,730	27,958
Idaho	11.94	9,981	6,387,708	25,861
Montana	6.76	9,935	6,358,657	25,744
Wyoming	6.63	6,487	4,151,977	16,810
Washington	4.24	2,886	1,846,928	7,477
Utah	2.19	1,861	1,190,831	4,821
Oregon	0.55	534	342,036	1,385
		42,475	**27,183,867**	**110,056**
16. Eastern ponderosa pine forest (*Pinus*)				
Montana	5.56	8,172	5,230,135	21,175
Nebraska	1.65	1,280	818,999	3,316
Wyoming	0.95	932	596,453	2,415
N. Dakota	0.07	52	33,451	135
S. Dakota	0.05	41	26,266	106
		10,477	**6,705,305**	**27,147**
17. Black Hill forest (*Pinus*)				
S. Dakota	3.39	2,611	1,671,189	6,766
Wyoming	2.00	1,952	1,249,238	5,058
		4,563	**2,920,427**	**11,824**
18. Pine-Douglas-fir forest (*Pinus-Pseudotsuga*)				
New Mexico	9.96	12,111	7,751,325	31,382
Colorado	10.04	10,451	6,688,486	27,079
Wyoming	3.29	3,220	2,061,077	8,344
Arizona	2.28	2,604	1,666,350	6,746
Utah	0.75	641	410,066	1,660
		29,027	**18,577,304**	**75,212**
19. Arizona pine forest (*Pinus*)				
Arizona	4.29	4,891	3,130,124	12,673
Utah	1.53	1,297	829,973	3,360
New Mexico	0.04	51	32,582	132
		6,239	**3,992,680**	**16,165**
20. Spruce-fir-Douglas-fir forest (*Picea-Abies-Pseudotsuga*)				
Utah	3.15	2,676	1,712,435	6,933
Arizona	0.65	745	477,034	1,931
		3,421	**2,189,468**	**8,864**
21. Southwestern spruce-fir forest (*Picea-Abies*)				
Colorado	5.87	6,110	3,910,394	15,832
New Mexico	2.00	2,510	1,606,306	6,503
Utah	0.42	359	229,637	930
Arizona	0.24	271	173,170	701
		9,249	**5,919,507**	**23,966**
22. Great Basin forest (*Pinus*)				
Nevada	1.89	2,089	1,336,737	5,412
California	0.04	71	45,637	185
		2,160	**1,382,374**	**5,597**

Type/state	Percent of state	Mile²	Acres	Km²
23. Juniper-pinyon woodland (*Juniperus-Pinus*)				
New Mexico	26.11	31,742	20,315,052	82,247
Utah	28.15	23,902	15,297,095	61,932
Arizona	16.87	19,231	12,308,120	49,830
Nevada	15.03	16,618	10,635,211	43,058
Colorado	9.09	9,463	6,056,503	24,520
California	2.37	3,754	2,402,466	9,727
Idaho	0.74	619	396,012	1,603
Oklahoma	0.60	420	268,939	1,089
Wyoming	0.22	212	135,859	550
		105,961	**67,815,258**	**274,556**
24. Juniper steppe woodland (*Juniperus-Artemisia-Agropyron*)				
Oregon	3.58	3,476	2,224,861	9,008
Nevada	2.50	2,761	1,767,101	7,154
California	0.82	1,294	827,987	3,352
Idaho	1.32	1,107	708,314	2,868
Utah	0.07	62	39,366	159
		8,699	**5,567,630**	**22,541**
25. Alder-ash forest (*Alnus-Fraxinus*)				
Oregon	0.16	158	100,982	409
Washington	0.20	136	87,151	353
		294	**188,133**	**762**
26. Oregon oakwoods (*Quercus*)				
Oregon	0.99	962	615,664	2,493
Washington	0.06	42	26,816	109
		1,004	**642,840**	**2,601**
27. Mesquite bosques (*Prosopis*)				
Arizona	0.23	260	166,635	67,464
		260	**166,635**	**67,464**
28. Mosaic: 2 (*Thuja-Tsuga-Pseudotsuga*) and 26 (*Quercus*)				
Oregon	4.35	4,225	2,703,711	10,946
		4,225	**2,703,711**	**10,946**
29. California mixed evergreen forest (*Quercus-Arbutus-Pseudotsuga*)				
California	3.39	5,379	3,442,340	13,937
Oregon	0.21	204	130,299	528
		5,582	**3,572,639**	**14,464**
30. California oakwoods (*Quercus*)				
California	10.91	17,313	11,080,031	44,858
		17,313	**11,080,031**	**44,858**
31. Oak-juniper woodland (*Quercus-Juniperus*)				
Texas	1.46	3,906	2,499,713	10,120
Arizona	3.32	3,788	2,424,376	9,815
New Mexico	0.81	988	632,096	2,559
		8,682	**5,556,185**	**22,495**
32. Transition: 31 (*Quercus-Juniperus*) and 37 (*Cercocarpus-Quercus*)				
Arizona	5.83	6,647	4,254,094	17,223
New Mexico	0.02	25	16,291	66
		6,672	**4,270,385**	**17,289**
33. Chaparral (*Adenostoma-Arctostaphylos-Ceanothus*)				
California	8.74	13,874	8,879,672	35,950
Arizona	0.09	102	65,347	265
Nevada	0.05	56	35,864	145
		14,033	**8,980,882**	**36,360**
34. Montane chaparral (*Arctostaphylos-Castanopsis-Ceanothus*)				
California	0.63	993	635,659	2,574
Oregon	0.28	275	175,904	712
		1,268	**811,563**	**3,286**

Type/state	Percent of state	mi²	Acres	km²
35. Coastal sagebrush (*Salvia-Eriogonum*)				
California	2.37	3,759	2,405,726	9,740
		3,759	**2,405,726**	**9,740**
36. Mosaic: 30 (Quercus) and 35 (*Salvia-Eriogonum*)				
California	0.65	1,039	664,997	2,692
		1,039	**664,997**	**2,692**
37. Mountain mahogany-oak scrub (*Cercocarpus-Quercus*)				
Utah	5.34	4,531	2,899,985	11,740
Colorado	3.36	3,497	2,238,273	9,062
Nevada	0.55	611	391,240	1,584
Wyoming	0.57	554	354,558	1,435
Arizona	0.01	10	6,535	26
Idaho	0.01	10	6,439	26
		9,214	**5,897,031**	**23,875**
38. Great Basin sagebrush (*Artemisia*)				
Nevada	35.55	39,307	25,156,741	101,849
Utah	11.80	10,021	6,413,429	25,965
Arizona	7.32	8,437	5,342,123	21,628
Colorado	2.93	3,050	1,951,906	7,902
California	1.89	2,995	1,916,757	7,760
New Mexico	1.41	1,711	1,094,765	4,432
Oregon	0.17	163	104,239	422
		65,594	**41,979,960**	**169,959**
39. Blackbrush (*Coleogyne*)				
Utah	5.34	4,536	2,903,266	11,754
Arizona	0.22	250	160,100	648
		4,787	**3,063,366**	**12,402**
40. Saltbush-greasewood (*Atriplex-Sarcobatus*)				
Nevada	19.95	22,058	14,117,248	57,155
Utah	20.36	17,284	11,061,935	44,785
California	3.16	5,017	3,210,895	13,000
Colorado	3.61	3,754	2,402,852	9,728
Wyoming	3.77	3,692	2,362,617	9,565
Oregon	3.65	3,548	2,270,466	9,192
New Mexico	2.55	3,095	1,981,003	8,020
Idaho	2.08	1,736	1,110,766	4,498
Texas	0.14	366	234,451	949
Arizona	0.04	51	32,674	132
		60,601	**38,784,906**	**157,024**
41. Creosote bush (*Larrea*)				
California	15.75	24,999	15,999,056	64,774
Nevada	7.78	8,599	5,503,445	22,281
Arizona	3.99	4,549	2,911,212	11,786
Utah	0.45	384	246,039	996
		38,531	**24,659,752**	**99,837**
42. Creosote bush-bursage (*Larrea-Franseria or Ambrosia*)				
Arizona	21.61	24,633	15,764,980	63,826
California	5.25	8,333	5,333,019	21,591
New Mexico	0.09	107	68,423	277
		33,073	**21,166,421**	**85,694**
43. Palo verde-cactus shrub (*Cercidium-Opuntia*)				
Arizona	8.19	9,337	5,975,989	24,194
California	1.09	1,737	1,111,589	4,500
		11,074	**7,087,578**	**28,695**
44. Creosote bush-tarbush (*Larrea-Flourensia*)				
New Mexico	5.00	6,079	3,890,324	15,750
Arizona	1.84	2,093	1,339,615	5,424
Texas	0.04	114	72,647	294
		8,285	**5,302,586**	**21,468**

Type/state	Percent of state	mi²	Acres	km²
45. Cenza shrub (*Leucophyllum-Larrea-Prosopis*)				
Texas	1.13	3,018	1,931,746	7,821
		3,018	**1,931,746**	**7,821**
46. Desert: vegetation largely absent				
Utah	5.33	4,526	2,896,705	11,728
Nevada	1.28	1,416	906,373	3,670
Idaho	1.44	1,202	769,487	3,115
Arizona	0.29	327	209,111	847
California	0.09	143	91,274	370
Colorado	0.07	77	49,374	200
		7,691	**4,922,323**	**19,928**
47. Fescue-oatgrass (*Festuca-Danthonia*)				
California	0.85	1,355	867,105	3,511
		1,355	**867,105**	**3,511**
48. California steppe (*Stipa*)				
California	12.69	20,134	12,885,955	52,170
		20,134	**12,885,955**	**52,170**
49. Tule marshes (*Scirpus-Typha*)				
California	1.87	2,975	1,903,718	7,707
Nevada	0.42	469	299,951	1,214
Utah	0.46	395	252,601	1,023
		3,838	**2,456,269**	**9,944**
50. Fescue-wheatgrass (*Festuca-Agropyron*)				
Washington	9.41	6,411	4,102,795	16,611
Idaho	1.75	1,459	933,687	3,780
Oregon	0.21	204	130,299	528
		8,073	**5,166,782**	**20,918**
51. Wheatgrass-bluegrass (*Agropyron-Poa*)				
Oregon	6.81	6,612	4,231,471	17,131
Washington	6.53	4,452	2,849,163	11,535
Idaho	2.59	2,163	1,384,433	5,605
Utah	0.50	420	269,003	1,089
Nevada	0.35	392	251,046	1,016
		14,039	**8,985,116**	**36,377**
52. Alpine meadows and barren (*Agrostis-Carex-Festuca-Poa*)				
Colorado	5.30	5,519	3,531,863	14,299
Washington	3.61	2,462	1,575,420	6,378
Montana	1.28	1,882	1,204,416	4,876
Wyoming	1.38	1,346	861,543	3,488
California	0.74	1,177	753,012	3,049
Oregon	0.45	438	280,144	1,134
Utah	0.50	420	269,003	1,089
Idaho	0.26	216	138,443	561
New Mexico	0.16	193	123,813	501
Nevada	0.02	20	13,041	53
		13,673	**8,750,698**	**35,428**
53. Grama-galleta steppe (*Bouteloua-Hilaria*)				
New Mexico	15.11	18,378	11,762,203	47,620
Arizona	8.74	9,965	6,377,874	25,821
		28,344	**18,140,077**	**73,442**
54. Grama-tobosa prairie (*Bouteloua-Hilaria*)				
Texas	2.22	5,913	3,784,242	15,321
New Mexico	0.03	31	19,549	79
		5,943	**3,803,791**	**15,400**
55. Sagebrush steppe (*Artemisia-Agropyron*)				
Idaho	44.79	37,431	23,955,918	96,988
Oregon	30.29	29,404	18,818,481	76,188
Wyoming	29.07	28,435	18,198,449	73,678
Nevada	13.86	15,324	9,807,086	39,705

Type/state	Percent of state	mi²	Acres	km²
Washington	20.04	13,654	8,738,552	35,379
Colorado	5.24	5,452	3,489,072	14,126
California	3.17	5,037	3,223,934	13,052
Montana	3.08	4,532	2,900,498	11,743
Utah	4.25	3,609	2,309,491	9,350
		142,877	**91,441,480**	**370,208**
56. Wheatgrass-needlegrass shrubsteppe (*Agropyron-Stipa-Artemisia*)				
Wyoming	10.46	10,231	6,547,730	26,509
Colorado	0.09	93	59,248	240
		10,323	**6,606,979**	**26,749**
57. Galleta-threeawn shrubsteppe (*Hilaria-Aristida*)				
Utah	2.05	1,743	1,115,379	4,516
		1,743	**1,115,379**	**4,516**
58. Grama-tobosa shrubsteppe (*Bouteloua-Hilaria-Larrea*)				
New Mexico	14.63	17,793	11,387,507	46,103
Arizona	13.95	15,898	10,174,538	41,192
Texas	0.09	232	148,596	602
		33,923	**21,710,641**	**87,897**
59. Trans-Pecos shrub savanna (*Flourensia-Larrea*)				
Texas	10.64	28,383	18,165,021	73,543
New Mexico	4.50	5,473	3,502,595	14,181
		33,856	**21,667,616**	**87,723**
60. Mesquite savanna (*Prosopis-Hilaria*)				
Texas	3.36	8,962	5,735,801	23,222
		8,962	**5,735,801**	**23,222**
61. Mesquite-acacia savanna (*Prosopis-Acacia-Andropogon-Setaria*)				
Texas	9.75	26,009	16,646,041	67,393
		26,009	**16,646,041**	**67,393**
62. Mesquite-live oak savanna (*Prosopis-Quercus-Andropogon*)				
Texas	1.01	2,698	1,727,014	699
		2,698	**1,727,014**	**699**
63. Foothills prairie (*Andropogon-Festuca-Stipa*)				
Montana	12.19	17,932	11,476,600	46,464
Wyoming	0.45	440	281,658	1,140
Utah	0.05	41	26,244	106
		18,413	**11,784,503**	**47,711**
64. Grama-needlegrass-wheatgrass (*Bouteloua-Stipa-Agropyron*)				
Montana	41.50	61,030	39,059,377	158,135
Wyoming	17.90	17,505	11,203,379	45,358
Nebraska	0.26	198	126,750	513
		78,734	**50,389,506**	**204,006**
65. Grama-buffalo grass (*Bouteloua-Buchloe*)				
Colorado	38.14	39,705	25,410,979	102,878
Texas	12.78	34,094	21,820,480	88,342
New Mexico	15.26	18,557	11,876,241	48,082
Nebraska	11.44	8,846	5,661,494	22,921
Kansas	9.39	7,724	4,943,570	20,015
Oklahoma	7.52	5,258	3,365,105	13,624
Wyoming	4.43	4,328	2,770,194	11,215
S. Dakota	0.01	5	3,283	13
		118,518	**75,851,446**	**307,090**
66. Wheatgrass-needlegrass (*Agropyron-Stipa*)				
S. Dakota	56.85	43,842	28,058,897	113,599
N. Dakota	47.01	33,237	21,271,544	86,120
Montana	7.78	11,446	7,325,489	29,658
Wyoming	6.92	6,767	4,330,913	17,534
Colorado	2.19	2,278	1,458,169	5,904
Nebraska	1.52	1,173	750,749	3,039
New Mexico	0.20	239	153,137	620
		98,983	**63,348,897**	**256,473**
67. Wheatgrass-bluestem-needlegrass (*Agropyron-Andropogon-Stipa*)				
N. Dakota	32.12	22,710	14,534,496	58,844
Nebraska	20.79	16,082	10,292,740	41,671
S. Dakota	16.60	12,805	8,195,063	33,178
Kansas	0.71	582	372,737	1,509
Colorado	0.02	21	13,166	53
		52,200	**33,408,201**	**135,256**
68. Wheatgrass-grama-buffalo grass (*Agropyron-Bouteloua-Buchloe*)				
S. Dakota	1.25	964	617,256	2,499
		964	**617,256**	**2,499**
69. Bluestem-grama prairie (*Andropogon-Bouteloua*)				
Kansas	42.35	34,842	22,298,830	90,279
Oklahoma	18.19	12,717	8,138,780	32,951
Nebraska	2.73	2,112	1,351,999	5,474
Texas	0.06	150	95,762	388
Colorado	0.10	108	69,123	280
		49,929	**31,954,493**	**129,370**
70. Sandsage-bluestem prairie (*Artemisia-Andropogon*)				
Kansas	7.38	6,069	3,884,312	15,726
Oklahoma	5.48	3,834	2,454,072	9,936
Colorado	3.41	3,549	2,271,189	9,195
Nebraska	2.91	2,250	1,439,749	5,829
Texas	0.01	21	13,209	53
		15,723	**10,062,530**	**40,739**
71. Shinnery (*Quercus-Andropogon*)				
Texas	2.25	5,990	3,833,774	15,521
New Mexico	2.06	2,510	1,606,306	6,503
Colorado	2.12	1,481	948,012	3,838
		9,981	**6,388,092**	**25,863**
72. Sea oats prairie (*Uniola-Andropogon*)				
Texas	0.20	537	343,422	1,390
		537	**343,422**	**1,390**
74. Bluestem prairie (*Andropogon-Panicum-Sorghastrum*)				
Nebraska	23.19	17,936	11,478,988	46,474
Kansas	16.78	13,804	8,834,522	35,768
S. Dakota	13.98	10,784	6,901,451	27,941
N. Dakota	7.67	5,420	3,468,877	14,044
Oklahoma	4.60	3,215	2,057,387	8,330
		51,158	**32,741,225**	**132,556**
75. Nebraska sandhills prairie (*Andropogon-Calamovilfa*)				
Nebraska	27.75	21,465	13,737,736	55,618
S. Dakota	1.48	1,144	732,171	2,964
N. Dakota	0.05	37	23,416	95
Wyoming	0.01	5	3,314	13
		22,651	**14,496,637**	**58,691**
76. Blackland prairie (*Andropogon-Stipa*)				
Texas	6.55	17,486	11,190,921	45,307
Oklahoma	1.42	993	635,369	2,572
		18,479	**11,826,290**	**47,880**
77. Bluestem-sacahuista prairie (*Andropogon-Spartina*)				
Texas	4.62	12,337	7,895,394	31,965
		12,337	**7,895,394**	**31,965**

Type/state	Percent of state	mi²	Acres	km²
78. Southern cordgrass prairie (*Spartina*)				
Texas	0.87	2,332	1,492,563	6,042
		2,332	**1,492,563**	**6,042**
81. Oak savanna (*Quercus-Andropogon*)				
N. Dakota	2.03	1,432	916,560	3,711
		1,432	**916,560**	**3,711**
82. Mosaic: 74 (*Andropogon-Panicum-Sorghastrum*) and 100 (*Quercus-Carya*)				
Kansas	11.64	9,579	6,130,543	24,820
Oklahoma	6.62	4,628	2,961,696	11,991
		14,207	**9,092,239**	**36,811**
84. Cross timbers (*Quercus-Andropogon*)				
Oklahoma	27.22	19,031	12,179,595	49,310
Texas	3.76	10,030	6,419,342	25,989
Kansas	2.17	1,783	1,141,098	4,620
		30,874	**19,740,035**	**79,919**
85. Mesquite-buffalo grass (*Prosopis-Buchloe*)				
Texas	10.81	28,832	18,452,306	74,706
Oklahoma	10.37	7,249	4,639,205	18,782
		36,080	**23,091,512**	**93,488**
86. Juniper-oak savanna (*Juniperus-Quercus-Andropogon*)				
Texas	9.60	25,602	16,385,172	66,337
		25,602	**16,385,172**	**66,337**
87. Mesquite-oak savanna (*Prosopis-Quercus-Andropogon*)				
Texas	1.33	3,550	2,271,866	9,198
		3,550	**2,271,866**	**9,198**
88. Fayette prairie (*Andropogon-Buchloe*)				
Texas	1.10	2,925	1,872,308	7,580
		2,925	**1,872,308**	**7,580**
98. Northern floodplain forest (*Populus-Salix-Ulmus*)				
N. Dakota	11.05	7,814	5,000,937	20,247
Kansas	6.23	5,124	3,279,432	13,277
S. Dakota	6.38	4,920	3,148,664	12,748
Nebraska	5.33	4,123	2,638,997	10,684
Montana	1.86	2,733	1,748,878	7,080
Oklahoma	0.41	289	184,896	749
Colorado	0.07	72	46,082	187
		25,075	**16,047,886**	**64,971**
100. Oak-hickory forest (*Quercus-Carya*)				
Texas	6.07	16,196	10,365,388	41,965
Oklahoma	6.33	4,423	2,830,588	11,460
Kansas	3.37	2,769	1,772,136	7,175
Nebraska	2.44	1,889	1,208,999	4,895
		25,277	**16,177,110**	**65,494**
111. Oak-hickory-pine forest (*Quercus-Carya-Pinus*)				
Texas	7.60	20,272	12,974,071	52,527
Oklahoma	7.93	5,542	3,546,639	14,359
		25,814	**16,520,710**	**66,885**
112. Southern mixed forest (*Fagus-Liquidambar-Magnolia-Pinus-Quercus*)				
Texas	1.15	3,065	1,961,466	7,942
		3,065	**1,961,466**	**7,942**
113. Southern floodplain forest (*Quercus-Nyssa-Taxodium*)				
Texas	1.42	3,787	2,423,764	9,813
Oklahoma	1.20	840	537,879	2,178
		4,628	**2,961,643**	**11,990**
Large lakes (>100 mi² or 260 km²)				
Great Salt Lake		1,681	1,076,013	4,356
Salton Sea		270	172,769	699
Pyramid Lake		199	127,153	515
Lake Tahoe		194	123,879	502
Flathead Lake		191	122,091	494
Goose Lake		178	114,097	462
Sevier Lake		169	108,257	430
Utah Lake		138	88,574	359
Lake Pend Oreille		136	87,008	352
Yellowstone Lake		135	86,154	349
Walker Lake		112	71,727	290
Bear Lake		111	71,475	289
Honey Lake		102	65,196	264
		3,616	**2,304,360**	**9,370**

[1]Rounding procedures made some column totals not equal to sum of individual rows. Km² were determined from hectare values (data not shown).

Bailey (1976, 1978) Ecoregions in the 17 Conterminous Western United States[1]

Ecoregion/ state	Percent of state	mi²	Acres	km²	Bailey mi²
M2111. Douglas-fir forest					
Washington	14.71	10,025	6,415,740	25,975	
Idaho	3.44	2,878	1,841,681	7,456	
		12,902	**8,257,421**	**33,431**	**11,400**
M2112. Cedar-hemlock-Douglas-fir forest					
Montana	13.42	19,733	12,629,326	51,131	
Idaho	21.51	17,971	11,501,476	46,565	
Washington	1.12	762	487,958	1,976	
		38,467	**24,618,760**	**99,671**	
2215. Oak-hickory forest					
Oklahoma	4.19	2,928	1,874,175	7,588	
		2,928	**1,874,175**	**7,588**	
2311. Beech-sweetgum-magnolia-pine-oak					
Texas	1.79	4,771	3,053,740	12,363	
		4,771	**3,053,740**	**12,363**	
2320. Southeastern mixed forest					
Texas	8.97	23,942	15,322,910	62,036	
Oklahoma	7.38	5,160	3,302,118	13,369	
		29,102	**18,625,027**	**75,405**	
2410. Willamette-Puget forest					
Washington	14.92	10,166	6,506,103	26,341	
Oregon	3.26	3,167	2,026,672	8,205	
		13,332	**8,532,775**	**34,546**	**13,000**
M2411. Sitka spruce-cedar-hemlock forest					
Washington	6.42	4,377	2,801,239	11,341	
Oregon	3.26	3,167	2,321,461	9,399	
		8,004	**5,122,700**	**20,740**	**6,300**
M2412. Redwood forest					
California	3.51	5,567	3,562,942	14,225	
Oregon	0.18	173	110,546	448	
		5,740	**3,673,488**	**14,872**	**5,100**

Ecoregion/ state	Percent of state	mi²	Acres	km²	Bailey mi²
M2413. Cedar-hemlock-Douglas-fir forest					
Oregon	16.99	16,496	10,557,121	42,741	
Washington	5.55	3,784	2,421,716	9,805	
California	2.22	3,527	2,257,152	9,138	
		23,806	**15,235,989**	**61,684**	**2,200**
M2414. California mixed evergreen forest					
California	3.20	5,072	3,245,822	13,141	
		5,072	**3,245,822**	**13,141**	**4,300**
M2415. Silver fir-Douglas-fir forest					
Washington	25.32	17,354	11,042,302	44,706	
Oregon	10.97	10,652	6,816,989	27,599	
		27,905	**17,859,291**	**72,305**	**25,300**
2511. Oak-hickory-bluestem parkland					
Kansas	16.45	13,534	8,662,076	35,069	
Oklahoma	12.25	8,562	5,479,731	22,185	
		22,097	**14,141,807**	**57,254**	
2512. Oak + Bluestem parkland					
Texas	23.74	63,328	40,529,818	164,088	
Oklahoma	31.19	21,810	13,958,142	56,511	
Kansas	1.86	1,533	980,962	3,972	
		86,670	**55,468,922**	**224,571**	**80,400**
2521. Mesquite-buffalo grass					
Texas	12.94	34,530	22,098,960	89,469	
Oklahoma	0.40	279	178,493	723	
		34,809	**22,277,453**	**90,192**	**32,200**
2522. Juniper-oak-mesquite					
Texas	9.84	26,257	16,804,606	68,035	
		26,257	**16,804,606**	**68,035**	**24,100**
2523. Mesquite-acacia					
Texas	10.71	28,572	18,286,302	74,034	
		28,572	**18,286,302**	**74,034**	**27,300**
2531. Bluestem prairie					
Nebraska	31.90	24,667	15,793,145	63,940	
Kansas	18.59	15,299	9,791,108	39,640	
South Dakota	17.92	13,823	8,846,515	35,816	
North Dakota	14.65	10,360	6,630,405	26,844	
Oklahoma	1.91	1,339	856,766	3,469	
		65,497	**41,917,938**	**169,708**	
2532. Wheatgrass-bluestem-needlegrass					
Nebraska	47.09	36,428	23,313,691	94,387	
North Dakota	35.76	25,280	16,178,926	65,502	
South Dakota	19.21	14,812	9,479,739	38,380	
		76,519	**48,972,356**	**198,269**	**49,400**
2533. Bluestem-grama prairie					
Kansas	50.16	41,269	26,411,929	106,931	
Oklahoma	31.07	21,726	13,904,594	56,294	
Nebraska	3.56	2,751	1,760,908	7,129	
Texas	0.47	1,242	795,057	3,219	
		66,988	**42,872,488**	**173,573**	**62,000**
2610. California grassland					
California	14.45	22,939	14,680,815	59,437	
		22,939	**14,680,815**	**59,437**	**20,200**
M2610. Sierran forest					
California	22.55	35,793	22,907,295	92,742	
Nevada	0.90	991	634,443	2,569	
Oregon	0.74	720	460,607	1,865	
		37,504	**24,002,345**	**97,175**	**32,600**
M2620. California chapparal					
California	22.15	35,151	22,496,903	91,081	
		35,151	**22,496,903**	**91,081**	**33,500**

Ecoregion/ state	Percent of state	mi²	Acres	km²	Bailey mi²
3111. Grama-needlegrass-wheatgrass					
Montana	51.28	75,402	48,257,513	195,375	
Wyoming	14.05	13,742	8,795,031	35,607	
		89,145	**57,052,544**	**230,982**	**83,800**
M3111. Grand fir-Douglas-fir forest					
Oregon	21.29	20,670	13,228,643	53,557	
Idaho	17.72	14,811	9,479,238	38,377	
Washington	0.66	452	289,160	1,171	
		35,933	**22,997,042**	**93,105**	**32,600**
3112. Wheatgrass-needlegrass					
South Dakota	62.87	48,481	31,027,986	125,619	
North Dakota	49.59	35,062	22,439,949	90,850	
Montana	10.59	15,576	9,968,603	40,359	
Wyoming	11.22	10,997	7,024,962	28,441	
Nebraska	1.93	1,490	953,825	3,862	
		111,586	**71,415,325**	**289,131**	**102,800**
M3112. Douglas-fir forest					
Montana	23.99	35,281	22,579,705	91,416	
Utah	33.02	28,032	17,940,227	72,633	
Wyoming	19.00	18,582	11,892,652	48,148	
Idaho	18.57	15,517	9,930,631	40,205	
Colorado	5.67	5,901	3,776,768	15,289	
		103,312	**66,119,593**	**267,691**	**94,500**
3113. Grama-buffalo grass					
Colorado	43.01	44,770	28,652,809	116,003	
Texas	14.70	39,216	25,098,492	101,613	
New Mexico	19.41	23,596	15,101,184	61,138	
Nebraska	15.52	12,009	7,685,631	31,116	
Kansas	12.93	10,643	6,811,205	27,576	
Oklahoma	11.61	8,116	5,194,142	21,029	
Wyoming	5.60	5,474	3,503,262	14,183	
		143,823	**92,046,725**	**372,659**	**131,000**
M3113. Ponderosa pine-Douglas-fir forest					
Colorado	45.68	47,548	30,431,007	123,202	
New Mexico	11.11	13,507	8,644,261	34,998	
Wyoming	6.51	6,367	4,074,847	16,497	
Utah	0.10	86	55,144	223	
		67,509	**43,205,618**	**174,922**	**60,200**
3120. Palouse grassland					
Washington	13.84	9,432	6,036,217	24,438	
Oregon	3.97	3,858	2,468,855	9,995	
Idaho	1.42	1,185	758,339	3,070	
		14,474	**9,263,412**	**37,504**	**12,400**
M3120. Upper Gila mountains forest					
Arizona	26.44	30,136	19,287,009	78,085	
New Mexico	8.09	9,836	6,295,149	25,486	
		39,972	**25,582,158**	**103,571**	**36,100**
3131. Sagebrush-wheatgrass					
Idaho	37.20	31,090	19,897,373	80,556	
Oregon	30.69	29,796	19,069,144	77,203	
Nevada	15.82	17,494	11,196,051	45,328	
Washington	16.12	10,985	7,030,205	28,462	
California	3.69	5,859	3,749,484	15,180	
Utah	2.50	2,125	1,360,222	5,507	
		97,348	**62,302,479**	**252,237**	**89,800**
P3131. Juniper-pinyon woodland + sagebrush mosaic					
Utah	28.11	23,867	15,274,927	61,842	
Arizona	14.05	16,015	10,249,668	41,497	
Colorado	2.72	2,836	1,814,861	7,348	
		42,718	**27,339,456**	**110,686**	**39,600**

Ecoregion/ state	Percent of state	mi²	Acres	km²	Bailey mi²
3132. Lahontan saltbush-greasewood					
Nevada	31.20	34,492	22,074,880	89,372	
California	1.71	2,711	1,734,836	7,024	
		37,203	**23,809,716**	**96,396**	**33,300**
P3132. Grama-galleta steppe + juniper-pinyon woodland					
New Mexico	36.14	43,940	28,121,919	113,854	
Arizona	13.72	15,642	10,010,876	40,530	
Colorado	0.72	745	476,630	1,930	
Utah	0.10	86	55,144	223	
		60,413	**38,664,570**	**156,537**	**55,100**
3133. Great basin sagebrush					
Nevada	42.48	46,971	30,061,396	121,706	
Utah	4.47	3,791	2,426,342	9,823	
		50,762	**32,487,738**	**131,529**	**46,900**
3134. Bonneville saltbush-greasewood					
Utah	30.35	25,763	16,488,098	66,753	
Nevada	0.71	787	503,822	2,040	
		26,550	**16,991,920**	**68,793**	**22,200**
3135. Ponderosa shrub forest					
Oregon	8.16	7,917	5,066,681	20,513	
California	2.55	4,051	2,592,927	10,498	
Washington	1.62	1,101	704,828	2,854	
		13,069	**8,364,435**	**33,864**	**11,200**
3140. Mexican highland shrub steppe					
Arizona	12.87	14,666	9,386,344	38,001	
New Mexico	3.99	4,848	3,102,737	12,562	
		19,514	**12,489,082**	**50,563**	**17,500**
A3141. Wheatgrass-needlegrass-sagebrush					
Wyoming	13.87	13,569	8,684,402	35,160	
Montana	0.72	1,054	674,293	2,730	
		14,623	**9,358,695**	**37,889**	**13,100**
A3142. Sagebrush-wheatgrass					
Wyoming	29.75	29,098	18,622,603	75,395	
Colorado	2.20	2,291	1,466,555	5,937	
Utah	0.98	833	533,060	2,158	
Idaho	0.14	113	72,223	292	
		32,335	**20,694,440**	**83,783**	**29,200**
3211. Grama-tobosa					
New Mexico	15.65	19,028	12,177,795	49,303	
Texas	0.10	254	162,625	658	
		19,282	**12,340,421**	**49,961**	**18,200**
3212. Tarbush-creosote bush					
Texas	16.75	44,694	28,603,969	115,806	
New Mexico	5.62	6,838	4,376,115	17,717	
		51,531	**32,980,084**	**133,523**	**45,900**
3221. Creosote bush					
California	17.34	27,515	17,609,516	71,294	
Nevada	8.89	9,826	6,288,448	25,459	
Arizona	3.98	4,535	2,902,236	11,750	
Utah	0.37	316	202,195	819	
		41,191	**27,002,396**	**109,321**	**36,700**
3222. Creosote bush-bur sage					
Arizona	28.95	33,006	21,123,867	85,522	
California	6.63	10,522	6,734,148	27,264	
		43,528	**27,858,015**	**112,785**	**40,800**

[1]The Bailey mi² column is from Bailey (1978). We listed all values that Bailey gave—some were not given. Rounding procedures made some column totals not equal to sum of individual rows. Km² were determined from hectare values (data not shown).

State Summaries of Küchler and Bailey Vegetation Categories

	Küchler map			Bailey map		
State	Vegetation type	Percent of state	km²	Eco-region	Percent of state	km²
Arizona	18	2.28	6,746	M3120	26.44	78,085
	19	4.29	12,673	P3131	14.05	41,497
	20	0.65	1,931	P3132	13.72	40,530
	21	0.24	701	3140	12.87	38,001
	23	16.87	49,830	3221	3.98	11,750
	27	0.23	675	3222	28.95	85,522
	31	3.32	9,815			
	32	5.83	17,223			
	33	0.09	265			
	37	0.01	26			
	38	7.32	21,628			
	39	0.22	648			
	40	0.04	132			
	41	3.99	11,786			
	42	21.61	63,826			
	43	8.19	24,194			
	44	1.84	5,424			
	46	0.29	847			
	53	8.74	25,821			
	58	13.95	41,192			
California	1	0.01	40	M2412	3.51	14,425
	2	2.00	8,235	M2413	2.22	9,138
	5	12.97	53,344	M2414	3.20	13,141
	6	2.18	8,961	2610	14.45	59,437
	7	1.77	7,259	M2610	22.55	92,742
	8	2.14	8,790	M2620	22.15	91,081
	9	0.14	581	3131	3.69	15,180
	10	1.92	7,892	3132	1.71	7,024
	22	0.04	185	3135	2.55	10,498
	23	2.37	9,727	3221	17.34	71,294
	24	0.82	3,352	3222	6.63	27,264
	29	3.39	13,937			
	30	10.91	44,858			
	33	8.74	35,950			
	34	0.63	2,574			
	35	2.37	9,740			
	36	0.65	2,692			
	38	1.89	7,760			
	40	3.16	13,000			
	41	15.75	64,774			
	42	5.25	21,591			
	43	1.09	4,500			
	46	0.09	370			
	47	0.85	3,511			
	48	12.69	52,170			
	49	1.87	7,707			
	52	0.74	3,049			
	55	3.17	13,052			
	Water	0.39	1,623			
Colorado	12	0.10	267	M3112	5.67	15,289
	15	10.37	27,958	3113	43.01	116,003
	18	10.04	27,079	M3113	45.68	123,202
	21	5.87	15,832	P3131	2.72	7,348
	23	9.09	24,520	P3132	0.72	1,930
	37	3.36	9,062	A3142	2.20	5,937
	38	2.93	7,902			
	40	3.61	9,728			
	46	0.07	200			
	52	5.30	14,299			

State	Küchler map: Vegetation type	Küchler map: Percent of state	Küchler map: km²	Bailey map: Ecoregion	Bailey map: Percent of state	Bailey map: km²
	55	5.24	14,126			
	56	0.09	240			
	65	38.14	102,878			
	66	2.19	5,904			
	67	0.02	53			
	69	0.10	280			
	70	3.41	9,195			
	98	0.07	187			
Idaho	11	10.40	22,519	M2111	3.44	7,456
	12	4.17	9,028	M2112	21.51	46,565
	13	7.68	16,621	M3111	17.72	38,377
	14	10.67	23,093	M3112	18.57	40,205
	15	11.95	25,885	3120	1.42	3,070
	23	0.74	1,605	3131	37.20	80,556
	24	1.33	2,870	A3142	0.14	292
	37	0.01	26			
	40	2.08	4,501			
	46	1.44	3,118			
	50	1.75	3,784			
	51	2.59	5,610			
	52	0.26	561			
	55	44.87	97,145			
	Water	0.23	509			
Kansas	65	9.39	20,015	2511	16.45	35,069
	67	0.71	1,509	2512	1.86	3,972
	69	42.35	90,279	2531	18.59	39,640
	70	7.38	15,726	2533	50.16	106,931
	74	16.78	35,767	3113	12.93	27,576
	82	11.64	24,820			
	84	2.17	4,620			
	98	6.23	13,277			
	100	3.37	7,175			
Montana	11	4.04	15,390	M2112	13.42	51,131
	12	15.38	58,581	3111	51.28	195,375
	13	0.44	1,170	3112	10.59	40,359
	15	6.76	25,744	M3112	23.99	91,416
	16	5.56	21,175	A3141	0.72	2,730
	52	1.28	4,876			
	55	3.08	11,793			
	63	12.19	46,464			
	64	41.50	158,135			
	66	7.78	29,658			
	98	1.86	7,080			
	Water	0.13	494			
Nebraska	16	1.65	3,316	2531	31.90	63,940
	64	0.26	513	2532	47.09	94,387
	65	11.44	22,921	2533	3.56	7,129
	66	1.52	3,039	3112	1.93	3,862
	67	20.79	41,671	3113	15.52	31,116
	69	2.73	5,474			
	70	2.91	5,829			
	74	23.19	46,474			
	75	27.75	55,618			
	98	5.33	10,684			
	100	2.44	4,895			
Nevada	5	0.29	818	M2610	0.90	2,569
	8	0.14	396	3131	15.82	45,328
	22	1.89	5,412	3132	31.20	89,372
	23	15.03	43,058	3133	42.48	121,706
	24	2.50	7,154	3134	0.71	2,040
	33	0.05	145	3221	8.89	25,459
	37	0.55	1,584			
	38	35.55	101,849			
	40	19.95	57,155			
	41	7.78	22,281			
	46	1.28	3,670			
	49	0.42	1,214			
	51	0.35	1,016			
	52	0.02	53			
	55	13.86	39,705			
	Water	0.34	964			
New	18	9.96	31,382	3113	19.41	61,138
Mexico	19	0.04	132	M3113	11.11	34,998
	21	2.06	6,503	M3120	8.09	25,486
	23	26.11	82,247	M3132	36.14	113,854
	31	0.81	2,559	3140	3.99	12,562
	32	0.02	66	3211	15.65	49,303
	38	1.41	4,432	3212	5.62	17,717
	40	2.55	8,020			
	42	0.09	277			
	44	5.00	15,750			
	52	0.16	501			
	53	15.11	47,620			
	54	0.03	79			
	58	14.63	46,103			
	59	4.50	14,181			
	65	15.26	48,082			
	66	0.20	620			
	71	2.06	6,503			
North	16	0.07	135	2531	14.65	26,844
Dakota	66	47.01	86,120	2532	35.76	65,502
	67	32.12	58,844	3112	49.59	90,850
	74	7.67	14,044			
	75	0.05	95			
	81	2.03	3,711			
	98	11.05	20,247			
Oklahoma	23	0.60	1,089	2115	4.19	7,588
	65	7.52	13,624	2320	7.38	13,369
	69	18.19	32,950	2511	12.25	22,185
	70	5.48	9,936	2512	31.19	56,511
	71	2.12	3,838	2521	0.40	723
	74	4.60	8,330	2531	1.91	3,469
	76	1.42	2,572	2533	31.07	56,294
	82	6.62	11,991	3113	11.61	21,029
	84	27.22	49,310			
	85	10.37	18,782			
	98	0.41	749			
	100	6.33	11,460			
	111	7.93	14,359			
	113	1.20	2,178			
Oregon	1	3.07	7,728	2410	3.26	8,205
	2	13.28	33,393	M2411	3.74	9,399
	3	5.94	14,942	M2412	0.18	448
	4	3.03	7,623	M2413	16.99	42,741
	5	1.13	2,835	M2415	10.97	27,599
	10	9.25	23,277	M2610	0.74	1,865
	11	4.43	11,131	M3111	21.29	53,557
	12	0.24	607	3120	3.97	9,995
	14	7.86	19,769	3131	30.69	77,203
	15	0.55	1,385	3135	8.16	20,513

State	Küchler map: Vegetation type	Küchler map: Percent of state	Küchler map: km²	Bailey map: Ecoregion	Bailey map: Percent of state	Bailey map: km²
	24	3.58	9,008			
	25	0.16	409			
	26	0.99	2,493			
	28	4.35	10,946			
	29	0.21	528			
	34	0.28	712			
	38	0.17	422			
	40	3.65	9,192			
	50	0.21	528			
	51	6.81	17,131			
	52	0.45	1,134			
	55	30.29	76,188			
	Water	0.06	145			
South	16	0.05	106	2531	17.92	35,816
Dakota	17	3.39	6,766	2532	19.21	38,380
	65	0.01	13	3112	62.87	125,619
	66	56.85	113,599			
	67	16.60	33,178			
	68	1.25	2,499			
	74	13.98	27,941			
	75	1.48	2,964			
	98	6.38	12,748			
Texas	31	1.46	10,120	2311	1.79	12,363
	40	0.14	949	2320	8.97	62,036
	44	0.04	294	2512	23.74	164,088
	45	1.13	7,821	2521	12.94	89,469
	54	2.22	15,321	2522	9.84	68,035
	58	0.09	602	2523	10.71	74,034
	59	10.64	73,543	2533	0.47	3,219
	60	3.36	23,222	3113	14.70	101,613
	61	9.75	67,393	3211	0.10	658
	62	1.01	6,992	3212	16.75	115,806
	65	12.78	88,342			
	69	0.06	388			
	70	0.01	53			
	71	2.25	15,521			
	72	0.20	1,390			
	76	6.55	45,307			
	77	4.62	31,965			
	78	0.87	6,043			
	84	3.76	25,989			
	85	10.81	74,706			
	86	9.60	66,337			
	87	1.33	9,198			
	88	1.10	7,580			
	100	6.07	41,965			
	111	7.60	52,527			
	112	1.15	7,941			
	113	1.42	9,813			
Utah	12	4.89	10,758	M3112	33.02	76,633
	15	2.19	4,821	M3113	0.10	223
	18	0.75	1,660	3131	2.50	5,507
	19	1.53	3,360	P3131	28.11	61,842
	20	3.15	6,933	P3132	0.10	223
	21	0.42	930	3133	4.47	9,823
	23	28.15	61,932	3134	30.35	66,753
	24	0.07	159	A3142	0.98	2,158
	37	5.34	11,740	3221	0.37	819
	38	11.80	25,965			
	39	5.34	11,754			
	40	20.36	44,785			
	41	0.45	996			
	46	5.33	11,728			
	49	0.46	1,023			
	51	0.50	1,089			
	52	0.50	1,089			
	55	4.25	9,350			
	57	2.05	4,516			
	63	0.05	106			
	Water	2.40	5,286			
Washington	1	5.47	9,662	M2111	14.71	25,975
	2	18.26	32,244	M2112	1.12	1,976
	3	6.95	12,268	2410	14.92	26,341
	4	6.58	11,617	M2411	6.42	11,341
	10	0.07	122	M2413	5.55	9,805
	11	4.73	8,346	M2415	25.32	44,706
	12	13.31	23,491	M3111	0.66	1,171
	13	0.55	964	3120	13.84	24,438
	15	4.24	7,477	3131	16.12	28,462
	25	0.20	353	3135	1.62	2,854
	26	0.06	109			
	50	9.41	16,611			
	51	6.53	11,535			
	52	3.61	6,378			
	55	20.04	35,379			
Wyoming	12	11.83	29,970	3111	14.05	35,607
	15	6.63	16,810	3112	11.22	28,441
	16	0.95	2,415	M3112	19.00	48,148
	17	2.00	5,058	3113	5.60	14,183
	18	3.29	8,344	M3113	6.51	16,497
	23	0.22	550	A3141	13.87	35,160
	37	0.57	1,435	A3142	29.75	75,395
	40	3.77	9,565			
	52	1.38	3,488			
	55	29.07	73,678			
	56	10.46	26,509			
	63	0.45	1,140			
	64	17.90	45,358			
	65	4.43	11,215			
	66	6.92	17,534			
	75	0.01	13			
	Water	0.14	349			

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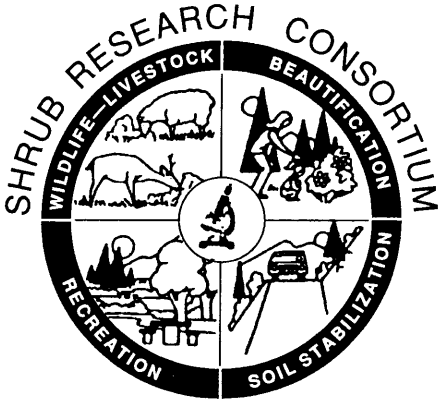

Vegetation Dynamics

Predicting Shifts in Australian Shrublands with Changing Climates and Land Uses

John A. Ludwig
Stephen G. Marsden

Abstract—Future changes in global climate and land use will likely have severe impacts on the arid and semiarid shrublands of Australia, and around the world. Current climate change models are predicting shifts in the patterns of rainfall in the shrubland and woodland regions of eastern Australia. Mean annual temperatures are expected to rise by about 2 °C by 2050. Winter rainfall may decrease, while summer rainfall may increase both in amount and in intensity of local storms. The impact of these changing rainfall patterns may be evident in subtle shifts in the balance between shrubs and grasses at the landscape scale. The mode of action may be through the way limited water and nutrient resources are differentially conserved and utilized within these semiarid landscapes. Our flow-filter landscape model has been used to predict changes in water, nutrient and productivity in a tall shrubland/woodland system using climate change and land degradation scenarios. Simulation results indicate that even if land degradation increases only slightly, that these impacts will be far greater than those expected from changes in climate.

The arid and semiarid regions of Australia cover about 5.5 million sq. km (75% of its land area; fig. 1). Except for the arid sandy desert regions, the semiarid areas are used extensively as rangelands for grazing sheep and cattle (Harrington and others 1984). These rangelands are drought-prone and have a high risk of becoming desertified, that is, being impacted by human activities and drought to become more desert-like (Mabbutt 1978).

Global climate modellers have used the El Niño—Southern Oscillation (ENSO) phenomenon to predict rainfall likelihood in various regions of Australia (Hunt 1994). This ability to easily predict rainfall likelihood has greatly improved through the development of software packages such as "Australian Rainman" (Clewett and others 1994). Pastoralists in semiarid rangelands can incorporate the latest estimates of the Southern Oscillation Index (SOI) into Rainman to obtain the probability of rainfall in the coming season for their region (McKeon 1994). This helps them minimize the risk of making an inappropriate management decision, thus reducing economic risks and impacts on the land (Muchow and Bellamy 1991). For example, if a drought has started and the long-term forecast is for no rain, stock should be sold (or moved) to avoid severe land degradation, which can occur by keeping too many stock on the land during drought.

Because Australian rainfall and its general vegetation respond strongly to ENSO (Nicholls 1988, 1991), it is likely that semiarid shrublands and woodlands will also respond strongly to future climatic changes. It is predicted that over the next thirty years, the semiarid rangelands of eastern Australia could experience higher temperatures, higher summer rainfalls (in fewer but more intense storms) and lower winter rainfalls. The species composition of grasslands and shrublands could significantly change in response to these climatic shifts, for example, C4 grasses may increase in areas currently dominated by C3 grasses and shrubs (Hattersley 1992).

Since its settlement by Europeans, the vegetation of Australia has undergone many impacts and changes (Saunders and others 1990). It is estimated that about 8% of Australia's rangelands (some one-half million sq. km) have undergone severe desertification (Dregne 1983), that is, areas showing signs of severe soil erosion such as gullies and with vegetation in poor range condition. Eroded and degraded semiarid rangelands do not efficiently conserve re-

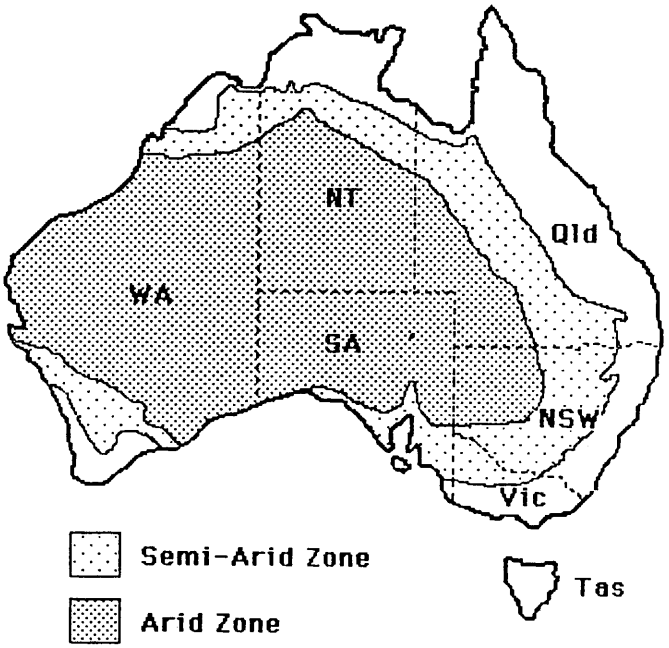

Figure 1—Arid and semiarid climatic zones of Australia. Non-stippled areas are wetter tropical and temperate zones (after Christie 1986).

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sources and have low levels of annual net primary production (NPP) compared to similar but undegraded landscapes (Ludwig and Marsden 1995).

The aim of this modelling study was to simulate the likely impacts of climate change and land degradation on resource conservation, species composition and NPP for the semiarid rangelands of eastern Australia, and to compare the importance of these two scenarios relative to a natural or undegraded tall shrubland/woodland system.

Semiarid Tall Shrublands/ Woodlands

In the semiarid zones of eastern Australia, including parts of Queensland, New South Wales, Victoria and South Australia (fig. 1), much of the upland vegetation is a mosaic characterized by tall shrublands and woodlands dominated by *Acacia* spp. and *Eucalyptus* spp. (Harrington and others 1984). Grasslands and riverine woodlands and forests occur on floodplains and along creeks and rivers. The climate varies from subtropical in Queensland to temperate in the southern States. Upland soils are mainly hard setting massive red earths of low fertility while lowland soils are cracking clays of moderate fertility.

Many of these semiarid landscapes in eastern Australia are patchy, runoff-runon systems (Ludwig and Tongway 1995). For example, a common feature observed is where thickets or patches of mulga (*Acacia aneura*) are interspersed with more open, grassy interpatches (Tongway and Ludwig 1990). This patchiness also occurs as smaller scale features such as log mounds-intermounds, or as grass clumps-interclumps. In a top-view diagram, these patchy semiarid landscapes appear as a number of discrete units dispersed

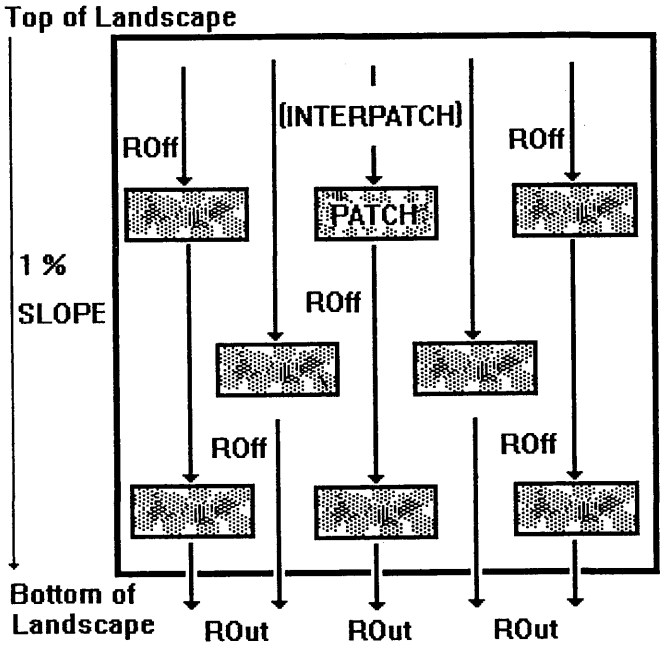

Figure 2—Top-view diagram of a typical semiarid landscape in eastern Australia, with patches separated by open interpatch areas (after Ludwig and others 1994).

across gentle slopes of less than 1% (fig. 2). Runoff will flow down these slopes unless it is captured by a patch. Runout occurs from the landscape unit when runoff is not captured.

Semiarid Landscape Function

Patchiness functions to concentrate and conserve limited water and nutrient resources, hence increase plant production (Ludwig and others 1994). This resource concentration effect is based on the theory that arid and semiarid lands function as source-sink or runoff-runon systems (Noy-Meir 1973). Given limited resources, this theory predicts that NPP will be higher in arid and semiarid environments if water and nutrients are concentrated to form resource-rich, productive patches than if such resources are uniformly dispersed in low concentrations over the entire landscape.

Landscape studies have demonstrated that patchiness is maintained by physical processes such as surface winds and surface water flows which redistribute resources into patches (Ludwig and Tongway 1995; Thiery and others 1995). For example, patches capture runoff water which recharges soil moisture stores, captured runoff sediments rebuild soil nutrient pools and trapped wind-blown litter contributes to soil organic carbon. Patches are maintained by biological and chemical processes, for example, plants growing in the patch utilize water and nutrients from the patch and then through death and decay return organic carbon and nutrients to the patch.

Simulation Models of Landscape Function and Production

To quantify how runoff flows down, and possibly out of a landscape, a "flow-filter" simulation model was developed (Ludwig and others 1994). When the amount of rainfall (R) exceeds the water infiltration rate (IR) or water storage capacity (SC) of the soil then runoff (ROff) occurs within interpatch areas (fig. 3). If not captured by patches, this ROff will runout (ROut) of the system, that is, if the IR and SC of the patch is exceeded then ROut occurs. Following a rainfall event at time (t), the total ROut from a landscape is also a function of the slope (S), area of interpatch (AI) and area of patch (AP):

$$ROut_t = f(R,IR,SC,S,AI,AP)_t$$

Another simulation model, SEESAW, was linked to the flow-filter landscape model to estimate annual net plant production (NPP) for the system. SEESAW was designed to simulate the ecology and economics of semiarid woodlands (Ludwig and others 1992, 1994). At time (t), a submodel within SEESAW computes NPP as a function of plant available moisture (PAM) and available nutrients (AN), and as a function of temperature (TEMP):

$$NPP_t = f(PAM,AN,TEMP)_t$$

Another submodel, called WATDYN, computes PAM by estimating soil water balance dynamics (Walker and Langridge 1996).

Four plant functional groups: ephemerals (forbs and grasses), C3 grasses, C4 grasses, and shrubs, were included in this simulation study. Plant processes modelled included

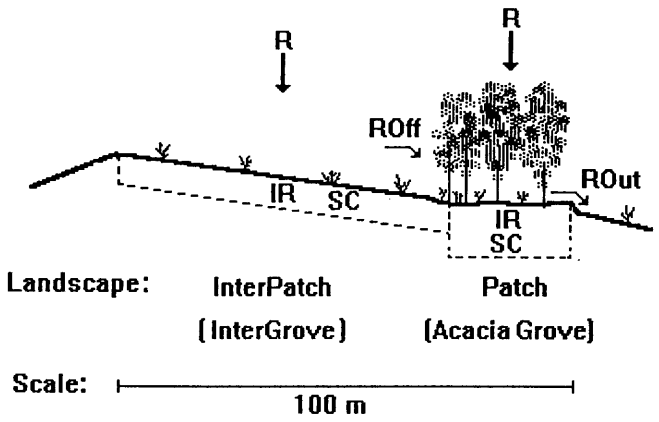

Figure 3—Cross section of a typical semiarid *Acacia* shrubland/woodland landscape in eastern Australia. The flow of resources is depicted following a rainfall event (R) with runoff (ROff) occurring when the amount and intensity of the rainfall exceeds the infiltration rate (IR) or the water storage capacity (SC) of the soil. Resources not captured by the patch runout (ROut) of the landscape system. Soils within patches are deeper, thus have a greater SC, and also have a higher IR (after Ludwig and others 1994).

growth, senescence, death, decay and consumption. Given initial or starting biomass values for leaf, stem and root components, annual NPP was computed using a weekly time-step for both patch and interpatch areas. However, the WATDYN submodel used a daily time-step to compute soil water dynamics by rainfall event within each rainy day.

Temperature and rainfall amount and intensity data used to "drive" the simulations was based on a 31.5 yr record (mid-year 1962 through 1994) collected from a Class A weather station at Cobar, New South Wales. Cobar is located near the centre of the semiarid tall shrublands/woodlands of eastern Australia.

Climate Change and Rangeland Degradation Scenarios

For the simulations three scenarios were simulated: (1) an undegraded or natural semiarid landscape, (2) a similar but degraded landscape, and (3) a natural landscape being impacted by climate change. We used a semiarid landscape system of fixed size, shape and patch structure (fig. 2). The landscape unit was assumed to be a rectangular area of 1 ha (10000 m^2) and having a uniform slope (S) of 1%. Patches were dispersed regularly over the 1 ha area and occupied 30% of the area. Undegraded semiarid woodland landscapes in eastern Australia typically have *Acacia* thickets occupying about 30% of the surface area (Tongway and Ludwig 1990).

Each of the three scenarios included parameter values reflecting differences in rainfall and soil infiltration rates (IR), and in soil depth which is related to soil water storage capacity (SC) (table 1). Actual field measurements taken in the semiarid woodlands of eastern Australia were used to estimate the parameter values for natural and degraded

Table 1—Inputs and parameter values used to simulate three scenarios for semiarid landscapes in eastern Australia.

Environmental inputs and landscape values	Scenario: Natural system	Scenario: Degraded system	Scenario: Climate change
Precipitation at Cobar, NSW	Actual for 1962-94	Actual for 1962-94	+10% S* −10% W
IR (mm/hr)			
Patch	60	30	60
Interpatch	10	5	10
Soil Depth (cm)			
Patch	100	75	100
Interpatch	45	30	45

* S = summer (Dec-Feb); W = winter (Jun-Aug)

landscape systems (Greene 1992). The climate change scenario assumed a 10% rise in mean summer rainfall (fewer events and more intense) and a 10% drop in mean winter rainfall, and included a two degree centigrade rise in mean annual temperature.

Results

Over the 31.5 year simulation run the natural semiarid landscape had a NPP of about 330 kg/ha/yr (fig. 4). The degraded landscape NPP only averaged about 160 kg/ha/yr, probably because it lost more rainfall as ROut (about 135 mm/yr) compared to the other scenarios (about 75 mm/yr; fig. 5). The impact of climate change was to increase NPP to about 425 kg/ha/yr relative to the 330 kg/ha/yr for the natural system.

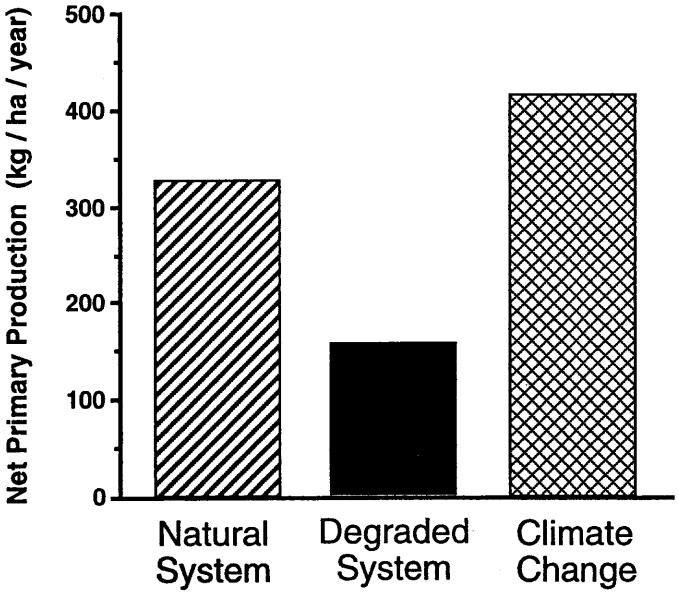

Figure 4—Average yearly net plant production (NPP) over a 31.5 year period (mid-1962-1994) for a semiarid landscape for three scenarios: natural, degraded and climate change.

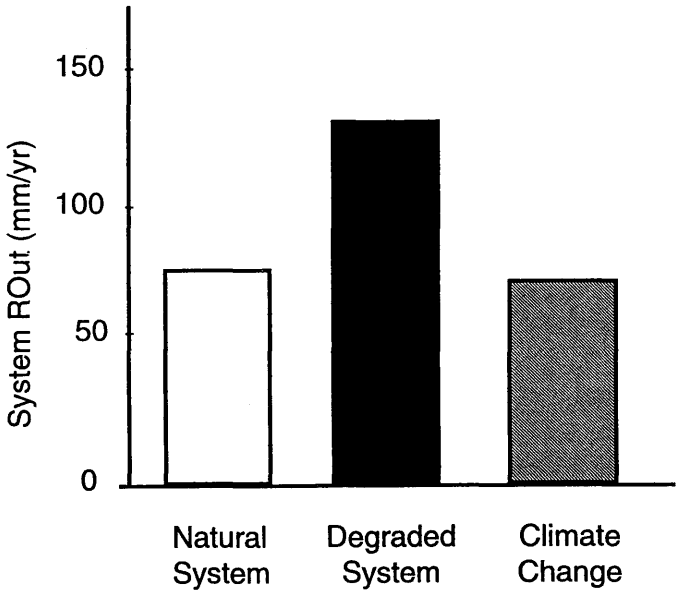

Figure 5—Mean annual loss of runoff after rains from a semiarid landscape (ROut) for three scenarios: natural, degraded and climate change

A natural semiarid landscape in eastern Australia subjected to the impacts of climate change is likely to experience a significant shift towards a dominance of C4 grasses (fig. 6) along with increased annual NPP. However, under climate change other plant functional groups changed little compared to the natural system. All plant functional groups declined under the land degradation scenario, particularly C4 grasses and ephemerals. Shrubs only declined slightly under the degradation scenario compared to the natural system and climate change scenarios.

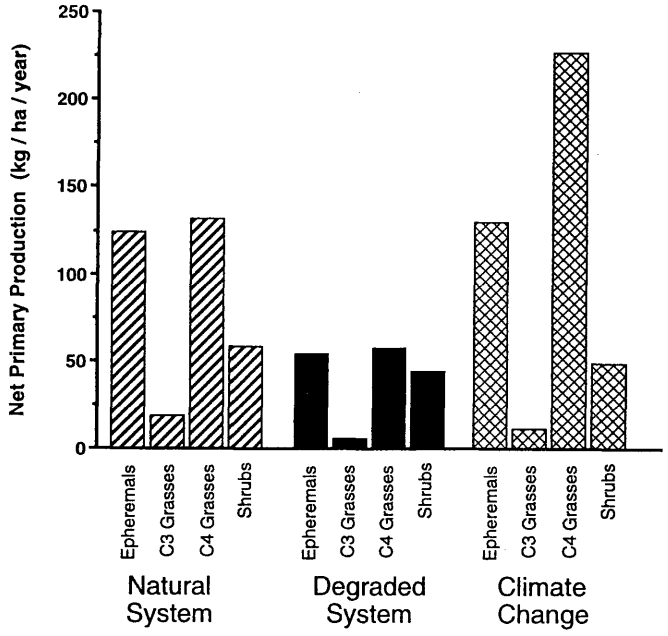

Figure 6—Yearly net primary production (NPP) for four plant guilds averaged over a 31.5 year period (mid-1962-1994) for a semiarid landscape system and three scenarios: natural, degraded and climate change.

Discussion

The likely impacts of land degradation are far greater than those impacts expected from climate change based on the modelling results of this study for semiarid regions of eastern Australia. Land degradation can lead to the loss of water and nutrients from a landscape. Since resources are already very limited in these landscapes, the result can be significant declines in plant production, particularly for grasses and forbs although perhaps less so for shrubs and trees. A loss of small-scale patchiness due to land degradation can lead to a decline in the capacity of the landscape system to capture resources (Tongway and Ludwig 1994).

This simulation study predicted a significant increase in C4 grasses under the impacts of a climate change scenario. This increase might be expected since C4 pathway plants have a higher rate of photosynthesis for a given CO_2 level compared to plants with the C3 pathway under warmer temperatures and higher light intensities (Solbrig and Orians 1977). Thus, a scenario of greater summer rainfall with warmer temperatures will tend to favor C4 grasses relative to C3 grasses (Hattersley 1992).

Patchiness appears to be a common natural phenomenon in arid and semiarid landscapes around the world. It has been documented by field studies in the semiarid tall shrublands/woodlands of eastern Australia (Ludwig and Tongway 1995; Tongway and Ludwig 1990), in the savannas of the Serengeti, East Africa (Belsky 1989), in the 'tiger bush' of West Africa (Thiery and others 1995), in semiarid grasslands of Chihuahua, Mexico (Montaña 1992) and in the shrublands of Western Australia (Tongway and Ludwig 1993).

Many degraded rangeland areas can be rehabilitated by restoring landscape patchiness and processes through appropriate rehabilitation treatments and land management practices. One treatment known to effectively restoration landscape processes is by constructing surface obstructions to water flow (Tongway and Ludwig 1993). Tree and shrub branches can be piled in clusters along contours to create patches. These obstructions function to capture limited water and nutrients flowing as runoff and blowing as dust and litter about the landscape. These processes rebuild patches natural to the system. These patches also provide valuable habitats for plants and animals.

Further simulation studies are needed to substantiate the findings of this study for other rangeland regions that have different levels of degradation, and which have different climate change scenarios. Where available, long-term rainfall amount and intensity and temperature data will be used.

Acknowledgments

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Elevational Relationships of Introduced Woody Species on the Islands of Lanai and Hawaii

Jack D. Brotherson

Abstract—The extreme isolation of the Hawaiian island chain has produced a highly unusual native island flora. Scientists estimate the native flora to consist of about 1,000 species of flowering plants, 89 percent of which are endemic. The native plant communities have been heavily impacted by the introduction of alien animal and plant species thought to be in excess of 5,000 taxa. Especially impacted have been the land areas below 1,500 ft elevation where the native plant communities have been almost totally decimated. These introductions are partitioning the available niches in ways uncharacteristic to their native habitat. An assessment of the patterns of colonization and distribution of several introduced woody species onto the islands of Lanai and Hawaii shows the invading species to have adapted to moisture regimes and distributed themselves in almost perfect bell-shaped curves along the entire elevational gradient. The areas of colonization stretch across the lower slopes of three shield volcanos from sea level to 3,000 ft (914 m) elevation.

The Hawaiian archipelago is one of the most isolated island chains in the world. It is 2,390 miles (3,854 km) from California, 2,300 miles (3,710 km) from Alaska, 2,400 miles (3,871 km) from the Marquesas Islands, and 3,850 miles (6,210 km) from Japan. The island system comprises a chain of about 132 islands, reefs and shoals of volcanic origin in the mid-Pacific ocean (Armstrong 1993). The islands are thought to have formed successively over a fixed "hot spot" beneath the northwestward moving Pacific tectonic plate (Carson and Clague 1995). Because of the extreme isolation of the islands, they support one of the most unusual and remarkable oceanic island biota's in the world (Carlquist 1980; Carlquist 1995). For example, Wagner and Funk (1995) state that endemism in this biological array ranges from 50 percent for the mosses, 89 percent for angiosperms, and 99 percent for insects. The colonization of these islands by plant species is hypothesized to have occurred in a variety of ways (Carlquist 1980) and from multiple sources (Funk and Wagner 1995). It is thought that the approximately 1,000 angiosperm species originated from about 235 original introductions, these coming in at the rate of about one per 100,000 years (Carlquist 1980). Much of the angiosperm flora evolved in place, making the Hawaiian archipelago an unparalleled example of insular evolution (Wagner and Funk 1995).

The islands of the Hawaiian archipelago, like most islands in the Pacific, have experienced major perturbations of their biota, resulting in loss of species and ecosystem stability. The conversion of the natural ecosystems in Hawaii, often into actively manipulated cultural landscapes, began with Hawaii's colonization by the Polynesians about 400 A.D. (Kirch 1982; Cuddihy and Stone 1990). Captain James Cook came to the islands in 1778. In the 200 years following that first European visit to Hawaii, human intruders have inundated the islands' fragile ecosystems with some 5,000 introduced plant species, and 3,000 insect and animal species. In time, these aliens have displaced hundreds of native species.

For example, Dolan (1990) states that, "much of native Hawaii—its lush rain forests and noisy, colorful birds that inhabit them—is gone forever, and its remnants are hurling toward some oblivion in the worst extinction crisis in the nation." The change in plant communities has been caused by several major factors: (1) the introduction of large herbivorous ungulates; (2) the introduction of exotic plants; (3) the burning of the vegetation in the lowland areas of the islands and the concurrent expansion of agriculture; and (4) commercial logging of lowland forests for firewood, sandalwood (*Santalum* sp.), and Koa (*Acacia koa*) (Tomich 1969; Kirch 1982; Cuddihy and Stone 1990).

The alteration of the native vegetation in the Hawaiian Islands has progressed upslope from sea level since settlement by the Polynesians, but has been much accelerated since the coming of the Europeans in 1778. Estimates are that 10 percent of the native Hawaiian flora has gone extinct with another 40-50 percent being threatened with extinction (Cuddihy and Stone 1990). Particularly impacted are the dry and mesic ecosystems below 3,000 ft (914 m) where invasion by alien grasses have resulted in an increase in the frequency, size, and intensity of fire (Muller-Dombois and others 1981).

Because of the enormous human impact on the native Hawaiian ecosystems and their corresponding floristic elements, it becomes evident and important to establish baseline data. Stone and Stone (1989) suggest that available time and resources be focused on field studies and analyses on native Hawaiian plants and their associated ecosystems, to provide data on the biology, evolution and ecosystem relationships of important native taxa. Such data will contribute to developing conservation and management strategies of these highly impacted Hawaiian ecosystems. Management of native areas in Hawaii is possible, although expensive, and an added benefit of basic field studies is that knowledge gained will

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contribute to our ability to manage highly invaded island ecosystems, and will ultimately prove useful for conservation of both island and continental systems (Loope and others 1988). Also, those ecosystems that have been damaged or degraded by alien introductions and past land use may have the "capacity for significant recovery" if the agents of disturbance are understood and controlled (Jokobi and Scott 1985).

To establish baseline data on conditions existent in the vegetative communities between sea level and upland areas (3,000 ft/914 m elevation), the colonization and distribution patterns of several introduced woody species were studied. The purpose was to determine alien tree and shrub species distribution and to correlate those patterns with elevation and precipitation patterns.

Methods

Three transects (65 study sites) were placed below 4,200 ft (1,280 m) on the lower slopes of three volcanos (Lanai, Mauna Kea, Mauna Loa) on the islands of Lanai and Hawaii. Two were located on Hawaii and one on Lanai. Those on Hawaii were located at South Point, the southern most point of the island, and along the saddle road about 20 miles (32 km) north of the town of Kailua-Kona. The Lanai transect was located on the slopes of the old shield volcano about 5 miles (8 km) northwest of Lanai City. Transect placement was in the more arid areas on the volcanos leeward sides where the climate tends to be sunny and dry. Transects and study sites were positioned on the shield volcano's lower slopes where little or no erosion has taken place and where the precipitation gradient mimics the elevation gradient, increasing gradually as elevation increases. Transects began at sea level and extended upslope. Study site number and placement varied depending on transect length and steepness of the elevation and on associated precipitation gradients.

The South Point transect contained 20 study sites placed at 100 foot (30.5 m) elevational increments, was 11 miles (18 km) long, and ranged from 0 to 1,900 ft (0 to 579 m) in elevation. The Saddle Road transect contained 22 study sites placed at 200 foot (61 m) elevational increments, was 22 miles (35 km) long, and ranged from 0 to 4,200 ft (0 to 1,280 m) elevation. The Lanai transect contained 20 study sites placed at 100 foot (30.5 m) elevation increments, was 7 miles (11 km) long, and ranged from 0 to 1,900 ft (0 to 579 m) in elevation. The steepness of the elevational gradient along each transect varied. Precipitation patterns also varied ranging from 10 to 50 inches (256 to 1,282 mm) along the elevational gradient at South Point, and from 10 to 40 inches (256 to 1,026 mm) on the Saddle Road and Lanai transects.

Data collection was accomplished using two 100 yard (91 m) transects at each study site, one placed perpendicular to the elevation gradient and one placed parallel to the elevation gradient. These two transects intersected at a cross at their 50 yard (46 m) midpoints. Each site was subsampled with 20, one m^2 quadrats placed every 10 yards (9 m) along the transects. Canopy coverage by species was estimated according to Daubenmire (1959). Abundance of each species was ocularly estimated at each study site along a 440 yard (400 m) walking transect, set parallel to the slope and centered on the study site, using abundance classes as follows: 1 = rare; cover small, less than 1 percent; 2 = scarce; cover small, less than 5 percent; 3 = infrequent; cover between 5-25 percent; 4 = frequent; cover between 25-50 percent; 5 = prevalent; cover between 50-75 percent; 6 = abundant; cover between 75-100 percent. Average cover was computed for each species encountered by site and then compared with the abundance estimates of the same site as a check of that species importance at that site. Elevation was determined at each site using a Thommen TX mechanical/barometer altimeter. Precipitation was estimated for each site from island maps with isohyetal estimation lines.

Results

Fourteen species of woody plants with origins from 11 different geographical areas of the world (table 1) were encountered on the study sites located along the three transects. All have origins in tropical or sub-tropical climates and with one exception, were introduced to Hawaii before 1900. Areas colonized by these species have been altered to such an extent that only one indigenous taxon and no native endemic taxa were encountered at the 65 study sites. Numbers of species encountered at each study site varied from 2 to 9, averaging 5.7 per site.

All species were not present on each of the three transects (figs. 1-3), but when a single species occurred on more than one transect, its relative importance varied from transect to transect. For example, *Opuntia ficus-indica* was found only on the Saddle Road, and *Psidium guajava* and *Schinus terebenthifolia* showed greater importance on Hawaii than on Lanai. Conversely, *Leucaena leucophala* showed greater importance on Lanai. The individual species showed changing patterns of importance with respect to the elevational gradient. For example, *Schinus terebenthifolia* was important at the higher elevations, *Leucaena leucophala* and *Lantana camara* were important at mid-elevations, and *Prosopis pallida* and *Waltheria indica* were important at or near sea level. The individual plant species placement along the elevational gradient in relationship to other species was highly predictable. For example, *Prosopis pallida* was always found along the sea coast and below *Lantana camara* along the gradient which was always below *Schinus terebenthifolia*. These patterns would suggest colonization, and subsequent success by invading species are random with respect to location, but controlled by evolutionary history as to the species interaction with the environment.

Species distribution patterns show that while some are narrowly restricted in distribution to a single elevational level (figs. 1-3), the majority peak in importance at specific points along the gradient and then decline as elevation either increases or decreases. Where the elevational gradient and the corresponding moisture gradient change gradually, as they do on all three of the transects, the species sort along the gradient where they form nearly perfect "bell-shaped" curves relative to their patterns of distribution. The elevational distribution of the individual plant species growing along the three gradients was generally similar in position with respect to all other species. However, an individual species relative position with respect to elevation varied some from transect to transect. For example, *Indigofera*

Table 1—Woody species encountered along the three transects on the lower slopes of the shield volcanos—Lanai, Mouna Kea, and Mouna Loa. Species' common names (in parentheses—Hawaiian names underlined), origins, and dates of introduction (where known) are included. All species are alien introductions having naturalized in Hawaii, except *Sida falax* which is indigenous.

Species	Origin	Introduction date[1]
Agave sisalana (AGSI) (Sisal, Sisal hemp, Malina)	Yucatan, Mexico	1893
Casuarina equisetifolia (CAEQ) (Common ironwood, Paina)	Australia	1882
Chamaecrista nictitans (CHNI) (Partridge tea, Lauki)	Neotropics	1871
Indigofera suffruticosa (INSU) (Indigo bush, Iniko, Inikoa, Kolu)	Java	1836
Lantana camara (LACA) (Lanatana, Lakana, La'au kalakala, Lanakana, Mikinolia hihiu)	West Indies	1858
Leucaena leucocephala (LELE) (Koa haole, ekoa, Lilikoa)	Neotropics	1837
Opuntia ficus-indica (OPFI) (Prickly pear, Panini, Papipi)	Mexico	Before 1809
Prosopis pallida (PRPA) (Algaroba, Mesquite, Kiawe)	Peru, Colombia, Equador	1828
Psidium guajava (PSGU) (Common guava, Kuawa, Kuawa ke'oke'o, Kuawa lemi, Puawa)	Neotropics	Early 1800's
Schinus terebenthifolia (SCTE) (Christmas berry, Wilelaiki, Naniohilo)	Brazil	Before 1911
Sida falax (SIFA) (Ilima)	Pacific islands to China	?
Solanum linnaeanum (SOLI) (Apple of Sodom, Popolo kikania)	Africa	1895
Verbesina encelioides(VEEN) (Golden crown-beard)	Mexico	Before 1871
Waltheria indica (WAIN) (Uhaloa, 'Ala'ala pu loa, Hala'uhaloa, Hi'aloa, Kanakaloa)	Pantropical	Before 1779

[1]Mostly from Wagner and others 1990.

suffruticosa peaked in importance at 400 ft (121 m) elevation on the Saddle Road transect and at 900 ft (274 m) on the South Point transect. Similarly, *Lantana camara* peaked in importance at around 750 ft (229 m) on South Point but was most important at 1,500 ft (457 m) on Lanai.

When data from the three transects were combined (fig. 4), the ecological relationships of the different species with respect to each other and to elevation became much more difficult to delineate. As shown in figure 4, the species distribution curves that were developed from the combined data intersect the elevation gradient across a much broader segment of the gradient. For example, *Sida falax* intersects the elevation gradient from 200 to 700 ft (61 to 213 m) on South Point gradient, while on the basis of the combined data the species intersects the elevational gradient from 100 to 3,100 ft (33 to 945 m), a 6 times greater range of distribution elevationally. When all species are considered in this analysis, the mean intersect of a species on the combined transect gradient is significantly greater ($p < 0.01$), on average of 2.4 times greater, than the mean species range of intersect on the individual transects.

Discussion and Conclusions

The terrestrial flora of the Hawaiian Islands along with aspects of its ecology and conservation has been well studied (Carlquist 1970, 1974, 1980; Kay 1972; St. John 1973; Wallace 1973; Williamson 1981; Muller-Dumbois and others 1981; Stone and Stone 1989; Stone and Scott 1985; Whiteaker 1983; Cuddihy and Stone 1990; Wagner and others 1990; Stone and others 1992; Wagner and Funk 1995). The island flora, as has been stated previously, is highly endemic, and several ideas have been proposed concerning its origin. Historically (pre-colonization by man), the majority of the species appear to have had their origins in southeast Asia. The Carolina and Marshall Islands of Micronesia appear to have acted as bridges for the migration of plants from Asia to Hawaii. Only about 20 percent of the native vascular plants appear related to plant groups of North and South America (Carlquist 1970, 1980). The Hawaiian flora is most endemic in the more advanced elements (i.e. 89 percent of the angiosperm species are endemic) and less so in the ferns (65 percent), liverworts (75 percent), mosses (65 percent), and lichens (38 percent).

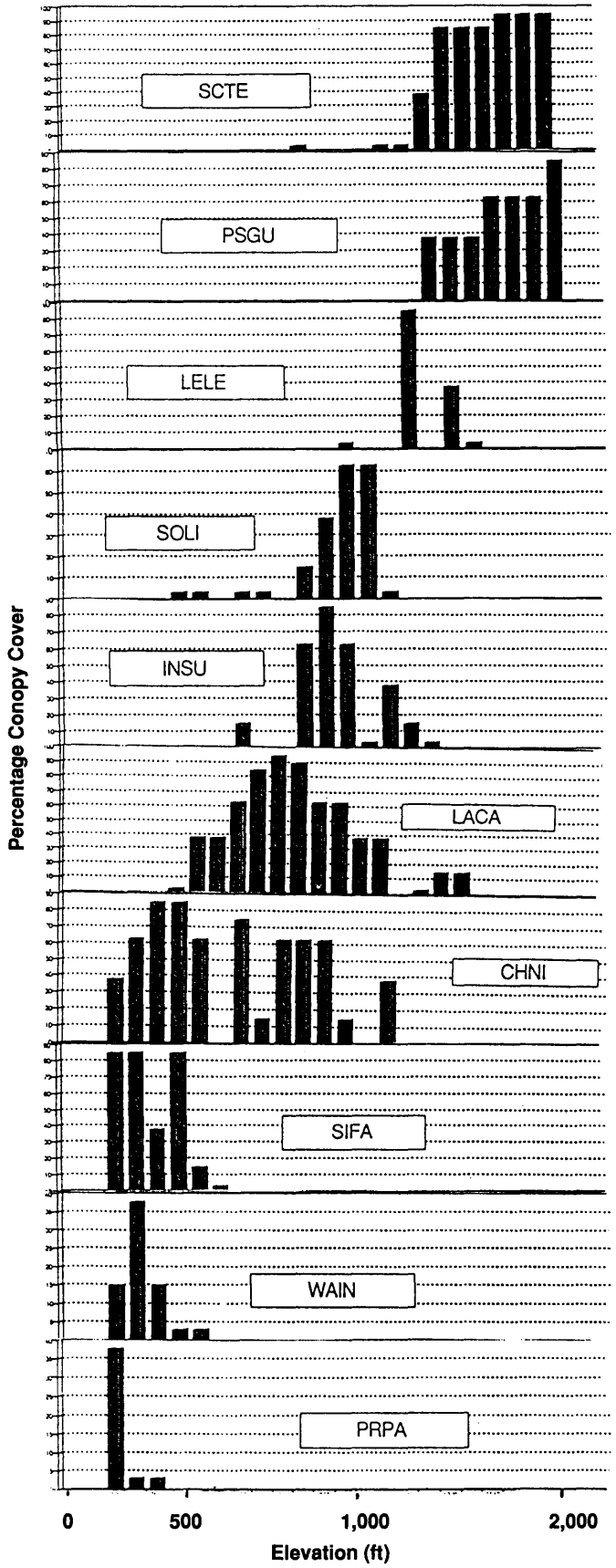

Figure 1—The distribution of woody species along the elevation/moisture gradient along the South Point transect on the island of Hawaii. See table 1 for species symbols.

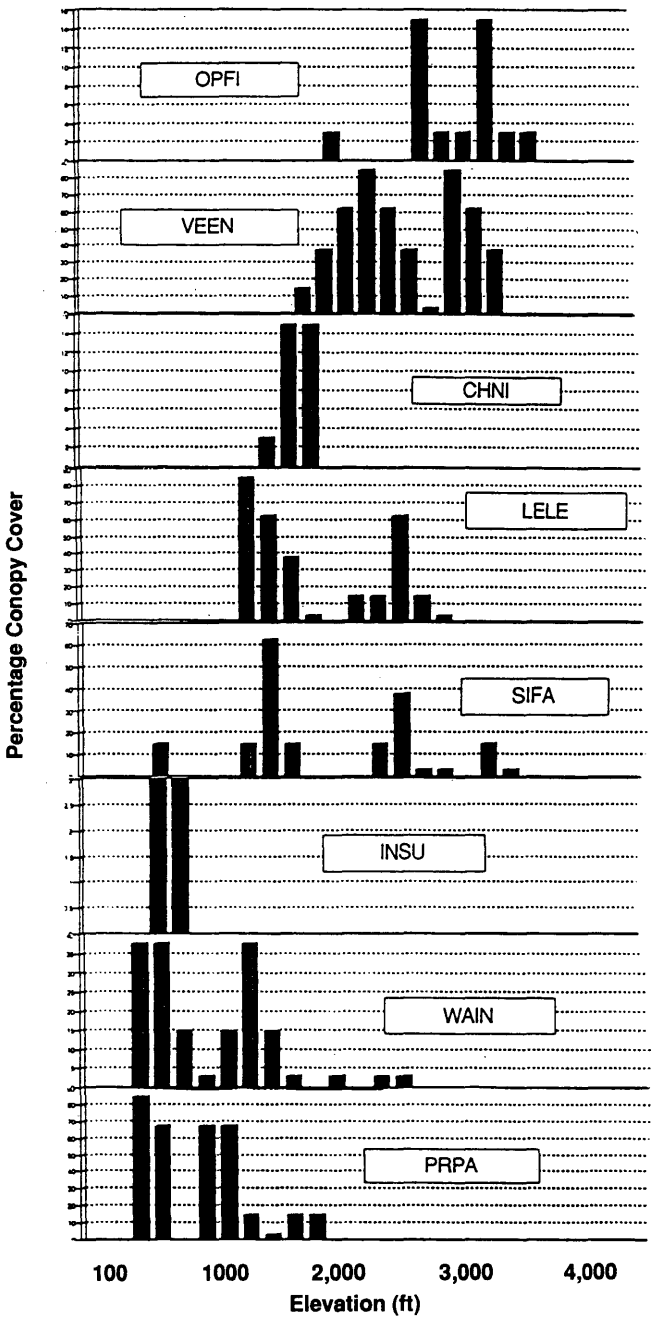

Figure 2—The distribution of woody species along the elevation/moisture gradient along the Saddle Road transect on the island of Hawaii. See table 1 for species symbols.

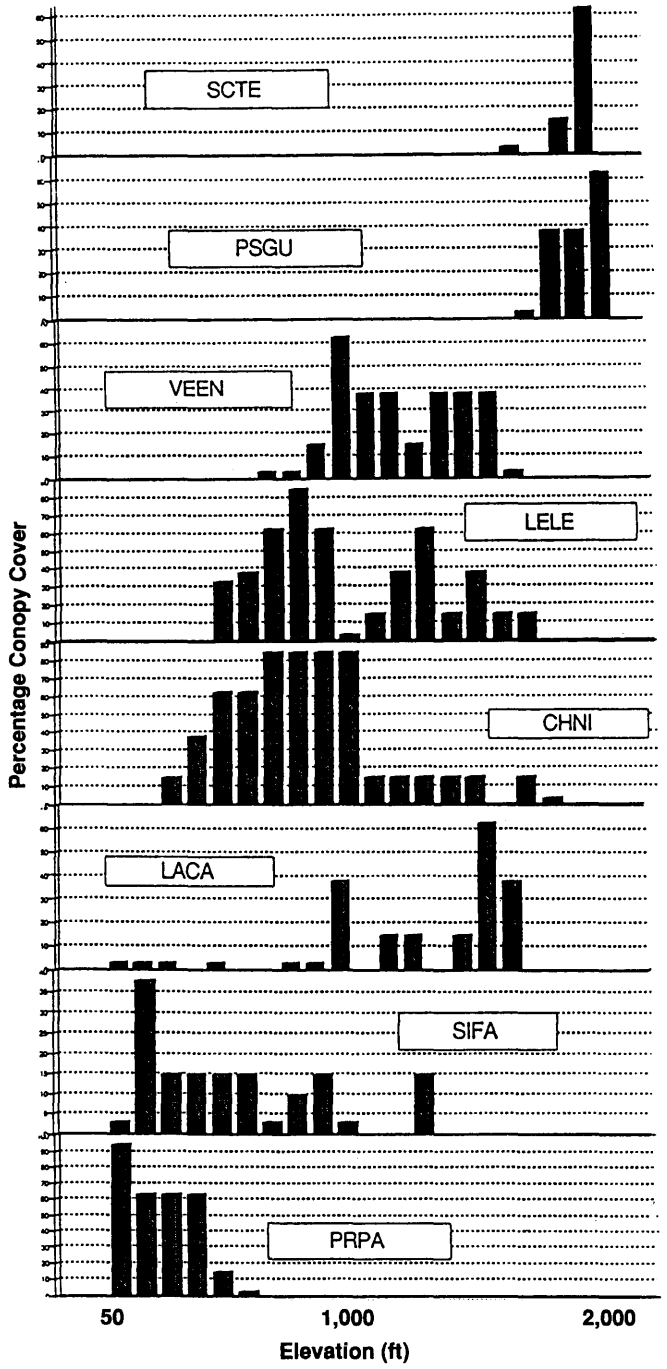

Figure 3—The distribution of woody species along the elevation/moisture gradient along the Lanai transect on the island of Lanai. See table 1 for species symbols.

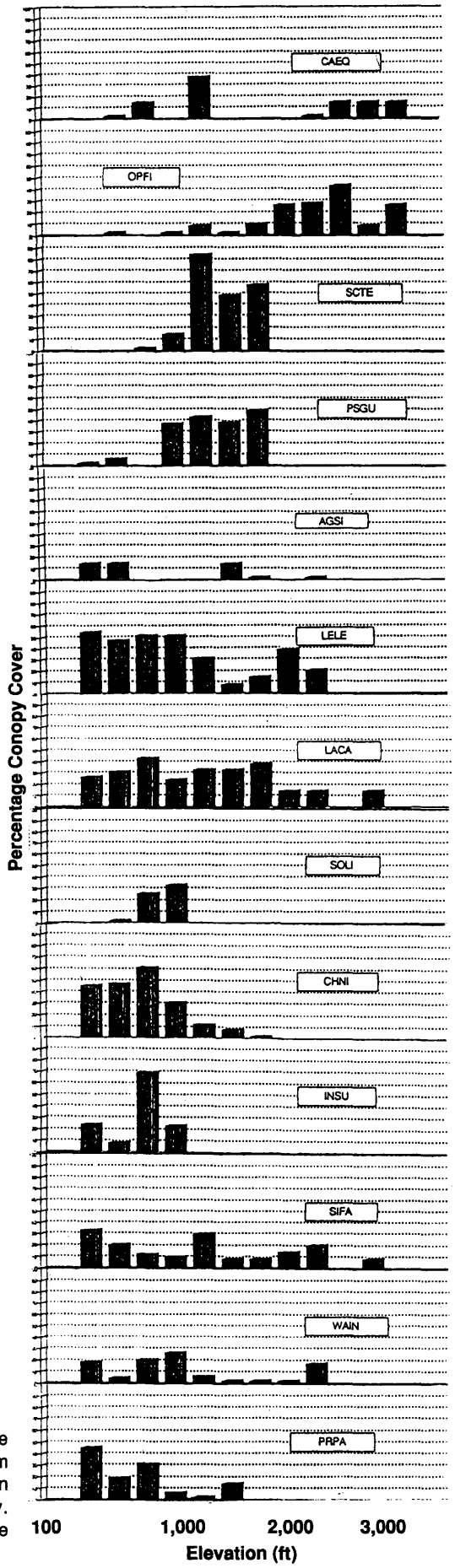

Figure 4—The distribution of woody species along the elevation/moisture gradient. Data were combined from the South Point, Saddle Road and Lanai transects on the islands of Hawaii and Lanai, respectively. *Verbensina encelioides* omitted from this figure. See table 1 for species symbols.

The first alien species (about 25 plant species plus the pig, dog, jungle fowl, and rat) were introduced to the islands with the coming of Polynesian immigrants roughly 400 A.D. (Armstrong 1973). A second immigration of people into the islands together with the plants they brought occurred around 1200 A.D. (Kirch 1982). The islands were discovered by Europeans in 1778, and since that time the introduction of alien plant species into the island system has occurred at an extremely elevated pace, making today's flora a changing mixture of exotic and endemic species (Diong 1982; Wagner and others 1990). Strong attempts are presently being made to control and eliminate the further introduction of alien plant species, which are still freely being introduced to the islands (Stone and Stone 1989).

The most important climatic factors governing plant distribution in Hawaii seem to be average annual rainfall at elevations below about 5,000 ft (1,524 m), and temperature and rainfall at higher elevations (Armstrong 1973). At present, vegetation types are characterized and identified by reference to their dominant species. When examining vegetation maps of the Hawaiian Islands, it becomes apparent that the dominant or characteristic plant species in all vegetation zones at lower elevations are species introduced to Hawaii since 1778.

Studies done on the relationships of plant communities to environmental gradients on the volcanos (Mouna Kea and Mouna Loa) of the island of Hawaii placed the existent vegetation into broad categories of zonation and emphasized its correlation with moisture and temperature gradients only in broad subunits (Muller-Dombois and others 1981). Less emphasis has been placed on the relationship of individual species (especially introduced aliens) to these same gradients. A single paper does exist which describes the ecological distribution of C_3 and C_4 grass species in relation to the altitudinal gradient on Mouna Loa volcano (Rundel 1980). Anderson and others (1992) discuss the distribution and spread of alien plants as a group and their relationships to elevation in the Kipahulu valley in Haleakala National Park on Maui. The distribution and successful colonization of alien plants, to island areas where they have invaded, is closely related to the species adaptive potential, the climatic factors and physical characteristics of the landscape as well as to man's disturbance.

The characteristics of abiotic gradients and associated vegetation in the Hawaiian Islands vary from sharp, unpredictable, highly dissected landforms (changing rapidly and unpredictably across short distances) to smooth, predictable, non-dissected landforms (changing slowly and predictably across long distances). For example, gradients found on highly eroded islands (Kauai) are highly disjunct and therefore so is the distribution patterns of associated plants. Where smooth gradients have been disrupted by erosion of the landscape, creating a wide variety of available habitats, introduced species will invade and colonize available niches. Under such conditions, species distribution becomes patchy, making it difficult to perceive the habitat relationships between the many alien species that have been freely introduced into the islands (Stone and Stone 1989). Conversely, where gradients are smooth and predictable, invading alien species distribution becomes continuous, with no sharp boundary lines between species.

The coming of Polynesian and European settlers heavily impacted native plant communities on all islands below 3,000 ft (914 m) elevation. These impacts paved the way for species introduced into the islands to succeed and in many cases to become serious pests (Stone and others 1992). The aftermath of man's disturbance of natural ecosystems leads to decreases in the diversity (species richness) of that system (Carlquist 1980). Numbers of alien taxa encountered in this study were low, ranging from 2 to 9 and averaging 5.7 species per site. These figures differ from work done by Anderson and others (1992) in the Kipahulu valley in Haleakala National Park on the island of Maui who found that numbers of alien species per site averaged 16.4 and varied from 10 to 25 for similar elevations. The communities they studied showed both a decrease in numbers of alien species per site as well as a decrease in vegetative cover provided by alien introduced species as elevation increased. In contrast, this study showed no pattern in either number of species per site or vegetative cover provided by alien species with respect to changing elevation.

Species introduced from widely divergent areas of the world into the same environment, such as along the transect at South Point on the island of Hawaii, come to the islands preadapted to distinct elevation and/or climatic regimes since they would have a genetic fitness for the environment of their origin. Under such conditions they would be expected to partition the environment along encountered gradients and into unique geographical niches in their new habitat. This creates a variation in dominant species extending across the island landscape that would match the variation of the island environment itself. Further, where the introduced species encounter environments similar in character to the ones they emigrated from, they should be able to establish viable populations where their greatest success would be at the optimal conditions of their range. Also, selection would impose severe limitation of the populations at the periphery of their genetic tolerance, thus restricting further expansion of range. However, if an introduced species carries with it unexpressed genetic capacity, and if the unexpressed genetic capacity were to be adaptive in the new habitat, species could become a severe weedy problem.

On Hawaii and Lanai the elevation and moisture gradients change gradually because of the lack of major erosion effects on the shield volcanos. This gradual change in the two gradients gives opportunity for species introduced to these environments to spread and sort to positions along the gradients where they are best adapted. Thus, the 14 woody species encountered in this study exhibited distribution patterns along gradients (figs. 1-3) and formed almost perfect bell-shaped curves. Studying plant species relationships with respect to these smooth gradients allows for quick insight into the ecological relationships between the species as well as the environments they occupy.

Plotting the distribution patterns of individual species with respect to a single transect (figs. 1-3), in contrast to combining data from several transects (fig. 4), yields more precise information as to differences in the ecology of several species growing together along the elevational and/or moisture gradient. Where data from several transects were combined, differences in the elevational/moisture requirements of the various species become much more difficult to

delineate. Although, combining data from several transects does yield greater information about a single species distribution and ecology in the islands because of an increased sample size, combining tends to obscure understanding of interrelationships between multiple species because the effects of microhabitat factors are masked when data are lumped. For example, *Sida falax* peaked in importance at about 450 ft (137 m) on the South Point transect and showed a rather narrow range of distribution along that transect, intersecting only 21.3 percent of the transects length. However, when the South Point, Saddle Road, and Lanai transect data were combined, it became much more difficult to determine where along the elevation transect this species peaks. Also, difficult to determine was how broad a tolerance range *Sida* had relative to elevation since *Sida* in the combined data intersected 80 percent of the measured gradient. It is not unlikely that *Sida* grows across a wide elevational gradient, but it is not readily apparent that its distribution encompasses 80 percent of the precipitation gradient as well.

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Time Series Analysis of Data for Raingauge Networks in the Southwest

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L. J. Lane
R. Gibbons

Abstract—The ability to evaluate shrubland ecosystem dynamics in a changing environment requires a historical perspective and quantitative analysis of one of the primary ecosystem inputs, precipitation. Historical time series of precipitation data collected from 25 raingauges on the USDA Jornada Experimental Range since as early as 1915 are examined. Time series analyses are conducted to test for trends, autocorrelation, and periodicities in the data and establish an association between mean annual precipitation and time. These results are compared with precipitation data from the Walnut Gulch Experimental Watershed and records from 25 raingauges on the Santa Rita Experimental Range in Southeastern Arizona. Because segments of the historic record can reveal increasing annual precipitation, decreasing annual precipitation, or no trend in annual precipitation, caution must be exercised in attempting to assign either natural variations in weather and climate or rangeland use and management practices as the cause of changes in vegetation over time.

Research conducted on experimental ranges and watersheds such as the Jornada Experimental Range near Las Cruces, New Mexico, the Santa Rita Experimental Range near Tucson, Arizona, and more recently the Walnut Gulch Experimental Watershed near Tombstone, Arizona to address management of arid and semiarid rangelands in the southwestern US has resulted in extensive multidisciplinary databases. During the past century changes in vegetation have been documented at all three sites. These changes may be a response of desert vegetation communities to gradual changes in climate and seasonal precipitation patterns, or changes associated with land use and management. The ability to evaluate shrubland ecosystem dynamics in a changing environment requires a historical perspective and quantitative analysis of one of the primary ecosystem inputs, precipitation.

The purpose of this paper is to describe temporal changes in precipitation measured over raingauge networks at rangelands sites in the Chihuahuan Desert and the Sonoran Desert, and at a site located in the transition zone between the two deserts.

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Site Descriptions

Figure 1 shows the locations of three experimental areas discussed in this paper.

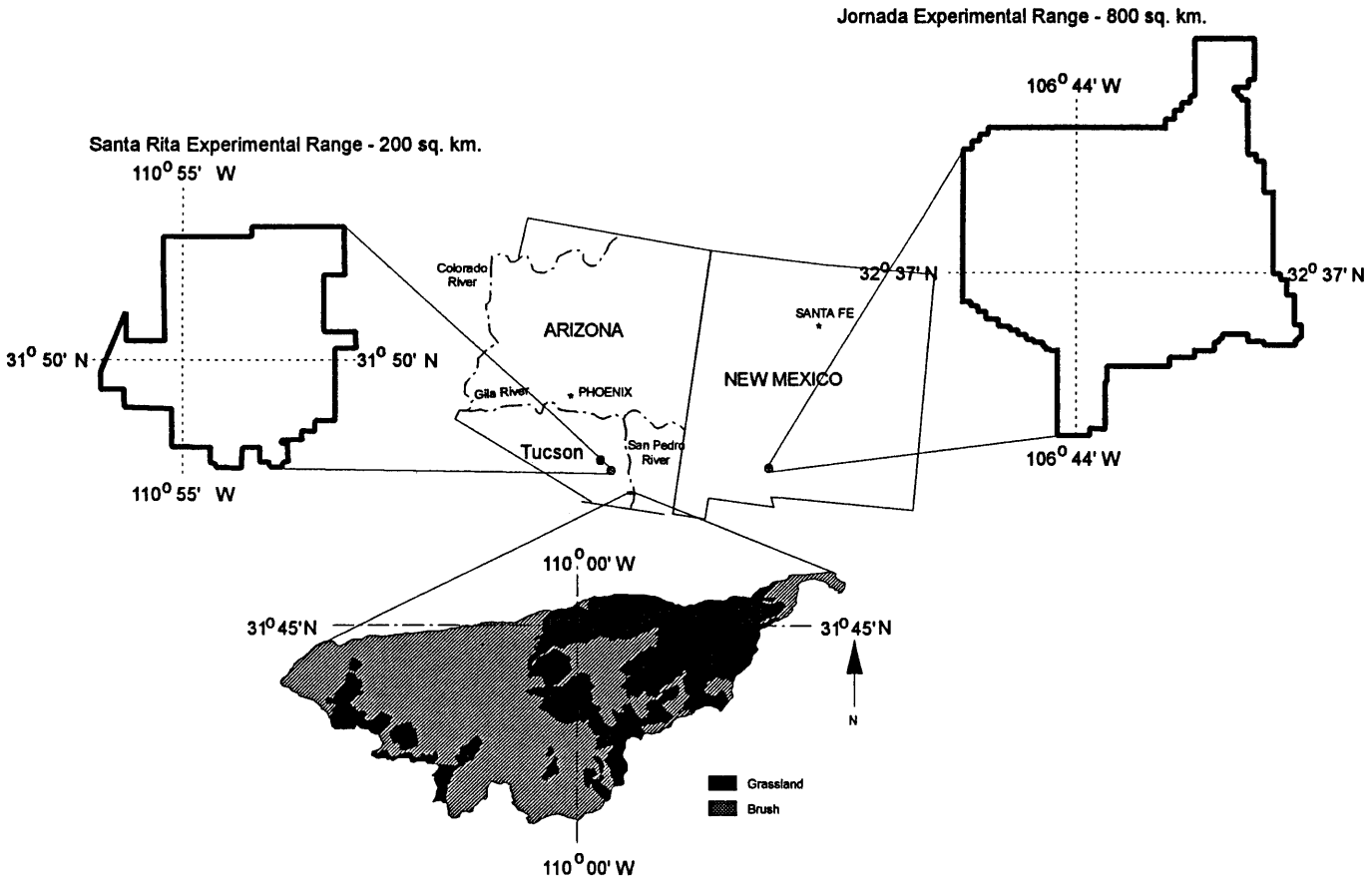
Walnut Gulch Experimental Watershed, Tombstone, Arizona

An extensive hydrologic database has been developed on the 150 sq km Walnut Gulch Experimental Watershed in Southeastern Arizona. The watershed is located in the transition zone between the Sonoran and Chihuahuan Deserts and is representative of approximately 60 million hectares of brush and grass covered rangeland found throughout the semiarid southwest (Renard and others 1993). Although initially instrumented to address water supply issues, the watershed has been the site of multidisciplinary research and database development since the late 1950's. Precipitation, runoff, sediment, topographic, channel networks, vegetation, soils, and landuse data have been collected. A recording raingauge network was initiated in 1954 to quantify and characterize precipitation on the Walnut Gulch Watershed. Continuous precipitation data currently are recorded by 85, 24 hour time scale, raingauges.

Vegetation on the watershed has changed from a grassland to a watershed that is dominated by shrubs on the lower $\frac{2}{3}$ of the watershed during the past century (Hastings and Turner 1965). Shrub canopy ranges from 30-40% and grass canopy cover ranges from 10-80%. Shrub species include creosote bush (*Larrea tridentata*), whitethorn (*Acacia constricta*), tarbush (*Flourensia cernua*), snakeweed (*Xanthocephalum sarothrae*), and burroweed (*Isocoma tenuisecta*). Grasses include black grama (*Bouteloua eriopoda*), blue grama (*Bouteloua gracilis*), sideoats grama (*Boutelous curtipendula*), bush muhly (*Muhlenbergia porteri*), and Lehmann lovegrass (*Eragrostis lehmanniana*).

Jornada Experimental Range near Las Cruces, New Mexico

The 800 sq km Jornada Experimental Range (JER) is a site for research to determine the processes resulting in desertification of semiarid grasslands and associated changes in ecosystem properties. The Jornada Experimental Range is located on the northern edge of the Chihuahuan Desert. The Chihuahuan Desert is separated from the Sonoran Desert by a high plain at the lower end of the Rocky Mountains that separates southeastern Arizona and southwestern New Mexico.



Walnut Gulch Experimental Watershed - 150 sq. km.

Figure 1—Location map—Santa Rita Experimental Range, Jornada Experimental Range, and Walnut Gulch Experimental Watershed.

Major grasses on the JER include black grama (*Bouteloua eriopoda*), mesa dropseed (*Sporobolus flexuosus*), and red threeawn (*Aristida purpurea* var. *longiseta*). Shrubs include honey mesquite (*Prosopis glandulosa* var. *glandulosa*), four-wing saltbush (*Atriplex canescens*), soaptree yucca (*Yucca elata*), and snakeweed. Brush invasion on the range has converted much of the grass covered range to shrub covered range (Buffington and Herbel, 1965). Precipitation data have been collected using weighing bucket raingauges since 1915 at the JER headquarters. Additional data collection for shorter periods has taken place at other locations on the JER.

Santa Rita Experimental Range near Tucson, Arizona

Research began on the 200 sq km Santa Rita Experimental Range (SRER) in 1903 to investigate the management of semiarid rangelands. The range is currently managed by the University of Arizona and is used for ecological and rangeland research. The SRER is representative of about 8 million hectares of semi-desert grass-shrub ecosystems in southern Arizona, New Mexico, and Texas (Martin and Cable 1975).

Monthly precipitation data have been collected since 1923 from weighing bucket gauges. A total of 25 annual precipitation records were analyzed, including 11 records for the time period 1923-1991.

Methods

Time Series Analysis

Linear trend analyses are conducted to test and quantify long term changes in annual precipitation with time. For each gauge annual precipitation totals were regressed against time using the simple linear regression model. Using this model, a significant trend is represented by a statistically significant regression slope at the 95% confidence level, i.e. the P-value for the slope is <0.05.

As previously reported, data from 6 Walnut Gulch raingauges with continuous 35 year records were examined for linear trends (Nichols and others 1993). A total of 25 JER continuous records with time periods ranging from 21 to 76 years (table 1), and 25 continuous records from SRER with time periods from 20 to 69 years were examined for linear trends (table 2). The slope and corresponding P-values of the linear trend are shown in tables 1 and 2 for each JER and SRER record examined. The P-value indicates the smallest value of α such that the $(1-\alpha)$ confidence interval for the slope does not include 0. Thus, the slope is significant at all confidence levels less than $(1-\alpha)$.

Autocorrelation analyses are conducted to examine seasonal and stochastic components of the time series. The autocorrelation coefficient r_k of a time series is the serial

Table 1—Summary of Jornada Experimental Range Raingauge precipitation and linear trend analysis.

Gauge name	Period of record	Mean ppt (mm/yr)	Variance (mm/yr)	Linear trend Slope	Linear trend P value
Headquarters	1915-1990	241.1	283.6	0.813	.068
West Well	1918-1991	225.1	282.9	0.406	.366
Red Lake	1918-1991	207.7	321.7	1.219	.013*
Dona Anna	1926-1990	236.2	270.3	1.092	.046*
Middle Well	1926-1990	223.0	356.4	0.559	.385
Road Tank	1926-1990	239.2	333.5	0.914	.132
Stuart	1926-1990	255.5	336.7	1.016	.100
Yucca	1926-1990	224.9	241.6	0.432	.421
Aristida	1927-1990	216.0	278.0	0.991	.081
Brown Tank	1927-1990	222.8	231.6	0.406	.429
New Well	1927-1990	270.4	317.8	0.864	.157
Rabbit	1927-1990	235.8	304.9	1.524	.010*
Restoration	1934-1990	227.1	323.3	2.083	.003*
Co-op Well	1937-1990	210.8	212.8	0.914	.160
Ash Canyon	1937-1976	321.0	390.1	0.533	.695
Mesquite	1937-1990	211.3	278.6	1.956	.007*
Taylor Well	1937-1990	227.3	236.4	1.499	.025*
Antelope	1938-1990	221.8	351.4	2.134	.010*
Parker	1942-1990	228.9	274.5	3.404	.001*
Excl A	1959-1990	243.5	171.4	1.727	.176
Excl B	1959-1989	226.3	205.9	1.854	.209
NE Excl	1959-1990	237.5	208.9	2.896	.036*
BER	1961-1990	232.2	150.8	0.686	.603
Past 2	1965-1990	244.7	271.6	3.150	.150
IBP	1970-1990	226.6	200.1	1.321	.622

*Linear trend with time in years significant at the 95% confidence level.

Table 2—Summary of Santa Rita Experimental Range precipitation and linear trend analysis.

Gauge name	Period of record	Mean ppt (mm/yr)	Variance (mm/yr)	Linear trend Slope	Linear trend P value
Florida	1923-1991	542.6	884.7	2.057	.021*
Box	1923-1991	383.8	502.9	1.753	.009*
Desert Station	1923-1991	312.9	353.8	1.245	.028*
Eriopoda	1923-1991	364.0	385.5	1.499	.011*
Forest	1923-1991	448.6	658.5	0.762	.328
Huerfano	1923-1991	371.7	453.9	1.245	.047*
Muhlenbergia	1923-1991	341.5	363.4	1.524	.007*
NW	1923-1991	290.6	298.4	1.651	.001*
Parker	1923-1991	436.7	572.7	0.483	.507
Road	1923-1991	373.6	395.0	0.889	.143
Whitehouse	1923-1991	417.8	555.2	0.737	.316
130	1939-1982	360.5	273.9	2.108	.032*
164	1940-1991	309.8	321.2	0.686	.410
205	1947-1982	344.4	310.8	3.556	.011*
41	1972-1991	419.0	735.3	5.994	.270
45	1937-1991	369.2	366.4	2.286	.004*
Amado	1967-1991	330.1	456.3	3.150	.301
Desert Grass	1933-1991	103.4	413.9	1.245	.112
Desert Rim	1935-1991	318.8	309.6	1.016	.182
Gravelly Ridge	1932-1991	321.3	336.2	0.686	.318
Limestone	1965-1991	363.2	326.2	2.286	.325
McGibbon	1947-1991	486.1	743.1	4.699	.002*
Pa 11A	1971-1982	334.1	254.3	5.740	.420
PAS 21	1971-1991	408.9	480.2	6.248	.119
PAS 3	1971-1991	304.9	358.1	2.845	.421

*Linear trend with time in years significant at the 95% confidence level.

correlation coefficient of the first N-k years of the series with the last N-k years, and the autocorrelation function is defined by $r(k) = r_k$. Autocorrelation coefficients are considered significant if they lie outside the 95% confidence interval for the autocorrelation coefficients of a random time series which is given by

$$((\pm 1.96 * \sqrt{(N-k-1)})-1) / N-k$$

It should be noted, however, that even for a random time series it is expected that 1 in 20 autocorrelation coefficients will appear significant at the 95% confidence level. The seasonal (periodic), stochastic, or random components of a time series common in hydrologic processes are revealed by the presence or absence of characteristic significant contribution to the autocorrelation function (each has a particular shape). For each gauge the autocorrelation function of the time series of annual values was computed and plotted together with the 95% confidence bands.

Spectral density analyses are conducted to compliment autocorrelation analysis. The spectral density function is defined as the Fourier cosine transform of the autocorrelation function. It is useful for detecting periodicities which are not multiples of the fundamental frequency (fundamental frequency is 1 year for our analyses). For an interval in the frequency domain the relative area under the spectral density curve is a measure of the amount of the variation of the series accounted for by frequencies in that interval. Thus, broad peaks in the spectral density function may indicate significant periods in the time series. The spectral density function was calculated and plotted for each time series of annual values.

Autocorrelation and spectral density analyses were conducted on records from 1956-1990 at all three sites. Additional autocorrelation and spectral density analyses were conducted on the longest available records at JER and SRER including 1 record from 1915-1990, 2 records from 1918-1991, 5 records from 1926-1990 and 4 records from 1927-1990 at JER (table 3), and 11 records from 1923-1991 at SRER (table 4).

Results and Discussion

Previous analyses of precipitation data collected on the Walnut Gulch Experimental Watershed have shown that interpretations of linear trends depends on the period of record examined (Nichols and others 1993). The longest time period evaluated was 1956-1990, a 35 year period that included drought years during the 1950's as well as later years of above average precipitation in the 1980's. The 6 records examined revealed significant positive linear trends with time ($P \leq .10$).

As previously reported, spectral density analyses did not reveal any consistently dominant periods in the Walnut Gulch records from 1956-1990. Subsets consisting of records from 1956-1990 were analyzed for the 12 longest records available from the JER, and for the 11 longest available records from the SRER. In contrast to results of the Walnut Gulch analysis, there is a suggestion of a 3 year cycle in the 1956-1990 records from both the JER and the SRER.

Because the 1956-1990 records are comparatively short, the analyses have been extended to the JER and SRER precipitation records that are available for 76 and 69 years respectively. The analyses of the long term JER and SRER records are described in the following sections.

Table 3—Summary of spectral density analysis of long record JER raingauges.

Gauge	Period of record	Apparent periodicity (years)	
		Raw data	Without linear trend
Headquarters	1915-1990	76,38,3	
West Well	1918-1991	18,15,3	
Red Lake	1918-1991	74,37,6,2	74,37,6,2
Dona Anna	1926-1990	64,16,5,3	64,16,9,3
Middle Well	1926-1990	64,32,3,2	
Road Tank	1926-1990	64,32,13,5,3	
Stuart	1926-1990	64,32,16,21,5	
Yucca	1926-1990	64,16,13,3	
Aristida	1927-1990	64,32,21,4,3	
Brown Tank	1927-1990	64,32,3	
New Well	1927-1990	64,32,9,3	
Rabbit	1927-1990	64,32,3	64,32,3

Table 4—Summary of spectral density analysis of long record SRER raingauges.

Gauge	Period of record	Apparent periodicity (years)	
		Raw data	Without linear trend
Florida	1923-1990	68,34,3,6,	34,6,3,4
Box	1923-1990	68,5,3	5,3
Desert Station	1923-1990	68,5,6	7,6,5,3
Eriopoda	1923-1990	68,5,3	5,3
Forest	1923-1990	23,3	
Huerfano	1923-1990	70,35,5,4	70,35,5,4
Muhlenbergia	1923-1990	68,6,5,3	6,5,3
NW	1923-1990	68,6,5,3	7,6,5,3
Parker	1923-1990	4,3	
Road	1923-1990	68,34,6,5	
Whitehouse	1923-1990	34,6,5,4	

Jornada Experimental Range

Overall 9 of the 25 records evaluated have a positive linear trend with time ($p \leq 0.05$) (table 1). Figure 2 is a plot of annual precipitation recorded at the JER Headquarters raingauge. The linear trend is shown for the entire record as well as for the period from 1915 to 1960. The 1915-1960 decrease is an apparent short term oscillation in a time series that increased over the period from 1915-1990.

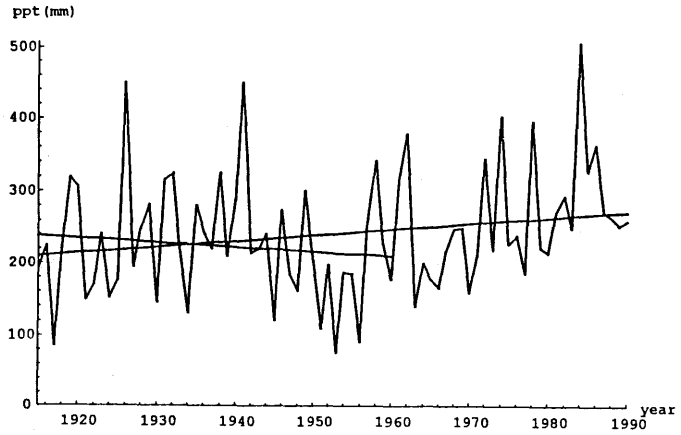


Figure 2—JER Headquarters raingauge showing linear trends from 1915-1990 and 1915-1960.

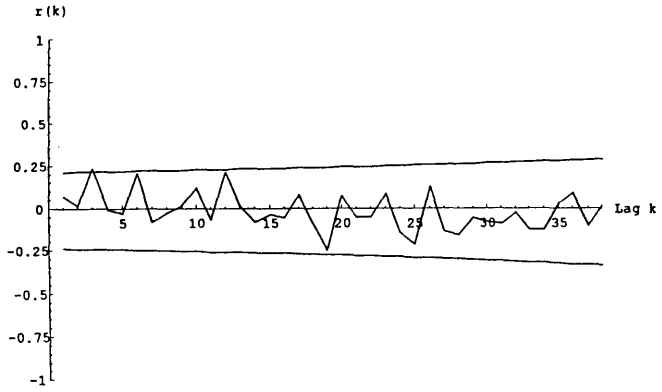


Figure 3—Autocorrelation—JER Headquarters raingauge.

Figure 4—Spectral density—JER Headquarters raingauge.

Figures 3 and 4 show the autocorrelation and spectral density plots for the JER Headquarters raingauge. These plots are representative of the JER annual precipitation records. Although there are significant autocorrelation coefficients and corresponding peaks in the spectral density function, their occurrence is not unexpected in a random time series. However, there is a suggestion of a 3 year period based on the occurrence of a 3 year cycle in 10 of the 12 records examined (table 3).

Santa Rita Experimental Range

Overall 11 of 25 records show a significant positive linear trend with time ($P \leq 0.05$). Of the 11 longest records (1923-1991), 7 have a significant positive linear trend with time (table 2). Autocorrelation and spectral density analyses of the 1923-1991 SRER records suggest a possible 3 year period (table 4).

Preliminary spectral density data for JER and SRER are summarized in tables 3 and 4, respectively. In each table the prominent peaks are listed for each record examined. In addition, records that revealed a significant linear trend

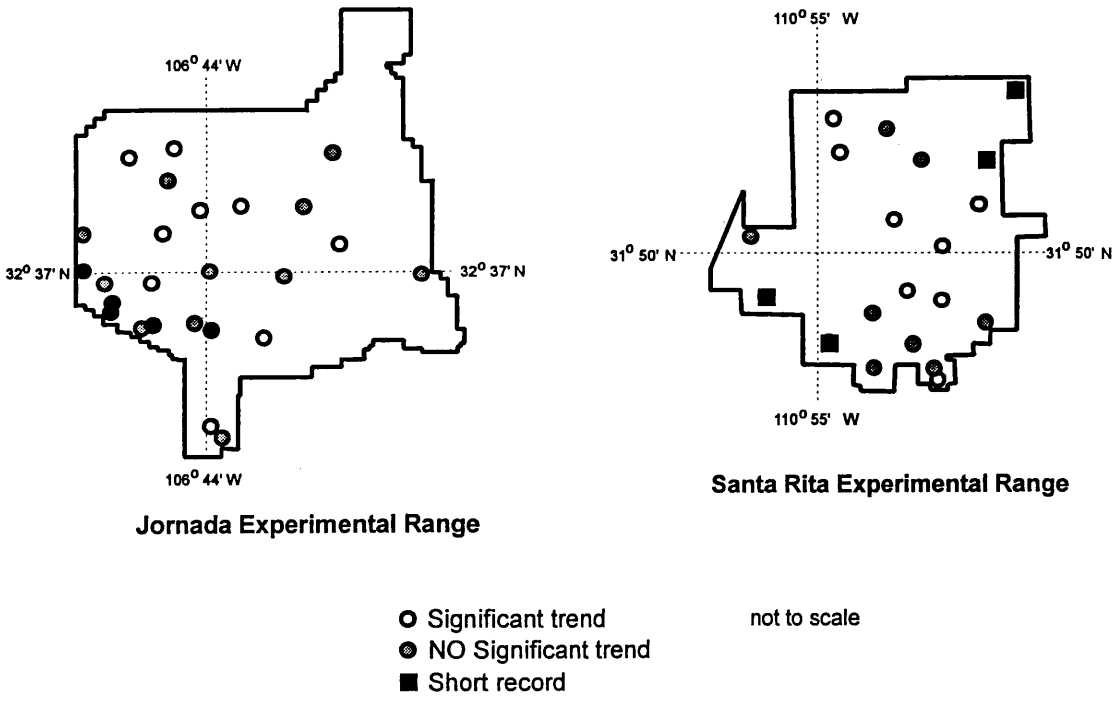


Figure 5—Distribution of raingauges with linear trends—Santa Rita Experimental Range and Jornada Experimental Range.

with time were reanalyzed after being detrended, and prominent peaks are listed for the detrended records. Note that apparent periodicities listed in the tables are calculated as 1/frequency and are rounded to whole years.

The spatial distributions of the 25 JER and 25 SRER raingauges showing significant trends and no significant trends plotted in figure 5 do not reveal any obvious spatial pattern in the distributions.

Conclusions

The particular period of record examined greatly influences interpretations of trends in precipitation records. Therefore, long term historical records are required to determine the effects of drought and periods of above average precipitation on vegetation changes over time, as well as to predict the future response of vegetation to climate change.

Precipitation records from 1956-1990 at Walnut Gulch do not reveal any dominant cycles, however records from the JER and SRER for the same time period suggest a 3 year cycle. A 3 year cycle in annual precipitation was also found during analyses of the longest available records from the JER and the SRER. In addition to total annual precipitation amount, the timing and distribution of precipitation in semiarid regions impact the germination, establishment, rate of growth, length of life and seeding characteristics of grasses and shrubs. Additional analyses are required to evaluate changes in the timing, intensity, or distribution of precipitation that may be reflected in changes in vegetation.

Acknowledgments

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Shrublands and Grasslands of the Jornada Long-Term Ecological Research Site: Desertification and Plant Community Structure in the Northern Chihuahuan Desert

Laura Foster Huenneke

Abstract—Semidesert grasslands of southern New Mexico have been replaced in this century with shrublands (chiefly creosote bush and mesquite). The Jornada Long-Term Ecological Research Program has been monitoring aboveground plant productivity, plant species composition, and other aspects of ecosystem function in 15 sites. Plant diversity differs significantly among vegetation types, with grasslands being the most diverse. Aboveground net primary productivity does not differ significantly among vegetation types. Productivity is correlated with plant species richness in some seasons; however, diversity has not been correlated with smaller fluctuation of production between years in the first few years of study. These results have implications for sustainable management of diversity and of productivity.

In this symposium we have heard much about the history of vegetation change and the alteration of ecosystem structure here in southern New Mexico (Buffington and Herbel 1965). My presentation will focus not on the causes and mechanisms of this change, but instead on the results of that change as seen in plant diversity and productivity. I address the following questions.

First, how does plant community structure in remnant grasslands of the Jornada basin compare with that in the "desertified" shrublands?

Second, has there been a major decline in the productive potential of the ecosystem? I assessed productivity as aboveground net primary production (NPP) of all species, not just economic or forage production. The conversion of grassland to shrubland is one stage of the desertification process (Schlesinger and others 1990), and it is important for purposes of sustainable management to determine whether the change in vegetation has been associated with a permanent and substantial decline in the system's productivity (Verstraete and Schwartz 1991).

Finally, I take this opportunity to address a very basic theoretical question in ecology: is there any association between the biological diversity of a system and its productivity? That is, is there some ecosystem "function" of plant diversity?

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Patterns of Plant Diversity

First, what are the patterns of plant species diversity? In the Jornada LTER program, we have been monitoring 15 sites scattered across the Jornada Experimental Range and the NMSU College Ranch (Chihuahuan Desert Rangeland Research Center): 3 grasslands, 3 grass-dominated playas, 3 creosote bush sites, 3 mesquite sites, and 3 tarbush sites, since 1989. We have compiled lists of all plant species present in permanent study quadrats, 3 times each year (winter, spring, and late summer), and have measured their biomass and productivity (methods described below). In addition, several environmental variables (precipitation, soil moisture, etc.) are monitored on each site. We can therefore compare the number of species present at a particular sample date, or cumulative over time—the total species list for a site.

At all sample dates, grasslands have more plant species present than do shrub-dominated systems (Huenneke, unpublished data). From 1989 through 1994, these numbers are approximately 40-50 species per site (during the growing season) for grasslands, in comparison with 20-35 species in a creosote bush area and 10-15 in mesquite sites. Of course, no one sample date represents all the species present in a site; many of the plants of semi-desert regions are ephemeral annuals or short-lived perennials, and no single sample (even in a "good" season) can capture the entire species list. Thus all sites have continued to "accumulate" species over time; that is, the cumulative species list for each site continues to grow, even after 5 years of data collection. Total species numbers are roughly 100 or so for grassland sites thus far, compared to 50-60 in creosote bush sites and 20-40 in mesquite sites.

Over time, the graph of cumulative species numbers is steepest for the grassland sites. That is, not only do the grasslands have the highest species richness at any given point in time, but they demonstrate the greatest diversity over time. This reflects in part an impressive amount of seasonal and annual variation. In sum, the grasslands contain the largest and most dynamic pool of species.

Inspection of the identity of species in the various sites reveals a great deal of overlap in the species lists. My initial hypothesis was that grassland species might have been displaced, replaced by distinct species' assemblages representative of Chihuahuan desert shrub systems. One would then expect little overlap between species lists of grassland and shrubland sites. However, nearly all plant species found in the shrub-dominated sites are also found in grasslands.

This suggests that conversion of grassland to shrubland took place via the impoverishment of (and alteration of relative abundances within) the grassland flora. In most of the creosote bush and mesquite sites, we have encountered no plant species absent from the grasslands.

Productivity of Jornada Ecosystems

Given that these ecosystems have altered substantially in structure, how much has this change in structure altered ecosystem function, especially productivity? While there is an undoubted decline in forage and economic productivity as grassland is replaced by desert scrub, it is not obvious whether there has been a permanent decline (as of yet) in the productive capacity of the landscape. The LTER program is interested in determining whether there has been any decrease in net primary productivity - the amount of carbon fixed by plants in photosynthesis per unit area in a fixed time period.

The 15 sites being followed in detail provide an opportunity to assess whether aboveground productivity differs between shrub- and grass-dominated systems. We have sampled each site three times per year, in winter, spring, and late summer or fall, since 1989. Non-destructive measures of aboveground plant size are made for all species, in 49 permanent 1-m^2 quadrats per site. Then an estimate of live biomass for each species in each quadrat is made, based on regressions developed for individual species from harvests over the past several years. Productivity is measured as the increases in biomass from one sample period to the next, summed for all species in a quadrat. This figure is definitely an underestimate, as we miss some production and loss of tissue over the season, but has proven to be a useful index for between-site comparisons. Our approach allows us to sample shrublands and grasslands with equivalent methods and equal intensity; it also yields non-destructive estimates that include a measure of variation over space-that is, variation from one square meter to another.

Thus far we have found few significant differences among ecosystem types in the average aboveground standing crop (g/m^2), except in winter when those systems with shrubs definitely have more living tissue aboveground. (However, a sample size of three sites per ecosystem type means we have a fairly weak ability to detect differences.) Of course, aboveground biomass is distributed on the surface differently; in grasslands, there is not much variation in biomass from one quadrat to another (low range of values), but in shrublands there is tremendous variation. Some patches have very high biomass, while others are completely bare (on the scale of 1-m^2 quadrats).

Does net aboveground productivity differ between grasslands and shrublands? On average, there is no meaningful difference among ecosystem types. In some seasons, playas have very high productivity (when they have filled with water and herbaceous growth has been great); in other seasons, they may have virtually zero productivity aboveground. Other than when playas have extremely low productivity, however, there are rarely significant differences among vegetation types. At least one or two shrub-dominated sites each season have productivity as high as that of grasslands, but these productive sites are not always the same ones each year. Again, three sites per type allows only a weak test, but it appears there is no gross difference in average productivity.

Relationship Between Plant Diversity and Productivity

Recently, we have become interested in applying our data to a more basic ecological question: that of the relationship between diversity and productivity of a biological system. While there are theoretical and conceptual reasons to suppose that greater diversity in plant growth forms and species, for example, might allow more efficient production in a system over time, there are few empirical studies of these relationships. There are at least two contrasting views (Schulze and Mooney 1993): one suggests that the more diverse a system is, the more productive and efficient it will be (with more complete use of resources, alternative species succeeding under varying conditions, and so on). The alternative view is that above some minimum number, extra species do not add much to ecosystem function - that is, there may be some "redundancy" in ecological communities. Our data afford a preliminary opportunity to address this topic.

When one arranges the 15 sites in order of species richness during a given sample period, there is a strong positive correlation with aboveground productivity at some (but not all) sample dates. Sites do receive different amounts of rainfall, even in a single season, because of the patchiness of summer storms. We have precipitation data for individual sites, so I was able to calculate the ratio between productivity and rainfall as an index of efficiency of production. The hypothesis was that a larger number of species in a system should allow more efficient use of rainfall (that is, a positive correlation between species number and efficiency of production in a given season). But there was no significant correlation.

Also, when one calculates the average annual production at a site, and plots it against the cumulative species number for that site over the first few years of sampling, there is no significant correlation. I also hypothesized that where conditions vary greatly from year to year (as in deserts), perhaps having a large species pool means a greater ability to produce SOMETHING each year. That is, species may substitute for one another from year to year, and NPP (net primary production) may remain more constant than it would for a less diverse system. The hypothesis, then, was that the range or fluctuation in NPP values should decrease as number of species in system increases - a negative correlation or slope. However, this was not the case! The most species-rich systems, if anything, had larger (not smaller) ranges of NPP values.

Conclusions

In the Jornada basin of southern New Mexico, desert shrublands contain fewer species than do the remnant semi-desert grasslands. In general, the shrub sites contain only plant species that are also present in grasslands, while the grasslands contain many unique species. Thus the grasslands are important reservoirs of plant diversity.

There is no large-scale difference in the mean biomass or average primary productivity of grasslands and shrublands (although of course these are distributed differently across the surface). These results suggest that as of yet there has been no severe impact of desertification on the productive capacity of the system.

While there is some tendency for more species-rich systems to have higher productivity than others, this higher species richness does NOT seem to provide the buffering against year-to-year variability one would expect. Further analysis may focus on growth form diversity or on some index of diversity more sophisticated than simple species richness. Certainly the LTER data will be a rich source of information on the relationships between ecosystem structure and function in this diverse and complex landscape.

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Winterfat Shrubland Boundary Dynamics Under Different Grazing Histories

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Abstract—This study examined boundary areas between winterfat (*Ceratoides lanata*) shrublands and adjacent blue grama (*Bouteloua gracilis*) grasslands in northern New Mexico. Vegetation response to defoliation was compared for interior and peripheral winterfat shrubland community positions on two locations having different grazing histories. Whittington locations were removed from domestic grazing in 1973, while adjacent lands sustained season long grazing. Seedlings and mature plants of winterfat and forbs were affected by community position, depending on grazing history, while basal cover of grasses was not. Defoliation may diminish the importance of community positions. Winterfat recruitment was affected by defoliation and community position.

Landscape boundaries have recently received much attention in ecology (Correll 1991; Holland and others 1991; Risser 1993; Turner and others 1991; Wiens and others 1985). Boundaries are recognized by both composition and structure of vegetation (van der Maarel 1976). Transition zones, where one plant community begins to grade into another, may be useful as indicators of vegetative change (Holland and others 1991). These ideas are not new to ecology. Many years ago Daubenmire (1947) recognized that plant distributions may reveal the limits to growth. As an extension of these ideas, we suggest that plants in boundary positions may be more sensitive to changes in biotic and/or abiotic factors when compared to individuals of the same species positioned interior to a community. Additionally, given that winterfat (*Ceratoides lanata*) is a valued forage on western range and the distribution of these shrublands is known to be limited under grazing (Stevens and others 1977), we selected the boundary between winterfat shrublands and adjacent blue grama (*Bouteloua gracilis*) grasslands to study the importance of community position for winterfat plants that may be constrained by past grazing history.

Methods and Materials

Study Site and Plot Layout

Winterfat-dominated communities and surrounding grass communities, dominated by blue grama, were used to test our hypotheses that winterfat plants in interior and peripheral community positions would respond differently to defoliation, and that these differences may also be altered by grazing history. Research sites were on lands owned by the National Rifle Association Whittington Center located in Colfax County, approximately 10 km south of Raton, New Mexico.

Three visually-recognizable winterfat communities were studied. Each of these communities is bisected by fence lines constructed prior to 1945. The Whittington side of this fence line has been protected from domestic grazing since 1973. The other side has been seasonally grazed by cattle from May to October until and during the time of the study. Both of these locations receive wildlife use, primarily by mule deer, elk, bear, and many small mammals.

Within interior and peripheral positions of each of three communities, six 4 x 2.5 m plots were fenced to exclude ungulate herbivory. "Interior" locations within each community were defined and visibly recognizable as winterfat-dominated areas that were surrounded by similarly dominated areas and were not adjacent to "peripheral" locations (fig. 1). "Peripheral" locations were positioned on the boundary of a winterfat community and adjacent vegetation dominated by grassland. Peripheral plots were aligned so that the longest axis of the rectangular plot was perpendicular to the community boundary. Study plots cover an 11-m^2 area and were located in peripheral and interior locations.

Plots were randomly assigned to one of three defoliation treatments. Plants in control plots were not clipped (treatment C = control). A second defoliation treatment involved clipping all grass, forbs, and shrubs (treatment A = all plants defoliated except yucca *Yucca glauca*, cacti, *Opuntia* sp. and *Echinocereus* sp., and broom snakeweed *Gutierrezia*

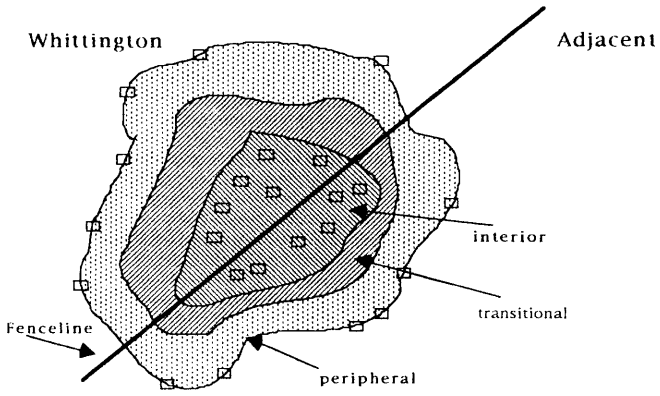

Figure 1—Community locations (Whittington and adjacent) and positions (interior and peripheral). Rectangles represent 11 sq. m areas.

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sarothrae). Grasses and forbs were clipped in June 1992, August 1992, June 1993, and June 1994, to a 2.5-cm stubble height. At the same time, shrubs were clipped to remove one half of all externally accessible new crown growth above 2.5 cm in height. A third defoliation treatment defoliated shrubs in the same manner as in treatment A, except that herbaceous plants were not clipped, and defoliation of browse plants was conducted in June 1992, September 1992, September 1993 and September 1994 (treatment B = browse). This treatment was initiated in June 1992 to begin the study but was defoliated in the fall 1992, 1993, and 1994.

Mature Plant Records

Basal cover of vegetation by species, bare ground, litter, and intact root crowns were recorded from permanent line transects in each plot. The plot width was traversed by four permanent line transects across the width of the plot. Each line was 2.5 m long resulting in a total of 10 m of line transect per plot. Transects were read as continuous line transects to a 0.5-cm resolution to create a linear map of basal cover. Cover data were recorded twice between May and September for three consecutive summers. Clipping treatments were not applied until after initial basal cover and winterfat crowns were recorded. Vegetative biomass from clipping treatments was removed from plots by species, dried and weighed. Total crown growth of winterfat individuals within plots was recorded for each plant. All individual winterfat plants found in the plots were permanently marked and measured for basal circumference, height, and two crown diameters. Winterfat plants were monitored for crown volume in June 1992, 1993, and 1994. The 1992 data were collected prior to application of defoliation treatments. Canopy volume for winterfat shrubs was calculated as the volume included under half of a spheroid, to represent the natural shape of the canopy comparable to Ludwig and others (1975) on broom snakeweed (*Gutierrezia sarothrae*). In this computation, canopy volume was = $4/3\ \pi\ r^2\ h$; where h is plant height and r is the average radius. The average radius for these data was obtained by adding two measures of the canopy diameter (the maximum diameter and the diameter perpendicular to the maximum) and dividing their sum by four. By numbering winterfat plants, we also recorded winterfat density.

Seedling Records

A seedling study was conducted to assess establishment of species under each treatment in comparable locations and positions. Adjacent to each end of the mature plant study plots, two seedling areas 0.2 m x 2.5 m (0.5 m^2 area) were marked resulting in a total of 144, 0.5 m^2 seedling areas. Within the seedling areas, seedlings were marked by species as they emerged, and their progress was followed for the duration of the study or until the seedling's death. Seedling plots were clipped identically to the mature plant plot to which they were attached. Seedling emergence and survival were recorded for three years, at least twice between May and September, of each growing season. We recorded total number of seedlings by species that emerged, and the survival of those seedlings on each measuring date until the conclusion of the study. Seedlings were identified and marked so that on subsequent measuring dates the species of dead seedlings was known.

Experimental Design and Data Analysis

The experimental design for the mature plant study was a split split-plot arrangement of a randomized block design, with three winterfat communities serving as blocks. Main plots represented locations that differed in grazing history. Subplots were interior or peripheral positions within a community. Sub-sub plots were the three defoliation treatments assigned to two plots at each location and position in each community. Sampling date was included as a repeated measure. Biomass, cover, winterfat dimensions, and seedling data were subjected to an analysis of variance appropriate to the experimental design.

Because of the numerous species recorded in some of the data collected, analysis was at times completed on groupings of species such as all grasses, forbs, or shrubs. All data were tested for conformance to assumptions of normality (Shapiro and Wilk 1965) and sphericity (Mauchley 1940). When violations of sphericity assumptions occurred, adjustment to F-test degrees of freedom was completed using Greenhouse-Geisser estimates of the degree to which sphericity was violated by a particular data set (Geisser and Greenhouse 1958). When three-way and higher order interactions occurred, F-tests of interacting treatment factors within a level of the third interacting factor were completed using error terms specific to the test. Additionally, mean separation within interactions was accomplished with Least Significant Differences calculated using error terms specific to the contrast. This approach to higher level interactions is based on recommendations by Milliken and Johnson (1984).

Results and Discussion

Mature Plants

Winterfat Density—Density of mature winterfat individuals was not different between Whittington and adjacent locations or defoliation treatments. Density of mature winterfat plants was greater in interior than in peripheral positions (2.01 and 0.45 plants per m^2, respectively). Additionally, the mean density of winterfat plants decreased over the three years of the study from mean of 1.26 plants per m^2 in 1992 to 1.20 plants per m^2 in 1994. Winterfat density on Whittington plots was slightly greater than that of adjacent plots, with 1.58 and 0.89 plants per m^2 respectively.

Winterfat Canopy Volume—Winterfat canopy volume per plant differed between defoliation treatments and between community positions, and these differences depended on sampling date. At the beginning of the study, canopy volume of winterfat plants was similar in all three defoliation treatments (fig. 2). Canopy volume did not change in control or browse-only defoliated plots. However, canopy volume did decrease when both herbaceous and browse plants were defoliated, and this effect was apparent by the second year of the study. By 1994, winterfat canopy volume was lower in defoliated plots, (regardless of the type of defoliation) than in control plots.

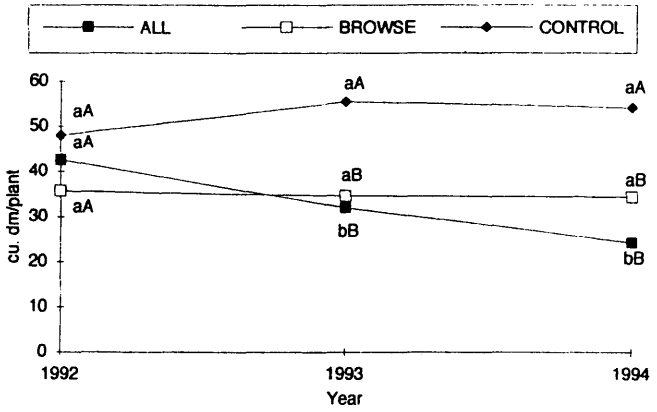

Figure 2—Winterfat canopy volume by defoliation and year. Means within a defoliation treatment with the same lower case letter do not differ. Means within a year with the same upper case letters do not differ (P>0.05, LSD).

Despite the foregoing defoliation effects, defoliation treatments did not interact with grazing history or community position effects. Thus, regardless of defoliation treatment effects, canopy volume of winterfat plants was greater in interior than in peripheral positions at the beginning of the study. However, while canopy volume remained stable in peripheral positions, canopy volume of winterfat plants on the interior positions decreased between 1992 and 1994 (fig. 3).

Winterfat Basal Area—Winterfat basal area differed between grazing histories and between years. Basal area increased between 1992 and 1993. Also, basal area of winterfat plants at Whittington locations was less than basal area of plants at adjacent locations. There were no effects of defoliation treatment or position on winterfat basal area.

Basal Cover of Grasses—Basal cover of all grasses averaged across all dates and treatments was 16.1% of the total ground cover. Within total grass cover, the most prevalent species was blue grama which accounted for 96.8% of

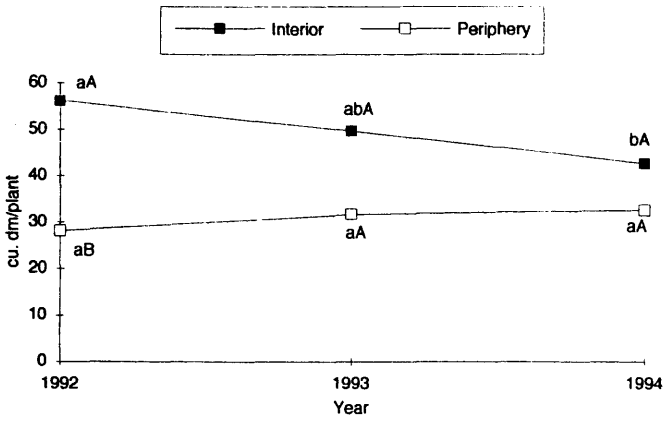

Figure 3—Winterfat canopy volume by position and year. Means within a position with the same lower case letter do not differ. Means within a year with the same upper case letter do not differ (P>0.05, LSD).

grass basal cover. Galleta grass (*Hilaria jamesii*), western wheatgrass (*Pascopyron smithii*), and buffalo grass (*Buchloe dactyloides*) each totaled 0.1% of the total basal cover and 1.1%, 0.9%, and 0.6 % of the total grass cover, respectively. Other grasses found on line transects were in trace amounts of less than one percent of total grass cover. In order of decreasing basal cover, these included squirrel tail (*Sitanion hystrix*), three-awns (*Aristida* sp.), ring muhly (*Muhlenbergia torreyi*), Foxtail barley (*Hordeum jubatum*), vine mesquite (*Panicum obtusum*), wolf tail (*Lycurus phleoides*), alkali sacaton (*Sporobolus airoides*), and sideoats grama (*Bouteloua curtipendula*). Because species other than blue grama and its root crown contributed so little to basal cover of grasses, results presented here are basal cover of all grass species together.

Basal cover results revealed no effects of grazing history or position on grasses. Basal cover of grasses increased on plots under defoliation treatment A by 1993 (fig. 4). Although basal cover of all grasses was not different between

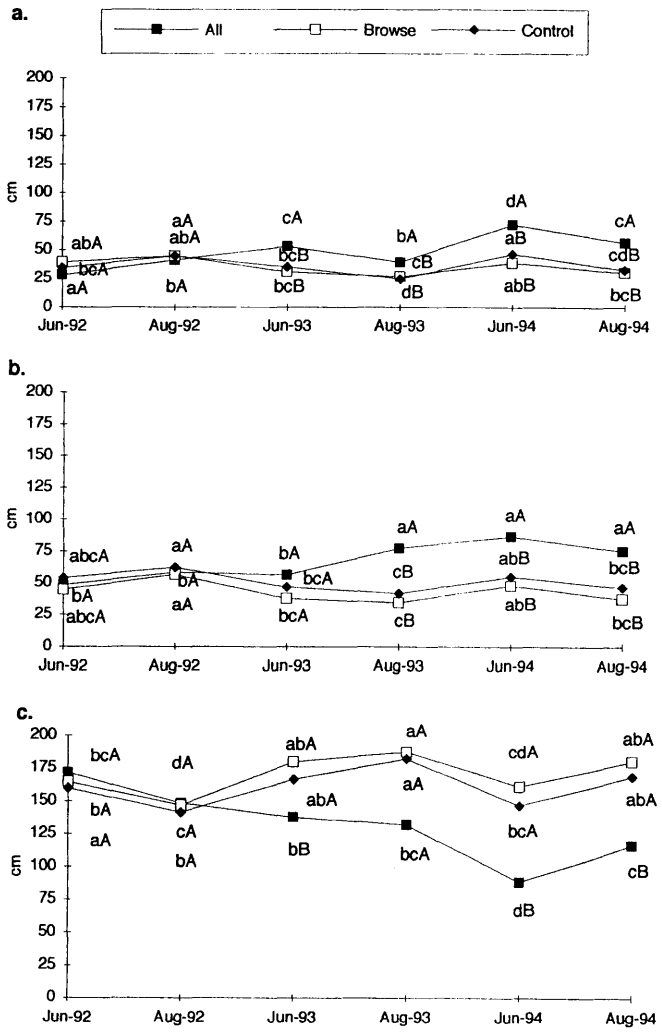

Figure 4—Basal cover of (a) grasses, (b) bare ground, and (c) litter by defoliation and date. Means within a defoliation treatment with the same lower case letters do not differ. Means within a date with the same upper case letters do not differ (P>0.05, LSD).

browse-defoliated and control plots, these two defoliation treatments differed from treatment A defoliation plots in 1993 and this difference was maintained throughout the remainder of the study.

Bare Ground and Litter Cover—By June 1993, bare ground was also greater in plots with defoliation of both browse and herbaceous plants than in plots with defoliation of browse only or control plots, and this difference was maintained throughout the remainder of the study (fig. 4). Bare ground was not significantly affected by location or position treatments.

Litter cover showed trends opposite to those shown by grasses or bare ground (fig. 4) by decreasing immediately following application of defoliation treatments. However, both browse-defoliated plots and control plots recovered litter cover in June 1993, while litter cover continued to decrease in plots where both browse and herbaceous vegetation was clipped. The lower cover of litter on the treatment A plots persisted for the remainder of the study.

Seedling Emergence

Annual Forb Seedling Emergence—Emergence of annual forbs was affected by grazing history and date. Analysis of these data was completed on ranked data; mean separation was completed on ranked means, and means presented in figures are means from the original data. For both grazing histories, emergence of annuals differed significantly between June and August sampling dates for each year (fig. 5). There was greater emergence of annual forbs at grazed adjacent land locations than on locations recently removed from grazing (Whittington) in August 1992 and in both June and August 1994. In all summers, early emergence of annual forbs prior to June was greater than emergence from June to August. In general, there was greater emergence of annual forbs at adjacent locations than at Whittington locations. Mean emergence of annual forbs was 6.0 and 4.1/m^2 for adjacent and Whittington plots, respectively.

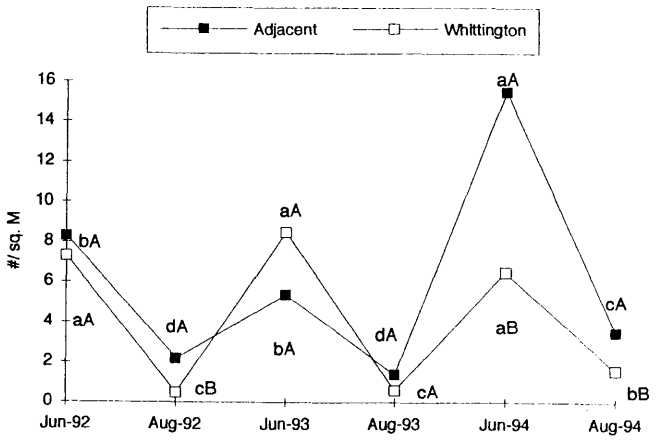

Figure 5—Annual forb seedling emergence by location and date. Means within a location with the same lower case letters do not differ. Means within a date with the same upper case letters do not differ (P>0.05, LSD).

Perennial Forb Seedling Emergence—Emergence of perennial forbs was affected by grazing history and depended on both position and date. Analysis of these data was also completed on ranks. At interior positions, emergence of perennial forbs differed between grazing history locations on June 1992 and June 1994 (fig. 6a and 6b). On peripheral positions, emergence was different for the two grazing histories in August 1992 and June 1994. For these dates, on both the interior and periphery positions, there was greater perennial forb emergence at adjacent locations than at Whittington locations. Although an apparent reversal of differences between grazing histories takes place on the periphery in June 1993, grazing history mean perennial forb emergence was not different. In both locations and positions, August dates had lower emergence of perennial forbs than did June dates. Defoliation treatments did not differ in emergence of perennial forbs, nor did defoliation interact with any other treatment.

Winterfat Seedling Emergence—On the initial sampling date (June 1992), winterfat seedling emergence occurred only at Whittington locations (fig. 7); most of these

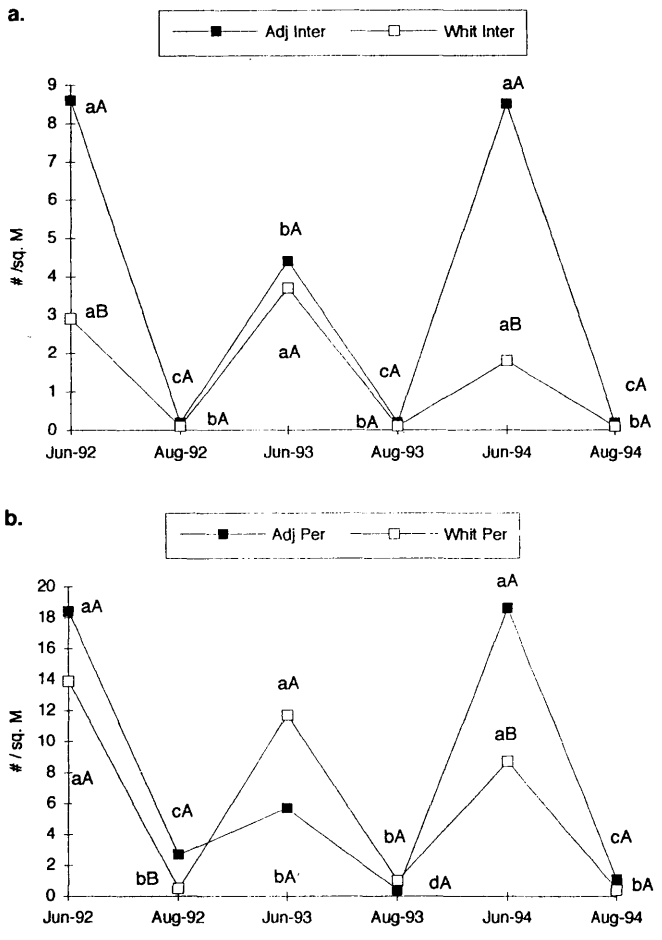

Figure 6—Perennial forb seedling emergence on (a) interior and (b) peripheral positions by location and date. Means within a location and position with the same lower case letters do not differ. Means within a date and position with the same upper case letters do not differ (P>0.05, LSD).

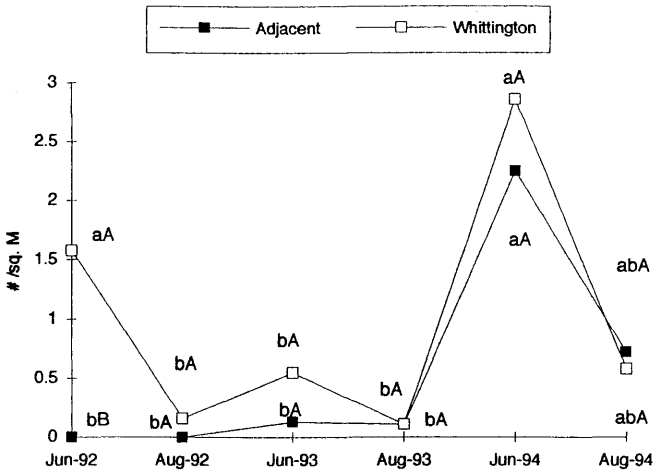

Figure 7—Winterfat seedling emergence by location and date. Means within a location with the same lower case letters do not differ. Means within a date with the same upper case letters do not differ (P>0.05, LSD).

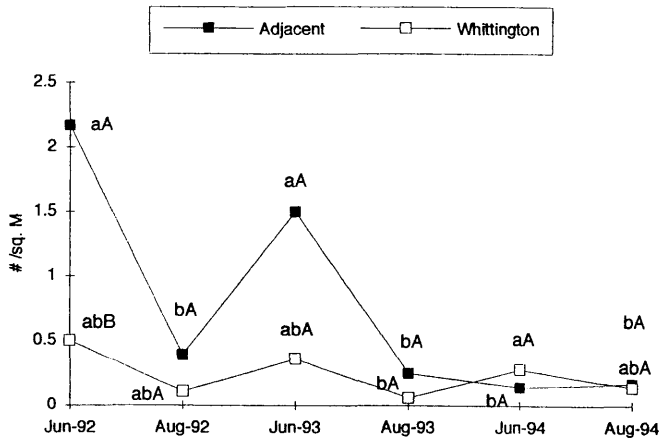

Figure 8—Emergence of other shrub seedlings by location and date. Means within a location with the same lower case letters do not differ. Means within a date with the same upper case letters do not differ (P>0.05, LSD).

seedlings emerged in interior positions. Winterfat seedling emergence was similar between locations on all other sampling dates. At Whittington locations, more seedlings emerged in June 1992 and June 1994 than on any other sampling date; at adjacent locations, emergence of winterfat seedlings was higher in June 1994 than at any other sampling date (fig. 7).

Location and position interacted in their effects on winterfat seedling emergence. At Whittington locations, emergence was greater in interior positions than in peripheral positions; emergence at these two positions did not differ at adjacent locations. Additionally, emergence was similar between locations at interior and peripheral positions. Defoliation treatments also affected winterfat seedling emergence. Winterfat seedling emergence was greater in control plots than in defoliated plots.

Other Shrub Seedling Emergence—Shrubs other than winterfat emerged differently between the two grazing histories (fig. 8). Analysis of ranked data indicated that emergence of these species was greater on adjacent than at Whittington locations only on the initial sampling date. Greatest shrub emergence at adjacent locations occurred in June of the first two field seasons and shrub emergence tended to be lower on dates later in the summers.

Seedling Survival

Winterfat Seedling Survival—The total number of winterfat seedlings that survived differed between defoliation treatments. Survival of winterfat seedlings was greater in controls than in either of the defoliated treatments.

Composition of Seedling Survivor Totals—There were significantly more total seedling survivors on peripheral positions than on interior positions at the end of the study. Mean numbers of survivors was 7.2/m^2 and 15.9/m^2 for interior and periphery, respectively. There were no other treatment impacts on total number of seedling survivors.

Seedling survivors were divided into three groups: perennial forbs, winterfat, and shrubs other than winterfat. These three groups were analyzed for their respective contributions to the total number of perennial survivors. (For example, the contribution of other shrubs to perennial survivors equals the number of other shrub survivors/number of total perennial survivors.)

Perennial Forb Contribution to Seedling Survivors—Perennial forbs were more important in peripheral positions than in interior positions, irrespective of location or defoliation treatments. Mean contribution of perennial forbs to total numbers of seedling survivors was 44.8% on the interior and 84.7% on peripheral positions (fig. 9).

Contribution of perennial forbs to seedling survivors at adjacent locations did not differ between defoliation treatments (fig. 10). At Whittington locations, there was greater proportion of forbs seedling survivors in plots under browse-only defoliation than in controls or plots under defoliation of both browse and herbaceous plants. For browse-defoliated plots, grazing histories did not differ in the contribution made by perennial forbs. However, contribution of perennial

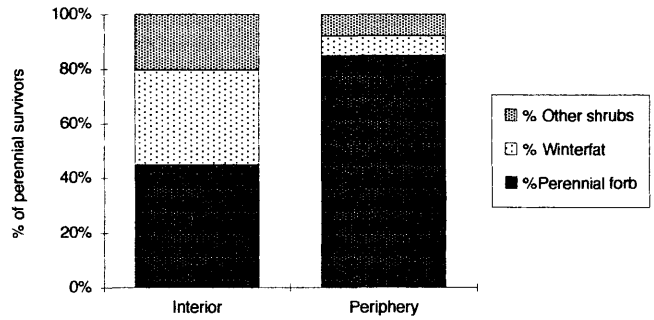

Figure 9—Composition of seedling survivors by position. Position means within each vegetation type differ (P<0.05, LSD).

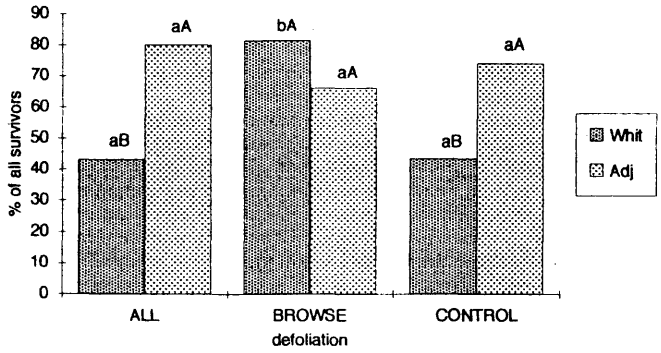

Figure 10—Contribution of forbs to seedling survivors by location and defoliation. Means within a location with the same lower case letter do not differ. Means within a defoliation treatment with the same upper case letter do not differ (P>0.05, LSD).

forbs to seedlings survivors was greater at adjacent locations than at Whittington locations in plots under defoliation of both browse and herbaceous plants and control plots.

Winterfat Contribution to Seedling Survivors—Control plots had greater proportions of winterfat seedlings than did browse-defoliated plots. Winterfat survivors in plots with defoliation of both browse and herbaceous plants were intermediate to and not different from either controls or browse-defoliated plots. Additionally, winterfat survivors contributed more to survivorship on interior positions than on peripheral ones (mean contributions were 34.8% on interior positions and 7.3% on peripheral positions). This trend is reversed for perennial forb portions of seedling survivors (fig. 9).

Contribution of Shrubs (exclusive of Winterfat) to Seedling Survivors—Shrubs (exclusive of winterfat) also made greater contributions to total number of seedling survivors on interior positions than on peripheral ones (fig. 9). Mean shrub contribution was 20.3% of the total perennial survivors on interior positions and 7.9% on the periphery.

Summary

Importance of Defoliation

Defoliation of both browse and herbaceous plants (defoliation treatment A) decreased mature winterfat canopy volume, litter ground cover, and winterfat seedling emergence, and increased grass basal cover and bare ground, relative to controls. Browse-only defoliation had similar effects on winterfat canopy and seedling emergence but did not effect basal cover of grasses, bare ground and litter. These effects were independent of grazing history and position. In addition, browse-only defoliation at Whittington locations had greater portions of forbs within seedling survivors than did control plots or plots under defoliation of both browse and herbaceous plants.

Importance of Position

Differences in canopy volume of mature winterfat, emergence and survival of winterfat seedlings, and survival of shrub and forb seedlings between interior and peripheral community positions have been documented in this study. Winterfat seedling emergence at Whittington locations was primarily on interior positions. Canopy volume of interior winterfat decreased from 1992 to 1994 while peripheral canopy volume did not. Consequently, although initial winterfat canopy volume was greater on interior positions, it did not differ from peripheral positions in 1993 and 1994. Growth of winterfat canopies on the periphery is more stable over time and we suggest that this position effect may express the presence of different competitive interactions in the two positions. Winterfat and shrub seedling survival was a greater portion of all survivors on interior positions while forbs constituted a larger portion of survivors on peripheral positions. These effects are independent of location and defoliation treatments.

Importance of Grazing History

Grazing history treatments affected seedlings and winterfat basal cover, while ground cover, basal cover of grasses, and mature winterfat canopy volume did not reflect differences in grazing history. Basal cover of mature winterfat plants was greater at adjacent locations than at locations with twenty-year removal of cattle. Additionally, on dates when the two locations differed, emergence of annual and perennial forbs and shrubs other than winterfat was greater at adjacent locations, while emergence of winterfat seedlings was greater at Whittington locations. Grazing history had little impact on seedling survival once seedlings had emerged (see interaction with defoliation effects above).

Conclusions

Many of the results of this study were not surprising. Prior studies have documented increase in basal cover of grasses under clipping as well as decreased canopy volume of shrubs with crown defoliation. Additionally, a history of past defoliation is known to increase emergence of forbs and nonpalatable shrubs.

Winterfat seedling results (initial emergence of winterfat only at Whittington locations) may reflect past grazing history. Increased litter and shade and decreased bare ground have been identified as important to winterfat emergence and survival (Woodmansee and others, 1971). Additionally, smaller basal size of winterfat plants at Whittington locations may indicate renewed winterfat regeneration within the past 20 years of grazing removal.

One interesting result is the apparently greater stability of peripheral winterfat canopies when compared to decreasing canopies on interior positions. Although it is not surprising that canopies decreased (⅔ of the plots in each position were subjected to defoliation), it is interesting that peripheral plants were able to recover their canopy volume before

the next sampling date, while interior plants did not. This suggests a very real impact of community position on mature winterfat crown growth and this difference may partially express competitive interactions.

An additional impact of position is apparent on the increased survival of shrub and winterfat seedlings on interior positions. Interior positions are more favorable for survival of shrubs than are periphery positions. Perennial forbs, however, differed between positions and were more numerous on peripheries.

Finally it is note-worthy that differences in grazing history and in community position were not documented on basal cover from line transects. Line transects documented change in grass basal cover due to defoliation treatments. Grass basal cover was not greatly changed by a twenty year removal of grazing or by shifts from periphery to interior positions within winterfat communities. This suggests that either the effects of grazing history and community position are not important to grass basal cover or that these impacts are not expressed in grass bases. Either statement has great ramifications for range management.

Many studies use exclosures to document the impacts of grazing and its removal on grasslands. However, problems with their use have also been noted. Painter and others (1989) have found that grazing history can cause intraspecific populations to respond differently to defoliation and competitive interactions. In our study, grazing history differences were seen in mature shrubs and in seedling dynamics. These data show that a short (20 year) removal of grazing can alter populations of many species, while the same removal may go unnoticed in grass basal cover. We suggest that comparisons of protected and grazed ranges be monitored via many different parameters.

Acknowledgments

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Invasion of Alien Annuals and Ecological Consequences in Salt Desert Shrublands of Western Utah

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Renée Van Buren
Stanley G. Kitchen

Abstract—Vegetation plots in experimentally grazed pastures at the Desert Experimental Range in west-central Utah have been mapped periodically since 1935. The pastures have been grazed at the same intensity and in the same season by sheep from 1935 to the present. Records show that *Bromus tectorum* and *Salsola pestifer* were observed on mapped plots in 1958, although the latter species was reported from the range in 1937. *Halogeton glomeratus* appeared first in 1969. All of these species had become common on both grazed and ungrazed plots by 1989, although plant density and vigor of these aliens were reduced on ungrazed sites. Frequency of occurrence of these species has increased steadily since their first appearance. Experimental studies suggest that soils from areas dominated by *Halogeton* and *Salsola* are associated with lower survival of *Ceratoides lanata* seedlings than soils from healthy *Ceratoides* stands.

The Desert Experimental Range (DER) is a 55,000 acre experimental area in Millard County, west-central Utah. Sheep grazing trials were initiated there in experimental pastures in 1935 and have continued uninterrupted and with only minor changes to the present (Clary and Holmgren 1982). The grazing treatment design and early results were described by Hutchings and Stewart (1953). More recently, grazing effects on shrubby species have been reported by Harper and others (1990). This paper represents an attempt to evaluate the role of annual plant species in the salt desert shrublands that dominate the DER. Prior to this study annual species had been pooled together without reference to individual species. Hutchings and Stewart (1953) show that all minor herbaceous species including annuals rarely contributed more than 18% of the above ground production.

The vegetation under consideration was initially dominated by shrubs, primarily shadscale (*Atriplex confertifolia*) and winterfat (*Ceratoides lanata*). Perennial grasses including Indian ricegrass (*Stipa hymenoides*), galleta grass (*Hilaria jamesii*), three-awn (*Aristida purpurea*), and sand dropseed (*Sporobolus cryptandrus*) occur as subordinate species on better managed ranges. In years of above-average precipitation, native annual species such as sixweeks grama (*Bouteloua barbata*), Hooker's eriogonum (*Eriogonum hookeri*), Palmer's buckwheat (*E. palmerianum*), thymeleaf spurge (*Euphorbia serpyllifolia*), broadlobe gilia (*Gilia hutchinsifolia*), western stickseed (*Lappula occidentalis*), desert pepperplant (*Lepidium montanum* var. *montanum*), false buffalograss (*Munroa squarrosa*), and crenulate phacelia (*Phacelia crenulata*) were a conspicuous part of the vegetation prior to the advent of aggressive alien annuals.

Long-term (1951-1980) precipitation records at the DER show an average annual total of 6.12 inches. Average annual temperature for that period was 49.0 °F with means of 26.4° and 73.8° for January and July, respectively. About 53% of the annual precipitation was received during the growing season (May 1 and Sept. 30) in the period 1951 to 1980 (National Oceanic and Atmospheric Administration 1982).

Methods

The grazing trials considered here have been applied to 20 fenced pastures (240-360 acres in size). Three grazing intensities (arbitrarily referred to as light, moderate, or heavy) that have averaged about 10, 14, and 17 sheep days per acre have been applied to various pastures. Stocking rates have been varied annually within the foregoing limits depending upon annual forage production in order to achieve a somewhat uniform degree of utilization from year-to-year for key forage species (Hutchings and Stewart 1953). Each grazing intensity class was applied in each of three seasons (Nov. 15-Jan. 3, Jan. 4-Feb. 23, and Feb. 24-Apr. 10). Every grazing intensity-season of use combination was replicated at least twice, except for moderate use in midwinter which is represented but once in the research design. The preceding statement assumes that split season use in which pastures are grazed in the early and midwinter season is not significantly different from early winter or midwinter grazing alone. It is further assumed that any split season combination of early or midwinter use with late winter use does not differ significantly from late season grazing alone. Both of the preceding assumptions are compatible with conclusions drawn by Blaisdell and Holmgren (1984) and Harper and others (1990). Any one pasture has been grazed at the same intensity and in the same season throughout the 54 year period covered by this study (1935-1989) (Hutchings and Stewart 1953).

Two 1 acre exclosures were constructed in 16 of the 20 pastures in 1935. Two permanently marked monitoring

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plots were placed in each exclosure at time of construction. These plots are 100 ft^2 (5 ft by 20 ft) in area. At least two additional plots were established at the same time on sites of comparable terrain, soils, and vegetation in grazed areas near each exclosure. Most plots in and adjacent to exclosures were mapped in 1935 using a 1.0 ft^2 grid marked off in .01 ft^2 subunits (Clary and Holmgren 1987). The mapping grid frame was secured to heavy steel pegs permanently driven into the soil at the corners of the 100 ft^2 monitoring plots. The plots considered in this paper were chosen because they appeared to belong to a range site type with the potential of supporting similar vegetation under uniform grazing use. The 48 plots used in this study were remapped periodically using the same procedures as in 1935 and a standardized form for recording results. The plots were reinventoried in 1935, 1936, 1937, 1959, 1968, 1975, and 1989. For our summary analyses, each map was subdivided into ten 2 ft x 5 ft subunits. The number of individuals (density) of each annual plant species was determined for each 10.0 ft^2 subplot for each year of record. Our summary analyses also report the percentage of all 2 ft x 5 ft subplots that contain any individuals of each species (frequency of occurrence). The location of plots and grazing treatments applied to the plots and subplots used in this paper are reported in table 1.

In an attempt to learn something of the separate effects of grazing intensity and season of grazing, all grazed plots are analyzed in two different ways. In a first analysis, plots were sorted into two groups: (1) light or moderate grazing intensity with season of use being ignored and (2) heavy grazing intensity again with season of use ignored. In a second analysis, all plots were sorted into two groups: (1) plots grazed in early or midwinter or (2) plots grazed in late winter. These groupings were suggested by results of earlier studies (Blaisdell and Holmgren 1984; Harper and others 1990) which show little vegetational difference between areas grazed at either light or moderate intensities, but significant differences between areas grazed at those intensities and areas grazed heavily. Likewise, those workers have concluded that early and midwinter use does not differ significantly, but late winter use has a more damaging effect on the ranges here considered.

We have evaluated the influence of soils that have supported dense stands of halogeton and Russian thistle since 1970 on winterfat seedling establishment. Surface soil samples were collected from an area where flood waters resulted in the death of winterfat in 1969. The dieoff area is located in the southeast ¼ of section 11, T.25 S., R.17 W. (the 4 unnumbered pastures, fig. 4 of Hutchings and Stewart 1953). A large stand of nearly pure winterfat occupied the area prior to the flooding event. Minor local differences in elevation resulted in the flood waters overflowing winterfat plants on an irregularly shaped area across the extreme southeasterly corner of the quarter section of concern. The winterfat plants thus irrigated by the July 1969 flood greened up and grew vigorously until cold weather arrived in late autumn. For unknown reasons, the flood irrigated plants did not survive the 1969-70 winter. The dieoff area was immediately invaded by halogeton and Russian thistle. Those species have continued to dominate the site from 1970 to the present. Although winterfat still exists in healthy stands along the margins of the dieoff area, that species has not reoccupied the flooded area.

In 1987, workers familiar with the dieoff event initiated a study to determine why winterfat was not reoccupying the area from which it had been displaced. Soil samples (top 2.0 inches of the profile) were taken at 10 locations within the dieoff zone and the adjacent, intact winterfat stands in May 1987. Subsamples were analyzed for texture, pH, electrical conductivity and exchangeable sodium by the Soil Analysis Laboratory, Department of Agronomy and Horticulture, Brigham Young University. The remainder of each soil sample was placed directly into 5.0 inch diameter, drained pots for winterfat seeding trials under greenhouse conditions. Seed used for these initial trials was obtained from field collections at the DER.

We also attempted to determine whether the barrier to winterfat invasion of the site was biological (competition) or abiotic (soil chemistry). Toward that end, two experiments were initiated in the summer of 1987. (1) All competing plant cover was removed from 10 milacre (43.6 ft^2) circular plots within the chenopod annual stand and within 5 ft of the winterfat-annual ecotone, and (2) 10 soil sample pairs were collected along the winterfat-annual ecotone and seeded with winterfat under greenhouse conditions. Each member of a soil sample pair was collected within a few yards of each other but in either the intact winterfat stand or in the chenopod annual stand. The competition removal trial was run through the growing seasons of both 1988 and 1989. The initial winterfat seeding trial was conducted under greenhouse conditions during the months of February and March 1988.

In July of 1988, 40 additional pairs of soil samples were collected along the winterfat-chenopod annual ecotone described above. Half of these soil samples from both winterfat and chenopod annual zones were immediately placed into individual plastic bags and fumigated for 40 hours with methyl bromide in an attempt to destroy soil microbes. After treatment, each fumigated soil sample was subdivided and placed in three 5.0 inch diameter drained pots. Non-fumigated soil samples were likewise divided into three equal subsamples and placed in 5.0 inch diameter pots. Twenty of the original soil samples were thus fumigated and 20 were reserved as untreated controls from both the chenopod annual area and the intact winterfat stand.

Table 1—Pastures, grazing treatments, and number of plots used in each treatment class. Basic data are on file at the Shrub Sciences Laboratory, Intermountain Research Station, U.S. Forest Service, Provo, UT.

Grazing treatment	Pastures used	No. plots used
Ungrazed exclosures	4, 6, 8, 10, 13, 15	18
Light grazing		
Early and/or midwinter	4, 13	10
Late winter	10	4
Moderate grazing		
Early and/or midwinter	—	—
Late winter	6	4
Heavy grazing		
Early and/or midwinter	8	4
Late winter	15	8
Total plots		48

For the second seeding trial, winterfat seed was collected near the dieoff area and hand sorted to produce seed lots that showed no mechanical damage and were uniform in plumpness and size. Seeds were soaked overnight in distilled water and hand planted (4 per pot) into pots that contained prewetted soil from the dieoff or intact winterfat stand sites. Half of the pots from each site contained soil that had received methyl bromide fumigation in late July 1988 and stored dry in individual plastic bags until used for the seeding trials. Pots were sown with winterfat seeds in early September 1988. Pots were maintained in an outdoor lathe house for this portion of the study which ran from early September through October. Pots were rewetted as needed to maintain moist but not saturated conditions. Pots were monitored on Mondays, Wednesdays, and Fridays to provide records of seedling emergence and survival. The experiment was terminated at the end of the final week of October 1988.

Plant nomenclature in this paper follows that of Welsh and others (1993). Species identification was facilitated by Goodrich's (1986) flora for the DER. Statistical tests employed included unpaired t-tests based on a model proposed by Snedecor and Cochran (1967).

Table 2—Native annual species encountered at any time on the plots considered.

Scientific name	Common name
Allionia incarnata	Trailing four-o'clock
Bouteloua barbata	Sixweeks grama
Camissonia boothii ssp. *alyssoides*	Alyssum evening primrose
Chaenactis macrantha	Bighead chaenactis
Chenopodium fremontii	Fremont's goosefoot
Cryptantha circumscissa	Opening cryptanth
Descurainia pinnata	Pinnate tansy mustard
Eriogonum hookeri	Hooker's eriogonum
E. palmerianum	Palmer's buckwheat
E. schockleyi	Schockley's wild buckwheat
Euphorbia serpyllifolia	Thymeleaf spurge
Gilia depressa	Depressed gilia
G. hutchinsifolia	Broadlobe gilia
Lappula occidentalis	Western stickseed
Lepidium montanum var. *montanum*	Desert pepperplant
Machaeranthera canescens	Hoary aster
Munroa squarrosa	False buffalograss
Phacelia crenulata var. *corrugata*	Crenulate phacelia
Townsendia florifer	Showy townsendia

Results

Dates of First Appearance

Only four alien species appeared on the plots considered in this study during the 54 year period of observation. Tumbling orach (*Atriplex rosea*), cheatgrass, and Russian thistle were first observed on mapped plots in 1958. The first two species were uncommon on the plots in that year: each occurred in only 0.1% of the 480 2 ft x 5 ft subplots sampled. Russian thistle, however, had a frequency of occurrence of 10.1% in those subplots in 1958. Hutchings and Stewart (1953) show that Russian thistle made a measurable contribution to plant community biomass in 1937 (their table 7) at one site on the DER. Halogeton's first appearance on plots considered in this study was in 1969, when it showed a frequency of occurrence of 4.3%. Since the intervals between samples are large in this study, it is unclear when each alien first arrived in the area. However, since all of the plots of concern were mapped in 1935, 1936, and 1937 and no mention was made of any nonnative species on the plots, they probably were not widespread on the DER prior to the 1940's.

Native Annuals

Native annual species encountered at any time on the plots considered in this paper are noted in table 2. Floristic richness for the study area is low with only 19 species of annuals being encountered over the 54 year period of concern. The performance of individual annual species through that period is reported in table 3. The most common of the native annuals were sixweeks grama, thymeleaf spurge, western stickseed, desert pepperplant, false buffalograss, and crenulate phacelia. Half of these species have the C-4 photosynthetic pathway (sixweeks grama, thymeleaf spurge, and false buffalograss), while the remainder utilize the C-3 photosynthetic pathway. Species in the former group are warm season species dependent on precipitation falling in the summer season (June through September), while C-3 species germinate in response to cool season precipitation. Annual species that carry out C-3 or C-4 photosynthesis form two rather distinct assemblages at the DER and are rarely seen simultaneously in roughly equal abundance (table 3 and fig. 1). The census years 1935, 1936, and 1975 were "C-4 years," while 1937, 1959, 1968, and 1989 were decidedly "C-3 years" for native annuals. It will be noted, however, that alien C-3 and C-4 annual species are much less dependent than native species on distinctly cool or warm season precipitation for germination and growth (table 3).

Although we analyzed the data to identify annual species that were seriously handicapped by the more stressful grazing treatments, preferred the ungrazed exclosures, or were indifferent to treatments, ambiguous patterns of response were the rule. Five species show no apparent response to any grazing treatment: sixweeks grama, thymeleaf spurge, western stickseed, desert pepperplant, and showy townsendia (table 3). Three species show a slight preference for ungrazed exclosures (pinnate tansy mustard, hoary aster, and crenate phacelia), but their responses fell far short of statistical significance. A single species (false buffalograss) has a tendency to perform best under moderate grazing treatments (early or midwinter or light to moderate use), but again the response was too variable to yield statistical significance (table 3). The 3 alien annuals (cheatgrass, halogeton, and Russian thistle) are highly intrusive in ungrazed exclosures (table 3), but those plants rarely become large under such conditions. Figure 2 shows that although cheatgrass became large enough to alter the aspect of the landscape in pastures grazed heavily in late winter (DER pasture 14 and 15), it was too small to be seen from a distance in an adjacent pasture grazed moderately in early winter (DER pasture 16). Both halogeton and Russian thistle are similarly suppressed in well managed pastures at the DER, even though they may dominate burrow-mound

Table 3—Density (average number of individuals/100 ft² plot) response of annual species to the various grazing treatments at the DER over the period 1935-1989. All species that had an average density of over 1.0 individual per 100 ft² for any inventory period or grazing treatment are reported. Numbers in parentheses below each species name describe species origin and photosynthetic pathway (see footnotes for explanation). Treatments are as follows: Excl. = exclosures (ungrazed); L. or M. = light or moderate intensity grazing (season ignored); heavily = heavy intensity grazing (season ignored); E. or M. = early or midwinter grazing (intensity ignored); and late = late season grazing (intensity ignored).

Species	Grazing treatment	1935	1936	1937	1959	1968	1975	1989
					Ind./100 ft²			
Bouteloua barbata	Excl.	20.3	46.4	0.0	0.0	1.8	7.5	0.0
(1,2)	L. or M.	26.3	46.1	0.0	3.2	0.0	0.9	0.0
	Heavily	1.9	73.0	0.0	0.0	0.3	0.0	0.0
	E. or M.	2.9	38.8	0.6	0.0	0.1	0.9	0.0
	Late	29.2	68.6	0.0	0.3	0.4	0.1	0.0
Bromus tectorum	Excl.	0.0	0.0	0.0	0.1	0.0	0.0	29.5
(3,4)	L. or M.	0.0	0.0	0.0	0.1	0.0	0.0	1.8
	Heavily	0.0	0.0	0.0	0.0	0.0	0.0	53.7
	E. or M.	0.0	0.0	0.0	0.0	0.0	0.0	1.9
	Late	0.0	0.0	0.0	0.0	0.0	0.0	90.8
Descurainia pinnata	Excl.	0.0	0.0	0.0	6.5	0.0	0.0	0.0
(1,4)	L. or M.	0.0	0.0	0.0	0.1	0.0	0.0	0.0
	Heavily	0.0	0.0	0.0	0.5	0.0	0.0	0.0
	E. or M.	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	Late	0.0	0.0	0.0	0.4	0.0	0.0	0.0
Euphorbia serpyllifolia	Excl.	5.6	11.2	0.0	0.0	1.5	15.1	0.0
(1,2)	L. or M.	5.6	12.9	0.0	0.0	0.1	5.9	0.0
	Heavily	2.2	36.0	0.0	0.1	8.5	13.5	0.0
	E. or M.	7.5	28.8	0.0	0.0	0.5	22.4	0.0
	Late	2.9	5.3	0.0	0.1	0.3	7.9	0.0
Halogeton glomeratus	Excl.	0.0	0.0	0.0	0.0	0.1	1.9	130.2
(3,2)	L. or M.	0.0	0.0	0.0	0.0	0.0	0.4	0.0
	Heavily	0.0	0.0	0.0	0.0	6.3	7.3	2.2
	E. or M.	0.0	0.0	0.0	0.0	0.0	0.7	0.0
	Late	0.0	0.0	0.0	0.0	3.1	5.5	1.6
Lappula occidentalis	Excl.	0.6	0.0	0.0	2.7	8.8	0.4	0.1
(1,4)	L. or M.	0.0	0.0	0.0	0.0	6.5	0.6	0.0
	Heavily	0.0	0.0	0.0	4.9	5.4	4.8	0.0
	E. or M.	0.0	0.0	0.0	5.2	0.0	1.4	0.0
	Late	0.0	0.0	0.0	5.5	0.1	1.9	0.0
Lepidium montanum	Excl.	0.0	3.4	0.3	6.6	6.3	0.8	0.0
(1,4)	L. or M.	6.4	7.1	4.4	14.9	6.1	0.8	0.0
	Heavily	0.0	0.3	0.0	3.8	1.6	2.0	0.0
	E. or M.	7.0	1.7	0.4	24.6	1.0	1.1	0.0
	Late	2.8	10.5	6.8	11.7	3.7	4.1	0.0
Machaeranthera	Excl.	0.0	0.0	0.0	1.1	1.4	0.7	0.0
canescens (1,4)	L. or M.	0.0	0.0	0.0	0.0	1.0	0.3	0.0
	Heavily	0.0	0.0	0.1	0.9	0.0	0.4	0.0
	E. or M.	0.0	0.0	0.0	0.0	0.0	0.5	0.0
	Late	0.0	0.0	0.1	0.7	0.1	0.5	0.0
Munroa squarrosa	Excl.	3.6	7.2	0.0	0.0	0.1	4.8	0.0
(1,2)	L. or M.	6.2	17.4	0.0	0.0	0.6	3.4	0.0
	Heavily	0.3	15.5	0.0	0.0	1.1	1.1	0.0
	E. or M.	6.7	24.5	0.1	0.0	0.1	4.4	0.0
	Late	3.0	7.6	0.0	0.0	3.1	4.4	0.0
Phacelia crenulata	Excl.	0.7	0.3	0.3	21.7	1.1	0.0	0.0
(1,4)	L. or M.	0.6	0.9	0.0	2.5	0.0	0.0	0.0
	Heavily	0.0	0.0	0.0	11.3	0.5	0.5	0.0
	E. or M.	0.0	0.0	0.0	1.3	0.0	0.0	0.0
	Late	0.6	1.5	0.0	9.4	0.0	0.9	0.0
Salsola pestifer	Excl.	0.0	0.0	0.0	2.7	18.3	4.4	16.2
(3,2)	L. or M.	0.0	0.0	0.0	7.4	7.3	2.5	0.4
	Heavily	0.0	0.0	0.0	14.5	262.8	14.7	24.6
	E. or M.	0.0	0.0	0.0	0.0	10.1	2.6	0.4
	Late	0.0	0.0	0.0	10.9	131.3	3.6	17.6
Townsendia florifera	Excl.	0.0	0.0	0.0	0.1	1.3	0.1	0.0
(1,4)	L. or M.	0.0	0.0	0.0	2.7	0.3	0.1	0.0
	Heavily	0.0	0.0	0.0	0.0	1.1	0.3	0.0
	E. or M.	0.0	0.0	0.0	3.5	0.0	0.1	0.0
	Late	0.0	0.0	0.0	2.7	0.1	0.0	0.0

(con.)

Table 3—(Con.)

Species	Grazing treatment	1935	1936	1937	1959	1968	1975	1989
Total native individuals in sample		1418	4251	91	1371	886	1018	2
C-4 Native Individuals		1269	4036	0	58	193	852	0
C-3 Native Individuals		149	215	91	1313	693	166	2
Total alien individuals in sample		0	0	0	360	3693	429	4171

1. Native species
2. C-4 photosynthetic pathway
3. Alien species
4. C-3 photosynthetic pathway

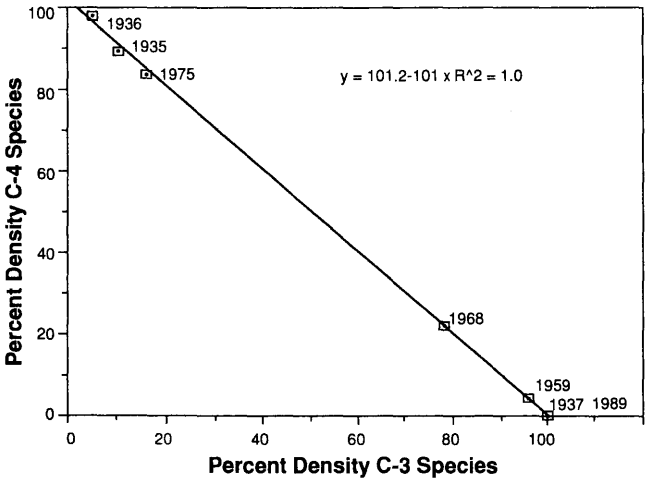

Figure 1—The relative density of C-3 and C-4 native annuals at the DER in years of record. The density of individuals of the two groups is significantly and negatively correlated.

complexes regularly disturbed by kangaroo rats or pocket gophers in such pastures. Careful analysis of the basic data (table 3) demonstrate that cheatgrass and Russian thistle are favored by the two most stressful grazing treatments (heavy grazing or any grazing treatment in late winter). Halogeton seedling number was also favored by stressful grazing treatments in 1968 and 1975, but in 1989 halogeton had the greatest number of seedlings in exclosures, but seedlings remained smaller in exclosures than in grazed areas. Under either of the more stressful grazing treatments, cheatgrass, halogeton, and Russian thistle display more than an order of magnitude increase in size (fig. 2) in favorable years.

Comparative Ecology of Natives and Aliens

The average 100 ft^2 plot rarely supports more than 4 or 5 annual species at the DER (table 4), a fact that again emphasizes the low species richness of the salt desert shrub

Figure 2—A view of the fence line separating pastures 14 and 16 at the DER, early June 1995. Pasture 14 lies to the left of the fence line (arrow): it is grazed heavily in mid- and late winter. The darker color is due to an abundance of cheatgrass in the mature color phase of reddish brown. Pasture 16 to the right of the fence line is grazed at moderate intensity in early winter. The lighter color is due to year-old foliage of Indian ricegrass and new foliage of winterfat.

Table 4—Some comparative ecological characteristics of native and alien annuals at the DER. For this analysis, all plots have been pooled, regardless of grazing treatment. Frequency is for 2 ft x 5 ft subplots.

Characteristic	Year						
	1935	1936	1937	1959	1968	1975	1989
Natives							
Average No. Species Per 100 ft^2 Plot	1.5	3.2	0.7	3.4	2.3	3.4	0.2
Average No. Individuals Per Species Per Plot	19.5	26.4	4.4	10.7	8.7	9.2	0.5
Average Frequency % Per Species	8.2	24.3	3.4	7.9	5.2	8.5	0.5
Aliens							
Average No. Species Per 100 ft^2 Plot	0	0	0	0.6	0.4	0.6	0.4
Average No. Individuals Per Species Per Plot	—	—	—	13.5	154.3	15.3	213.3
Average Frequency % Per Species	—	—	—	4.1	22.1	13.3	11.2

type of west-central Utah. By 1968, when the three alien species (cheatgrass, halogeton, and Russian thistle) had become well established, it was readily apparent that the alien annuals were unlike native annuals in many ways. The alien species average far larger in size than the native annuals which are often diminutive (usually less than 6 inches tall with delicate, fragile branches). The aliens also appear broader niched than the native annuals existing on a greater variety of microsites (greater frequency values) and at much greater densities (table 4).

Although our results (table 4) show a sharp decline in number of native species per plot in 1989, that result probably should not be inferred to mean that native annual species have disappeared from the study area. It is more likely that 1989 was simply an unusual year in which few native annuals found conditions suitable for germination. More frequent inventory of the study plots used for our study is needed before one can accurately assess the role of alien annuals on performance of native annuals.

Winterfat Reproduction and Alien Annuals

Where runoff water results in the death of winterfat, alien chenopod annuals (halogeton and Russian thistle) quickly invade and become the dominant plant cover. Sites exist at the DER where these annuals have held dominance for over 2 decades. At the winterfat dieoff site described in METHODS, we collected soil samples in 1987 to determine whether the chenopod annuals had altered surface characteristics from those prevailing under intact, adjacent winterfat stands that still existed just a few decimeters away.

As shown in table 5, surface soils from sites dominated by the annuals did differ significantly from those still supporting winterfat in respect to exchangeable Na and electrical conductivity. The chenopod annuals appear to have "pumped" Na from the soil profile and deposited it at the surface as annual leaf and stem growth have died and fallen to the surface.

Although winterfat seed was produced at the study site in both 1987 and 1988 and seed was observed on the competition removal plots, no winterfat seedlings were ever observed in 1988 or 1989. Reasons for the failure of winterfat seedlings to establish on the competition free plots could not be discerned from field observations.

The initial winterfat seeding experiment conducted under greenhouse conditions did result in seedling establishment on both winterfat and chenopod annual soils. By the end of March 1988, there were significantly more winterfat seedlings in pots with winterfat soil than in pots with soil taken

Table 5—Average values (N = 10 in each case) for characteristics of soils from an intact winterfat stand and an immediately adjacent site a few inches lower in elevation where flood waters had caused the death of all winterfat plants 17 years earlier. Chenopod annuals have occupied the dieoff site continuously since the flood. Means followed by the same letter do not differ significantly. Identified significant differences differ at the p≤.05 level.

Characteristic	Vegetation on site	
	Winterfat	Chenopod annuals
Texture		
Sand (%)	65a	57a
Silt (%)	17a	21a
Clay (%)	18a	22a
pH	7.9a	8.1a
Exchangeable Sodium (ppm)	5a	279b
Electrical conductivity (mmhos x 10^3)	0.86a	1.35b

Table 6—Average values for winterfat seedling survival after 30 days. Seeds were germinated and grown in soils taken from beneath healthy winterfat stands and from adjacent areas where chenopod annuals had grown as essentially the only plant cover for the preceding 18 years. Means followed by different letters differ significantly at the .05 probability level.

Treatment	Sample size (no. pots)	% survival (after 30 days)	Total seedlings emerged
Winterfat soil			
untreated	60	47.4a	155a
fumigated	62	55.9a	148a
Chenopod annual soil			
untreated	59	36.6a	148a
fumigated	59	50.3b	160a

from beneath the chenopod annuals. Nevertheless, results were not readily interpretable, because observations had not been adequate to determine whether the observed difference was caused by differential mortality of seedlings in the two soil types or by use of seed of unequal viability in the two soils.

Results of the second seeding trial demonstrate that seedling emergence did not differ between winterfat and chenopod annual soils or between fumigated and nonfumigated soils from either source area (table 6). Although fumigation did enhance seedling survival on soils from the intact winterfat site, the difference was not statistically significant at the $p<.05$ level. Fumigation did significantly increase winterfat seedling survival on soils from the chenopod annual site (table 6).

Discussion

The foregoing results suggest that alien annuals may greatly alter ecological relationships in the salt desert shrub communities of the Great Basin. Since the alien annuals are apparently better able to establish seedlings at a greater variety of sites (for example, have larger frequency values) and in larger numbers (larger density values) than native annuals, we predict that they will become increasingly serious competitors with both native annuals and perennials for safe sites for seedlings. Native annual species that are narrowly adapted to the salt desert shrublands of western North America can be expected to steadily decline in even relatively undisturbed segments of the salt desert shrublands of the Intermountain West. More detailed studies are needed to determine which of the native annuals are at greatest risk. Hunter (1990) has arrived at a similar conclusion concerning the probable impact of alien annuals on native plant species in the Mojave Desert at the Nevada Test Site managed by the U.S. Department of Energy.

Although major alien species such as cheatgrass, halogeton, and Russian thistle do reproduce and set some seed in even quite virgin communities, figure 2 graphically shows that salt desert shrub vegetation can greatly suppress growth of the alien annuals, if they are grazed at moderate rates in early or midwinter only. Whether such grazing treatments could hold the alien annuals at bay indefinitely is unknown at the present time, although some (Svejcar and Tausch 1991; Tausch and others 1994) suggest that aliens will eventually come to dominance on even the best managed of Great Basin landscapes. It is important that many high condition rangelands be carefully monitored to learn whether any management schemes can preserve examples of the presettlement vegetation of the Great Basin.

It has long been understood that some alien annuals greatly shorten the fire return cycle (Whisenant 1990) on semiarid and arid lands throughout western America. Shortened fire return intervals are known to eliminate fire intolerant shrubs and herbs from natural vegetations and disrupt many natural processes in associated systems (Billings 1994). Our results (table 6) suggest that alien annuals may disrupt natural communities in yet another way. The data suggest that annual chenopods have enhanced the likelihood that soil microbes will kill emerging seedlings of at least winterfat. We have preliminary agar plate culture data for microbial growth from fumigated and nonfumigated soil dilutions which suggest that fumigation with methyl bromide was particularly effective in reduction of microfungal growth. Several microfungal genera are known to be facultative pathogens that exist primarily as saprobes feeding on soil organic matter. Under some conditions, however, such saprobes may attack and kill germinating seeds and seedlings. Such attacks are described as "damping-off disease" (Agrios 1989).

Recent field observations suggest that other native perennials in addition to winterfat may be inhibited from invading dense stands of alien annuals by either competition, soil pathogens or both. The chenopod annual stand considered in tables 5 and 6 is essentially free of all perennial vegetation. Although even the adjacent, intact winterfat stand has few perennial plant associates, the near absence of native perennials in stands of alien chenopod annuals seems unusual and suggestive of severely adverse interactions between the native perennials and the alien annuals. Dead and dying winterfat and perennial grass plants (primarily Indian ricegrass) along ecotones between the alien annuals and adjacent native communities suggest that the disturbance area is slowly expanding. The "damping-off" fungi are known to be weak parasites of the root systems of adult plants as well as devastating to seedlings (Agrios 1988).

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Plant Community Changes Over 54 Years Within the Great Basin Experimental Range, Manti-La Sal National Forest

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Abstract—Plant community changes and natural succession over time impact forage values, watershed quality, wildlife habitat, and ecosystem dynamics. Comparisons were made between a vegetation map of community types completed in 1937 by the U.S. Forest Service, and vegetation maps compiled in 1990 of the same areas by satellite imagery, and through 1991 areal photo interpretation combined with ground truthing. The study area includes nearly all of the drainage in Ephraim Canyon located in central Utah which consists of 6,027 acres (2,439 ha). Elevation ranges from 6,600 to 10,400 feet (2,040 to 3,210 m). Vegetation types ranged from pinyon-juniper woodland through oakbrush, mountain shrub, aspen, conifer and subalpine herbland. The comparison showed significant plant community changes and successional trends over the 54 year period.

Natural succession is a dynamic property of plant communities. Over time intermountain rangelands have been exposed to a number of management practices that may accelerate community dynamics and succession of the vegetation types within these communities. Such management practices include the suppression of wildfire, grazing of domestic livestock, changing numbers of wildlife populations, and the introduction of exotic plant species that can compete with and displace native vegetation (Ellison 1949, 1960; Ellison and others 1951; Monsen and McArthur 1995; Walker and others 1995).

Changes in plant communities impact forage values, watershed quality, wildlife habitat, and ecosystem dynamics. Some vegetative communities seem to be more stabile or at least change at a slower rate. While other communities can change at a more rapid rate, undergoing a complete conversion from one community type to an other in a relatively short period of time.

Loss of aspen (*Populus tremuloides*) and subsequent conversion to conifer forests on the Wasatch Plateau is a concern to forest managers. Aspen is being displaced at an estimated rate of 1,600 acres per year (U.S. Department of Agriculture 1986). These changes are generally slow and are quite difficult to quantify, without the use of long-term ecological study sites. Harniss and Harper (1982) and Mueggler (1994) have documented long term demographics of aspen communities on the Wasatch Plateau, and show aspen is succeeding to conifer dominance on some study sites as well as on a broad scale.

This study was undertaken in an effort to better understand the community dynamics and changes that are occurring on the Great Basin Experimental Range of the Wasatch Plateau. A 1937 map of the vegetation or community types of the Great Basin Experimental Range and adjoining areas of Ephraim (Cottonwood) Canyon was used to compare with present distribution and occupancy. Comparisons between mapping dates offered an opportunity to quantify changes by vegetation types over a 54 year period. To compare present distribution of the major vegetation types to the information from the 1937 map, remote sensing techniques were used.

As the study was undertaken it presented an opportunity to compare vegetation censusing techniques. This paper compares the applicability of two censusing techniques as well as presenting quantified vegetative community changes.

Study Area

The study took place on the Great Basin Experimental Range, which is located on the west front of the Wasatch Plateau, about 5 miles (8 km) east of Ephraim, on the Manti-La Sal National Forest in central Utah. The Great Basin Experimental Range has been a focal point for conducting research dealing with community ecology and management practices affecting watersheds, rangelands, and forest types since it was established as the Utah Experiment Station in 1912 (Keck 1972; McArthur and Monsen in press).

The study area ranges in elevation from 6,600 to 10,400 ft (2,040 to 3,210 m). The area includes all of Ephraim Canyon, which is about 5 miles (8 km) long by 0.9 to 2.5 (1.4 to 4.0 km) miles wide. Total area of the study is 6,027 acres (2,439 ha). The major vegetation types occurring throughout the canyon include, big sagebrush (*Artemisia tridentata* ssp.), pinyon-juniper (*Pinus edulis-Juniperus osteosperma*), oakbrush-mountainbrush (*Quercus gambelii*, *Acer grandidentatum*, *Amelanchier alnifolia*, *Symphoricarpos* sp., *Cercocarpus* sp., *Prunus virginiana*, *Sambucus* sp.), aspen, aspen-conifer, spruce-fir (*Picea engelmannii*, *Picea pungens*, *Abies lasiocarpa*), mountain fir (*Abies concolor*, *Pseudotsuga menziesii*), and sub-alpine (including mostly grasses, tall

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forbs, sedges and shrubs), all interspersed with small meadows and small riparian corridors.

Methods

The historic vegetation map from 1937 was meticulously made. The vegetation communities were divided into 224 distinct vegetative types, including overstory and understory composition. This detail allowed a high confidence of the vegetative components of this area in 1937. The vegetation was subdivided into units as small as 0.25 acres (0.10 ha).

To acquire present vegetation coverage of the study area, remote sensing data from the Utah GAP Analysis project was suggested. As part of the GAP Analysis, Utah's land cover has been classified into 31 cover-types and 5 land-use classes. This classification was done using Landsat TM data from 1985-1993, modelling and ancillary data. Details of the process are contained in Edwards and others (1995). National GAP Analysis guidelines required individual pixel cover-type data be aggregated to a minimum mapping unit of 247 acres (100 ha), but through classification process minimum mapping unit data at 12.3 acres (5 ha) was made available for our project.

The UNESCO hierarchical classification system of vegetation (Driscoll and others 1984) has been adopted by the GAP Analysis project. Of the 31 cover-types or vegetation-type classifications in Utah, 19 appear within the Ephraim canyon study area. This compares to 224 vegetation types for the 1937 map.

To compare the 1937 Map with the GAP Analysis cover, the 1937 Map was scanned using a VEMCO Multiscan 5000 scanning and the CadImage/SCAN Version 1.3 software. ARC/INFO (ESRI, Redlands, CA) software was used to digitize and then register the 1937 Map coverage to UTM coordinates. The boundary of the 1937 map was used to clip out the same area from the GAP coverage.

To compare the vegetation categories of the 1937 map to the GAP Analysis vegetation cover-types, the 1937 vegetation types were reclassified to fit within the GAP codes.

In comparing the 1937 map to the GAP Analysis, it became clear that the detail of the GAP was greatly reduced. Whereas, the 1937 map was very accurate and detailed. For instance, white fir, as a major overstory species, is contained in 20 separate vegetation types. In the GAP Analysis, white fir is the primary tree species in one class and associated in only five other classes.

After initial comparison between the two coverages and conducting some ground truthing, it became apparent that the GAP Analysis had been designed for more broad area applications and would not be applicable to this detailed analysis. It was evident that another method of inventorying the present vegetation was necessary to accurately census the distribution of present vegetative communities. We commenced mapping vegetative communities using 1991 color aerial photos (1:13,000 scale). After acquiring the aerial photos of the study area, we proceeded to outline distinct vegetation types, and verified with ground truthing. When field work was completed, these photos were then scanned using the previously described scanning equipment. The images were then digitized and registered with the ARC/INFO software to UTM coordinates, and finally clipped to the 1937 map boundary.

Results and Discussion

In comparing the three vegetation coverages, distinct problems were found with the GAP for some vegetative types. For example the alpine herbland type, through ground truthing and other observation was expected to show little change. Yet, comparing the three coverages, the GAP showed significantly less sub-alpine area than was present in 1991 or 1937 (table 1).

Another vegetation type causing concern was the oakbrush. The GAP showed oakbrush decreasing from 907 acres (366 ha) in 1937 to 425 acres (172 ha) in 1989. This is much less than the 1,404 acres (567 ha) of oakbrush shown to be present in the 1991 photos (table 1). Through ground truthing we discovered the GAP coverage classified much of the oakbrush as aspen. This is also demonstrated by the large acreage shown by the GAP for aspen, and the small area shown for the aspen/conifer type. For other vegetation types including juniper, the GAP analysis correlated better with

Table 1—Area in acres[1] and percent of total area of specific vegetation types for three sampling methods.

Cover type	Method					
	1937-Map		1989-Gap		1991-Photo	
	Area	Percent	Area	Percent	Area	Percent
Aspen/Conifer	1,404	23	35	1	689	11
Alpine	1,194	20	70	1	1,018	17
Oak	907	15	425	7	1,404	23
Aspen	872	15	2,424	40	450	8
Conifer	734	12	1,727	29	1,171	19
Pinyon	208	4	208	4	262	4
Sagebrush	183	3	133	2	54	1
Mt.shrub	171	3	519	9	156	3
Total[2]	5,673		5,541		5,204	

[1]Multiply by 0.404 to obtain ha.
[2]Difference between totals, result from other minor cover types not included in the table.

our mapping (table 1). These differences and misclassification may be due to the specific spectral signature associated with the cover types.

Due to the ambiguity of the GAP analysis, comparisons among community types will only be made between the 1937 map and the 1991 photo interpretation.

Aspen-conifer association is of great concern for land managers who recognize that aspen is being displaced by conifer at an accelerated rate. From current mapping it is apparent that aspen has been reduced 422 acres (171 ha), a 48% reduction. Aspen stands are being maintained and spreading in some areas, but at a rate slower than it is being displaced by conifer. Less than half of the aspen present in 1937 (872 acres) are still pure stands in 1991 (450 acres). Sites consisting of a mixed aspen-conifer coverage in 1937 have been reduced from 1,404 acres (567 ha) to 689 acres (278 ha) in 1991, a 51% reduction. Sites initially supporting a mixture of aspen and conifer, are now mostly dominated by conifers.

Information obtained prior to this study indicated that conifer was displacing the aspen and mixed aspen types (U.S. Department of Agriculture 1986). The results of our findings support this information and confirm a definite increase in area and density of conifer. Conifers are also expanding into the alpine areas. Oakbrush is also expanding, while Big sagebrush is being lost (table 1).

Conclusions

Using the percentages as a guide (table 1), the study area can be characterized in 1937 as one dominated by mixtures of aspen/conifer, pure aspen, pure conifer, alpine herbland, with strong contributions from oakbrush. In 1937 the contribution from pinyon, sagebrush and mt. shrub were minor. From the areal photo data of 1991 the study area has changed from a two-level to a three-level system. In 1991 study sites were dominated by oak, pure conifer and alpine herblands. Presently there is a middle level of importance represented by aspen/conifer and aspen. Pinyon, mt. shrubs and sagebrush communities are rather minor components. Alpine herblands have remained quite constant, with about the same acres recorded in 1937 as in 1991. This is also represented in the percentage data (table 1).

In assessing the techniques used, it is apparent that the GAP analysis is not adequate for small areas and requires extensive ground truthing. Using aerial photographs to closely map the vegetation was much more accurate on the scale of this study. However, more information is required to increase the accuracy of this method.

The techniques used in this study demonstrate that pinpointing areas to equate ecological changes is possible and necessary. Management decisions can be addressed more specifically regarding each area. These techniques can be used in assessment of all major vegetation types throughout many environments. Managers have the opportunity to address questions and decisions within specific vegetative types, and determine if conversion patterns influenced by land management practices are desirable and acceptable. If not, perhaps management strategies need to be reevaluated and changed. A more proactive management can then be applied to alter conversion patterns.

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Seral Stage Classification and Monitoring Model for Big Sagebrush/Western Wheatgrass/Blue Grama Habitat

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Abstract—An ecological classification model for seral stages was developed for big sagebrush (*Artemisia tridentata*) shrub steppe habitat in Thunder Basin National Grassland, Wyoming. Four seral stages (early to late succession) were defined in this habitat type. Ecological seral stages were quantitatively identified with an estimated 92% level of accuracy when this model was applied in the field. The number of plant species was greater in the early seral stage and decreased throughout to the late seral stage. This model will assist range managers to monitor and evaluate management alternatives by assessing changes in species composition and trends over time within and between seral stages. Canopy cover (%) and frequency of occurrence (%) for big sagebrush, western wheatgrass (*Agropyron smithii*), and blue grama (*Bouteloua gracilis*) are the only required variables to measure in the field to determine and monitor seral stages. The developed model may only be applied to this habitat type, and caution is expressed when applying it beyond Thunder Basin National Grassland.

Determination of proper management alternatives in sagebrush communities is important but difficult when managing for multiple-use objectives. The ability to identify a range of alternatives and relate them to prescribed management activities is essential to achieve a desired condition (Dyksterhuis 1985; Uresk 1990; UCT 1995). Determination of seral stages using multivariate statistical models of plant succession allows managers to monitor prescribed practices. Plant succession has been used for rangeland monitoring for many years (Sampson 1919; Humphrey 1949; Dyksterhuis 1949; MacCracken and others 1983; Hanson and others 1984; Dyksterhuis 1985; Hoffman and Alexander 1987; Girard and others 1989; Westoby and others 1989; Uresk 1990). However, accurate and repeatable quantitative procedures that do not rely on subjective interpretations are often lacking.

Over the last few decades, the rangeland condition classification concept has provided resource managers a framework for evaluating vegetation changes in response to natural events (weather, fire) and management practices (Dyksterhuis 1949; Westoby and others 1989; Smith 1988; Holechek and others 1989). Range classification methods used by the Forest Service (USDA-USFS 1968) and Soil Conservation Service (USDA-SCS 1976) have not been sensitive enough to detect slow plant succession in arid rangeland (Tausch and others 1993; Samuel and Hart 1994). Other multivariate and ordination techniques (Mueller-Dombois and Ellenberg 1974; del Moral 1975; Foran 1986; McLendon and Dahl 1983; Mosely and others 1986) have refined vegetation classification, but did not provide simple practical tools, such as quantitative equations or models, for range managers to determine successional course using measurements of vital vegetation attributes as variables.

The use of range condition based on climax plant communities as a management tool has been strongly criticized (Pendleton 1989; Friedel 1991; Tausch and others 1993; Borman and David 1994; National Research Council 1994; UCT 1995) because of (1) difficulty of determination of the climax vegetation in some habitat types and (2) replacement of climax community by other disclimax plant associations after major disturbances. While the above is true, this research effort provides a classification model that does not require identification of climax vegetation nor does it rely on the comparison of present vegetation to climax vegetation as defined by the USDA-SCS's (1976) procedures. The developed procedure evaluates the full range of plant succession from early to late seral stages within a habitat type that is present today (Uresk 1990). The purpose of this study was to develop an ecological classification tool which will be used by range managers to determine seral stages can be used to decide management alternatives. The objectives were to (1) develop and test an ecological classification model for big sagebrush shrub steppe habitat type and (2) delimit possible applications for the classification model outside Thunder Basin National Grassland.

Study Area

The study was conducted in Thunder Basin National Grassland (TBNG), Wyoming, on the upland big sagebrush shrub steppe habitat type (Thilenius and others 1994). This area encompasses about 380,000 acres of National Forest Service lands.

Soils are predominately aridisols (crushman, forkwood, terro series) and entisols (grummit, samday, shingle, tassel series). Surface textures vary from fine-grayish brown loam (aridisols) to clay loam and grayish sandy loam (entisols) (USDA-SCS 1983, 1990). Elevations in TBNG range from

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3,937 ft (1,200 m) at the southeast corner to a maximum of 5,250 ft (1,600 m) on the surface of the Rochelle Hills. The maximum elevation at the northern part (Spring Creek) is about 4,265 ft (1,300 m) (von Ahlefeldt and others 1992). Climate of TBNG is interior continental with hot summers and cold winters. Strong winds, often up to 40 mph (66 km/h), occur any time of the year. Mean annual precipitation ranges from 12 inches (30 cm) in central TBNG to 16 inches (40 cm) in the northern part (Spring Creek). Mean annual temperatures range from 43 °F (6 °C) to 47 °F (8 °C). The highest temperatures range from 104 °F (40 °C) to 110 °F (44 °C) and the lowest temperatures range from –36 to –44°C. Frost free period averages 120 days (Martener 1986).

Methods

Data collection and analyses followed Uresk (1990). A preliminary ground reconnaissance of the entire TBNG upland big sagebrush shrub steppe habitat began in mid-June of 1993. The ground reconnaissance was conducted to assess the vegetation variability of the study area. Sites were selected so that the range natural variability of the vegetation would be explained by the sampling. Plots that had been excluded from grazing for 50 years were also included in the sampling. Plant nomenclature followed Flora of the Great Plains (Great Plains Flora Association 1986).

Data were collected on 121 macroplots (sites). Each macroplot was randomly selected within one of three perceived seral stages (early, mid, late). A total of 121 macroplots were permanently established throughout the entire big sagebrush shrub steppe habitat in 1993. At each macroplot, 2 parallel 99 ft (30 m) transects were set 66 ft (20 m) apart. Sampling of canopy cover and frequency of occurrence for each plant species occurring within each microplot, 8 x 20 in (20 x 50 cm), was completed at 3.28 ft (1 m) intervals along each transect (Daubenmire 1959). Plant litter, rock cover, and bare ground were also estimated. All macroplot data (60 microplots) for each site were averaged for each plant species (variable). Average canopy cover (%) was multiplied by frequency of occurrence (%) to produce an index value for the analyses (Uresk 1990).

Preliminary data examinations removed minor plant species that were highly variable. Twenty variables (from a total of 150) were subjected to further analyses. Principal component analysis (SAS Institute 1988) further reduced the number of variables to 6 major plant species: big sagebrush, western wheatgrass, blue grama, threadleaf sedge (*Carex filifolia*), prairie junegrass (*Koeleria cristata*), and needle-and-thread (*Stipa comata*). A non-hierarchical clustering procedure, ISODATA (Ball and Hall 1967; del Morel 1975), grouped the 121 sites into 4 distinct clusters (seral stages). Then stepwise discriminant analysis (Norusis/SPSS Inc. 1992) at 0.05 entry level selected big sagebrush, western wheatgrass, and blue grama as the best predictive variables to be used for seral stage classification and monitoring. Misclassification error rates were estimated using cross-validation procedures (SAS Institute 1988). The developed model was subjected to field testing by collecting additional data during the second year (1994).

Results

Four distinct seral stages (early to late) were defined in the TBNG sagebrush shrub steppe habitat. Stepwise discriminant analysis showed significant differences among these seral stages ($P < 0.05$). The developed model consisted of 3 variables (plant species) and 4 Fishers discriminant functions that define the seral stages (table 1). Variables were heavily weighted at individual seral stage, reflecting the biotic potential of each key plant species in predicting dynamics of the vegetation within the ecological system (fig. 1). Big sagebrush is dominant in late seral stage, western wheatgrass in late intermediate, and blue grama in early intermediate (table 2). All 3 plant species showed low percent covers and frequency of occurrences in early seral stage. Big sagebrush, western wheatgrass, and blue grama were the best indicators of seral stages.

This model classifies seral stages by multiplying index values associated with the 3 key plant species by the discriminant coefficients of each seral stage and then summing the products for each seral stage. The greatest of the four discriminant scores indicates assignment of the seral stage. An example of seral stage determination is presented in table 3: a site where the index value for big sagebrush = 4730,

Table 1—Fisher's discriminant coefficients for classification of seral stages in Thunder Basin National Grasslands sagebrush shrub steppe habitat type.

Species	Seral Stages			
	Late	Late Int.[1]	Early Int.	Early
Big sagebrush	0.00551	0.00154	0.00095	0.00113
Western wheatgrass	0.00241	0.01146	0.00505	0.00240
Blue grama	0.00216	0.00399	0.00932	0.00262
Constant	–15.000	–14.070	–15.643	–3.1503

[1]Int. = intermediate.

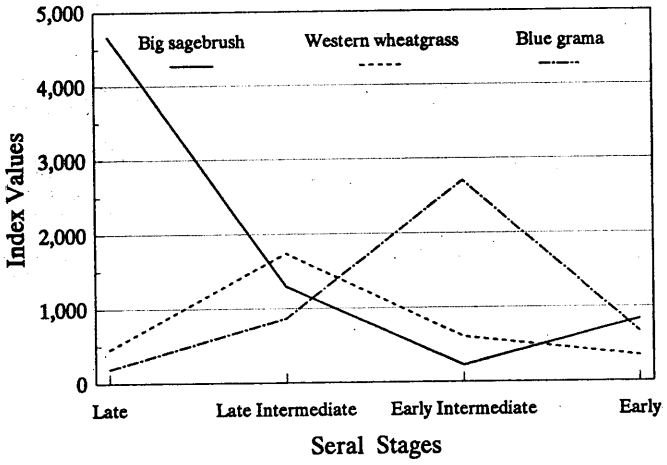

Figure 1—Key plant species with index values (canopy cover (%) x frequency of occurrence (%)) distributed throughout all seral stages in Thunder Basin National Grasslands sagebrush shrub steppe habitat.

Table 2—Canopy cover ($\bar{x} \pm$ SE) and frequency of occurrence ($\bar{x} \pm$ SE) for the key plants throughout the defined seral stages in Thunder Basin National Grassland sagebrush shrub steppe.

Seral stages		Big sagebrush	Western wheatgrass	Blue grama
	n	Canopy cover (%)		
Late	25	55 ± 2.1	8 ± 1.2	6 ± 0.8
Late intermediate	23	22 ± 3.1	20 ± 1.0	14 ± 1.7
Early intermediate	21	7 ± 0.9	8 ± 1.3	30 ± 1.8
Early	52	17 ± 1.6	7 ± 0.6	12 ± 0.9
	n	Frequency of occurrence (%)		
Late	25	85 ± 1.6	60 ± 4.9	32 ± 2.3
Late intermediate	23	60 ± 4.8	85 ± 1.7	61 ± 4.7
Early intermediate	21	27 ± 2.8	63 ± 5.9	87 ± 2.6
Early	52	51 ± 2.8	50 ± 2.6	57 ± 2.7

n = sample size

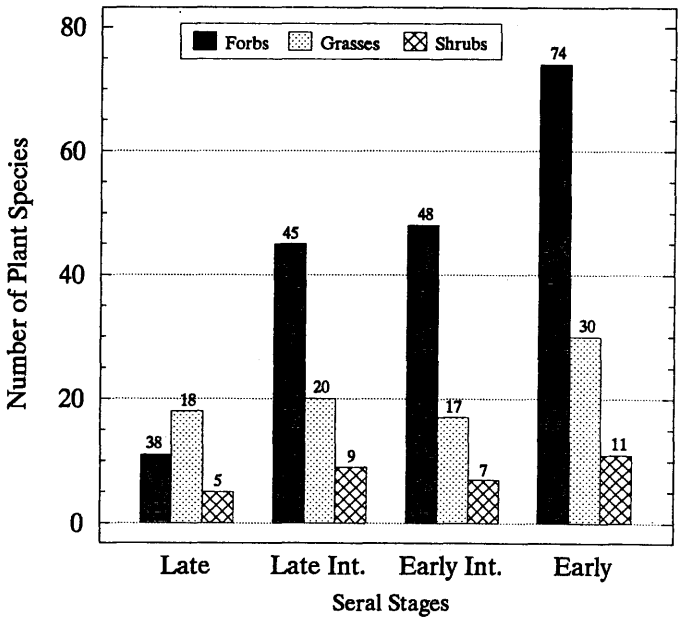

Figure 2—Number of plant species by category throughout all seral stages in the Thunder Basin National Grasslands sagebrush shrub steppe habitat type.

western wheatgrass = 976, and blue grama = 120 would be assigned to the late seral stage. In this example, 13.67 is the greatest score and is associated with the late seral stage. Monitoring of a site over time will show any changes in seral stages when the above procedures are applied.

Overall application accuracy, obtained from cross-validation procedures (SAS Institute 1988), was 92%. Specific cross-validation results showed classification errors that are likely to occur for each seral stage during applications of the developed model. These errors for each seral stage were less than 1% for late, 4% for late intermediate, 5% for early intermediate, and 10% for early.

The early seral stage had the greatest number of plant species with 74 forbs, 30 graminoides, and 11 shrubs. The number of plants decreased throughout to the late seral stage which had 38 forbs, 18 graminoides, and 5 shrubs (fig. 2).

Discussion

The developed seral classification and monitoring model was based on ecological concepts of plant succession (Clement 1916; Sampson 1919; Humphrey 1947; Dyksterhuis 1949; Daubenmire 1968). However, plant succession in this study is not used as defined by USDA-SCS's (1976) procedures that use percentage of climax to determine current range condition. With the developed model, successional status is obtained from using multivariate quantitative equations. These equations consist of interrelationships from a set of plant species occurring throughout the defined four seral stages. Thus, the developed model determines seral stages regardless of hypothetical past or future climax vegetation. It is difficult to predict long term (100 years or more) past or future climax conditions; at best such prediction becomes an ecological guess. Knowledge of hypothetical climax vegetation is not required when applying the developed model to determine seral stages because: (1) vegetation data that were used to develop the quantitative model were collected over a range of natural variation on a habitat type that is present today and (2) every plant species sampled occurring in the habitat type was included as a variable in a sequence of multivariate statistical analyses to determine the set of key plant species (perennial or annual) that best characterize the habitat type.

Although sagebrush steppe appears to be common on western rangelands, the application of the developed model

Table 3—An example of estimating the assigned seral stage using Thunder Basin National Grasslands Fisher's discriminant coefficients and data collected for the 3 plant species on a site.

	Big sagebrush		Western wheat.		Blue grama			
	Coeff[1].	Index	Coeff.	Index	Coeff.	Index	Const.	Score
Late	(0.00551 * 4730 +	0.00241 * 976 +	0.00216 * 120) −	15.00	=	13.67		
Late Int.	(0.00154 * 4730 +	0.01146 * 976 +	0.00399 * 120) −	14.07	=	4.88		
Early Int.	(0.00095 * 4730 +	0.00505 * 976 +	0.00932 * 120) −	15.64	=	−5.10		
Early	(0.00113 * 4730 +	0.00240 * 976 +	0.00262 * 120) −	3.15	=	4.85		

[1]Coeff. = Fisher's discriminant classification coefficient, Const. = constant values in Fisher's discriminant model, Int. = intermediate.

is limited to this specific habitat type. When applying this classification model outside TBNG, care must be taken to ensure that big sagebrush is the dominant shrub. Western wheatgrass and blue grama are the dominant grass species (table 2). Subspecies of big sagebrush were not differentiated in our study. However, Johnson (1979) reported that Wyoming big sagebrush (*Artemisia tridentata wyomingensis*) was the most dominant subspecies in this area. Küchler (1964) limited this habitat type to southeastern Montana and Wyoming while Bailey (1980) limited it to Wyoming Basin Province only. However, Johnson (1979) stated that the northeastern Wyoming sagebrush steppe was consistent with mixed grass prairie elsewhere, except for a greater dominance of sagebrush.

Management Implications

Rangelands with different seral stages may require several management strategies to maintain biodiversity. For instance, an adjustment in the level or timing of livestock grazing can change the seral stage to a preferred management alternative. As seral stages change, some plant species will be lost and others gained. These are trade-offs which can be evaluated. To maintain biological diversity, all defined seral stages must be maintained. The question is how much of each seral stage and where must it be maintained?

Managing for one particular seral stage does not meet multiple-use objectives. For instance, the early intermediate seral stage appears to be superior to the late seral stage for livestock production because of the abundance of palatable graminoides in this habitat type. Other seral stages may be more important to certain species of wildlife, such as sage grouse, which require an early seral stage for booming and a late seral stage for nesting. Samuel and Hart (1994) reported that biological diversity was greater in early seral stage sites that were not dominated by blue grama when they conducted a biological survey in northeastern Wyoming. We found that the early seral stage had a greater number of plant species which decreased throughout to the late seral stage (fig. 2).

Managers concerned with biological diversity must maintain all defined seral stages. The entire range, from late to early, is necessary for multiple use, such as livestock and wildlife production and recreation (Bowns and Bagley 1986; Uresk 1990; Samuel and Hart 1994). However, an early seral condition, where bare ground is high, may require additional considerations because of potentially high soil erosion (Benkobi and others 1994). The developed model provides a tool for range managers that can determine vegetation changes in response to management alternatives.

The developed classification model can also quantify the effect of various grazing intensities on secondary succession in order to determine grazing levels that will maintain, restore, or change the successional status of the vegetation for a management alternative. In addition, useful information about wildlife species' activities, livestock and wildlife interactions, and their relationships to seral stages in plant communities can be demonstrated (MacCracken and others 1983; Uresk and Paulson 1988; Uresk 1990; Rumble and Gobeille 1995).

Application of the developed model requires field measurements of index values (canopy cover (%) x frequency of occurrence (%)) for the three key plant species (big sagebrush, western wheatgrass, blue grama). Field measurements of canopy cover should follow Daubenmire's (1959) six cover classes. For each site sampled, two 99 ft (30 m) parallel transects should be established 66 ft (20 m) apart. Along each transect, sampling should be conducted at 3.3 ft (1 m) intervals, using an 8 x 20 inch (20 x 50 cm) quadrat frame. The obtained index values are applied to the classification model (table 1) as demonstrated in table 3. Variability in the data led to an estimate of 2 macroplots per section (640 acres) as a minimum requirement for seral stage classification and monitoring. Monitoring requires repeated measurements of the 3 key plant species over time on permanent plots to oversee management changes.

Conclusions

A classification and monitoring tool (model) of plant succession was developed for TBNG sagebrush shrub steppe habitat. Key plant species for classification and monitoring were defined by multivariate statistical methods. Percent cover and percent frequency of occurrence for big sagebrush, western wheatgrass, and blue grama can be used to measure succession or retrogression in this habitat type. The consistent overall accuracy (92%) of this classification system suggests wider applications for this model in management, conservation, and research.

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Estimating Latent Heat Flux in the Shrub-Steppe Using Lysimeter and Satellite Data

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Abstract—A map of instantaneous latent heat flux for a shrub-steppe site in south-central Washington was produced using Landsat Thematic Mapper data and simple ground based measurements. Latent heat flux ranged from <50 W m^{-2} in rocky areas with little green vegetation to 100 W m^{-2} at high elevations with cool temperatures to 160 W m^{-2} in areas of high temperature and leaf area index. Quantitative remote sensing allowed us to predict absolute values of latent heat flux rather than relative values. This work supports efforts to produce a more mechanistic model for general use.

Latent heat flux (LE) is the resultant of evaporation from the soil and plant transpiration. The prediction of LE at large scales is a critical component of landscape level process models (Graetz 1990). Models of LE can be complex (van de Griend and van Boxel 1989) making large scale applications difficult. Bolin (1988) suggests that models be simple with prediction based on variables that can be measured from satellites. We present a simple model that combines surface brightness temperature (T_s) and the normalized difference vegetation index (NDVI) measured with the Landsat Thematic Mapper satellite with leaf area index (LAI) measures to predict LE for a shrub-steppe ecosystem.

Remotely sensed T_s has been used to estimate regional LE rates for agricultural purposes using the energy balance equation (Brown and Rosenberg 1973; Reginato and others 1985). Less work has been done to estimate LE in non-agricultural conditions using remotely sensed data. Seguin and others (1985) analyzed LE for a varied landscape including agricultural and natural systems in southern France. They made use of an empirical simplification of the energy balance equation using net radiation (R_n), T_s, and air temperature (T_a) to predict LE. The analysis relied on ground based measures of R_n and T_a plus the Meteosat satellite for measurement of T_s. An evapotranspiration (ET) map was produced with rates ranging from 1 to 10 mm d^{-1}. Poor calibration of the satellite caused an uncertainty of 10-15 °C in T_s, but because ground based temperature sensors were used for calibration, error in T_s was estimated to be ± 2-3 °C.

Kustas and others (1994a) developed a model to predict LE in semiarid rangelands using aircraft and ground-based meteorological data. LE was predicted within 15% of Bowen-ratio measurements for three days. The model was sensitive to parameter values used in the calculation of sensible heat flux (H) and, thus LE. The approach of Kustas and others (1994a) is complex, requiring measures or estimates of several energy budget variables and parameters not easily obtained from satellites.

Another variable directly related to LE is plant community structure. LE is positively correlated with LAI when LAI is less than three (Seevers and Ottmann 1994). LAI is also correlated with NDVI obtained from satellite data (Huete and Jackson 1987; Sellers 1985). Running and Nemani (1988) demonstrated that transpiration can be related to NDVI through LAI and used in the estimation of regional ET rates for weekly intervals.

Most of the remote sensing literature has dealt with closed canopy crops with little effort expended on the 60% of the Earth's land surface composed of ecosystems where LAI <1 (Graetz 1990; Moran and others 1994a). Our purpose was to develop a simple approach for the prediction of instantaneous LE in a shrub-steppe ecosystem using satellite and easily obtained surface data.

Methods

Study Site

The study area is the Fitzner/Eberhardt Arid Lands Ecology (ALE) Reserve on the Hanford Site in south-central Washington. The 312 km^2 Reserve varies in elevation from 150 m to 1,100 m and is semiarid with hot dry summers and cool wet winters. Average yearly precipitation ranges from 260 mm at the higher elevations to 160 mm in the lower areas (Thorp and Hinds 1977). Vegetation is dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*), big sagebrush (*Artemisia tridentata* ssp. *tridentata*), Sandberg's bluegrass (*Poa sandbergii*), and downy brome (*Bromus tectorum*). Because of frequent fires, approximately 80% of ALE is dominated by bluebunch wheatgrass (Rogers and Rickard 1988).

Latent Heat Flux Data

LE was measured using weighing lysimeters; two in a bluebunch wheatgrass community and two in the big sagebrush-bluebunch wheatgrass community (Gee and others 1991). The lysimeters contain undisturbed monoliths of soil

In: Barrow, Jerry R.; McArthur, E. Durant; Sosebee, Ronald E.; Tausch, Robin J., comps. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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This paper is dedicated to the memory of Dr. Daniel E. Gibbons for his fundamental contributions to this work.

and vegetation. To measure T_s, an infrared-temperature sensor with a waveband of 8-14 μm and a 15° field of view was mounted on the end of a 1.83 m pipe and pointed down at the surface of one of the bluebunch wheatgrass lysimeters. The long axis of the viewed ellipse on the ground was 0.5 m. Data were acquired every 10 sec using a CR-7 datalogger (Campbell Scientific, Logan, UT) and converted to hourly averages.

Leaf Area Index Data

LAI (m^2 green leaf area/m^2 ground area) was measured for plants at peak biomass in a bluebunch wheatgrass community, a big sagebrush-bluebunch wheatgrass community, and in 2 communities dominated by downy brome. Sampling was conducted in 10 randomly located plots at each site. All herbaceous species were clipped at the ground level in a 0.5 m^2 circular area. Single-sided green leaf area was determined with a Licor 3100 Leaf Area Meter (Licor, Inc., Lincoln, NE). Leaf area of big sagebrush was estimated using a model relating leaf area to canopy measures taken on each shrub in 10 randomly chosen 50 m^2 plots (Link and others 1990a).

Topographic Map Preparation

A 3-D topographic profile of ALE was produced by draping satellite imagery over a U.S.G.S. digital elevation map. The profile was generated using a SPOT (Satellite Pour l'Observation de la Terre) 10 m panchromatic image and 3 Landsat bands. The SPOT image was registered to a UTM coordinate system and then the Landsat bands were registered to the SPOT UTM image. The 30 m Landsat image was then resampled to the 10 m scale of the SPOT image. The SPOT and Landsat images were subjected to a linear-contrast stretch to improve their appearance. A composite image was produced using bands 7 (red), 4 (green), and 1 (blue).

Landscape Thermal Measurements

Landsat Thematic Mapper (TM) band 6 thermal data were acquired on May 8, 1989. TM brightness temperatures (corrected for atmospheric conditions) were calculated for each pixel and compared with selected ground-truth plant community brightness temperatures. Concurrent with the overpass, field data were collected including: (1) radiosonde measurements (launched from the Hanford Meteorological Station), (2) hand-held radiometer temperature measurements of the vegetation and soil communities, (3) Columbia River temperatures (used to verify the atmospheric corrections modeled by the atmospheric computer code LOWTRAN6 [Air Force Geophysical Lab 1986]), and (4) thermal emissivities of vegetation and soil. The TM thermal channel (10.42-12.46 μm), with proper atmospheric and ground adjustments, yields T_s to within 0.6 °C of ground measurements (Gibbons and others 1989; Wukelic and others 1989).

To compare satellite (120 m pixel) determined T_s to ground-truth plant community brightness temperatures a field sampling technique was devised using hand-held radiometers (Gibbons and others 1990). Radiometer temperature measurements were collected concurrent with overpass near the weighing lysimeters. The TM images were registered to ground control points and TM digital numbers (DN) of the sampling plots were extracted for analysis. Atmospheric corrections using the local radiosonde data were determined using LOWTRAN6. Conversion tables of DN and TM determined atmospherically corrected temperatures were calculated as in Gibbons and others (1989). Temperatures obtained using average DN values of the river and sample plots for different communities were compared with ground-truth mean temperatures. Corrected water temperatures agreed to within 0.5 °C of ground-truth values. Corrected T_s compared well with ground-based mean temperatures for both homogeneous (<0.7 °C variance) and heterogeneous communities (<1.5 °C variance) (Gibbons and others 1990).

Temperature Map Preparation

An atmospherically corrected brightness temperature map was produced using conversion tables and color coded by computer. Two digital files were produced; one for the unsmoothed T_s values with 120 m pixels for use in the LE map and the other with 30 m pixels for the T_s map. Finally, box filters smoothed the 30 m digital temperature data to graphically present a contouring of temperatures.

Thematic Mapper Determination of NDVI

NDVI was determined from Landsat TM data using Bands 4 (near IR) and 3 (visible) as:

$$\text{NDVI} = \frac{\text{P(Band 4)} - \text{P(Band 3)}}{\text{P(Band 4)} + \text{P(Band 3)}}, \quad (1)$$

where P are atmospherically corrected reflectances. Atmospheric corrections are needed to derive reliable measures of vegetation (Huete 1988). Use of the soil-adjusted vegetation index (SAVI) was not required because of the presence of consistent light dry soils across the landscape and because of the low cover (<50%) of green vegetation (Huete 1988). NDVI is best for estimating low values of phytomass (Huete and Jackson 1987). Gibbons and others (1990) determined TM reflectances for all bands and compared them with mean ground-truth reflectances obtained with spectroradiometric measurements taken of plant communities on ALE using a Daeldalus Spectrofax AA440 concurrent with TM overpass. TM data were corrected using radiosonde data and a modified form of LOWTRAN6 to determine atmospheric effects. For all plant communities, the average deviation from the site mean reflectances was <4%. Look-up tables of TM DN's and atmospherically corrected reflectances were determined to produce an NDVI map.

Prediction of Latent Heat Flux

Our approach to predicting LE is derived from the energy balance equation:

$$\text{LE} = R_n - G - H, \quad (2)$$

where LE is latent heat flux, R_n is net radiation, G is soil heat flux, and H is sensible heat flux, all in units of W m^{-2}.

We empirically related LE to T_s as:

$$LE = b_0 + b_1 T_s, \quad (3)$$

where b_0 and b_1 are regression parameters estimated by relating diurnal lysimeter values of LE to diurnal ground-level measurements of T_s. The only component of Eq. 2 measured from the satellite is T_s (Jackson and others 1983). Thus, we chose to relate T_s to LE rather than make assumptions about how R_n, G, and H vary in the landscape. Diurnal changes in T_s are highly correlated with LE rates (Taconet and Vidal-Madjar 1988). It is difficult to provide accurate estimates of G in natural landscapes where heterogeneous surface characteristics create sampling and thus, modeling difficulties. This is also true of H which is a function of T_a, T_s, and wind speed (U). T_a and U are similarly difficult to predict across the landscape. Each of these terms is related to or can be empirically related to T_s. The assumptions we make are that the relationship is independent of variation in vegetative cover over the landscape and that temporal variation can be substituted for spatial variation.

The other predictor of LE is LAI (Link and others 1990a). To compute LAI from satellite data we related observed LAI from a bluebunch wheatgrass community, a big sagebrush-bluebunch wheatgrass community, 2 communities dominated by downy brome, and bare ground to NDVI as:

$$LAI = \begin{cases} b_0 + b_1 * NDVI & \text{if NDVI} < 0.3375 \\ 0.31 & \text{if NDVI} > = 0.3375 \end{cases} \quad (4)$$

where b_0 is the intercept and b_1 is the slope. We assumed a linear relationship between LAI and LE and relativized the relationship between LE and LAI to that occurring at the bluebunch wheatgrass lysimeter where LAI = 0.251. Rock surfaces have an LAI and LE of 0.

The model used to predict LE is:

$$LE = (b_0 + b_1 T_s) * (LAI/0.251). \quad (5)$$

This model makes simplifying assumptions about the distribution of driving variables in the landscape, namely that the whole landscape is like the weighing lysimeter. We assume that R_n, G, H, and U are consistent across the landscape. Such assumptions limit the relevancy of the model to this site and time.

Results

LE, measured by lysimetry, is strongly related to T_s (eq. 3; $b_0 = -10.44$; $b_1 = 2.82$; $R^2 = 0.94$; fig. 1). Predicted and observed LE are also graphed as a function of time (fig. 2). The coefficient of variation for the 4 lysimeters averaged 16% from 10:00 to 14:00 when LE was greatest.

The piece-wise relationship between LAI and NDVI (fig. 3) was significant for NDVI < 0.3375 (eq. 4; $b_0 = -0.418$; $b_1 = 2.158$; $R^2 = 0.96$; fig. 3). For NDVI > 0.3375, LAI was assigned the value of 0.31, the predicted value for the linear portion of the relationship when NDVI = 0.3375.

T_s ranged from 30 to 55 °C being the lowest at the highest elevation and the highest at the lowest elevations (figs. 4 and 5A). Two locations within the > 50 °C zone were 5 to 10 °C cooler than surrounding areas. The cool patch on the upper left (a) is composed of a dense community of annuals in an ephemeral playa. The cool strip (b) is a riparian area with trees.

The NDVI map (fig. 5B) indicates higher ratios (>0.4) at the higher elevations, in the playa, and riparian areas than at lower elevations and bare rock areas (c). NDVI in riparian areas is greater than 0.5.

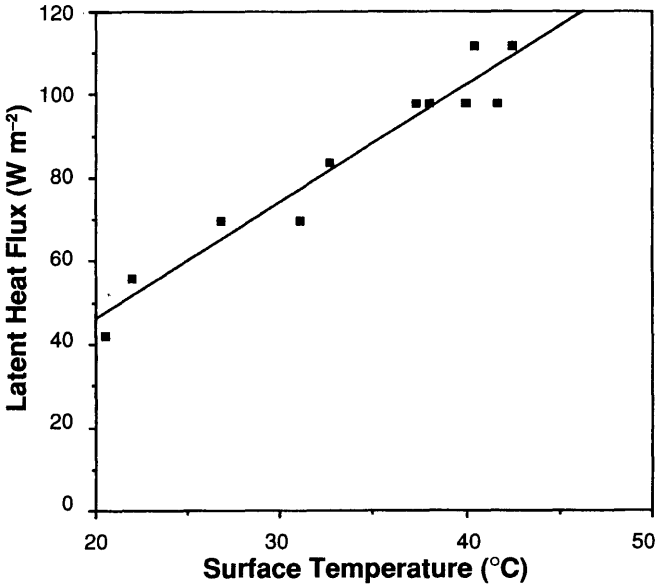

Figure 1—Relationship between latent heat flux and surface temperature measured on a bluebunch wheatgrass weighing lysimeter. Data were collected on May 8, 1988.

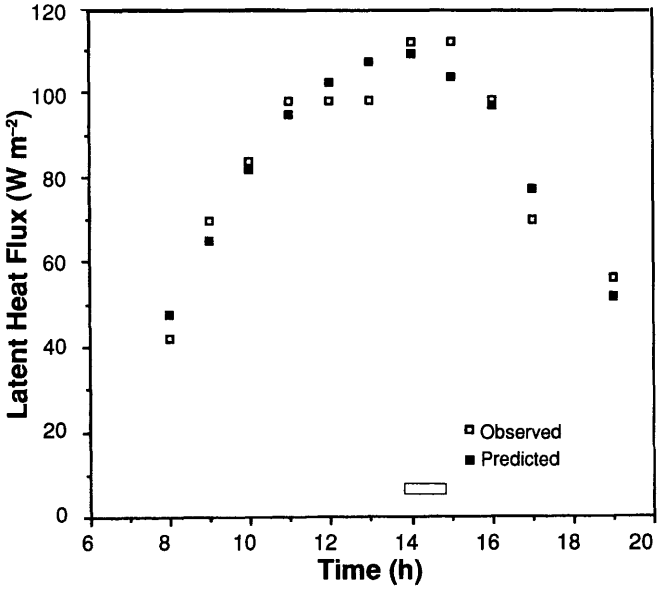

Figure 2—Predicted and observed latent heat flux at the bluebunch wheatgrass weighing lysimeter.

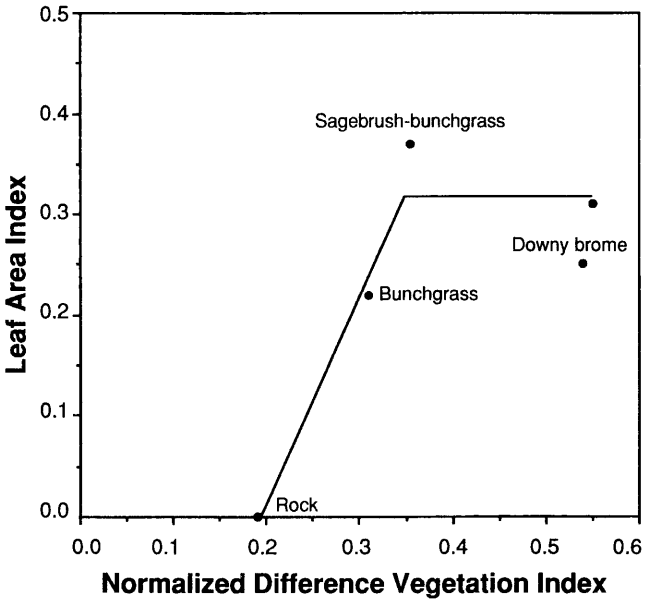

Figure 3—Piece-wise linear relationship between the leaf area index and the normalized difference vegetation index.

The LAI map (fig. 5C) indicates large areas with values of 0.31 at high and low elevations. The lowest LAI values occur in rocky areas and at the middle and low elevations where the dominant plant cover, Sandberg's bluegrass, had senesced.

LE ranged from 0 to 160 W m^{-2} across the landscape (fig. 5D). Lowest values are in rocky areas with little green vegetation (<75 W m^{-2}), low to middle elevation areas where Sandberg's bluegrass had senesced (100 W m^{-2}), and at high elevations with cool temperatures (<100 W m^{-2}). Highest values (>150 W m^{-2}) are at middle to low elevations having high LAI and T_s (>45 °C).

Discussion

We present a simple approach to predict LE across the landscape in the shrub-steppe using quantitative remote sensing satellite and lysimeter data. The range of LE values across the landscape (0-160 W m^{-2}) compares well with the micrometeorological observations of Kustas and others (1989) in the arid Owens Valley of California. This range of LE is lower than is commonly found in agriculture. Moran and others (1989) reported LE in cotton, wheat, and alfalfa fields of 400-700 W m^{-2}. The low values we found are because of the low LAI in the shrub-steppe. This ecosystem is water limited and thus plant growth is limited (Link and others 1990a). Quantitative remote sensing data allowed us to estimate absolute values of LE across the landscape rather than relative values (Pierce and Congalton 1988; Thunnissen and Nieuwenhuis 1989).

LE patterns are related to vegetation patterns. Most of ALE is dominated by bluebunch wheatgrass (Rogers and Rickard 1988). The LE model was developed from bluebunch wheatgrass-dominated lysimeters. The effects of soil water stress on LE are manifested through lower LAI and thus

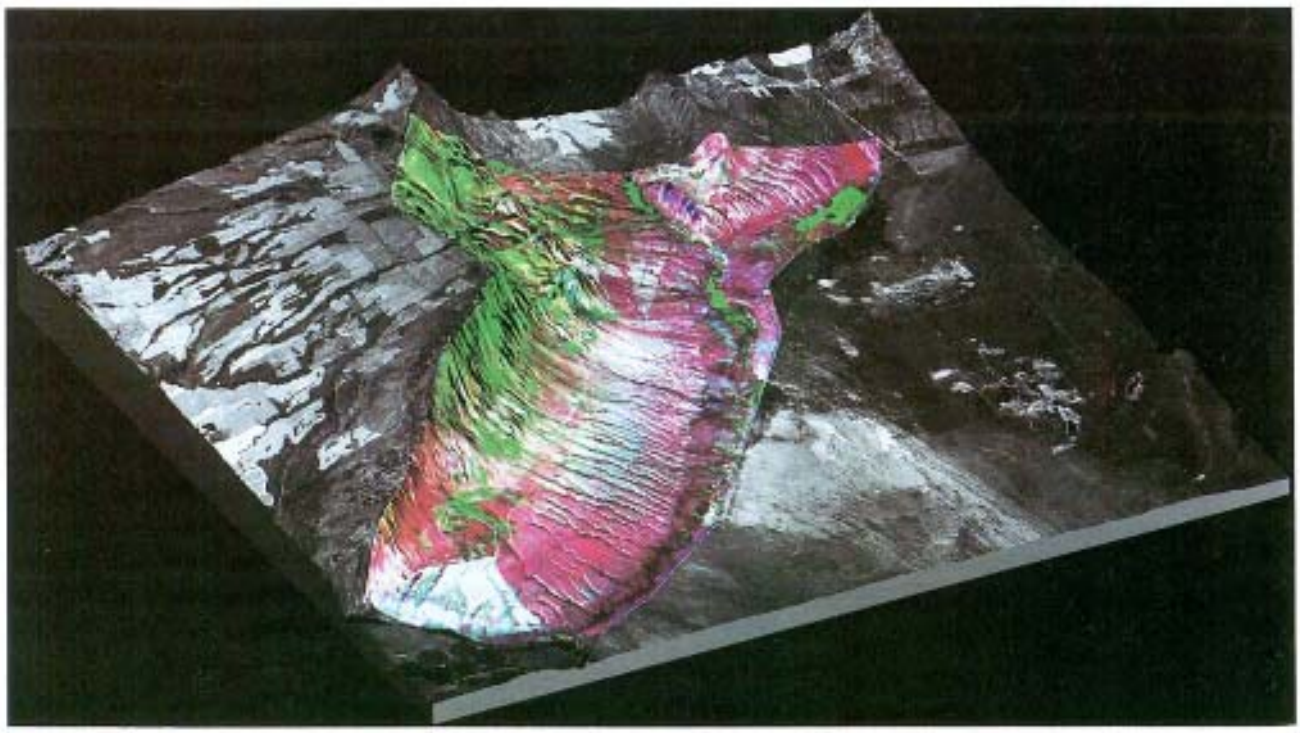

Figure 4—Topographic view of the Fitzner/Eberhardt Arid Lands Ecology Reserve on the Hanford Site in south-central Washington.

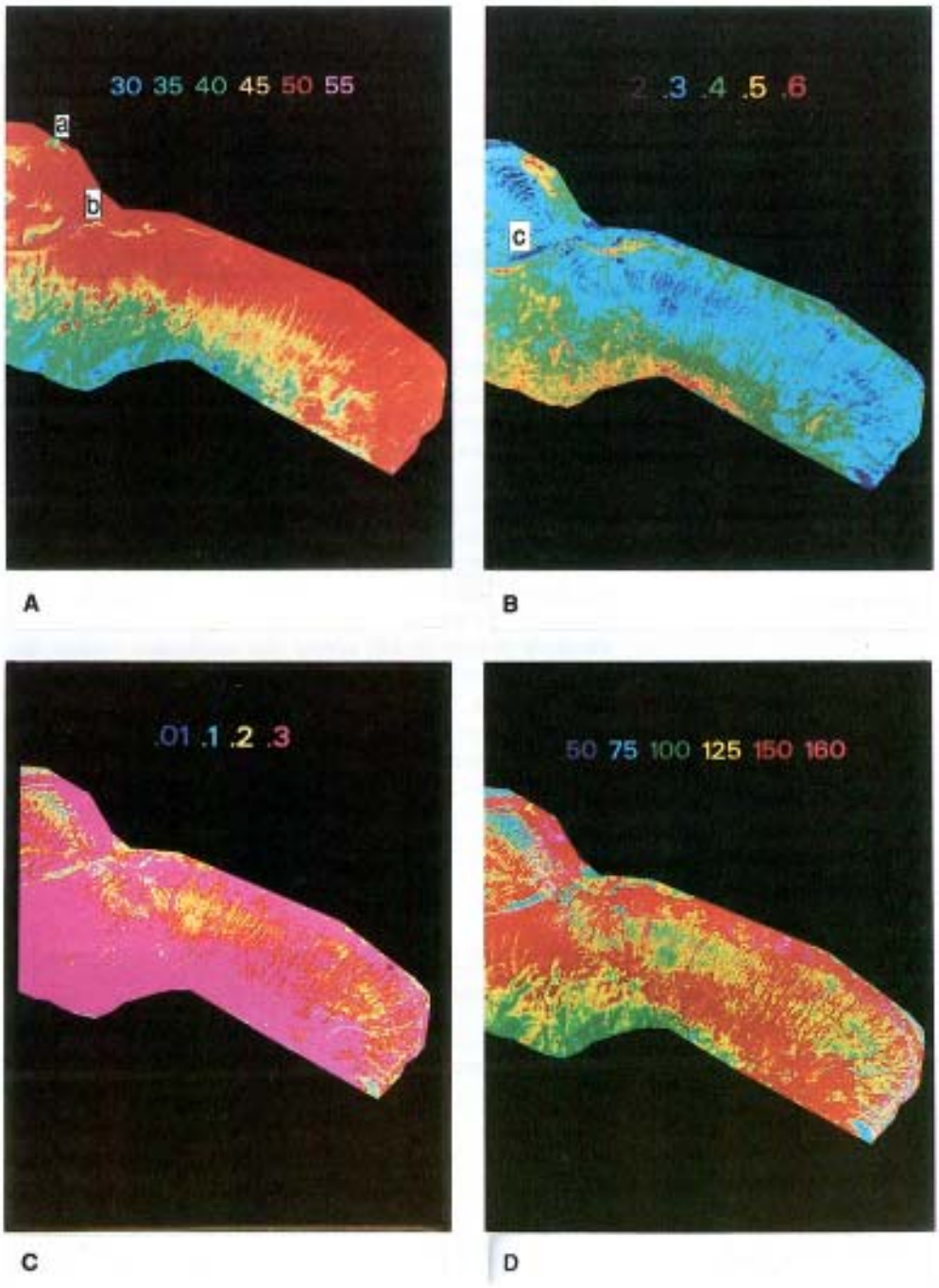

Figure 5—Map of (A) surface temperature (°C), (B) normalized difference vegetation index, (C) leaf area index, and (D) latent heat flux (W m^{-2}) from satellite imagery of the Fitzner/Eberhardt Arid Lands Ecology Reserve, Hanford, Washington, on May 8, 1989 at 11:16 PDT. The cool patch on the upper left (a) is an ephemeral playa and the cool strip (b) is a riparian area.

lower values of LE. Rocky areas where the dominant vegetation is the shallow rooted perennial grass (Sandberg's bluegrass) had low LAI and thus low LE even though T_s was near 50 °C. At lower elevations where LE was low, Sandberg's bluegrass, the dominant species had senesced and consequently had a low LAI (Link and others 1990b). At other low elevation areas where T_s and LAI were both high, the model predicted high LE.

Values of LAI in our study were less than 0.5 and were apparently nonlinear with NDVI. Generally, the relationship is linear up to LAI values of 3-4 (Nemani and Running 1989). Our relationship may be explained by differences in plant community structure. Bluebunch wheatgrass has a dense canopy up to 0.6 m tall with basal diameters up to 0.5 m. Interspaces are bare soil, cryptogamic crusts and Sandberg's bluegrass. The downy brome communities are homogeneous and generally less than 0.5 m tall. Interspaces are covered with litter with little bare soil showing. It is likely that the differing NDVI values of these communities can yield similar values of LAI due to this structural difference. If the bunchgrasses were clipped and the foliage arranged about the surface as in the downy brome communities we suspect the surface would have a higher NDVI.

Huete and Jackson (1987) investigated the suitability of spectral indices for evaluating vegetation in arid rangelands and found that the amount of senesced grass strongly

influenced the green vegetation signal. This complication would make it difficult to quantitatively measure green phytomass remotely using NDVI. In our case, we are relying on a site-specific relationship between NDVI and LAI to estimate LAI across the site. Thus, the relationship we found between NDVI and LAI is unique to the plant communities of ALE.

Most areas had high LAI, thus LE for these areas is a function of T_s. This is why LE is relatively low at the high elevations. In this ecosystem, where much of the surface is dominated by soil, it is likely that hot air rising from the soil increases the vapor pressure deficit, thus increasing transpiration. Soil temperature can be 30 °C higher than adjacent canopy temperature in this ecosystem (Gibbons and others 1990).

We did find a strong positive correlation between T_s and LE in time, thus we feel it is reasonable to expect LE to vary with T_s across the landscape. We were not able to test this expectation. The use of T_s to empirically predict LE has been proposed by others (Carlson and Buffum 1989). While this logic supports the use of T_s from satellites to estimate LE, it remains only an empirical attempt to predict a very complex process.

A playa (a) and a riparian area (b) where LE was poorly predicted had high NDVI and relatively low T_s (fig. 5A,B). In these areas LAI is likely to be greater than one reducing the effect of soil on observed T_s and lowering the observed T_s by evaporational cooling. Such areas are similar to agricultural sites. Our model is not adequate for such areas.

Mapping accuracy of LE will increase with improvements in our application of the energy budget equation after the inclusion of site level meteorological data as in Moran and others (1989), Kustas and others (1994a). Although the collection of meteorological data (Bowen ratio method for estimating LE) will likely improve our ability to estimate LE, it has not been used successfully in pheatophytic rangelands (Nichols 1992). Improvements in the estimation of LE for semiarid rangeland have been made (Kustas and others 1994a; Moran and others 1994b), but difficulties remain. The difficulty is, in part, the use of a single valued above-canopy bulk aerodynamic resistance term when plant and soil processes operate very differently in terms of the energy budget. LE from plants is, in part, driven by the sensible heat flux (H) of the soil in sparse canopy environments. The separation of plant and soil in the energy budget is very difficult. As pointed out by Moran and others (1989) in the case where T_s is dominated by soil rather than the transpiring vegetation, H is overestimated and LE is underestimated.

While our prediction of LE would be improved by measuring and estimating each of the terms in the energy budget equation across the landscape (Humes and others 1994; Kustas and Daughtry 1990; Kustas and others 1994b), the practicality of measuring and estimating R_n, G, T_a, U, and surface parameters for aerodynamic resistance for routine mapping in complex terrain (Moran and others 1989) at the regional scale is limited.

Although difficulties exist in making use of the energy balance equation at the regional scale, progress is possible. For example, surface parameters for aerodynamic resistance depend on plant community characteristics. Further improvements in the mapping of LE will be made by improved classification of plant communities, as has been done for ALE using AVHRR satellite data (Kremer and Running 1993), and relating characteristics of the communities to LE on the ground and then relating these measures to satellite data. This route will lead to a series of equations unique to each plant community.

A further generalization of such equations into an explicit prediction of LE using the energy budget will improve the prediction of landscape scale LE (Wu 1990). This will require the development of predictive systems models using a combination of ground based and satellite data to predict plant growth and as a consequence, LAI. Ecosystem simulation models have successfully predicted LE using remotely sensed data at the daily time scale in agricultural systems (Thunnissen and Nieuwenhuis 1989), at the weekly time scale (Running and Nemani 1988) and monthly time scale (Hoshi and others 1989) in forested ecosystems. The use of simulation models may improve our ability to predict LE in the landscape at shorter time scales.

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Mapping Plains-Mesa Grasslands of New Mexico Using High Temporal Resolution Satellite Data

Donald G. Vickrey
Albert J. Peters

Abstract—This research uses time-series satellite sensor data set to map and examine vegetation community dynamics within semiarid New Mexico grasslands. A multi-level image classification technique was used to extract and define grassland communities. Temporal vegetation response curves were then produced for grassland communities. Discrimination between grassland communities was possible by examination of their unique vegetation response curves. This technique shows potential for monitoring vegetation change in semiarid grasslands, and for producing timely regional-scale vegetation surveys.

Monitoring vegetation change in rangeland ecosystems is a primary concern of natural resource managers. In the state of New Mexico over 90% of the land area is in native vegetation that is grazed by wild and/or domestic herbivores (Gay and others 1984). Considering the vast rangeland ecosystems (in the western United States alone estimated at 70% of the land area), monitoring change over time becomes an enormous task (Hudson, 1991). Satellite remote sensing technology is well suited for regional studies and may provide an additional tool for land resource managers. The Advanced Very High Resolution Radiometer (AVHRR) onboard the National Oceanic and Atmospheric Administration (NOAA) meteorological satellites provides several advantages over other satellite sensors, including twice daily local coverage, high radiometric resolution (1024 brightness levels), and lower data cost. In addition, an extensive temporal database is accumulating from the AVHRR sensors. The first AVHRR sensors, the Television Infrared Observation Satellites (TIROS-N) series were put into orbit and began recording data in 1978, and new sensors have come on-line since then and still more advanced sensors are being planned for future satellites. This research uses a temporal AVHRR sensor data set to map and examine vegetation community dynamics within semiarid New Mexico rangelands. This research was focused on the following questions: Can AVHRR sensor data be used to delineate the Plains-Mesa grasslands within New Mexico rangelands? Can these grasslands be further stratified into grassland communities using AVHRR sensor data? What information can be derived from temporal vegetation response curves obtained from these grassland communities?

Study Area

The overall area chosen for this study covers the eastern half of New Mexico, extending from approximately 103° through 107° west longitude and 32° through 37° north latitude. This area was selected because, along with other vegetation types, it covers the majority of the Plains-Mesa grasslands within New Mexico (fig. 1). The overall study area was further reduced in size by the application of an iterative masking and multilevel classification process until only the core Plains-Mesa grasslands remained.

Grasslands are one component of the rangelands of New Mexico, along with desert shrublands, savanna woodlands, forests, and tundra. New Mexico grasslands are generally divided into three broad types: Desert, Montane, and the relatively homogeneous grassland areas of the eastern plains. This third type has been called Mixed-Prairie, Plains and Prairie, and Plains-Mesa. The Plains-Mesa grasslands are the most extensive vegetation feature within New Mexico, and were recently mapped at 6,947,618 hectares (Dick-Peddie 1993). The Plains-Mesa grasslands have been and are currently undergoing change. They are being reduced in size over time by the combined effects of urbanization, conversion to dry farming and irrigated agriculture, woody plant invasions, and grazing. Inventory and monitoring of change within this vast resource is of vital importance.

Climate

New Mexico receives most of its moisture from air masses that move inland from the Gulf of Mexico. Summer rains in June, July, and August contribute more than 40% of the annual total over most of New Mexico. However, the eastern plains are an exception. On the eastern plains May marks the beginning of the rainy season which continues into early autumn (September). The plains and mesas of the eastern third of the state receive over 70% of the annual precipitation (12-18 inches) over the growing season (April-September). Winter is the driest season on the plains with February often being the driest month (Tuan 1973). Elevation across the study area ranges from approximately 3,600 feet at the southern portion in the Pecos river valley to 6,500 feet at the upper elevation boundaries with pinyon juniper woodlands.

In: Barrow, Jerry R.; McArthur, E. Durant; Sosebee, Ronald E.; Tausch, Robin J., comps. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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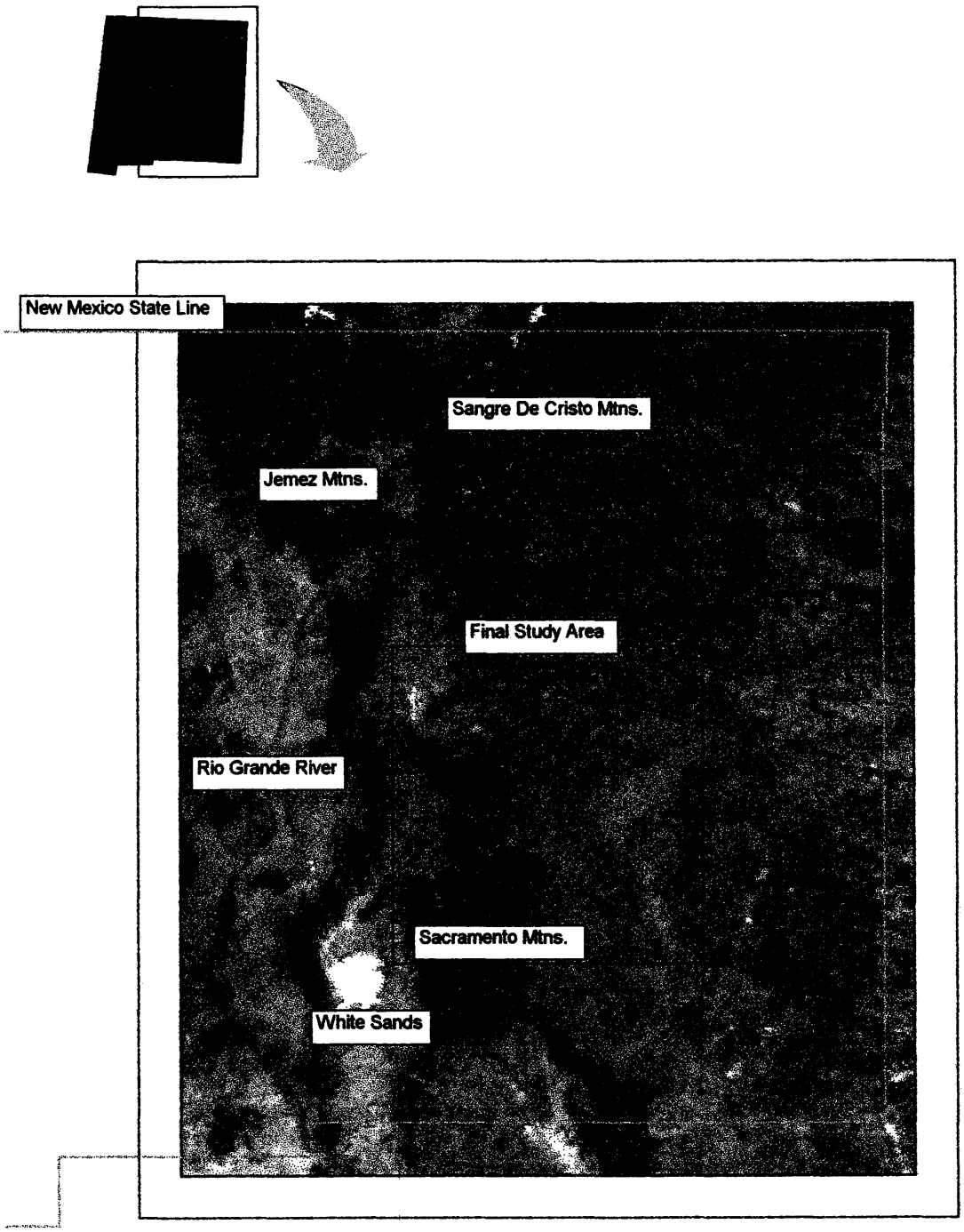

Figure 1—Overall and final study area.

Vegetation

Previous studies have defined the potential dominant vegetation of the Plains-Mesa grassland as blue grama grass (*Bouteloua gracilis*). The potential associated species vary with geographic locality and may include: buffalo grass (*Buchloe dactyloides*), threeawn species (*Aristida* spp.), western wheatgrass (*Agropyron smithii*), galleta (*Hilaria jamesii*), sideoats grama (*Bouteloua curtipendula*), little bluestem (*Schizachyrium scoparium*), Muhly species (*Muhlenbergia* spp.), black grama (*Bouteloua eriopoda*), hairy grama (*Bouteloua hirsuta*), tobosa (*Hilaria mutica*), burro grass (*Scleropogon brevifolius*), and others (Heerwagen in Weaver and Albertson 1956; Donart 1978; Dick-Peddie 1993).

AVHRR Satellite Data

AVHRR data is characterized by low cost, high temporal (twice daily local coverage) and radiometric resolution (10 bit-1024 brightness levels), and a spatial resolution of 1.21 km^2 at nadir. Nadir is defined as the path a line dropped from the satellite perpendicular to the earth would follow on the earth's surface. Another important feature of the AVHRR sensor for regional studies is its synoptic view. With a sensor scan angle of approximately ±55.4° the sensor images a 2,700 km swath perpendicular to nadir with each scan. The AVHRR sensor records energy in the visible red (.58-.68 mm), near infrared (NIR) (.725-1.1 mm), middle infrared

(MIR) (3.55-3.93 mm), and thermal infrared (TIR) (10.5-11.5 mm) regions (Kidwell 1991). The data are collected at the same local sun time on each overpass with either a 7:30 am/pm or a 2:30 am/pm equatorial overpass depending on satellite orientation.

Vegetation Indices

AVHRR data have been used extensively to delineate vegetation in global and regional studies. The primary method has been through the use of vegetation indices (VI). Vegetation indices are quantitative measures based on mathematical combinations of reflectance data that attempt to measure vegetation biomass or vigor. Several indices have been developed such as the simple vegetation index (VI), and the normalized difference vegetation indices (NDVI) (Goward and others 1991).

$$VI = (NIR - RED)$$

$$NDVI = \frac{(NIR - RED)}{(NIR + RED)}$$

The vegetation index used in this research is the soil adjusted vegetation index (SAVI).

$$SAVI = \left[\frac{(NIR - RED)}{(NIR + RED + L)}\right](1 + L)$$

SAVI was developed by A. R. Huete in 1988 to minimize soil influences on vegetation indices involving red and near-infrared spectral data. These indices all exploit the characteristics of healthy, actively photosynthesizing vegetation. The chlorophyll in such vegetation absorbs much of the visible red light (RED) to carry on photosynthesis and the mesophyll tissue reflects infrared radiation (NIR). It is this difference between the absorbed RED and reflected NIR that is utilized by the vegetation indices.

Methods

Data Selection

Seven images were selected for this research (table 1) from the NOAA-10 satellite (launched September 17, 1986). All images were from descending daytime overpass (7:30 am equatorial crossing) satellites. The criteria for image selection were: image dates were spread evenly across the growing season, image nadir tracks were centered as much as possible on the study area, and images contained a minimum of clouds or ground fog in the study area. The images contain five spectral bands, three of which were utilized in this study (table 2).

Preprocessing

After image selection, image preprocessing steps were completed to extract the study area from the images, apply geometric and solar zenith angle corrections, and to complete radiometric calibrations. A VAX 8530 minicomputer and the Nebraska AVHRR Processing software (NAPS) were used to complete the preprocessing steps (Di and Rundquist 1994). The last step in the preprocessing procedure was to convert the data into a format suitable for further processing using personal computer based Earth Resources Data Analysis System (ERDAS) software (ERDAS 1990).

Table 1—Core 1989 NOAA-10 data set.

Image date	Julian date	Image Nadir @Equatorial crossing	Scene ID No.
May 2	89122	111°42'	AV108912214494
May 19	89139	117°35'	AV108913915123
June 7	89158	112°05'	AV108915814505
July 4	89185	112°05'	AV108918514490
August 9	89221	111°40'	AV108922114474
September 18	89261	113°30'	AV108926114522
October 10	89283	115°31'	AV108928315000

Table 2—NOAA 10 data characteristics.

Satellite	Bands	Spectral range (μm)	Used in this research
NOAA-10	1	.58 - .68 (RED)	X
	2	.725 -1.10 (NIR)	X
	3	3.55 -3.93 (MIR)	
	4	10.50 -11.50 (TIR)	X
	5	Band 4 repeated	

Additional Image Processing

After the image preprocessing, additional image processing procedures were completed including: georeferencing and registration, image atmospheric standardization, and image masking (clouds, cloud shadows, and coniferous forested mountain areas). The final image processing step before image classification was to create a soil-adjusted vegetation index (SAVI) image for each image in the temporal data set. The RED and NIR bands, and the SAVI formula were used to create the vegetation index images for the overall study area. The seven SAVI images were then used in the classification process to define the vegetation within the overall study area.

Multi-Level Image Classification

1st Level Classification

The overall study area was "cut" from each of the seven SAVI images created in the previous image processing procedures. The images were then combined so that each SAVI image became one band in the resulting seven-band image. An unsupervised classification was then performed on the seven-band SAVI image. This classification produced an image containing 30 vegetation classes and an accompanying 30-class signature file. The signature file contained the statistical signature for each vegetation class (mean, standard deviation, etc.). The cloud and cloud shadow areas within this image were not classified and had a class value of zero.

2nd Level Post-Classification Grouping

The 30-class composite image was then grouped into five classes (table 3) to isolate the Plains-Mesa grasslands from the 30-class image. Existing vegetation maps, county soils maps, and personal knowledge guided this post-classification grouping process. The five class image isolating the Plains-Mesa grasslands is shown in figure 2.

Table 3—30-class to five class grouping.

Original classes	New class	Description
0	0	Masked Areas
1	1	Barren/Playas, Water, Sand Dune
2-8,10	2	Chihuahuan Desert Shrub
9,11-22	3	Plains-Mesa Grasslands
23-28	4	Closed Canopy Pinyon Juniper Woodlands, Shinnery Oak & Sandscrub Woodland
29-30	5	Irrigated Agriculture, Riparian, Remaining Coniferous Mountain Vegetation

3rd Level Classification

To establish vegetation class boundaries within the Plains-Mesa grasslands (Class 3 in fig. 2), the Plains-Mesa grasslands were isolated from the other rangeland vegetation using a binary image masking procedure.

Final Study Area

The final core grassland study area was then 'cut' from the seven SAVI images containing only the Plains-Mesa grasslands. The images were combined so that each SAVI image became one band in the resulting seven-band image, an unsupervised classification was repeated on only the Plains-Mesa grassland areas. A 7-class image was produced establishing vegetation class boundaries within the Plains-Mesa grasslands.

Field Work

Extensive field work was completed within the final study area. To assist in this task a 7-class field image map and a

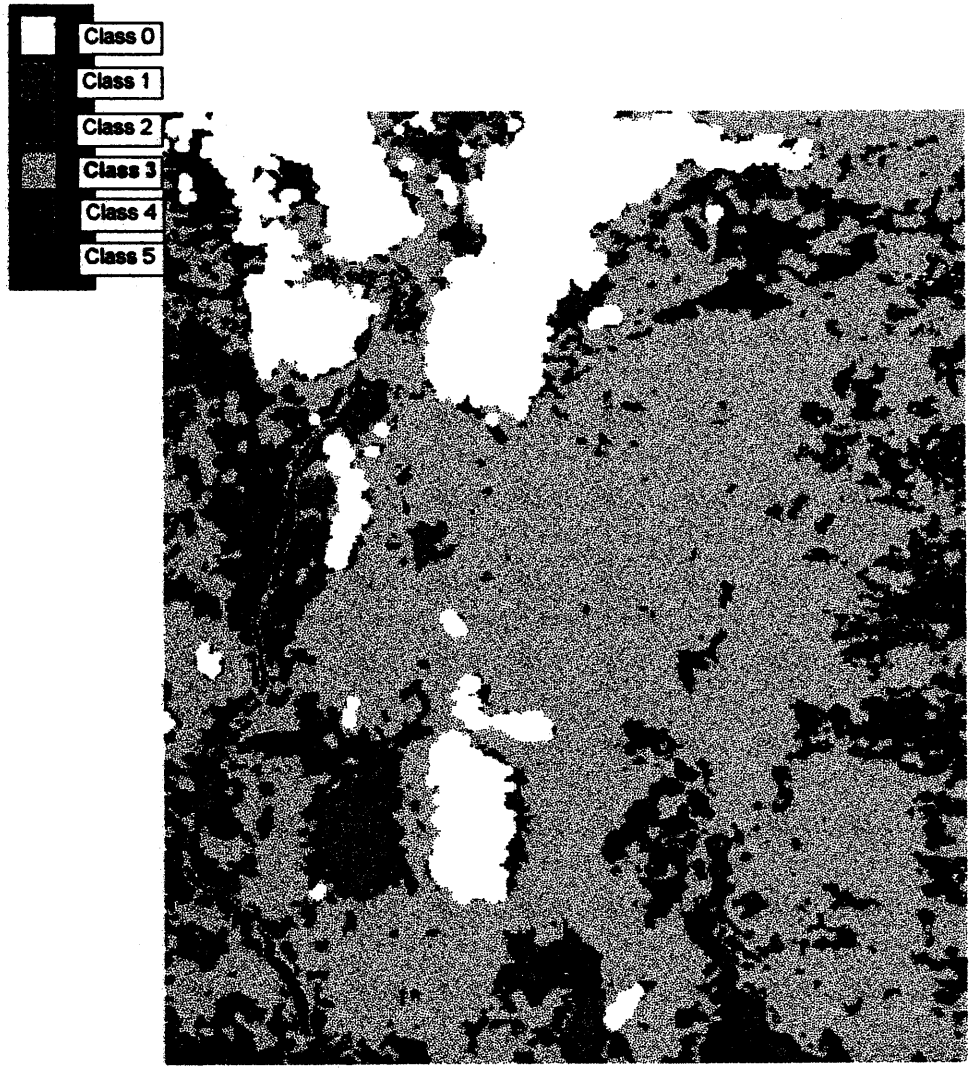

Figure 2—Five class image of overall study area isolating Plains-Mesa grasslands (class 3).

Global Positioning System (GPS) were utilized on the field trips. The main goal for the field trips was to obtain location data for vegetation classes observed in the field using the GPS. Additional goals were to obtain visual qualitative estimates of vegetation composition, and amount of cover/bare soil in the areas where GPS points were taken. The location data and estimates of composition and cover were used as an aid for the final grouping of the 7-class vegetation classification, and for forming qualitative vegetation class descriptions.

The 34 GPS points and accompanying vegetation descriptions were separated based on the class they were overlaying on the 7-class field image map. These data were then reviewed and summarized, and qualitative class descriptions were generated for the 7-class image map taken to the field.

Analysis of Grassland Classification

Before analysis the seven grassland classes were subjected to post-classification merging resulting in three vegetation classes corresponding to distinctive field classes. The three classes were a relatively homogeneous grassland class, a grassland/shrub mix class, and a juniper grassland class. In each of these classes, warm season grasses are the predominant vegetation. The classes are shown in table 4, and figure 3.

Table 4—Post-classification merging into 3 classes.

Original classes	New class	Class description
1,2	1	Grassland/shrub mix
3,4	2	Homogeneous grassland
5,6,7	3	Juniper grasslands

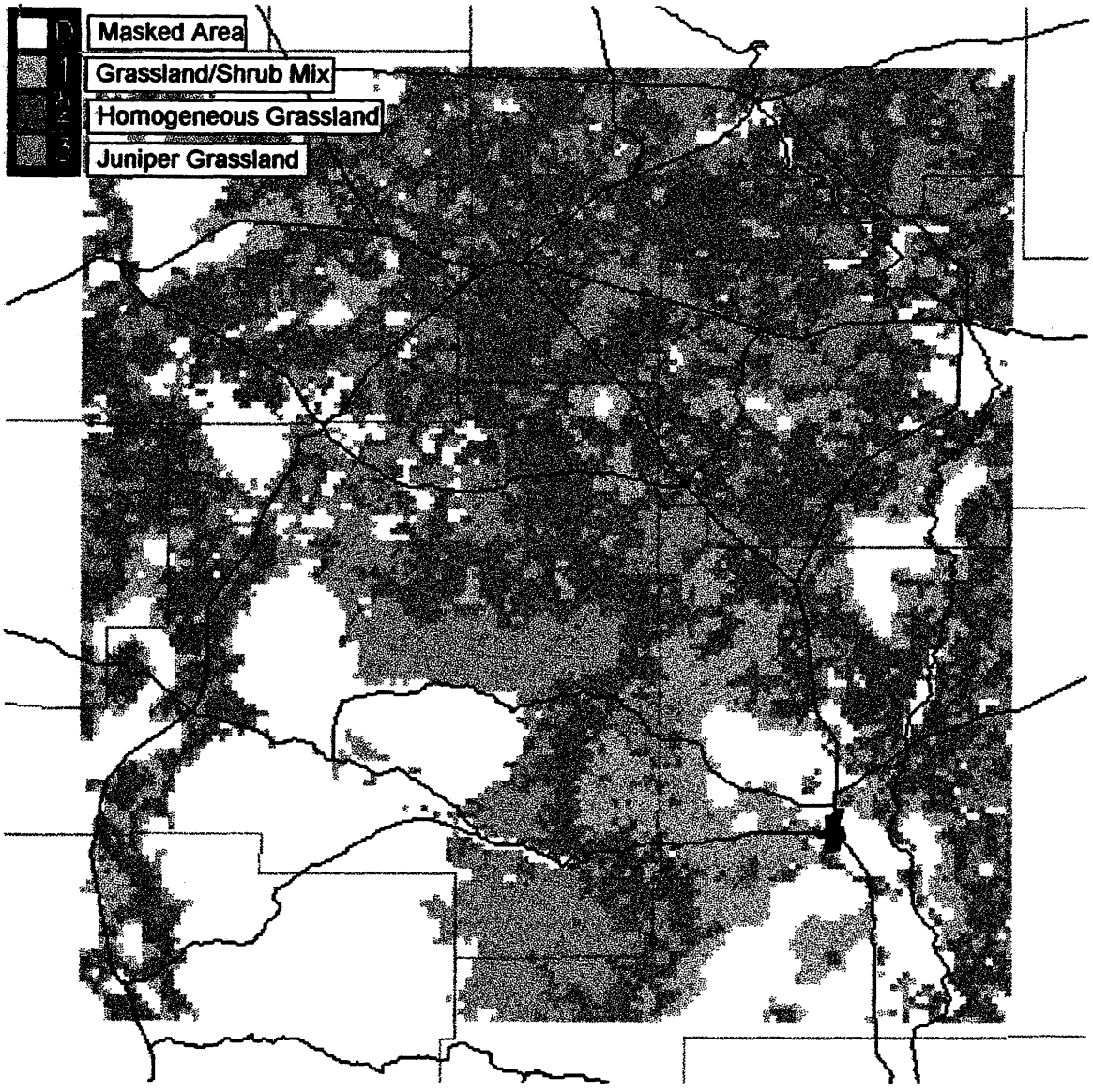

Figure 3—Final study area grassland classes.

Grassland/Shrub Mix Class Description

The Grassland/Shrub Mix class (number 1 in fig. 3) consists of 2,758 km^2 within the study area. The grassland/shrub mix class is found scattered at various sites throughout the study area and represents areas of transition. Blue grama grass dominates in this class with associated black grama and other grass species. This type occurs where brushy species such as mesquite (*Prosopis glandulosa*), and creosote (*Larrea tridentata*) have invaded degraded grasslands. It also occurs in areas where grasslands merge with fourwing saltbush (*Atriplex canescens*) communities such as those found around playa lakes. An example is the area surrounding the Laguna del Perro west of Vaughn, New Mexico. The grassland/shrub mix class also occurs in ecotonal/transition areas between the Plains-Mesa and desert grasslands found at the xeric lower elevation boundary of the study area.

Homogeneous Grassland Class Description

The Homogeneous Grassland class (number 2 in fig. 3) consists of 10,296 km^2 within the study area. This relatively shrub- and tree-free grassland class occurs throughout the study area. Blue grama grass is the dominant vegetation in this class with various associated grass species.

Juniper Grassland Class Description

The Juniper Grassland class (number 3 in fig. 3) consists of 5,086 km^2 within the study area. This class occurs throughout the study area at the mesic higher elevation boundary where the juniper grassland transitions to a juniper savanna are marked by higher densities of pinyon pine (*Pinus edulis*), and one-seed juniper (*Juniperus monosperma*). Blue grama and sideoats grama grasses dominate in this class.

Associated Species

In grassland/shrub mix areas associated non-grass species are fourwing saltbush, mesquite, creosote, and broom snakeweed (*Gutierrezia sarothrae*). In juniper grassland areas sideoats and blue grama grasses dominate with scattered one-seed junipers and pinyon pine. Other associated species that may occur in minor amounts throughout the study area are Mormon tea (*Ephedra* spp.), yucca (*Yucca* spp.), various cacti species (*opuntia* spp.), winterfat (*Ceratoides lanata*), sumac (*Rhus trilobata*), and Apache plume (*Fallugia paradoxa*).

Vegetation Response Curves

The third objective of this research was to produce a temporal vegetation response curve for each of the three Plains-Mesa grassland classes: Grassland/Shrub Mix class, Homogeneous grassland class, and Juniper grassland class. To produce the vegetation response curves the SAVI mean value for each class was extracted for each of the seven images in the data set. These data were then entered into a spreadsheet and plotted graphically. The SAVI mean values were plotted on the Y-axis, and the corresponding Julian dates were plotted on the X-axis. A curve was then placed through the data points using a cubic-spline fitting algorithm. This curve represents a best estimate of the class mean vegetation response over the seven dates (fig. 4). The SAVI mean, standard deviation, and range for the three grassland classes are shown in table 5.

Analysis of Vegetation Response Curves

In 1989 the mean annual precipitation across the study area was below normal, reflecting a spring and early summer drought that occurred across most of New Mexico. Growing season precipitation departure from normal for 1989 was approximately two inches below the thirty year normal across the study area (table 6).

The monsoon rains that normally begin in May on the eastern plains did not begin until mid-July in 1989 (Climatological Data Annual Summary for New Mexico, NOAA 1989). We believe this can be seen in the three vegetation response curves as they do not begin their strong photosynthetic response (greenup) until July (Julian date 185) after the late monsoon rains.

Curve Seasonal Patterns

One way to interpret these curves is as an indication of temporal vegetation phenological activity across the study area. Because warm season grasses are the dominant vegetation in all three of these classes, the class phenological activity represented by the curves is predominantly due to the seasonal activity of grasses and not other associated

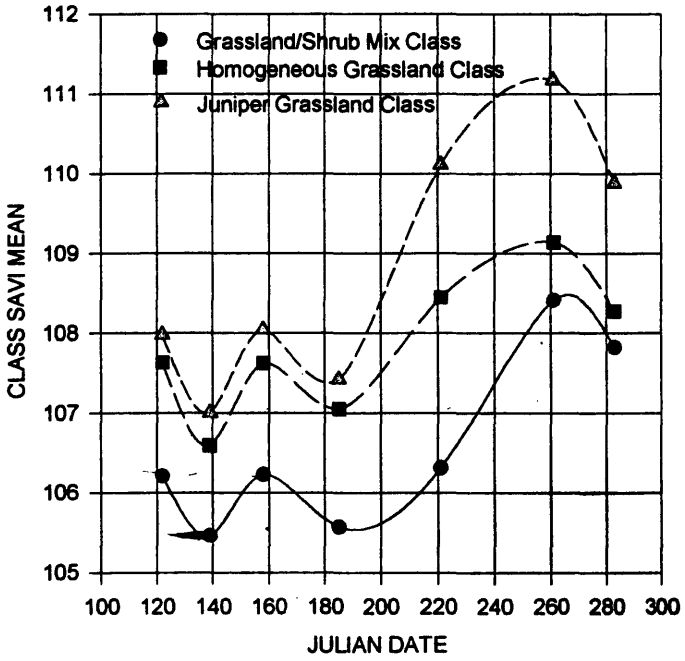

Figure 4—Grassland community response curves representing class means for seven dates through the 1989 growing season.

Table 5—SAVI data statistics—mean, standard deviation, and range for final study area three grassland classes.

Image date	Mean	Standard deviation	Range
Class 1—Grassland/Shrub Mix Class			
May 2, 1989	106.21	1.026	102-114
May 19, 1989	105.462	0.871	98-114
June 7, 1989	106.229	0.977	103-112
July 4, 1989	105.572	1.032	103-112
August 9, 1989	106.315	1.628	103-113
September 18, 1989	108.416	1.936	102-116
October 10, 1989	107.824	1.634	104-113
Class 2—Homogeneous Grassland Class			
May 2, 1989	107.632	1.198	105-118
May 19, 1989	106.591	0.955	100-113
June 7, 1989	107.626	1.139	104-118
July 4, 1989	107.050	1.226	104-115
August 9, 1989	108.449	1.848	104-123
September 18, 1989	109.142	1.457	104-117
October 10, 1989	108.274	1.261	104-116
Class 3—Juniper Grassland Class			
May 2, 1989	107.983	1.340	105-117
May 19, 1989	107.003	0.991	104-113
June 7, 1989	108.046	1.149	104-114
July 4, 1989	107.421	1.345	104-113
August 9, 1989	110.110	1.883	104-121
September 18, 1989	111.175	1.756	105-121
October 10, 1989	109.880	1.569	105-117

Table 6—Study area precipitation departure from normal in 1989 (30 year normal 1951-1980).

Climate division	1989 growing season (May-October) in.	1989 total departure in.
Northeast Plains (3)	+1.27	+0.25
Central Valley (5)	–1.19	–1.37
Central Highlands (6)	–1.69	–2.70
Southeast Plains (7)	–2.48	–2.77
Southern Desert (8)	–1.13	–1.59

vegetation such as shrubs in the grassland/shrub mix class or trees in the juniper grassland class. All three classes exhibit similar seasonal vegetation response patterns reaching an early season peak on June 7 (Julian date 158) and then decreasing rapidly due to the late arrival of the monsoon rains and increasing summer temperatures. After the monsoon rains began in mid-July, the warm season grasses began their greenup reaching a peak on September 18 (Julian date 261) and then began to fall again due to decreasing temperatures and associated fall season vegetation senescence across the study area.

Curve Amplitude

A second way to interpret these curves is as an indication of differences in cover between the three grassland classes. The SAVI curve representing the Juniper grassland class consistently has the highest mean values across the growing season, while the curve for the Grassland/Shrub Mix class has the lowest and the Homogeneous grassland class curve falls in between. We believe these differences in SAVI mean values are due to differences in the amount of cover or conversely the amount of bare soil between the three classes. The qualitative class descriptions recorded in the field indicate the greatest amount of bare soil in the Grassland/Shrub Mix class and the least in the Juniper grassland class. Bare soil in the Homogeneous grassland class fell in between these two.

Conclusions

The focus of this research was on the development of techniques for the delineation of Plains-Mesa grasslands and on the use of temporal vegetation response curves as an indicator of vegetation activity within the grassland classes. The Plains-Mesa grasslands are the most extensive vegetation feature within the state of New Mexico and their continued health is important economically and aesthetically to the citizens of New Mexico. We believe an initial grassland inventory and assessment of condition should be conducted, and the grasslands should be monitored on a regular basis. In particular, the ecotonal xeric and mesic boundaries of the Plains-Mesa grasslands should be monitored closely. Any expansion or contraction of the Plains-Mesa grasslands will be evident as change within these regions. We believe the techniques developed with this research are a step towards monitoring the health of the New Mexico Plains-Mesa grasslands.

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Using High Temporal Resolution Satellite Data to Assess Shrub Control Effectiveness

Marlen D. Eve
Albert J. Peters

Abstract—In 1988 and 1992, personnel with the Jornada Experimental Range in southern New Mexico chemically treated a large grassland area for mesquite (*Prosopis glandulosa*). The treatments were successful in defoliating nearly 100% of the mesquite plants present. Since treatment, plant recovery and invasion has resulted in current mesquite densities of about 2% cover. We assessed vegetation index information derived from meteorological satellite imagery recorded over seven growing seasons (1987-1993). The data were used to track the photosynthetic activity of mesquite canopy from pre-treatment through both treatments. Differences in seasonal landscape greenness characteristics derived by analysis of the satellite data show the effect of the chemical treatment, as well as the recovery of the mesquite. This research demonstrates the potential utility of satellite derived information in assessing vegetation response to implementation of range management strategies. Similar techniques applied over longer time periods could be utilized to monitor ecosystem health and aid in managing arid shrublands.

Much of southern New Mexico once dominated by grassland is now dominated by mesquite (*Prosopis glandulosa*). Mesquite is a thorny, long-lived, winter deciduous shrub that exhibits a C_3 photosynthetic pathway, and initiates vigorous leaf growth during the spring with fruiting during early- to mid-summer (Valentine and Norris 1960). It forms cream colored flowers that develop into seed pods that are four to eight inches long (Gay and others 1984). It is drought resistant, with a tap root system that can grow as deep as 60 feet (Gay and others 1984; Valentine and Norris 1960). The deep tap root often allows mesquite to draw upon ground water reserves. Mesquite also has long lateral roots, long-lived seed and a high germination rate even under adverse temperature and moisture conditions (Hennessy and others 1983). Underground mesquite stems contain dormant buds that sprout when the above-ground biomass is killed (Valentine and Norris 1960). Mesquite has little forage value, but the seed pods are sought out by livestock. New mesquite seedlings are often the result of the dispersal of seeds by livestock, rodents, and rabbits.

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It is believed that mesquite was originally dominant along washes. Native Americans used mesquite extensively, and pockets of mesquite dunes apparently formed around their campsites (York and Dick-Peddie 1969). Also, it has been reported that early ranchers would commonly carry a bag of mesquite pods with them to feed their horses (Gardner 1951). With increased grazing pressure, the expansion of mesquite from these areas was rapid (York and Dick-Peddie 1969). Between 1858 and 1963, the area of the Jornada Experimental Range in south-central New Mexico (fig. 1) dominated by mesquite increased ten-fold (Buffington and Herbel 1965). Mesquite tends to invade sandy soils, and dunes commonly form as grass cover is reduced and erosion increases (Buffington and Herbel 1965; Herbel and others 1983). Once dune formation has occurred, return of the area to grassland is highly unlikely (Gardner 1951).

Research on various treatments to control mesquite has been underway for most of this century, but escalated with the introduction of 2,4,5-trichlorophenoxy-acetic acid (2,4,5-T) in the mid-1940's (Valentine and Norris 1960). Research using 2,4,5-T and other chemicals to control mesquite has been extensive in southern New Mexico (see Herbel and Gould 1995; Herbel and others 1983; Gould 1982; Valentine and Norris 1960). While complete and long-term kill of the plants has not been accomplished, research does show that mesquite can be effectively managed using chemicals, however, this level of management may not be economically feasible (Herbel and Gould 1995). Chemical treatment of mesquite has been shown to decrease mesquite density, increase grass cover (Herbel and others 1983; Herbel and Gould 1995), and decrease soil erosion (Gould 1982). The greatest impact has been when treatment was applied during late May or early June following adequate spring moisture to generate vigorous mesquite growth (Herbel and others 1983). Effective single treatment should result in root kill exceeding 30%, and 50% from repeat treatments (see Herbel and Gould 1995).

In southern New Mexico, dominant perennial grasses are C_4 species that require relatively high night temperatures to produce new growth. Timing of green-up and maximum growth of desert grasses is primarily a function of water availability and temperature (Stephens and Whitford 1993). Because mesquite is growing actively in the spring while the C_4 grasses remain dormant, a temporal sequence of satellite derived images should be useful in detecting the effectiveness of chemical treatment, and the resulting plant community response. Ideally, chemical treatment would result in a decrease in mesquite (C_3 shrub) production and an increase in C_4 grass production (Herbel and Gould 1995). Using a temporal, satellite-derived vegetation index (VI), this ideal

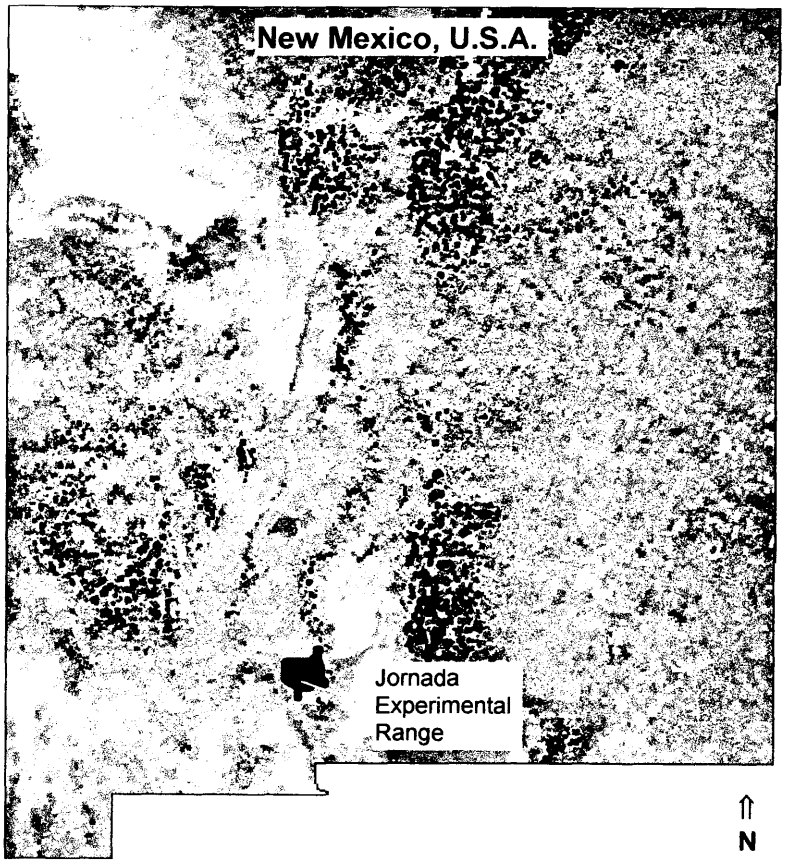

Figure 1—Location of the Jornada Experimental Range in southern New Mexico. The background image is a sample of NOAA-AVHRR satellite data.

treatment outcome resulting in a shift of photosynthetic activity from the spring to the monsoon season, would be seen to decrease VI values in the spring and increase values during the monsoon.

The question asked during our research was: Are these expected changes in plant community growth characteristics detectable with high temporal resolution satellite data? Therefore, the goals of our research were to show the ability of temporal satellite spectra to detect ecosystem response to chemical treatment of mesquite and to demonstrate their utility as a management tool.

Study Area

The Jornada Experimental Range (JER) lies within the Jornada del Muerto portion of the northern Chihuahuan Desert in southern New Mexico (fig. 1). Elevations on the JER range from 1,180 to 1,375 m. Precipitation is highly variable. Of the 230 mm. average annual precipitation, 52 percent comes in July, August, and September (Gibbens 1991). While summer precipitation is generally from localized, high-intensity, short-duration storms, winter moisture is commonly the result of synoptic, low-intensity, frontal storms (Gibbens 1991). High temperatures and low humidity result in large evaporation losses. Potential evaporation can be as much as ten times the annual precipitation of the area (Paulsen and Ares 1962). The frost-free period averages 200 days, but the effective growing season (the duration of favorable soil moisture and temperatures) is often less than 90 days (Paulsen and Ares 1962).

The JER lies at the boundary between the North American warm deserts to the south and west and the plains grasslands to the north and east. For this reason, Lowe (1967) refers to the area as an ecotone, with a climate that is intermediate between desert and grassland. Historically, the area has more commonly been referred to as desert grassland (see Dick-Peddie 1975; Humphrey 1958). Pre-settlement, the landscape was a mosaic of grassland with desert scrub occupying the hotter, drier sites (Gardner 1951; Buffington and Herbel 1965; York and Dick-Peddie 1969; Dick-Peddie 1975). Today the inverse is true, Chihuahuan Desert scrub dominates the landscape with grasslands limited primarily to more mesic sites (Dick-Peddie 1975).

The sites selected for this analysis are in a grass/shrub transition zone where active mesquite encroachment is ongoing. Pre-settlement, the area was dominated by black grama (*Bouteloua eriopoda*) (Dick-Peddie 1975; York and Dick-Peddie 1969). Mesquite was historically found along drainages, scattered or in thickets in the uplands (Humphrey 1958), and around Native American campsites (York and Dick-Peddie 1969). Presently, mesquite dominates much of the area around our study sites, and stands have thickened and spread since pre-settlement times. Mesquite can have widely varied sub-dominants depending upon the type of soil and level of degradation of the landscape. Our study area has mesquite growing in association with a grassland community made up primarily of gramas (*Bouteloua spp.*), sporoboluses (*Sporobolus spp.*), and soaptree yucca (*Yucca elata*). As mesquite invasion continues, coppice dune formation commonly occurs with soils and nutrients being stripped from inter-dunal spaces by wind and accumulated around the base of the mesquite plants. This is the condition to the north of the sites analyzed here.

It is very difficult for other species to establish and survive in these inter-dunal spaces. Where upland grasslands remain, gramas, sporoboluses, muhlys (*Muhlenbergia spp.*), and three-awns (*Aristida spp.*) dominate, with scattered individuals or patches of snakeweed (*Gutierrezia sarothrae*), soaptree yucca, mesquite, tarbush (*Flourensia cernua*), and/or creosote bush (*Larrea tridentata*) (Dick-Peddie 1986; Gay and others 1984).

Methods

Our data were derived from the National Oceanic and Atmospheric Administration's-Advanced Very High Resolution Radiometer (NOAA-AVHRR). These operational weather satellites were intended primarily for observation of cloud and sea-surface parameters, but their ability to monitor changes in land characteristics over large areas makes them invaluable for land-based studies (NOAA 1991; Tucker and others 1991). Multispectral data acquired by the AVHRR from NOAA-10 and NOAA-12 were obtained for the 1987

through 1993 growing seasons. Data from the High Resolution Picture Transmission (HRPT) mode of the NOAA sensors have a spatial resolution of 1.1 km at satellite ground track (nadir). Other characteristics include high radiometric resolution (1,024 gray levels), high temporal resolution (daily coverage), 2,400 km scanning view, and a 07:30 equatorial overpass time (NOAA 1991). All data acquired have satellite nadir in or very near the study area.

Image Preprocessing

We implemented a one-step algorithm for combining geometric and radiometric calibration, and solar zenith angle corrections (Di and Rundquist 1994). An image processing step accounts for per-date sensor scan-angle distortion by georeferencing each pixel to a latitude and longitude coordinate system. Subsequent image processing and analyses were conducted using the Earth Resource Data Analysis System (ERDAS) software on a Personal Computer. All georeferenced images were interactively coregistered to within one pixel locational tolerance, and 10-bit resolution was retained throughout our analysis.

Cloud obstruction in the imagery was minimized through image masking. To accomplish this we used the thermal channel of the AVHRR sensor (10.3-11.7 mm) to locate cloud pixels which are generally cooler than the land pixels. The red image band was utilized to mask pixels lying in cloud shadows. A binary cloud mask was produced for each date of imagery by designating clouds and cloud shadows as zero-value pixels and non-cloud pixels as one. Subsequent multiplication of the cloud mask and reflectance images resulted in elimination of clouds by conversion to a value of zero. Atmospheric attenuation was standardized for all red and near-infrared images using histogram minimization (Jensen 1996). The signal obtained from reflectance at the center of Elephant Butte Reservoir was used as the base value. Histograms were shifted downward for each date of imagery so that reflectance over Elephant Butte Reservoir was the same for all imagery, thereby normalizing atmospheric path radiance throughout the data.

Vegetation Indices

Successful vegetation discrimination on the basis of satellite data depends upon the contrast in spectral radiance between vegetation and the surrounding soil (Tucker 1979). Mesophyll tissue in actively growing vegetation strongly reflects near-infrared energy, while chlorophyll strongly absorbs red energy for photosynthesis. A mathematical quantity referred to as the Normalized Difference Vegetation Index (NDVI) is routinely calculated from AVHRR data due to its sensitivity to the presence of photosynthesizing vegetation and its ability to normalize atmosphere and background attenuation (Huete and Jackson 1987; Huete and Tucker 1991; Tucker and others 1991). Formulation for NDVI is: (NIR – RED)/(NIR + RED), where NIR equalsNear-Infrared reflected energy (0.725-1.10 mm) and RED equals Red-reflected energy (0.58-0.68 mm). Calculation of the NDVI results in pixels with an index value theoretically between –1.0 and +1.0. Vegetation will generally yield positive index values, water will yield negative values, and bare soil will result in values near zero due to the reflectance characteristics of these surface materials (Lillesand and Kiefer 1994; Tucker 1979).

Site Delineation

Sites used in the analysis of mesquite control effectiveness were delineated through unsupervised classification of 1993 NDVI images. This resulted in identification of one polygon (site) made up predominantly of the chemically treated area, and another to the north that is primarily untreated (fig. 2). We believe that the process of delineating polygons that remain consistent throughout our analysis provides for standardization of soil background (Peters and Eve 1995). These polygons resulted in a consistent spatial unit for all subsequent temporal analyses. Temporal changes in scene reflectance were then measured and compared. Soils at a given location do not change significantly during a growing season. In desert ecosystems with their inherent low vegetation cover, the ratio of vegetation to soil background remains relatively constant (Huete and Tucker 1991). Even though we do not know the exact effect of soil background in each site, relative changes in NDVI temporal patterns are still meaningful. Additionally, we have carefully selected our

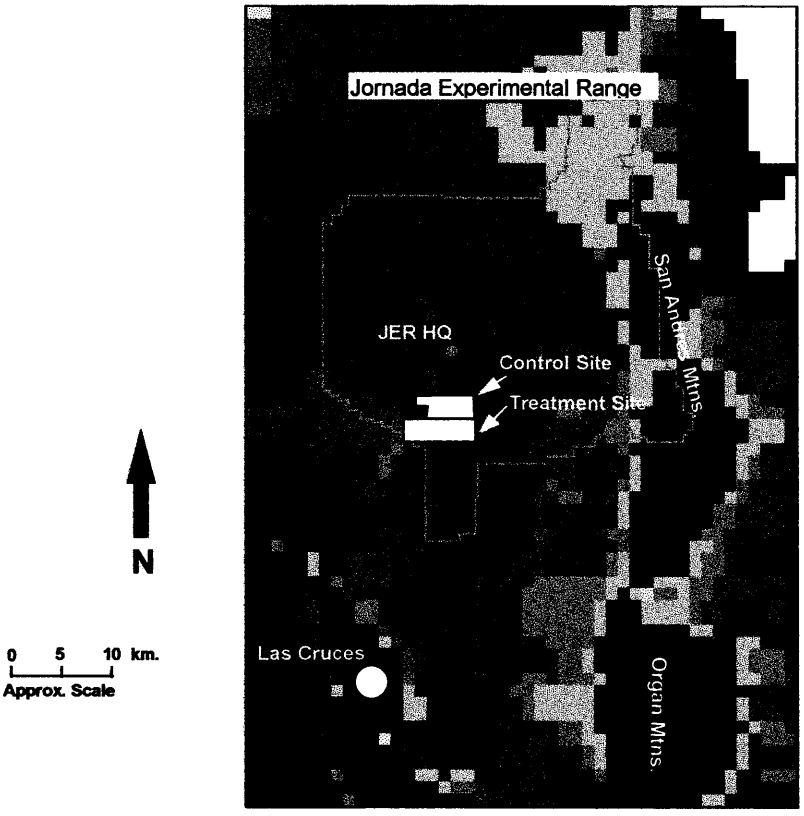

Figure 2—Location of the treatment and control sites on the Jornada Experimental Range.

single-date HRPT imagery to minimize the effects of soil moisture and off-nadir atmospheric attenuation.

Results and Discussion

The level of photosynthetic activity at each site (as measured by NDVI) was graphed for each of seven growing seasons from 1987 to 1993. These seven years exhibit temporally variable precipitation patterns, and variable NDVI growth patterns from year to year. In spite of this temporal variability, year by year comparison between chemically treated and non-treated (control) sites reveals the effect of the treatment on the photosynthetic activity of the plant community. The treatment site comprised 12 AVHRR pixels (14.52 km^2), and the control site 9 pixels (10.89 km^2). Each year was analyzed in sequence.

Prior to chemical treatment, the seasonal growth curves for 1987 are very similar for both sites (fig. 3). June was unusually wet, resulting in an NDVI spike in early July. Depending upon temperatures and nutrient availability, this could be photosynthetic activity of shrubs, grasses, and/or annuals. Both sites lie at the boundary of active mesquite invasion. The treatment site still contains the original black grama, along with other grasses and mesquite, while the control site is dominated by mesquite, dropseeds, and threeawns, and almost no black grama (table 1). These community composition differences account for the slight separation in the curves in the spring (treatment site having less photosynthetic productivity) and late summer (treatment site having more activity).

In 1988, precipitation patterns were more typical of this area, with minimal spring precipitation and monsoonal moisture starting in early July. The growth curves for the two sites begin the year almost identically. Upon chemical treatment in early June (fig. 4), the NDVI curve for the treated area drops, indicating defoliation of the mesquite. With the mesquite no longer competing for water and nutrients, the C_4 grasses of the treatment site are able to grow much more vigorously during the monsoon season than in the control site.

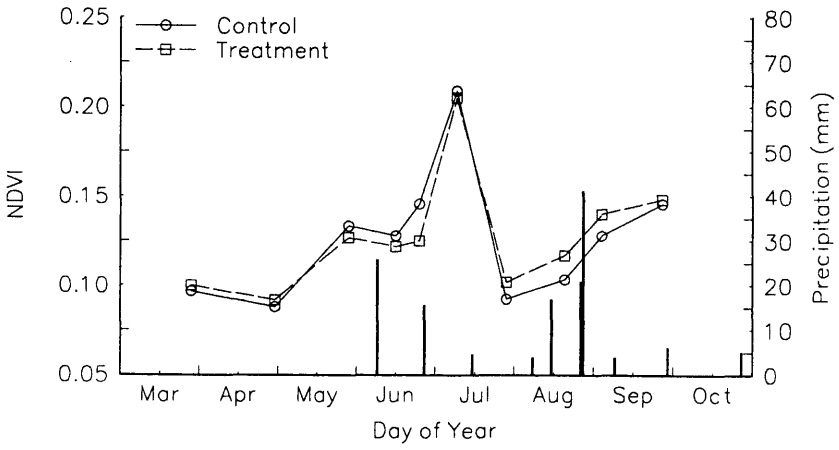

Figure 3—Temporal NDVI curves for treatment and control sites for the pre-treatment year 1987. Precipitation at Rabbit Rain Gauge is presented on the right y axis.

Table 1—Species cover and composition at the treatment and control sites.

	1994 Field Cover and Composition Data	
Species	**Control (%)**	**Treated (%)**
C_3 Species		
Prosopis glandulosa	12.70	1.91
Atriplex canescens	1.29	—
Gutierrezia sarothrae	3.38	4.31
C_4 Species		
Bouteloua eriopoda	0.03	13.14
Sporobolus flexuosus	5.80	5.37
Aristida longiseta	0.20	5.57
Erioneruron pulchellum	2.88	—
Muhlenbergia porteri	0.04	0.20
Hilaria mutica	—	0.10
CAM Species		
Yucca Elata	—	0.62
Total C_3 Species	17.37	6.22
Total C_4 Species	8.95	24.42
Total CAM Species	—	0.62

During 1989, the first full season after the chemical application, the effects of the treatment are very noticeable (fig. 5). The control (mesquite) site has a markedly higher spring peak, and the treatment (grass) site is higher from the onset of monsoonal moisture through senescence. This is to be expected as the treatment reduces shrub production and increases grass production.

Precipitation timing was unusual in 1990, especially during the monsoon period. From early July through the end of September frequent small rainfall events were recorded (fig. 6). Most of these did not even exceed 10 mm. Such small events are typically ineffective for plant biomass production (W.G. Whitford, personal communication). The temporal growth curves reflect this, as no strong monsoonal peak is obtained. Because of this, it is difficult to interpret plant growth patterns during the monsoon (fig. 6). The low point on the control site in late August appears anomalous. It could be due to localized wet soil, or unaccounted for atmospheric attenuation. During the spring of 1990, however, the two curves do show the expected separation. The treated site does not exhibit the level of photosynthetic activity that the mesquite dominated site does.

By 1991, the effect of the treatment is no longer evident (fig. 7). The separation in the NDVI curves is very subtle, as was the case during the pretreatment year (1987). Again the treatment (grass) site has slightly less photosynthetic activity in the spring, and a very slightly higher peak during the monsoon season. The similarity in these curves would indicate that the mesquite canopy cover has increased, and the 1988 treatment has lost its effect. One point of interest during the 1991 growing season is the response of vegetation to the large precipitation event in early July.

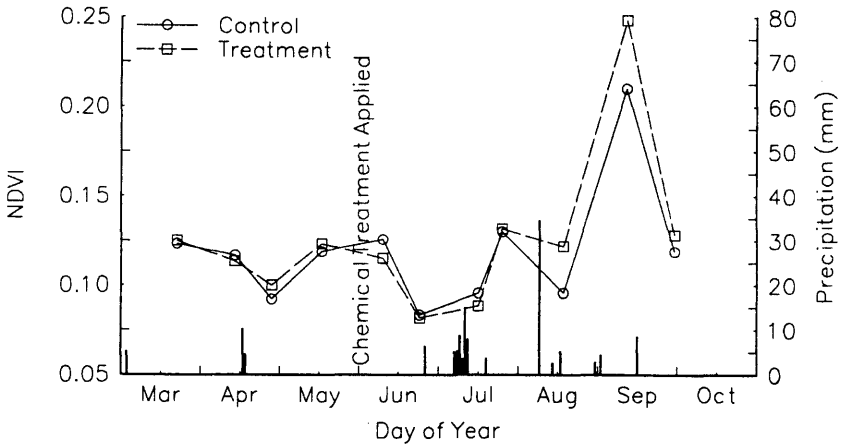

Figure 4—Temporal NDVI curves for treatment and control sites for the first treatment year 1988. Precipitation for the Rabbit Rain Gauge is presented on the right y axis.

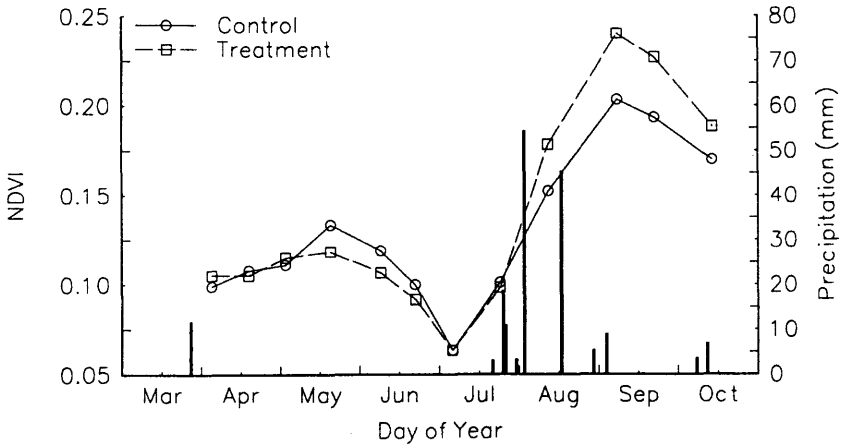

Figure 5—Temporal NDVI curves for treatment and control sites for the first full season post-treatment 1989. Precipitation at Rabbit Rain Gauge is presented on the right y axis.

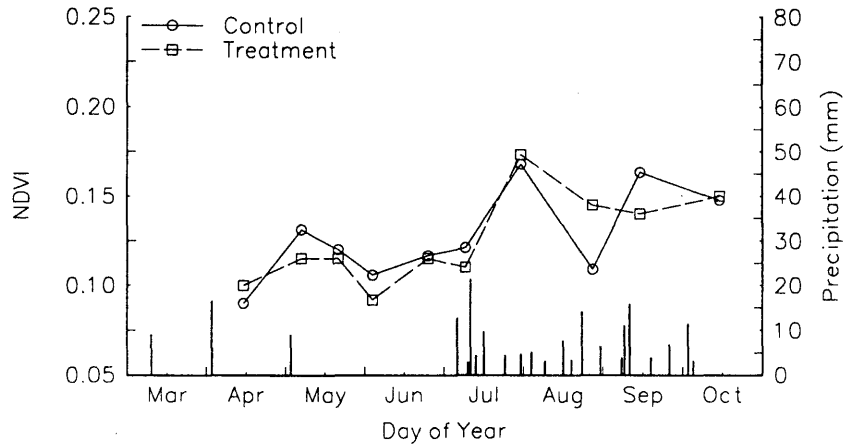

Figure 6—Temporal NDVI curves for treatment and control sites for the second season post-treatment 1990. Precipitation amounts at Rabbit Rain Gauge are presented on the right y axis.

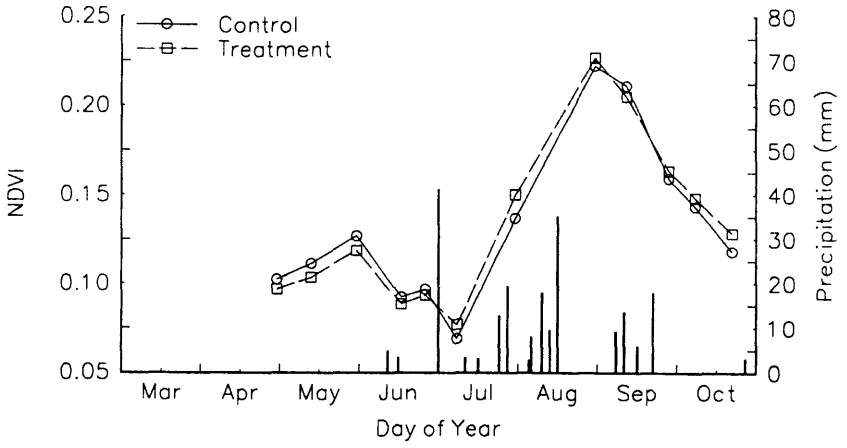

Figure 7—Temporal NDVI curves for treatment and control sites for the third year post-treatment 1991. Precipitation amounts recorded at the Rabbit Rain Gauge are presented on the right y axis.

The spring of 1992 was wetter than normal. Both NDVI curves are identical during the early spring season (fig. 8), reinforcing the conclusion from the 1991 curves that the treatment has lost its effectiveness. As in 1988, the curves separate coincidentally with the defoliation of the mesquite resulting from the chemical application. The unusually wet spring generated a large spring growth activity peak, reflecting a high level of spring biomass production. The monsoon season was drier than normal, and vegetation growth response during the spring probably used most of the available nutrients, resulting in minimal photosynthetic activity during the late summer. The treatment (grass) area was more productive than the control area as measured by NDVI. In fact, the control area did not peak at all during the 1992 monsoon.

In 1993, the first full season after the second chemical treatment, the effect is again noticeable (fig. 9). The grass dominated treatment site had lower spring vegetative activity and higher monsoon season. The differences, however, are not as pronounced as they were following the 1988 treatment. Before any comparisons of 1988 versus 1992 treatment effectiveness could be made, 1994 and 1995 data would need to be analyzed as well.

Conclusions

We expected chemical treatment would result in a reduction of C_3 mesquite production and an increase in C_4 grass production. This shift would be detected by satellite-derived vegetation index curves as a decrease in the index during the spring and an increase during the monsoon season. The sites analyzed show this expected pattern of response. A satellite-derived temporal comparison of treated versus untreated sites successfully provided an indication of plant community photosynthetic response to chemical treatment of mesquite. Furthermore, we were able to determine the length of time of treatment effectiveness. We believe that our research demonstrates the utility of high temporal resolution satellite data for monitoring regional landscape change. We show that carefully calibrated, satellite-derived inputs could be developed to aid monitoring of ecosystem health and managing arid shrublands.

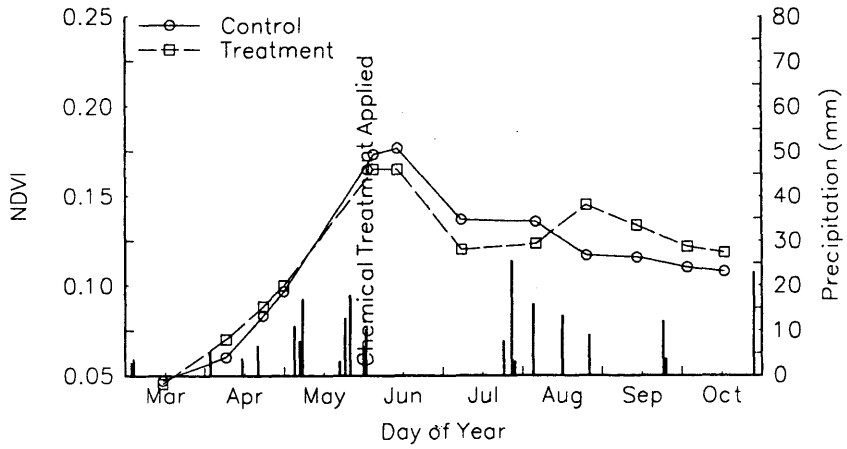

Figure 8—Temporal NDVI curves for treatment and control sites for the second treatment year 1992. Precipitation amounts at Rabbit Rain Gauge are presented on the right y axis.

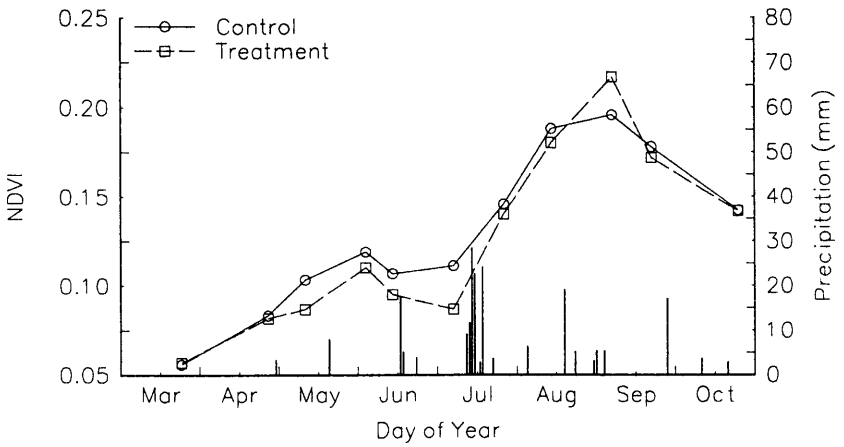

Figure 9—NDVI curves for treatment and control sites for the first year post-treatment 1993. Precipitation amounts at Rabbit Rain Gauge are presented on the right y axis.

Acknowledgments

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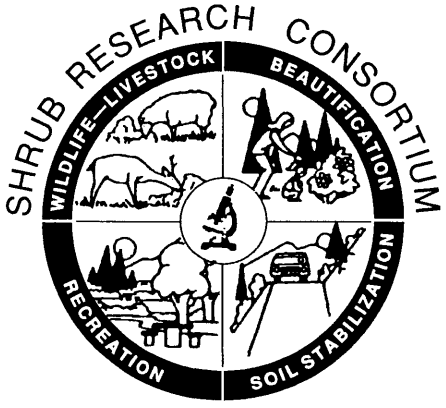

Management and Restoration Options

Past Changes, Present and Future Impacts, and the Assessment of Community or Ecosystem Condition

Robin J. Tausch

Abstract—Health, condition, and trend are widely used terms in ecosystem management, but their use is highly variable. Their application has been incompatible with the kinds of ecosystem changes that have occurred during the Quaternary and with our evolving understanding of ecosystem dynamics and present and future impacts from human activities. To manage for sustainability into the future, our concepts, definitions, and selection of standards should be appropriate for what we know about the influence of past, present, and future impacts. To avoid circularity in concepts and assessments of health, they should be based on values that are distinct from the sampled indicators and attributes applied in making the assessments. Definitions and concepts are needed that allow for the selection of standards of health and condition that are more appropriate for the nonlinear trajectories of ecosystem change and human alterations of those trajectories into the future.

References to ecosystem health, including range condition and trend, are widely applied to plant communities and whole ecosystems. Despite their importance, the interpretation or understanding of terms such as good or poor health vary greatly (National Research Council 1994; Scarnecchia 1995; West and others 1994; Unity in Concepts and Technology Task Group 1995a,b), are the subject of debate (Joyce 1993), and often do not supply answers to management questions (Unity in Concepts and Technology Task Group 1995a,b). Ecosystem health is determined by reference to a standard (West and others 1994). This standard varies, but it is based on judgement of what represents healthy or unhealthy condition from community composition. Clements (1916, 1936) was the first to apply an ecological standard based on plant succession. His monoclimax model, operating within a climate assumed to be fluctuating around an average, has largely dominated subsequent management applications.

This paradigm has created problems for the interpretation and understanding of the present and future states of the structure, function, and resilience of ecosystems. First, since the late 1950's, communities have been known to potentially have multiple endpoints (Olsen 1958). Second, the accumulating information from the past shows that climate has continually changed during the last 2 million years of the Quaternary (Betancourt and others 1993; Tausch and others 1993a,b). Third is the accumulating information on the potential impacts from the past, present, and future human activities altering ecosystem dynamics (Denevan 1992; Tausch and others 1993b). Last is a general failure to keep the concepts of health or condition separate from the ecological data and theories used or applied in making those assessments (Scarnecchia 1995).

Ecosystem Changes During the Quaternary

In much of our study and management of ecosystems we have demonstrated a limited understanding of how ecosystems function and change over the long term, in part because these efforts have usually occurred in a fragmented fashion over the short term. As paleoecological information accumulates on long-term ecosystem dynamics, it is apparent that a major part of why ecosystems behave as they do is rooted in their history of change through the Quaternary (Betancourt and others 1993; Tausch and others 1993b).

During the Pliocene, climate was generally more stable than during the Pleistocene where there have been an estimated 17 to 20 cycles of glacial advance and retreat with associated environmental changes (Winograd and others 1992). Interglacial climates, such as those of the present, only represented about 10 to 15 percent of the Quaternary period (fig. 1 in Tausch and others 1993b). Species present today are those that have managed to survive from the Pliocene, through the pounding of the repeated glacial cycles of the Pleistocene, followed by the human impacts of the Holocene.

Associated with these climatic cycles have been dramatic changes in species distributions and community dominance patterns (Betancourt and others 1993) as each species responded individualistically to the environmental changes (Foster and others 1990). The result has been a continual shifting in the species composition and competitive interactions of communities (Foster and others 1990; Nowak and others 1994a,b) that continues today. Communities have not responded as single units.

Several conclusions could be summarized from the results of paleoecological studies. Communities and ecosystems are unique at each location and transient over time. They are both dynamic and pluralistic because they function as a mosaic of successional stages and functional processes scattered across the landscape. Communities potentially have thresholds in the patterns of their successional trends and can change rapidly in response to environmental changes if those thresholds are crossed (Laycock 1991). Changes that result from crossing a threshold can be persistent for long

In: Barrow, Jerry R.; McArthur, E. Durant; Sosebee, Ronald E.; Tausch, Robin J., comps. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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periods (Tausch and others 1995). This landscape mosaic of dynamic processes and successional change are central to both understanding and managing ecosystems to maintain their resiliency (Arrow and others 1995). An existing community may be as much or more the result of the conditions of its formation as it is of the environmental conditions under which it currently exists.

Clearly, the better we understand how communities came to be through their history of development during the Quaternary, the better we will understand the nature of current changes, including their scale and the driving forces behind them. Management actions based on this understanding will be more appropriate for maintaining healthy ecosystems.

Paleoecological Implications for Ecosystem Health

Results from paleoecological research can provide guidance for the determination of ecosystem health and range condition. Range condition in this case is a specific application of the concept of ecosystem health. When determining the condition of a target community or site for management, it is necessary to compare the area to a reference or standard (West and others 1994). That standard is a benchmark that represents the climax or some preferred community composition (Unity Task Group 1995a,b). A benchmark represents an external standard for health assessment (West and others 1994).

Two alternatives exist for selecting a benchmark for this comparison. The first, and most preferred alternative is to have an actual benchmark community that represents the ecologic potential for the target community. With proper management the successional direction taken by the target community should result in its changing to increasingly resemble the benchmark community.

Suitable benchmark communities are relatively rare because of climate changes and the extensiveness of past human impacts on most ecosystems (Denevan 1992, Tausch and others 1993a,b). Thus, the second method is to come up with an estimation of what the benchmark community would look like and what its species composition would be, and to do so by some means such as a defacto expert system (West and others 1994).

Paleoecological information reveals several potential problems with the methods used for selecting a benchmark community, be it actual or estimated. The assumption is that the benchmark community is a valid standard or reference that is still representative of the potential for the target community, and that it represents the community composition needed to meet the management goals for the site. Because benchmarks are scarce, extra effort is often expended to find something that is representative. Once benchmarks are selected, attempts are usually not made to determine either accuracy or precision of their species composition and abundance, but are treated as if they are known without error.

All communities, however, continually change, but more recently the directions of change have often been altered by humans (Denevan 1992, Tausch and others 1993b). Thus, many potential problems exist for the representativeness of the selected benchmarks. A particularly relevant example are benchmark data that are from, as most are, a single location and point in time (West and others 1994). How benchmark communities can conflict with the assumptions used in their application for condition determination can be described by drawing on examples from history.

Example 1—The benchmark site and the target site were originally the same community at some arbitrary time in the past, but the benchmark site is no longer relictual nor representative of the target site because both have changed over time. The changes have proceeded in different directions because the two sites have experienced different environmental changes and disturbances. The benchmark currently represents a community we think existed on the target site in the past, or was possibly chosen because someone's preference was for such a community to have existed.

Example 2—The benchmark site is actually a relic, representing the potential for some other sites, but is not and never has been representative of the potential for the target site. There are many reasons why this can happen. An improper identification of the potential community type could occur because of error in identifying the history and ecology of either the target site or the benchmark site. An inappropriate selection of a benchmark site could occur because of the desire to have one despite their scarcity or absence.

Example 3—The benchmark site is a valid relic and was once representative of the subject site, but disturbance, introduced species, or other environmental factors have pushed the target site across one or more thresholds to where the benchmark site is neither representative nor attainable (Unity Task Force 1995a,b). The sustainable potential communities possible for the target site have changed, and current examples may not exist.

Example 4—The benchmark site is a valid relic that is still representative of some past composition of the target site. However, the benchmark community provides either inadequate productivity or inadequately protects important resources for current human needs (Unity Task Force 1995a,b). Other communities within the environmental constraints of the target site would perhaps be better able to supply the resource demands on a sustainable basis.

Example 5—The benchmark site is a relic that is representative of what existed on the target site at some arbitrary past time. However, the climate and other environmental conditions under which the benchmark community developed no longer exist. This could include past processes and stages of its development that are no longer possible, and past interactions with species that are no longer present. The benchmark site is now a relic that has persisted by vegetation inertia such as persistence of long-lived perennial community dominants (fig. 4 in Tausch and others 1993b). As such it is on the edge of a threshold and easily changed by even minor disturbance. Converting the target site to the same community as the benchmark site would take considerable effort, and the site would be difficult to maintain due to inherent instability. The possible communities for the target site that are sustainable are new for the location and probably did not exist in the past.

Example 6—When there is no actual benchmark site, and the composition of one must be estimated, one or more of the preceding five examples may still apply. An additional possible problem is that the estimated benchmark community is not real, even though it was based on experience or historical information. It possibly has never existed or at least is not a possibility for any of the target sites to which it has been applied.

The above complications may not always occur, but they and related problems are common enough to contribute to the current inappropriate use, confusion, and concern in the assessment of health described by the Unity Task Force (1995a,b) and the National Research Council (1994). Some selections of a benchmark for condition determination have been successful for management, but often because of luck. When a benchmark is used and any of the complications described in the examples above occur, then the goals set for the target site are in error in some way. All estimates of health or condition based on comparison with the benchmark site will usually be negatively affected. The greater the error in the selection of a benchmark, the more negative the affects on any estimate of health, condition, or trend are likely to be. Also, decades of experience (Unity Task Force 1995a,b) have shown that selection of pristine or climax vegetation usually used for benchmarks is not a necessity nor even particularly useful for assessing health or setting management goals.

Benchmark communities selected for determining target site health may have several problems. One has been the lack of any established procedures at any point in the process for judging the appropriateness of a benchmark community or for determining its suitability for meeting management needs. Lack of objective guidelines can lead to selections based on appeal of some pristine condition or, a reliance on some past magical time of supposed ecosystem perfection or when things were still "natural"—communities that may have never existed (Denevan 1992; Tausch and others 1993b).

Another problem arises when a static benchmark community is selected for health assessment and for management direction. A static community represents a defacto selection of, or a gamble on, the particular future environmental scenario favorable to the selected benchmark. But based on the accumulating climatic information we have for the past 2 million years, the least probable future event is for the climate to remain the same. Therefore, any benchmark picked is likely to be incorrect except over the relatively short term because we have limited ability to predict climate and environmental changes into the future.

Paradigms Needed for the Future

Procedures used for determining ecosystem health that involve any sort of standard, including benchmarks, are inadequate now and, unless changed will be inadequate for the future. One needed change concerns use of benchmarks of preferred community composition for health assessment. Paleoecological evidence clearly shows that plant communities are trajectories of change from the past, through the present, and into the future. The patterns and rates of these changes vary in time and space as a mosaic of dynamic processes of competition and community change scattered across the landscape.

Trajectories of community change from pre-history are increasingly being modified by impacts from human activities, resulting in new demands and problems (Golley and others 1994). The changes are often unnoticed until major differences have accumulated because the changes are occurring on spatial scales that encompass entire landscapes, and are occurring on times scales where cause and effect can be separated by one or more generations (Lee 1993).

Management decisions can only involve either maintaining or changing the many community trajectories in response to the new demands and problems. Better knowledge of the past, present, and likely future of these trajectories needs to be part of how we assess ecosystem health and how we make management decisions. Our current knowledge, however, is woefully inadequate. In many ways, we do not know how the world works, what the problems are, how serious they are, or how to cure them (Woodwell 1994). The result is a critical need for new information from monitoring and the continuing development of new methods (Golley and others 1994). This requires a broader, more forward-looking focus than the concentration on a single benchmark as a standard for both the assessment of health and the selection of management actions.

An attempt to develop better guidelines for assessing range health was recently published by the National Research Council (1994). This attempt was both confusing and clarifying, leading Scarnecchia (1995) to refer to the Council's proposal as "a change in terminology without a change in conceptuality—a confounding step sideways out of the line of fire." An example of the confounding was the concept of thresholds in community composition as an integral part of determining range condition. By the Council's definition, a community near a threshold is a community at risk, but a community must have crossed a threshold to be in poor condition.

Increasing evidence shows that there are often thresholds of change in communities (Laycock 1991). But the Council's definition incorporating a threshold as a requirement for an assessment of poor condition implies that all communities have only one threshold, or maybe only one important threshold. If any communities do not have a threshold, does that mean they cannot ever be in poor condition? For situations where more than one threshold may occur, the Council provides no way for determining which one should be used in the identification of poor condition. Another implication is that the threshold in the species composition of each community is located at just that point in a sere that identifies the critical point for management.

A common characteristic of thresholds is that changes in community composition are permanent, at least for management implications into the foreseeable future (Laycock 1991; Tausch and others 1993b; Tausch and others 1995; Unity Task Group 1995a,b). The result of a community crossing a threshold is the change to a new species composition that is functionally a new community. Resource needs and management goals can also dictate that many communities should be interpreted as in "poor" condition well before they are even at risk of crossing a threshold, else mitigation becomes unlikely, if not impossible.

The latest report from the Unity Task Group (1995b) also provides recommendations for new guidelines that are based first on the concept of an ecological site. The focus on a benchmark is a little less stringent. Proper identification of the ecological type allows for extrapolation of research and management experience to other areas of the landscape with the same ecological type. The Unity Task Group (1995a,b) also adds to the definitions for a Site Conservation Threshold and a Site Conservation Rating specific to the ecological site. These allow for identifying community status and change on ecological sites critical to management that are independent of thresholds.

The Task Group format also calls for the identification of different community types for a particular ecological site, but only those currently known to occur. They recommend that one be selected from those identified to be the Desired Potential Community, which is described in more general terms than the benchmark has been in the past, but vegetation status is still determined in terms of similarity to, and trend as movement toward or away from, the Desired Potential Community (Unity Task Group 1995a,b).

Remaining problems with the Task Group's definition of the Desired Potential Community are related to those of a benchmark in general. First, its selection involves significant proportion of value judgments, such as the selection of a Desired Potential Community that is based on an assumption that climate and environmental conditions favorable to it will be present in the future. The Task Group's definition assumes that the communities identified as currently representative of the ecological site cover all the possibilities. However, some or all of these communities could be relics of past conditions and not possible in the future.

These guidelines also assume that we know enough about the important ecological attributes and indicators of the ecological site to recognize it over all the communities currently occurring. For most sites such information is probably not available because, first, the level of change is ongoing, and second, no communities have ever been adequately identified and mapped (Estes and Mooneyhan 1994). Finally, the Task Group guidelines ignore the possibility that many, or even most, of the possible future communities may not yet exist (for example, they will only occur as conditions change in the future).

The procedures built into assessments are currently inappropriate, which confounds the process, (Scarnecchia 1995). Basically, our failure has been to not keep the value-based concepts of health, condition, or ecological status (EMAP from West and others 1994) separated from both ecological theory and ecological data. Scarnecchia (1995) points out that to accomplish this separation it is necessary "that the concept [of health] *per se be devoid and independent of any ecological theory, including theories involving succession, climax, stable states, and thresholds*" (emphasis from Scarnecchia 1995). He additionally stresses that a concept of ecosystem health or condition "must be designed to *apply, but not consist of*, regionally applicable, partially validated, ever evolving ecological theories" (Scarnecchia 1995). There are no directly measurable indicators of ecosystem health, only measurable changes over time in indicators and attributes of ecosystems. These changes must be interpreted using values that include cultural factors (Unity Task Group 1995a,b), to develop an appropriate assessment of health.

The assessment of ecosystem health thus involves three important, functionally discrete modules: (1) the social values upon which the associated concepts of ecosystem health or condition are based; (2) the ecological theories available for the ecosystem; and (3) the ecological data on attributes and indicators available for the ecosystem. When we fail to keep these three functionally discrete parts separate, we end up with the confounded and confused process described by Scarnecchia (1995). Inventory, monitoring, selection of the Site Conservation Threshold, determination of the Site Conservation Rating, and the assessment of condition for all possible communities are critical to the process of health determination. However, they need to be based as much as possible on attributes and indicators that are as independent as possible from a particular plant community and from values of health.

The procedures for determining a benchmark community as a standard for health assessment can be used to provide examples of how confounding can occur. Whether some on-the-ground benchmark is present or absent, the process comprises values as much as it comprises ecological theory or ecological data. Essentially, whenever there is a gap in either ecological data or theory, values tend to fill in the gap, confounding the process. Their identification as values is then usually lost. Even estimated benchmarks, however, are often treated as if they represent actual ecological data.

The Unity Task Group (1995a) report indicates a need for the development of a statistically valid inventory and condition assessment of rangelands. Statistical procedures for inventories of attributes and indicators (typical of field data) are established and widely used. Changes in those attributes and indicators over time can also be analyzed by conventional statistics. However, a statistically valid summary for the assessment of condition or ecological status, with its necessity for a high proportion of incorporated values and opinions, requires different assumptions and statistical techniques.

Assessing of an ecosystem's health should focus on the current trajectory of change. This requires baseline data and the application of adaptive management through the monitoring of future changes (West and others 1994) of not only all known communities for an ecological site, but for unrealized ones as they occur. Expanding on a description by Lee (1993), ecosystem health, range condition, and ecosystem sustainability are not fixed endpoints as a benchmark community is often interpreted, but directions (values) for guiding constructive change.

Again paraphrasing Lee (1993), these ideas (values) are worthwhile because they set a standard for responsible management. When the concepts of health are used appropriately, the focus will be on managing the ongoing trajectories of change in ecosystems and not on achieving a particular benchmark. The standard of comparison will be more functional than compositional.

Assessments need to be accomplished in the three parts described by Scarnecchia (1995). First are the field collection and statistical analysis of the ecological data on the ecosystem. Second is the application of available ecological theory for interpretation of analysis results. This is needed to improve our ecological understanding of what the states and changes measured mean for anticipating possible affects that future changes or trends will have on the structure,

functioning, and resilience of the ecosystem. Third is incorporating a framework of social values within which ecological data and theories can be organized into an assessment (Scarnnechia 1995).

All three parts must be involved and are always intimately interlinked. The ultimate successes of ecosystem management, for example, hinge on people because we are an integral part of ecosystems (Box 1995). Interaction between social values and ecological theory can also affect how we view ecosystems, which will influence the types of ecological data collected. However, unless we consistently recognize all three parts of the process, and focus on standards based on monitoring ecological attributes and indicators rather than on achieving fixed benchmark communities, the resulting confounding of our assessments will prevent accurate and timely understanding of the ecosystem changes. This will inhibit proper management to maintain ecosystem trajectories of change that sustain their functions and resiliency.

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Community Stability in a Salt-Desert Shrubland Grazed by Sheep: the Desert Experimental Range Story

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Abstract—The effects of 59 years of winter and spring grazing on a Great Basin salt-desert shrubland were analyzed using frequency and cover data. Spring grazing altered species composition more than winter grazing when compared to the nongrazed exclosures. Grazing in both seasons resulted in significant decreases in shrub importance. Introduced annuals increased in importance with spring grazing. Spring-grazed pastures show patterns of destabilization that are missing from winter-grazed pastures and nongrazed exclosures.

Traditionally applied concepts used in managing grazing on Western United States rangelands are founded in what has been called the "climax" (Friedel 1991) or the "successional" (Westoby and others 1989) model. The framework of this model was developed by Clements (1916) and applied to the management of rangelands by Sampson (1919). It is based on the assumption that: (1) a single climax state exists for each site; (2) each of a series of seral states predictably gives way in succession to subsequent states until the climax state is reached, implying a single pathway for succession to follow; (3) disturbance, such as that caused by grazing, has the opposite effect as succession; and (4) all changes in successional position are reversible. Consequently, all one must due to restore a community degraded by grazing is reduce or eliminate grazing, and successional forces will, in time, complete the restoration. The closed nature of the model renders irrelevant the concept of stability.

Vegetative communities on many arid and semiarid rangelands worldwide do not respond as predicted by the successional model (Friedel 1991; Laycock 1991). Alternative models have recently gained acceptance as more accurate tools in describing and explaining changes on rangelands (Laycock 1991). These models incorporate concepts of multiple stable states and successional pathways and generally hold that movement between states requires crossing thresholds. Reversibility, at least on a practical time-scale (several to many decades), is often lost.

In: Barrow, Jerry R.; McArthur, E. Durant; Sosebee, Ronald E.; Tausch, Robin J., comps. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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The two-dimensional ball and trough analogy is a useful method of presenting the multiple stable-state model (Laycock 1991; Tausch and others 1993). In figure 1, the ball symbolizes the composition of a community at a given point in time. It rests on a line curved to a contour of valleys and hills representing stable states (A and B) and intervening thresholds (C). The shape of the line is a function of the physical and biological environment. Trough depth depicts stability (Laycock 1991).

For as long as the ball (community composition) stays within a single trough (stable state) it more or less follows the successional model, meaning, the ball will always return to rest at the bottom of the trough (climax vegetation) whenever disturbance is removed. When a disturbance occurs with adequate force to overcome threshold height, the ball crosses into a new trough. At this point the Clementian model is no longer adequate to describe the possible compositional trajectories of a community. The reversibility of a move across a threshold depends upon threshold height. Constant disturbance, such as moderate grazing, may lack the full energy needed to move the ball over a threshold but will hold it on the slope of the trough. Such a ball (community), though stationary, is less stable than one in the trough bottom because of its more proximal position to the threshold crest. The breadth of the trough bottom is indicative of community flexibility, or the degree to which it can vary in composition without a change in stability.

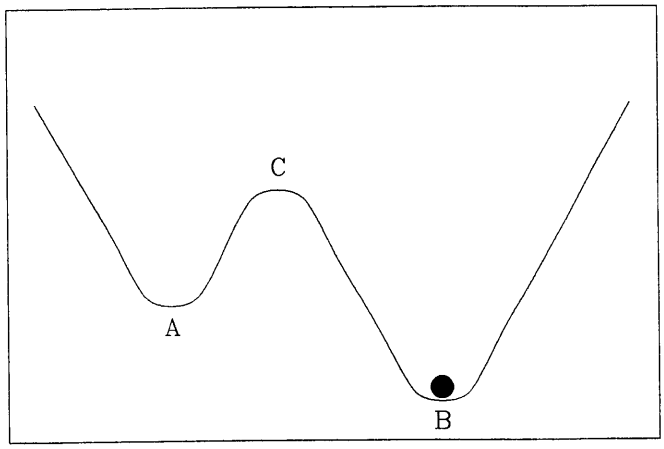

Figure 1—The two-dimensional ball and trough diagram can be used to illustrate relationships among stable states and intervening thresholds.

Abiotic and biotic changes in the environment, such as climate change and species introductions, alter relationships among thresholds and stable states and are expressed in the diagram as a change in line curvature (Tausch and others 1993). Such changes can alter the stability (depth) of a state (trough) as well as create new stable states. As a result, communities that have demonstrated considerable resilience to disturbance beforehand might become susceptible to lower levels of disturbance following changes in environmental parameters.

Study Site

The Desert Experimental Range was established in Pine Valley, Millard County, Utah, in 1933 as a site where long-term effects of fall, winter, and spring sheep grazing could be studied (Clary and Holmgren 1982). The experimental area of this site is representative of about 180,000 km^2 of mixed salt-desert shrubland found in the Great Basin and neighboring areas of the Western United States (Holmgren 1975).

Winters are cold and summers are warm. Mean January and July temperatures are –3.5 and 23.3 °C, respectively (Holmgren 1975). Approximately half of the 157 mm mean annual precipitation occurs during a 7-month period of soil moisture accumulation (October-April), mostly as light snowfalls of 5 cm or less.

Prior to establishment of the Desert Experimental Range, plant communities in Pine Valley had been significantly altered due to a half century of unrestricted access to public lands by livestock operators (Holmgren 1975). In 1934, 20 pastures of either 97 or 130 ha were established to study the long-term effects of sheep grazing on the desert community. In each of 16 pastures, two exclosures of 0.4 ha each were established in 1935. Treatment combinations of fall (early winter), midwinter, and spring (late winter) grazing at light, moderate, and heavy levels (average of 25, 35, and 42 sheep days per hectare, respectively) were assigned to each pasture (Hutchings 1966). Grazing treatments have been applied annually from 1935 to present with actual sheep use days adjusted according to available forage. Earlier investigations (Holmgren and Hutchings 1972) revealed no differences between the effects of fall and winter grazing treatments and led to a modification in which both dormant-season grazing treatments were applied during a single winter (dormant) period.

The long-term study conditions at the Desert Experimental Range are well suited for investigating the effects of sheep grazing on the stability of salt-desert plant communities. Here we examine differences in species composition and cover between paired grazed and nongrazed study areas and seek to characterize possible stable states. We consider the stability of communities under the different grazing treatments and explore the possible ramifications of species introductions on community stability. Finally, we make management recommendations based upon our conclusions.

Methods

The 16 pastures at the Desert Experimental Range with exclosures were used for this study. Grazed study areas (0.4 ha each), with similar soils and aspect, were located near to and paired with each of the 32 exclosures (two per pasture). Study area pairs were grouped by grazing season: 20 in pastures grazed in winter only, and 12 in pastures with spring grazing. Justification for ignoring grazing intensity is provided by Harper and others (1990) and Whisenant and Wagstaff (1991).

Within each study area, four 50 m parallel transects were spaced at 10 m intervals. On each transect, 10 nested sampling configurations were randomly located alternating on either side of the transect line. Each configuration had an area of 4.0 m^2 (200 x 200 cm) with smaller, nested plots of 1.0, 0.25, and 0.06 m^2. Transects were read in June and the first week of July 1994.

Study area summed frequency values (SFV's) were determined for each vascular plant species using a modification of methods described by Smith and others (1987). Maximum potential SFV for any species was 160. Relative differences in SFV's among paired study areas were determined for the 12 most abundant species using the formula: relative difference = [SFV(grazed) – SFV(nongrazed)]/SFV(nongrazed) x 100. Resulting values indicate the effect of grazing season on species frequency when compared to no grazing both in direction and magnitude.

We estimated canopy cover from 400 point intercept observations per study area (10 points per nested configuration). Mean cover percentages were calculated for total vegetation, shrubs, perennial grasses, and introduced annuals.

Summed frequency data were used to calculate species diversity values weighted for species abundance for each study area using MacArthur's Diversity Index (MacArthur 1972). An index of similarity between each pair of study areas was calculated for all species combined and shrubs and perennial grasses only (Ruzicka 1958) (table 1).

Plant nomenclature in this paper follows that of Goodrich (1986). Data were subjected to analysis of variance using the General Linear Model (Minitab). Significant differences ($p < 0.10$) among means were determined using Fisher's least significant difference (LSD).

Results

Fifty-eight species were encountered across all transects including: shrubs (10), perennial grasses (10), cacti (4), perennial forbs (17), annual forbs (16), and annual grass (1). All species except for the annual forbs halogeton (*Halogeton glomeratus*) and Russian thistle (*Salsola iberica*) and the annual grass cheatgrass (*Bromus tectorum*) are native to the site.

Table 1—Similarity indices (Ruzicka 1958) based upon SFV's for paired grazed and nongrazed study areas for all species, shrubs only, and perennial grasses only. Asterisks indicate significant differences ($p < 0.10$).

	Pastures		
	Winter		Spring
All species	62.6	*	54.8
Shrubs	65.2	*	46.5
Perennial grasses	70.9		68.7

Table 2—Mean SFV's for 12 species across all grazed and exclosed study areas. Asterisks indicate significant differences between treatment means for individual species ($p < 0.10$). Differences for winterfat and purple three-awn approached significance with p-values of 0.11 and 0.12, respectively.

Species	Summed frequency per study area		
	Exclosed		Grazed
Shrubs			
Shadscale	36.0	*	49.2
Winterfat	60.7		46.4
Budsage	68.7	*	30.8
Low rabbitbrush	20.6		19.8
Perennial Grasses			
Indian ricegrass	80.5	*	98.6
Sand dropseed	71.3		81.9
Galleta grass	45.5		48.6
Purple three-awn	34.5		24.1
Squirreltail	26.3	*	16.9
Perennial Forbs			
Gooseberryleaf globemallow	15.8		13.3
Introduced Annuals			
Cheatgrass	43.3		51.5
Halogeton	14.0	*	28.1

Mean SFV's for the 12 most common species are found in table 2. Grazing-related differences for Greenes low rabbitbrush (*Chrysothamnus greenei*), sand dropseed (*Sporobolus cryptandrus*), and gooseberryleaf globemallow (*Sphaeralcea grossulariifolia*) were not significant. Values for the shrubs budsage (*Artemisia spinescens*) and winterfat (*Ceratoides lanata*), and for the perennial grasses squirreltail (*Sitanion hystrix*) and purple three-awn (*Aristida purpurea*) are significantly lower for grazed areas (grazing season ignored) than for nongrazed areas. Significantly higher grazing-related values were found for the shrub shadscale (*Atriplex confertifolia*), the perennial grass Indian ricegrass (*Oryzopsis hymenoides*), and halogeton.

Grazing season effects on relative differences in sum frequency are illustrated in figure 2. A significant negative effect of spring compared to winter grazing was observed for budsage, Indian ricegrass, and squirreltail. This was in spite of the significant positive response of Indian ricegrass to grazing when season is ignored. Spring grazing significantly favored galleta (*Hilaria jamesii*) and halogeton, both warm season species, and had a near significant, positive effect for cheatgrass ($p = 0.11$).

Vegetative cover expressed both in absolute percentages and relative to total vegetative cover is shown in table 3. Shrub cover is significantly lower for both grazing seasons when compared to nongrazed exclosures. Perennial grass cover was highest in winter grazed pastures, although differences were not statistically significant. Spring grazing resulted in significantly higher cover percentages for introduced annuals compared to both winter grazing and nongrazed exclosures.

We detected no significant differences in species richness due to grazing treatment with a mean of 19.7 species detected per sample area. MacArthur's Diversity Index yielded 8.7 and 7.9 species of equal abundance (frequency) in

Table 3—Mean cover values for exclosures, winter-grazed, and spring-grazed study areas. Asterisks indicate significant differences ($p < .10$) among grazed and exclosed, or winter-grazed and spring-grazed study areas. Numbers in parentheses indicate relative cover percentages (proportional to total vegetative cover).

	Cover percentage				
	Grazing treatment				
	Exclosures		Winter		Spring
	Percent				
Total vegetation	23	*	21		20
Shrubs	9 (39)	*	5 (24)		4 (20)
Perennial grasses	12 (54)		15 (70)		12 (60)
Introduced annuals	1 (5)		1 (5)	*	4 (20)

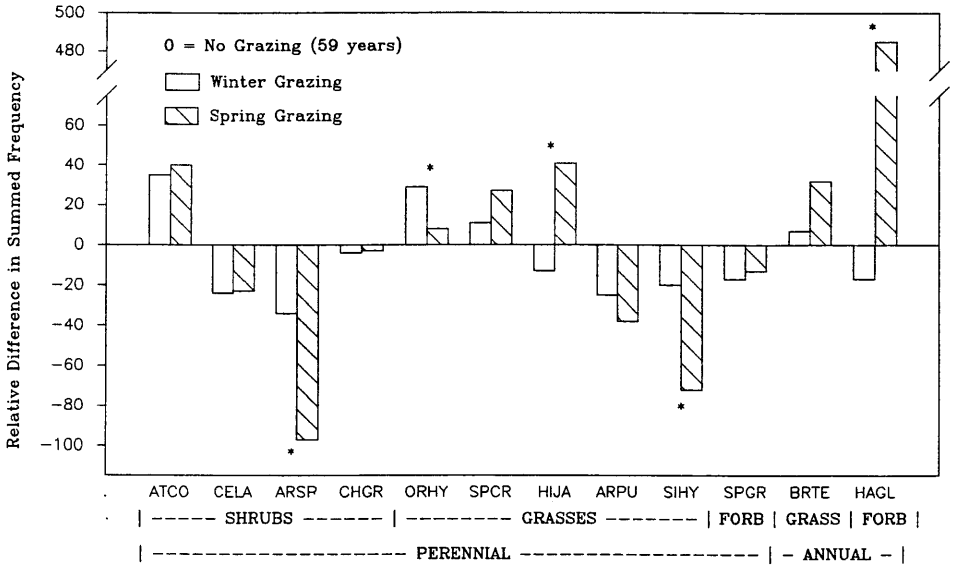

Figure 2—Relative differences in summed frequency for winter-grazed and spring-grazed pastures when compared to exclosures. Graph depicts both the direction and magnitude of that difference. Asterisks indicate significant differences ($p < 0.10$) between the effects of the two grazing seasons. ATCO = shadscale, CELA = winterfat, ARSP = budsage, CHGR = Greenes low rabbitbrush, ORHY = Indian ricegrass, SPGR = sand dropseed, HIJA = galleta, ARPU = purple three-awn, SIHY = squirreltail, SPGR = gooseberryleaf globemallow, BRTE = cheatgrass, and HAGL = halogeton.

nongrazed and grazed study areas, respectively. The difference in values approaches the statistical threshold for significance ($p = 0.13$). Differences in the indices associated with grazing season were not significant.

A mean similarity index of 60.1 was calculated across all species and study area pairs. Similarity values were higher for winter than for spring pastures for all species combined and for shrubs separately. Across all pairs, values for perennial grasses (mean 70.2) were significantly higher than those for shrubs (mean 59.4).

Discussion

Herbivory alters stability by disrupting competitive balance among individuals of co-occurring species, thus providing an opportunity for invasion and/or expansion of species affiliated with one or more alternate stable states (Harper 1969). The possible effects of pastoral activities on community stability are certainly not limited to those caused by herbivory. However, the effects of other grazing-related processes such as trampling, soil compaction, and disruption of cryptobiotic crusts are probably secondary in importance. Therefore, an examination of the mechanisms by which herbivory modifies competitive relationships should provide a satisfactory explanation for grazing-related differences in community composition.

Herbivory is the removal of living plant tissue from a plant for food. When vegetative parts are removed, photosynthetic capacity is at least temporarily reduced. At some point, this results in a reduction in growth rate and may reduce reproductive output and/or the ability of the plant to survive stress. When reproductive parts are removed, the capacity to replace dying individuals is impaired. Thus, herbivory may reduce the ability of plants to compete for limited resources and to leave progeny.

Herbivory is expressed selectively in all natural communities. Selectivity varies with species of herbivore, season of use, and density of target species (Harper 1969). Of particular interest at the Desert Experimental Range are changes in utilization due to seasonal differences in desirability of target species to sheep. For example, sheep consume smaller amounts of Indian ricegrass during winter when it is dormant than in the spring when succulent green shoots are available. Other species that are more highly selected in spring than in winter include budsage and squirreltail. As expected, these three species had significantly lower SFV's in spring-grazed versus winter-grazed pastures (fig. 2). We observed no seasonal differences for shrub species that provide forage of comparable palatability in both winter and spring (winterfat and shadscale). Higher SFV's for warm season herbaceous species (galleta, sand dropseed, and halogeton) are attributable to dormancy during grazing season and competitive release.

The magnitude of the impact of herbivory is inversely proportional to growth rate and to length of growing season. At the Desert Experimental Range, we observed that palatable species that grow slowly and only during the spring (budsage and squirreltail) were more negatively impacted by grazing than those that grow at moderate rates and are able, at least in some years, to "recover" after spring grazing (winterfat, shadscale, Indian ricegrass). Conversely, the rapid growth rate of cheatgrass more than compensated for the relatively high degree of overlap between its growing season and time of maximal use by grazers.

Plant species sometimes inhibit herbivory by allocating carbohydrate resources to structural and chemical characteristics that discourage foraging animals. The spines of shadscale and secondary metabolites of low rabbitbrush are examples at the Desert Experimental Range. These strategies are deployed at a cost to growth rate. This is generally a beneficial trade-off for perennials where the risk of herbivory is high.

Although single plant responses to herbivory are often negative and frequently lead to an increase in mortality rate, whole populations may compensate with increases in seedling survival. Consequently, herbivory has the effect of lowering mean plant age (Tilman 1988). Thus, species that reach reproductive maturity more quickly have an advantage over slower maturing species in communities with significant herbivory-related losses. Shadscale is a shorter lived, faster maturing species than winterfat or budsage (Blaisdell and Holmgren 1984). This relatively abbreviated life history contributes to the success of this species in grazing impacted communities.

In summary, species that succeed under grazing pressure do so through strategies of avoidance or tolerance. At the Desert Experimental Range, avoiding species are cool-season dormant, or employ protective structures or biochemistry to discourage herbivores. Tolerating species have fast growth rates, extended growing seasons, and/or shorter lifespans. Species most impacted by cool-season grazing possess traits that may be highly adaptive in the absence of herbivory but make the species susceptible to grazing damage. These traits include conservative growth rate, obligate summer dormancy, exposed meristems, long life-span, and a lack of protective strategies.

Grazing practices in northern Pine Valley prior to the establishment of the Desert Experimental Range were, in the absence of introduced annuals, probably not severe enough to cause irreversible changes in species frequencies. Therefore, the composition of communities in exclosures, where sheep have been excluded for 59 years, might approximate that of presettlement times.

Structurally, all protected communities were similarly dominated by shrubs and/or perennial grasses, often in roughly equal proportions (table 1). Budsage, winterfat, Indian ricegrass, and sand dropseed were the most frequently encountered species ($MSF > 50$). Shadscale, galleta, purple three-awn, squirreltail, and cheatgrass were also common ($50 > MSF > 25$). Though minor contributors to total biomass (Hutchings and Stewart 1953), several species of native forbs were encountered in most exclosed study areas. A total of 31 native forb species, representing a wide range in life-history strategies, were sampled.

The most abundant introduced annuals at the Desert Experimental Range are cheatgrass, halogeton, and Russian thistle (Harper and others, this proceedings). Their occurrence in the 32 exclosures was minor except on permanent rodent mounds where they have become the dominant vegetation.

Winter-grazed areas had fewer and smaller shrubs and more perennial grass plants than nongrazed areas. Among shrubs, shadscale increased in importance while winterfat and budsage decreased. Indian ricegrass and sand dropseed increased while the less abundant squirreltail decreased. Native forb abundance and diversity did not appear to be affected by grazing. However, low density size made the detection of significant differences difficult. The distribution of introduced annuals in winter-grazed pastures was similar to that of exclosures.

Shrubs in spring-grazed pastures were small, often of low vigor, and widely scattered. Budsage has almost been eliminated. The effects on perennial grasses were mixed. Cool-season grasses had frequencies equal to or lower than those in exclosures. Warm-season grasses generally did better than in exclosures. One exception was purple three-awn. This grass may suffer more from trampling or other secondary grazing effects than from herbivory. There were no measurable effects of spring grazing on native forbs. Introduced annuals were significantly more abundant in spring-grazed than in winter-grazed pastures and nongrazed study areas. This effect was amplified in 1995, a year of near record precipitation, creating clear contrasts among neighboring pastures of different-season grazing treatments (Harper and others, this proceedings).

Results suggest that winter-grazed study areas and their nongrazed pairs are not separated by any significant threshold and are probably equally stable, indicating plasticity in community stability. Conversely, reversion of spring-grazed study areas to shrub-dominated landscapes may require more than reductions or even elimination of livestock. Harper and others (1990) demonstrated that downward trends for budsage and winterfat in spring-grazed pastures have continued since establishment, while trends for the same species on winter and nongrazed areas have continued to rise during the same time period. Assuming the rates of change in community composition were somewhat constant in the spring-grazed pastures, it would take at least 120 years after elimination of grazing to fully restore these species to levels found in exclosures. This process could be slowed further by the virtual loss of seed sources and increased dominance of introduced annuals. Thus, we argue that, for all practical purposes, spring-grazed pastures have passed into an alternative compositional state of unknown stability.

Locations at the Desert Experimental Range with shrub/perennial grass communities have been almost completely displaced by introduced annuals (Harper and others, this proceedings). The rodent mounds mentioned previously, which make up approximately 10 percent of the area in experimental pastures, are a case in point. Alien annuals now dominate large areas on the fine-textured soils of valley bottoms that were once dominated by winterfat. Similar areas of annualization are found in many of the valleys of the Great Basin. There are probably many causes for the loss of perennial cover (McArthur and others 1990), including but not limited to, mismanagement of domestic livestock grazing. Apparently, intact perennial communities on some soil types are at risk of annualization regardless of how grazing is managed (Harper and others, this proceedings; Tausch and others 1994). At the Desert Experimental Range, this change in stability is due primarily to the advent of exotic weeds. In the ball and trough model, this community is represented by a change in line curvature, creating a new "valley," or stable state, dominated by annuals (Tausch and others 1993).

Management Recommendations

Continued winter (dormant season) grazing with sheep at moderate levels appears to pose little threat to the stability of these communities. Spring grazing increases the risks of shrub loss and conversion to annuals. Common sense suggests that the effects of spring grazing might be minimized under a conservative deferred grazing system. Using current technology, attempted restoration of annualized lands may not be prudent due to costs and high probability of failure. Even when restored, such communities may be highly unstable due to the presence of introduced annuals. More exhaustive studies are clearly needed to evaluate management options for annualized ranges in the Intermountain West.

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Influence of Fire on Understory Shrub Vegetation in Ponderossa Pine Stands

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Abstract—The effect of prescribed fire on understory shrub vegetation revealed that postfire development of understory shrubs is characterized by many factors including prefire composition of the stand, fire intensity, and regeneration characteristics of the different species. Recovery speed of understory vegetation is highly variable. Young shrubs of burned stands are mostly alive and vital compared to shrubs in unburned stands that have become old and decadent. Early results from two Oregon ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) sites indicate that the number of understory shrub species did not change significantly after prescribed underburning. The number of shrubs increased in a ponderosa pine/bitterbrush-greenleaf manzanita/needlegrass (*P. ponderosa/Purshia tridentata* (Pursh)—*Arctostaphylos patula* Greene/ *Stipa occidentalis* Thurb. ex Wats) community, but did not change in a ponderosa pine/snowberry (*P. ponderosa/Symphoricarpos* spp.) community. The percentage of live individual shrubs increased, and the percentages of standing-dead and dead-and-down decreased.

Prescribed fire is a useful tool for achieving many different management objectives. In addition to understory management, other goals include reduction of wildfire hazard and site preparation for forest regeneration. Since 1980 many large forest fires have occurred in the western United States despite fire suppression efforts (Mutch 1994). Fires were especially devastating in 1994. The need to decrease fire hazard in the forests is evident; it is probable that areas treated by prescribed fire will increase. Information about understory development after prescribed underburning will help decision makers achieve goals for successful understory management.

The interior Northwestern United States receives scant amounts of precipitation during the summer months, most of the annual precipitation falls as snow during the winter. Drought is commonly the main factor limiting the growth of vegetation, especially at low elevations. Plant communities occupying these lands are fairly drought resistant, but fire prone. Various ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) series cover 10.8 million hectares in the western United States, forming the second largest forest type in the area (USDA 1982).

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Historically, low-intensity fire occurred in ponderosa pine forests at 5- to 25-year intervals (Bork 1985; Martin 1982). Since 1920 human control has almost eliminated natural fire from the east side of the Cascade crest (Agee 1990). Fire exclusion has led to unnaturally high fuel loading in many of these forest stands, which increases the risk of intense wildfire.

Prescribed burning has been used as a silvicultural method to varying extent during this century (Agee 1990). In the past the main goal of prescribed fire has been wildfire hazard reduction (Norris 1990). Other considerations have been accelerating decomposition of slash and reducing understory competition with commercial conifer tree species. In recent years, reducing fire hazard in young and middle-rotation ponderosa pine forests through the use of prescribed fire has become a more important option because of the high fuel loadings that have accumulated in the forests due to fire exclusion (Mutch 1994; Mutch and others 1993). Prescribed burning may also reduce insect and disease hazard, but results are not obvious (Filip 1994; Mitchell 1990; Thies 1990).

Understory vegetation is a very important part of the forest ecological system. It has a marked effect on soil properties, nutrient cycling, and soil and forest floor microorganisms. Nitrogen fixing species like snowbrush (*Ceanothus* spp.) and antelope bitterbrush (*Purshia tridentata* Dougl.) contribute to soil productivity (Binkley and others 1982; Conard 1985; Youngberg and Wollum 1970; Youngberg and Wollum 1976). Understory vegetation is also habitat and browse for many wildlife species. Where vigorous stands occur, antelope bitterbrush is a major component of big game diet especially during winter (Giunta and others 1978; Kufeld and others 1973). Palatability of browse decreases when shrubs become older, more woody, and decadent (Wallmo 1981). Prescribed fire can be used successfully to rejuvenate shrubs (Merrill 1982).

Fire, even when it burns with low intensity, drastically affects the understory shrub coverage. Most shrub and other woody biomass above the surface is burned totally or damaged severely by fire (Covington and Sackett 1984). Postfire development of stands is characterized by many factors including prefire composition, fire severity, and regeneration characteristics of the different species (Morgan 1989; Pratt and others 1984).

Many species have the ability to sprout after losing their above-ground biomass due to fire. Sprouting individuals have a large root system to support rapid regrowth (Agee 1993; Kauffman 1990). Sprouting vigor depends on many factors including genotype, soil, moisture, season of disturbance, and temperature of the fire (Bunting and others 1985; Martin and Driver 1983). Some species like manzanita

(*Arctostaphylos* spp.) have lignotubers which allow extensive sprouting after disturbance (Agee 1993). Prescribed underburning temperatures are not normally high enough to kill below-ground reproductive biomass. A hot fire, however, can kill buds and prohibit sprouting (Driver 1983; Kauffman 1990).

Regeneration from seed is common after fire and especially important after severe burns (Driver 1983). The seed bank present in the ground is a significant factor in postfire succession (Morgan 1989; Morgan and Neuenschwander 1988; Pratt and others 1984). Seeds of many species stay viable in the ground for a very long time (Gratkowski 1962). Pratt and others (1984) found that the total number of seeds per square meter can be as high as 14000, representing 46 different species; however, under one percent of the seeds were from shrubs. Most seeds which stay viable for long periods of time need thermal treatment to germinate (Gill 1981; Stone and Juhren 1951; Wells 1969) and the heat created by fire usually stimulates vigorous germination of those species (Kauffman 1990). Seeds of pioneer species can spread to burned sites by wind or animals. If properties of burned surfaces are favorable for germination, establishment of new seedlings is common when sufficient moisture is present.

Species composition of understory shrubs in burned stands is the product of regeneration processes and is often more diverse after a fire than before burning (Attiwill 1994a, 1994b), especially if fires are sufficiently patchy so that many extant shrubs survive. The number of shrubs per hectare is usually higher after burning than before (Gratkowski 1962; Lathrop and Martin 1982; Merrill 1982), but the response is different for each species. For example, the number of bitterbrush individuals decreases after fire (Bunting and others 1985). Another factor determining postfire composition of shrubs is the growth rate of different species. Rapid initial growth rate is important especially for shade-intolerant species. Conspicuous occurrence of new shrub species that were not present in the stand before a fire is not common (Morgan 1989).

After a fire, the above-ground parts of shrubs are younger and therefore smaller than before fire. Growth rate of shrubs varies by species whether they establish from sprouts or seeds. Merrill (1982) found very rapid recovery rates after fire in ponderosa pine/common snowberry (*Symphoricarpos albus*) communities. Depending on the species, heights were similar one to four growing seasons after a fire and biomass of all species pooled was similar after three growing seasons. Young shrubs in burned stands consist primarily of live biomass and are vigorous compared to shrubs in unburned stands that have become old and decadent (Wallmo 1981).

The understory vegetation component of an ecosystem performs important ecological functions. Contemporary ecosystem management calls for increased use of prescribed fire to modify overstory species composition and reduce hazardous fuel buildups. In view of future potential increases in the application of prescribed underburning in the interior Northwestern United States, the response of understory vegetation needs definition. Here we report the response of understory shrubs to prescribed underburning in two ponderosa pine communities in Oregon.

Materials and Methods

Research was carried out at two sites in central Oregon–one on the Deschutes National Forest near Lava Butte and the other on the Mt. Hood National Forest near Bear Springs. The plant community at the Lava Butte site is ponderosa pine/bitterbrush-greenleaf manzanita/needlegrass, (*P. ponderosa/Purshia tridentata* (Pursh)-*Arctostaphylos patula* Greene/*Stipa occidentalis* Thurb. ex Wats) and the Bear Springs site is ponderosa pine/snowberry (*P. ponderosa/Symphoricarpos* spp.). Research began at the Lava Butte site in 1979 and at Bear Springs in 1986. Location and description of the sites are in table 1. The Lava Butte site was clearcut in the 1920's, slash was broadcast burned, and the site was regenerated naturally. The site was pre-commercially thinned in 1964, and the slash was left on-site, untreated. The Bear Springs site was clearcut in 1960 and planted in 1961 for ponderosa pine. The site was pre-commercially thinned in 1975, and the slash left on-site, untreated.

At the Lava Butte site, two replications of three treatments were applied in a randomized block design. The treatments were a control, a prescribed burn to achieve moderate fuel consumption, and a prescribed burn to achieve high fuel consumption (Landsberg 1992). Within each experimental unit, four to six 0.08-ha plots (sampling units),

Table 1—Description of the study sites.

Site	Lava Butte	Bear Springs
Location: latitude, longitude	44° 50' N, 121° 23' W	45° 8' N, 121° 32' W
Elevation	1450 m	2000 m
Soil classification	Typic Cryorthent of ashy over loamy skeletal.	Typic Xerumbrepts.
Percent sand	79.7%	50.3%
Percent clay	4.2%	10.8%
Annual precipitation	46 cm	82 cm
Slope and aspect	<2% to N and E	3% to N and E
Unit size	17 ha	8.5 ha
Site index, Hdom (100-year basis)	30.7 m	36.6 m
Initial age of dominant trees on site	45 years (1979)	30 years (1986)
Initial basal area of trees	25 m^2ha^{-1}	16.6 m^2ha^{-1}
Initial height of trees	12.9 m	10 m
Initial No. of trees	606 stems ha^{-1}	477 stems ha^{-1}
Diameter of stem of mean basal area	22.9 cm	22.4 cm

were established. The underburns were conducted in the spring of 1979; understory vegetation was measured immediately before and after the burns and again in the fall 1994, 15 years after underburning.

At the Bear Springs site, six replications of two treatments were applied in a completely randomized design to 0.16-ha treatment plots. The treatments were a control and an operational burn applied in the spring of 1988. Understory vegetation was measured in the fall 1994, six years after underburning.

Within each plot, understory vegetation that was rooted within four 2 x 15 m belt transects was measured. The belt transects originated at and bisected the plot corners and projected into the plots towards the plot center. Each shrub was recorded by species (or genus) and the following variables measured: maximum height, crown diameter, percentage of living (from above-ground parts), percentage of standing-dead, and percentage of dead-and-down. Lava Butte data were analyzed using analysis of variance in a split-plot over time design. Dates of measurements used in the analysis of variance were preburn 1979 and postburn 1994. When factors in the analysis of variance were significant ($\alpha = 0.10$), the treatments were compared using pairwise t-tests. At Bear Springs, the understory shrub cover was two-storied, so the data were divided into two classes. The classes were shrubs under 75 cm in height and shrubs 75 cm and taller in height. The classes were analyzed separately using analysis of variance for a completely randomized design using the 1994 post-treatment measurements. On all data the percentages of living, standing-dead, and dead-and-down were analyzed using the arcsine-square root transformation, and log transformation was used on shrubs per hectare to meet the assumption of the analysis of variance.

Model of analysis of variance for Lava Butte data was:

$$y = \mu + \rho_i + \alpha_j + \gamma_{ij} + \beta_k + \theta_{ik} + (\alpha\beta)_{jk} + \varepsilon_{ijk}$$

where

μ = overall mean, ρ_i = ith block effect, α_j = jth treatment effect, γ_{ij} = error term associated with treatment, β_k = kth year effect, θ_{ik} = error term associated with year, $(\alpha\beta)_{jk}$ = treatment-year interaction, and ε_{ijk} = error term associated with the interaction.

Model of analysis of variance for Bear Springs data was:

$$y = \mu + \alpha_i + \varepsilon_{ij}$$

where

μ = overall mean, α_i = ith treatment effect, and ε_{ij} = error.

Results

Lava Butte

Species Composition—Before treatment, seven shrub species (or genera) were identified at the Lava Butte study site: antelope bitterbrush, greenleaf manzanita, snowbrush ceanothus (*Ceanothus velutinus* Dougl.), birch (*Betula* spp.), cherry (*Prunus* spp.), currant (*Ribes* spp.), and rabbitbrush (*Chrysothamnus nauseosus* Cronq.). In the burned plots, all stems of snowbrush ceanothus and currant shrubs were destroyed by the fire or were not recognized after burning. No snowbrush ceanothus shrubs were found on the site in the immediate postburn measurement. In 1994, ten different shrub species were present in the study area; the number of species increased in all treatments including the control. New species were serviceberry (*Amelanchier* spp.), common princes-pine (*Chimaphila umbellata* Rydb.), and rabbitbrush goldenweed (*Haplopappus bloomeri* Gray).

Number of Shrubs—Before burning in 1979, the average number of shrubs per hectare was approximately the same in all treatments (table 2). Prescribed burning with moderate fuel consumption decreased density (number of shrubs) by 900 per hectare and prescribed burning with high fuel consumption decreased density by 1500 per hectare (table 2). Although the number of shrubs in the control increased between postburn 1979 and 1994, the increase was greater in the burned areas. Preburn 1979 was compared to postburn 1994 in split-plot analysis of variance over time. Time was the only significant factor ($p = 0.02$). When compared pairwise, the density on the moderate and the high fuel consumption treatment areas were changed during the study period. In 1994 the density on the moderate fuel consumption areas differed from the density on the other areas.

When response to burning was compared among the most important species–antelope bitterbrush, snowberry, and greenleaf manzanita–significant differences in numbers of shrubs per hectare were found in the high fuel consumption

Table 2—Lava Butte understory in 1979 (before and after burning) and in 1994. All species pooled. Means and standard errors by year and treatment. Standard error in parenthesis.

	Control			Moderate fuel consumption			High fuel consumption		
	1979 preburn	1979 postburn	1994 postburn	1979 preburn	1979 postburn	1994 postburn	1979 preburn	1979 postburn	1994 postburn
Shrubs per hectare	9300 (1900)	9300 (1900)	11000 (1420)	9400 (1380)	8500 (1000)	14200 (1090)	7800 (220)	6300 (170)	10200 (40)
Avg crown dia cm	63 (1.3)	63 (1.3)	64 (1.2)	67 (1.2)	51 (1.0)	36 (0.7)	77 (1.9)	49 (1.2)	44 (0.9)
Avg max height, cm	38 (0.6)	38 (0.6)	47 (0.7)	33 (0.5)	40 (0.8)	31 (0.5)	51 (0.8)	42 (0.9)	39 (0.6)
Amount live per shrub, %	45 (1.0)	45 (1.0)	54 (1.0)	46 (1.0)	17 (1.0)	80 (0.8)	51 (1.0)	5 (0.6)	84 (0.8)
Amount standing dead per shrub, %	39 (0.7)	39 (0.7)	34 (0.8)	37 (0.7)	69 (1.1)	14 (0.6)	36 (0.8)	76 (1.0)	11 (0.6)
Amount dead- and-down per shrub, %	16 (0.8)	16 (0.8)	12 (0.8)	17 (0.7)	14 (0.7)	6 (0.6)	13 (0.6)	19 (0.8)	5 (0.6)

areas. Number of antelope bitterbrush was 7360 shrubs per hectare in preburn 1979, 5530 in postburn 1979, and 6190 in postburn 1994. Time was the only significant factor for the number of antelope bitterbrush ($p = 0.02$). In pairwise comparisons no change was determined between preburn 1979 and postburn 1994 in any of the treatments. In 1994 the density on the high fuel consumption areas differed, having significantly less bitterbrush shrubs compared to the others.

For snowbrush ceanothus in the moderate fuel consumption areas, numbers per hectare were 14 in preburn 1979, 0 in postburn 1979, and 420 in postburn 1994. In high fuel consumption areas, snowbrush ceanothus were found only in postburn 1994, at a density of 150 shrubs per hectare. For the number of snowbrush ceanothus shrubs, the time x treatment interaction was significant ($p = 0.08$). When compared pairwise the densities on the burned areas changed during the study period. In 1994 the burned areas differed from the control, but not from each other.

The number of greenleaf manzanita shrubs ranged from 300 to 400 shrubs per hectare before burning in all treatments. In the control, the density remained relatively constant during the entire study period–1979 to 1994. At the end of the research period in 1994, the number of individual manzanita shrubs had increased to 2590 per hectare in the moderate fuel consumption areas and to 3550 per hectare in the high fuel consumption areas. When the number of greenleaf manzanita shrubs was analyzed, time x treatment interaction was highly significant ($p = 0.01$). In pairwise comparisons the results were similar to those for snowbrush ceanothus.

Crown Diameter and Height of Shrubs—Before burning, average crown diameter and average height, calculated as a mean of all species, were significantly greater in the high fuel consumption treatment areas (table 2). During the entire study period, average crown diameter in the control remained relatively constant. In the burned plots, average crown diameter decreased immediately on burning; crown diameter also decreased between postburn 1979 and 1994 (table 2). Treatment x year interaction was significant ($p = 0.07$). When compared pairwise, preburn 1979 was significantly different from 1994 in both moderate and high fuel consumption areas but did not differ significantly in the control. In 1994 the control differed significantly from both burned treatments, but burned treatments did not differ from each other.

In the control, average height increased during the study period. In the moderate fuel consumption plots, average height was greater immediately after burning but decreased after that. In the high fuel consumption areas, height was less immediately after burning and stayed stable between postburn 1979 and 1994. Treatment ($p = 0.06$) and treatment x year interaction ($p = 0.06$) were significant factors. In pairwise comparisons, the heights on the control and the high fuel consumption areas were significantly changed during the study period. In 1994 the height on the moderate fuel consumption areas differed significantly from the height on the other sites.

Live and Dead Percentage of Shrubs—The average live percentage of each individual shrub ranged from 45 to 51% before treatments. In the burned areas, average percentage live was low immediately after burning, but in 1994 it was significantly higher than in preburn 1979 or in the control areas in 1994 (table 2). Standing-dead percentage doubled immediately after burning in the burned areas but decreased between postburn 1979 and 1994. Dead-and-down percentage of the shrubs decreased immediately in the moderate fuel consumption areas (from 17 to 14%) and increased in the high fuel consumption areas (from 13 to 19%). In the period postburn 1979 to 1994, percentage of dead-and-down decreased in both burned areas.

When compared statistically, treatment, year, and their interaction were all significant for percentages of live and standing-dead shrubs. For dead-and-down percentages, year and treatment x year interaction were significant. When live and standing-dead percentages were compared pairwise, the burned plots in 1994 were significantly different from the control but did not differ from each other. When 1994 dead-and-down percentage was compared, all treatment areas differed from each other. Except for standing-dead in the control treatment, all live and dead percentage variables in all three treatments were significantly different from preburn 1979 to postburn 1994.

Bear Springs

Species Composition—At Bear Springs, the understory was dominated by snowbrush ceanothus and snowberry. Additional shrubs found in the diverse understory in 1994 in both the control and burned plots included: blackberry (*Rubus* spp.), California hazelnut (*Corylus cornuta* var. *californica* DC.), cherry, currant, golden chinkapin (*Castanopsis chrysophylla* Dougl.), northern twinflower (*Linnaea borealis* L.), Oregon hollygrape (*Berberis aquifolium* Pursh), rose (*Rosa* spp.), serviceberry, spreading dogbane (*Apocynum androsaemifoliun* L.), vine maple (*Acer circinatum* Pursh), western trumpet honeysuckle (*Lonicera ciliosa* Pursh), and yerba buena (*Satureja douglasii*). Creambrush ocean-spray (*Holodiscus discolor* Pursh) was found only on the burned plots in 1994.

Number of Shrubs—There were 65900 shrubs per hectare in the burned plots and 78000 shrubs per hectare in the control plots in 1994. Even though the difference in the number of shrubs was high, it was not statistically significant. Also, the difference in the number of shrubs less than 75 cm in height was not significant. There were twice as many shrubs taller than 75 cm on the control areas than on the burned areas (table 3), a statistically significant difference ($p = 0.02$). Of the number of small shrubs (height <75 cm), snowberry accounted for 82% in the burned and 90% in the control plots. No small snowbrush ceanothus were found on the burned areas and the proportion on the control areas was only 0.1%. Of shrubs taller than 75 cm, snowbrush ceanothus accounted for 32% and snowberry accounted for 50% on the control areas. On the burned areas snowbrush ceanothus accounted for 52% and snowberry accounted for 30% of the shrubs taller than 75 cm.

Shrub Size, and Live, and Dead Percentage of Shrubs—There was no statistically significant difference in the crown diameter of shrubs less than 75 cm in height, but the maximum height was significantly greater in the control areas ($p = 0.07$) (table 3). In the group taller than 75 cm the means for crown diameter and height were significantly greater in the burned areas ($p = 0.07$ and $p = 0.09$).

Table 3—Bear Springs understory in 1994. All species pooled. Means and standard errors by treatment and size class. Standard error in parenthesis.

	Shrubs <75 cm height		Shrubs >75 cm height	
	Control	Burn	Control	Burn
Number of shrubs per hectare	75900 (16530)	65000 (9150)	1960 (210)	930 (290)
Average crown diameter, cm	30 (1.1)	32 (1.0)	195 (11.3)	314 (57.5)
Average maximum height, cm	30 (1.7)	25 (1.7)	160 (10.2)	190 (12.7)
Average percent shrub live	87 (2.3)	92 (1.4)	73 (3.9)	82 (3.1)
Average percent shrub standing-dead	13 (2.3)	8 (1.4)	22 (3.4)	11 (1.9)
Average per cent shrub dead-and-down	0 (0)	0 (0)	5 (1.7)	7 (1.5)

Average percentage live by shrub was greater and standing-dead and dead-and-down were smaller in the control compared to the burn plots on both size groups. The differences were statistically significant for percentage live and standing-dead.

Discussion

The number of species on the two sites did not increase or decrease markedly between the preburn and the 1994 measurements which were six years after burning at Bear Springs and 15 years at Lava Butte. The new species present in 1994 were represented by only a single or a few individuals. The results are similar to those reported by Merrill (1982) and Morgan (1989).

At Lava Butte, the shrub density (number of shrubs) increased rapidly in both burn treatments which is similar to results in other studies (Gratkowski 1961; Lathrop and Martin 1982; Merrill 1982). Densities of bitterbrush decreased but densities of snowbrush ceanothus and greenleaf manzanita increased following burning at Lava Butte. The type of shrub regeneration was not determined and it is impossible to say which shrub plants regenerated from sprouts or from seed. Bitterbrush is said to be negatively affected by fire and sprouts poorly after burning, although ability to sprout differs between varieties (Bradley and others 1992; Noste and Bushey 1987). In this study, bitterbrush retained its dominant position despite burning. Biomass measurements would validate reliability of these conclusions.

Snowbrush ceanothus and greenleaf manzanita are well adapted to fire and both have the ability to sprout vigorously (Agee 1993; Noste and Bushey 1987). Ceanothus seeds stay viable in the ground for a very long time (Gratkowski 1962; Kauffman 1986). Because there were not many snowbrush ceanothus or greenleaf manzanita shrubs before burning at Lava Butte, most of the increase must be due to individuals that germinated from seed. The proportion of greenleaf manzanita increased markedly and fire seems to be favorable to the species.

At Bear Springs, the 1994 difference in total number of shrubs between treatments was high but not statistically significant. Snowbrush ceanothus and snowberry were the dominant species before burning and their position remained stable afterward due to their adaptations to fire. A dominant position in postfire succession is promoted by having the ability to sprout after fire or seeds which remains viable for many years (Bradley and others 1992; Noste and Bushey 1987). However, the shrub number per hectare did not increase due to prescribed underburning, perhaps because the site was occupied by a very dense snowberry and ceanothus stand before burning.

Although we did not age the shrubs in this study, it was apparent that most of the shrubs were younger in the burned areas and therefore smaller, especially at Lava Butte. However, at Bear Springs the mean crown diameter and mean maximum height of the shrubs taller than 75 cm was smaller in the control areas compared to the burned areas, partly because number of shrubs was higher in the control areas. At Lava Butte, shrub height recovered faster after fire than did crown diameter, but both were still less than in the control areas. Shrub response to burning, measured by mean crown diameter and maximum height, differed between the two sites—differences which can be caused by many factors like site properties, species composition, competition, and fire behavior. Recovery speed at these sites was slower than those reported by Merrill (1982).

In the burned plots, the percentage of living individual shrubs was higher several years after fire. Standing-dead and dead-and-down percentages of individual shrubs decreased in the burned plots; although, at Bear Springs, the percentage of dead-and-down was low in both the burned and control areas. Other studies have found fire decreases the amount of dead, woody material present (Covington and Sackett 1984; Landsberg 1992).

Conclusions

The number of understory shrub species did not increase markedly after prescribed underburning in these two ponderosa pine communities. Where bitterbrush had been the dominant understory shrub species prior to burning, it retained dominance although it decreased to some extent. The number of snowbrush ceanothus and greenleaf manzanita, which are fire-adapted, increased. At Lava Butte, which had a low initial understory shrub density, the number of shrubs increased after burning; at Bear Springs, which had a high initial understory shrub density, the number of shrubs per hectare did not increase. At both sites, the percentage of standing-dead shrubs decreased after the underburns and the percentage of live shrubs increased. More information is needed, however, to determine shrub crown cover and biomass response to prescribed underburning across a range of site conditions.

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Ecology of Two *Acacia* Species in Chihuahuan Desert Rangeland

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R. F. Beck
R. L. Steiner

Abstract—Whitethorn acacia (*Acacia constricta* Benth) and viscid acacia (*Acacia neovernicosa* Isely) are drought resistant and winter deciduous shrubs that exhibit sympodial growth patterns. Individual stands of whitethorn acacia and viscid acacia growing in southern New Mexico were evaluated. Measurements were made biweekly for two growing seasons; 1993 had near average rainfall while weather in 1994 was very droughty. The results of the study indicated that both species had lower growth rates in 1994 than 1993 in terms of twig diameter, leaf production, flower and pod production and number of side branches per twig. This difference is attributed to the low rainfall in 1994. Whitethorn acacia had a higher growth rate than viscid acacia in terms of percent increase in twig diameter and number of side branches/twig during both years. However, viscid acacia twigs produced more leaves, flowers, pods than whitethorn acacia.

Many grasslands in the United States have been changed into shrublands while others have become deserts. In New Mexico, aggressive shrub invasion has lead to economic losses to the state in the form of desertification, lower livestock production and huge expenditures on eradication of such species (Herbel and Gould 1995). In the Chihuahuan Desert, the increasing abundance of whitethorn acacia (*Acacia constricta* Benth) and viscid acacia (*Acacia neovernicosa* Isely) are causing various management problems. These shrubs are not considered a serious threat to rangelands by many researchers and managers, and therefore more emphasis has been placed on other shrub species, particularly on creosotebush (*Larrea tridentata* (DC.) Cov.) and mesquite (*Prosopis glandulosa* Torr.). Very little is known about the growth-behavior of these *Acacia* species in southern New Mexico. Because of their impending importance on rangelands, there is an immediate and growing need to conduct more research on these shrubs. Through this research the ecological requirements of these plants will be better understood leading to better management of Chihuahuan Desert rangeland.

The genus *Acacia* is part of the Fabaceae family. The members of this genus are found as shrubs or small trees. In deserts *Acacia* species play a vital role in stabilization and by providing forage for herbivores. In the United States, several *Acacia* species are found in the Southwest (fig. 1, Moore 1989).

Whitethorn acacia is an upright or spreading shrub or small tree commonly 1 m to 3 m tall and has a diameter up to 2 m, though larger plants sometimes occur. Bark of twigs is smooth, purple grey to reddish, becoming fissured and grey on older limbs and trunks. The twigs are often armed with paired white spines. The foliage of the plant is cold and drought deciduous (Johnson 1993). Occasionally some limbs of the plant are spineless or often an entire plant may be spineless. Yellow-orange, fragrant ball-shaped flowers dot the foliage. Pods are reddish brown, curved, about 10 cm long, and constricted between the seeds. Its habitats includes washes, gravelly plains, rocky hillsides and dry hills and mesas about 450 to 1,950 m in elevation throughout deserts (Mielke 1993). This species is distributed from Texas to Arizona and Mexico (Hiles 1992). The plant is occasionally browsed by game animals and cattle (Powell 1988) but generally has little forage value. The plant produces HCN under certain conditions (Parker 1972).

The plant has been reported to be used for several different medicinal purposes. The leaves and pods when ground into a powder make an excellent infused tea for diarrhea and dysentery, as well as a strongly astringent hemostatic and antimicrobial wash. The straight powder is used to stop superficial bleeding, and to stop body rashes. The powder is widely used by native Americans for treating the sore backs and flanks of their horses. The flowers and leaves as a simple tea acts as a sedative and are a good anti-inflammatory for

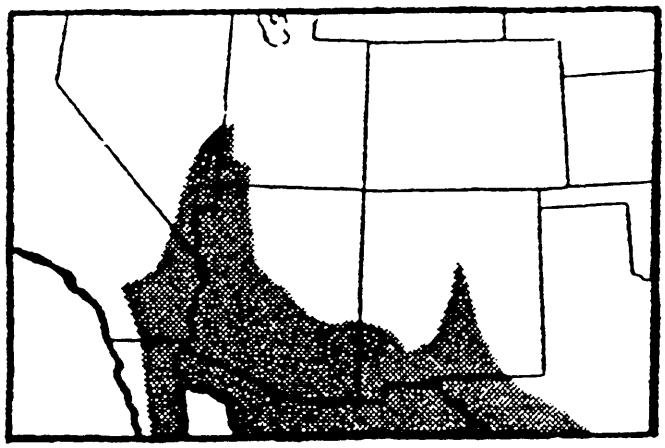

Figure 1—Current distribution of *Acacia* species in southwestern USA (Moore 1989).

In: Barrow, Jerry R.; McArthur, E. Durant; Sosebee, Ronald E.; Tausch, Robin J., comps. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

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stomach and esophagus in nausea, vomiting, and hangovers. The pods of the plant are used for conjunctivitis. The root is thick and mucilaginous and used as a tea is good for sore throats and mouth inflammations as well as dry, raspy coughing (Moore 1989).

Viscid acacia is an open, upright shrub, 2 to 3.5 m tall with a 1 to 3 m canopy spread. New bark has a pink to reddish color. The twigs of the plant are usually armed with paired white spines. The skeletal, open growth habit and sparse foliage provide an untamed appearance. The leaves are small, oily green in color, and are drought and cold deciduous (Johnson 1993). The entire plant, including the leaves, stems, and pods, are sticky from glandular secretions. The fragrant yellow ball-like flowers are sprinkled throughout the shrub from April to July (Mielke 1993). The plant is generally found at elevations from about 900 m to 1,500 m in desert plains, stream beds, canyons, mesas and rocky calcareous hills (Isely 1969) and on shallow caliche and limestone soils on dry slopes (Schmutz et al 1968). The species is distributed from Texas to New Mexico and Arizona, southward into Mexico (Martin and Hutchins 1980).

The major objectives of this study were to determine the growth characteristics and growth rates of these two *Acacia* species.

Study Area and Methods

In this study 2 different sites, Jornada Plain and lower bajada of Organ Mountains in the Chihuahuan Desert were chosen. The sites were about 12 km apart at an elevation near 1400 m above sea level. On each site one of the two *Acacia* species was studied from May to October during 1993 and 1994.

The climate of the area is typical for a continental interior location. Daytime temperature highs in the summer often exceed 35 °C with nighttime temperature nearly 15 °C lower. Freezing temperatures are common in winter. Annual precipitation averages 235 mm (fig. 2). Most summer precipitation comes from localized thunderstorms of high intensity while winter moisture comes from frontal storms producing low-intensity rainfall, occasionally snow. Springs are usually dry and windy.

Whitethorn acacia site was located on the Jornada Plain on the southern side of Dona Ana Mountains about 10 km northeast of Las Cruces, New Mexico. The topography of the site was flat with sandy and clayey soils (fig. 3). On this site, whitethorn acacia was the dominant shrub. Several grass and forb species were present. The most common grasses were tobosa (*Hilaria mutica* (Buckl.) Benth.) and burrograss (*Scleropogon brevifolius* Phil). The site was surrounded by other plant communities dominated by either creosotebush or mesquite plants.

Viscid acacia site was near Tortugas Mountain 2 km east of Las Cruces, New Mexico. This site is part of the lower bajada (with a west exposure) from the Organ Mountains to the Rio Grande flood plain. The study site was located at the top of a ridge with arroyos on both sides. Soils are shallow with little top soil, much of the surface is characterized by desert pavement (fig. 4). Very few herbaceous species grow on this site. Creosotebush communities grow near by.

Figure 3—Site dominated by whitethorn acacia at Jornada Plain in southern New Mexico.

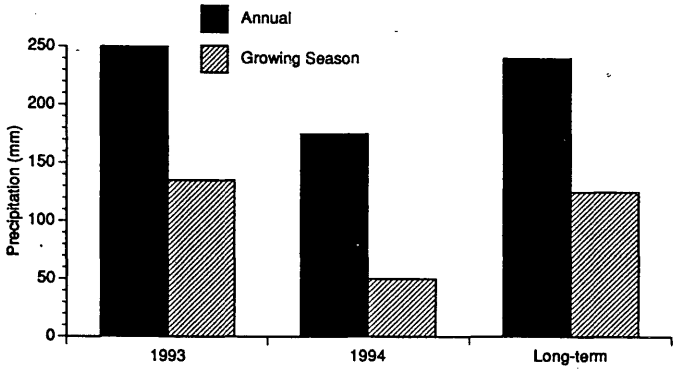

Figure 2—Precipitation records of Chihuahuan Desert in southern New Mexico. Long term records are for 1930-1994.

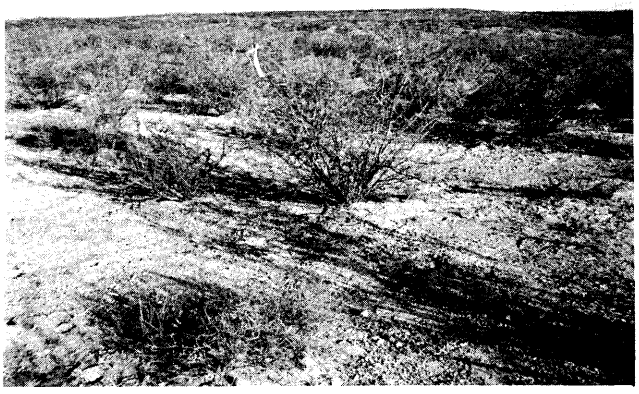

Figure 4—Site dominated by viscid acacia near Tortugas Mountain in southern New Mexico.

On each site, 5 small and 5 large acacia plants were randomly selected. For whitethorn acacia, the small plants were <1.0 m tall and the large plants were >2.0 m tall. For viscid acacia, the small plants were <0.5 m tall and the large plants were >1.0 m tall.

On each plant, 8 twigs (2 from each side of the plant, according to cardinal directions) were selected and tagged. The various growth parameters of these twigs were recorded every 15 days from May to October in 1993 and 1994. Growth was already initiated before the first sampling period in 1993. Basal diameter of the twigs was measured with a vernier calliper.

Total number of leaves, mature flowers, green immature pods per twig and side branches were counted at each sampling period. Plant size had little influence on attributes measured, so data presented in this paper are averages across large and small plants. Twigs sampled ranged in length from 100 mm to 200 mm for both species. Twigs grew on the average less than 2 mm during the study. Some twigs lost length because of the tip dying back.

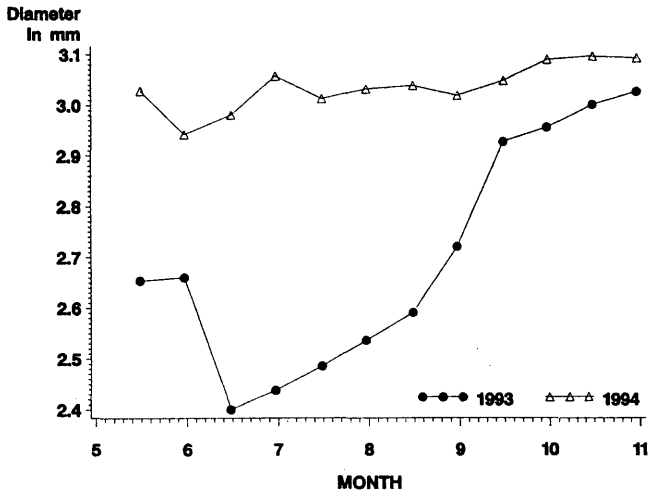

Figure 6—Average diameter of twig for viscid acacia by year.

Results and Discussions

Both *Acacia* species increased in average twig diameter during 1993 (fig. 5 and fig. 6). The average twig diameter for whitethorn acacia increased from 2 mm to 2.95 mm, a 47% increase in twig diameter in that year. For viscid acacia, twig diameter increased from 2.4 mm to 3.0 mm an increase of 25%. During 1994, twig diameter for both species increased very little.

On the average, whitethorn acacia produced 33 leaves/twig at the peak of its growing season in July 1993. But in 1994, leaf production was only 24 leaves per twig and moreover, leaf growth started later in this year (fig. 7). On the average, 73 leaves per twig were produced on viscid acacia during peak season of its growth in 1993 while only 52 leaves were produced per twig in 1994 (fig. 8). Whitethorn acacia produced by mid June (2nd sampling period of this species) in 1993 an average of 10 leaves/twig, while viscid acacia had produced on the average 10 leaves/twig by mid May (1st sampling period of this species) in the same year. From this it can be inferred that viscid acacia started its growth about one month earlier than whitethorn acacia in 1993. In 1994, we see a similar trend, the average number of leaves/twig of viscid acacia were near 10 by mid May (1st sampling period), while this number of leaves on whitethorn acacia did not appear until late June, one and a half months later. Neither species leafs-out as early as other shrub species in the area. Both species appear to be well adapted to the environmental extremes which characterize the area. Differences between time of green up may partly be explained by soil texture differences and soil moisture availability.

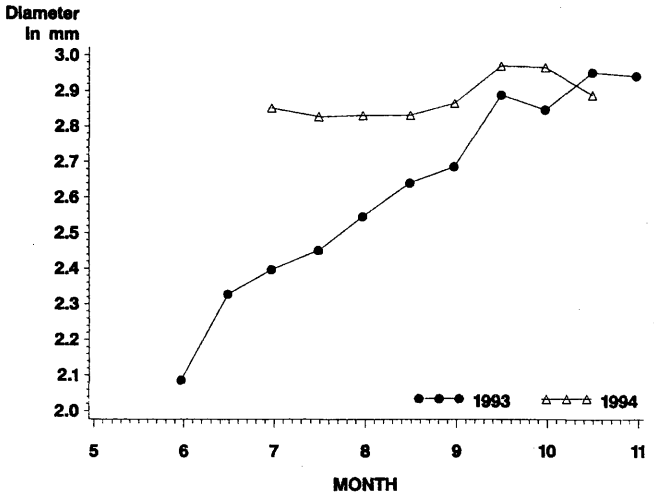

Figure 5—Average diameter of twig for whitethorn acacia by year.

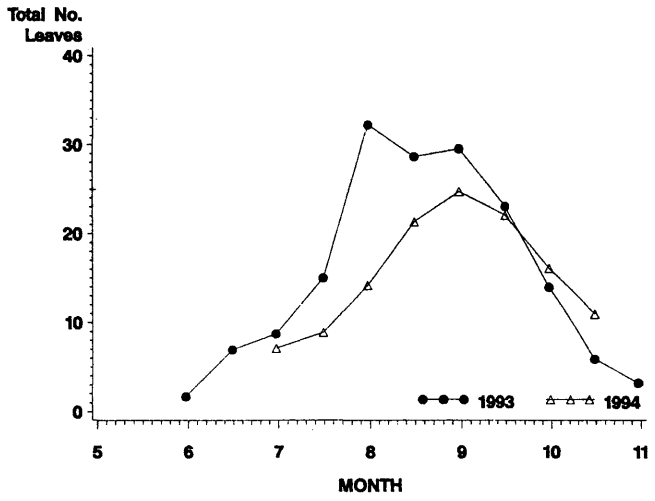

Figure 7—Average total leaves per twig for whitethorn acacia by year.

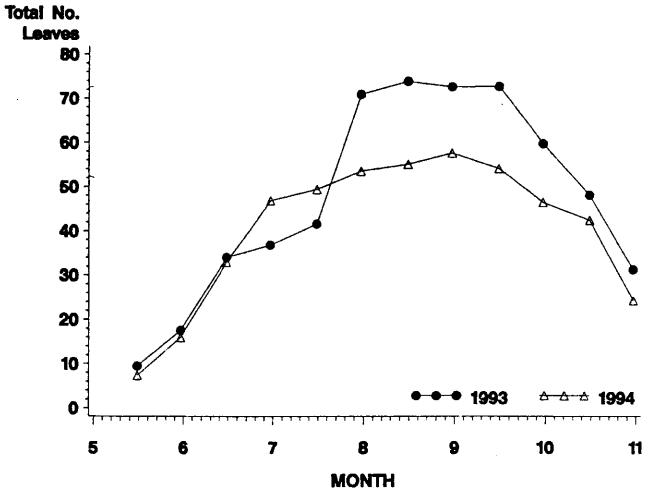

Figure 8—Average total leaves per twig for viscid acacia by year.

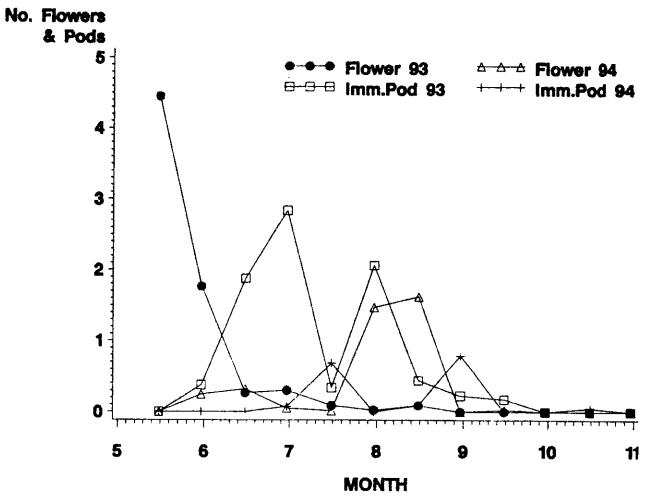

Figure 10—Average total mature flowers and green immature pods per twig for viscid acacia by year.

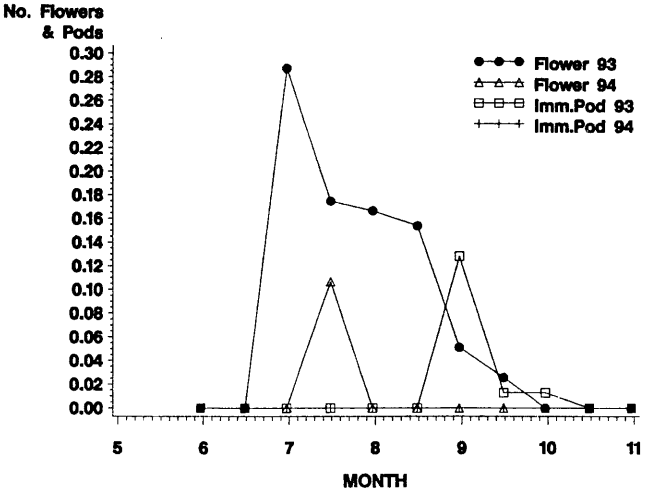

Figure 9—Average mature flowers and green immature pods per twig for whitethorn acacia by year.

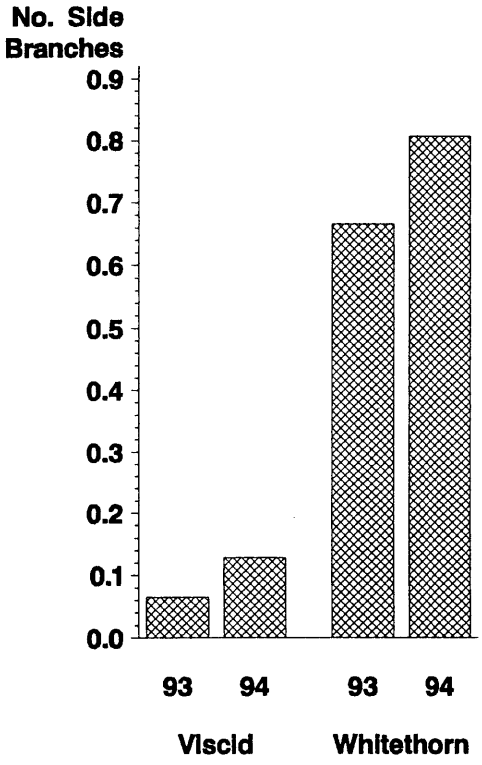

Figure 11—Average number of side branches per twig on viscid and whitethorn acacia by year.

Twigs of whitethorn acacia produced very few (<1/twig) mature flowers and green immature pods in 1993. But, in 1994, there was almost no production of flowers and pods (fig. 9). Viscid acacia, on the first sampling date, had 4-5 mature flowers per twig in mid May 1993 which indicates growth had initiated earlier. The number of green immature pods was greatest (3/twig) in early July (fig. 10). The number of flowers and pods declined during the remainder of the growing season. Flower and pod production was lower in 1994, averaging less than 2/twig at all sampling dates.

The twigs of whitethorn acacia on the average produced more side branches than viscid acacia in both years (fig. 11). This suggests that whitethorn acacia has more buds which may become active if somehow the terminal end of the primary twig is damaged or another possible explanation is that the growing region on the primary twig does not have as strong a hormonal control over the lateral buds as does viscid acacia. The difference in number of side branches between 1993 and 1994 in figure 11 is the number of new twigs that grew in 1994. For both species, this average increase was near 0.1 per twig.

Growth of both species in 1994 was limited by the below average rainfall for several months before initiation of growth and during the summer growing season. This period of low rainfall was also accompanied by high temperatures. In 1994, neither species appeared to put much energy into flower and seed production, and twig and side branch growth. The number of leaves produced in 1994 was 30% less than in 1993. Neither species showed any stress (wilting) because of low available water.

Conclusions

Viscid acacia started growth almost one month earlier than whitethorn acacia during both years and both species exhibited sympodial growth pattern.

Whitethorn acacia had a 47% increase while viscid acacia had a 25% increase in twig diameter during 1993 growing season but in 1994, there was no significant increase in twig diameter of these species.

During both years, viscid acacia produced more leaves/ twig than whitethorn acacia.

Whitethorn acacia produced more side branches per twig than viscid acacia during both years.

Overall whitethorn acacia had higher growth rate than viscid acacia.

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Modeling Mixed Brush Rangeland to Determine Economic Characteristics of Managing a Mexico-U.S. Watershed

Gary L. McBryde
C. Wayne Hanselka

Abstract—Range along the Texas-Mexico border was modeled using SPUR-91. Stocking at 12 acres per animal unit with cattle and goats induced the largest runoff and sediments, averaging 3.20 inches per year and 0.11 tons per acre. Lighter stocking, 25 acres per animal unit, also with cattle and goats induced the least runoff and sediments averaging 2.88 inches per year and 0.06 tons per acre. Plant transpiration rates were largest with the light combination stocking averaging 11.56 inches per year and smallest with heavy stocking, 5.69 inches per year. Overall, stocking rate was more influential on hydrologic properties than livestock types.

The lower Rio Grande region of south Texas and Mexico, which has a growing population, faces a condition where the demand for water is quickly exceeding available supplies (Schmandt 1993). Recent drought conditions in Mexico have brought the problem of water scarcity to the attention of residents of the region (Texas AgriNews 1995). More often alternate methods of increasing water supplies that include range management are being discussed (Griffin and McCarl 1989). Previous range hydrology studies have examined local conditions, but few range studies have attempted to address the issue of whether range management would be feasible to regulate regional water supplies (Thurow and others 1986; Weltz and Blackburn 1995).

Integral to making regional watershed management assessment studies would be field data that frequently does not exist, in particular for the mountainous areas in northern Mexico that drain into the lower Rio Grande. Several computer models were reviewed (Spaeth 1993; Botkin 1993; Srinivasan and Arnold 1994) as part of an economic study to address regional range watershed management in the lower Rio Grande area. Based on the review, the 1991 upgrade of the Simulation of Production and Utilization of Rangelands (SPUR-91) model was selected for additional assessment. The study area for the initial assessment includes rangeland that sheds water into the lower Rio Grande surrounding Garcias Creek in Starr County, Texas. This is an area for which there exist data to validate SPUR-91 for the climatic conditions holding for the larger region. Located in the Tampaulian biotic province, the study area is classified as a mixed thorn-brush savanna with dominant climax grasses of bluestem and bristlegrass (Jahrsdoerfer and Leslie 1988).

SPUR has five modules climate, soil-hydrology, plant, animal, and economic that were designed to study biophysical processes at the landscape scale (Wight and Skiles 1987). The original SPUR model had its inception with the Agricultural Research Service in 1980 and in part drew from existing bio-physical models. Sub-models adopted into SPUR included existing climate and soil hydrology modules. The climate module was incorporated into SPUR-91 with minimal alterations. The soil-hydrology and plant modules were modified from crop system models for short-grass prairies with distinct winter-summer growing seasons. The 1991 upgrade version was a cooperative task undertaken by the Natural Resource Conservation Service and the Texas Agricultural Experiment Station. Upgrade efforts focused on incorporating into the plant and hydrology modules features that would allow for more accurate modeling of woody species on rangeland. Key modifications were the addition of increased soil profiles and root growing depths for woody plant species (Carlson and Thurow 1992).

Objectives

In general the present study was conducted to evaluate those components of SPUR-91 that would be applicable for providing simulated input data into an economic study of rangeland watersheds along the lower Rio Grande in both Texas and Mexico. More specifically, the first objective in the validation process was to determine if SPUR-91 could model plant community dynamics on a mixed brush rangeland with growing seasons determined by water availability rather than temperature. One aspect of this involved determining if the model was capable of reflecting plant community compositional differences over the course of several years under alternate grazing pressures. Related to the verification of plant growth, plant-plant competition, and plant-animal interactions was the second objective of validating rates of litter decomposition. A third objective was the determination of the applicability of the animal and economic modules. Last, it was necessary to determine if the model would predict different hydrologic properties for the same range under a different state of plant succession and livestock management.

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Methods

Shannon (1975) describes the calibration and validation of simulation models as two separate tasks. Calibration was described as the task of verifying that simulation model output quantitatively matches an existing set of data. The data being similar, but not identical, to the situation for which the model will be applied for predictive purposes. Validation, on the other hand, was described as a qualitative assessment that determines how applicable a model will be for the simulation of events for which predictions are desired. In particular, can the results from a model simulation be rationally interpreted. The use of SPUR-91 for the economic study involved some calibration but primarily validation checks. For example, one phase of the testing of SPUR-91 required a routine calibration check of the simulated 10 day average temperatures from the climate module, CLIMGEN, against existing temperature averages. Widespread use of CLIMGEN and its previous documentation in other models dictated simple graphical comparisons for the present study (Carlson and Thurow 1992).

Contrasted to the case of weather data and the climate module, limitations in detailed plant growth data and the behavior of the plant growth model exist. These data limitations precluded exhaustive calibration tests of the plant and hydrology modules and justified a more heuristic series of validation checks. Also, population growth and water shortages in the Lower Rio-Grande region are triggering decisions on water use that will likely affect land management. Rather than wait for additional data and fail to contribute to the policy making process, the approach adopted is to utilize existing knowledge and add qualified advice into the policy formulation process (Dinar and Lochman 1994; Musser and Tew 1987). While recognizing existing shortfalls in data, limitations in calibration checks, or the validity of a SPUR-91 module for a particular task, adopting sensitivity analysis of key variables in the economic analysis can be used to assist in characterizing the economic stability of a decision relative to data obtained from SPUR-91. Also, the economic analysis can play a role in defining future range hydrology research agenda items.

Given these considerations, several working assumptions were adopted. These were assumptions not subject to direct validation checks. Foremost it was assumed that the climate and hydrology models would be essentially correct if qualitative accurate plant compositions could be simulated for the study area. This included validating organic matter decomposition rates. Accurate direct simulations, however, of plant-animal interactions were not assumed as a condition for useful hydrologic simulations. In particular, altering animal preferences for plants and stocking rates in the animal module and inducing realistic plant community responses was a tested validation check.

Additional working assumptions to achieve the simulation results were based on soil and hydrologic data from a 100 acre representative field composed of four range sites. These sites varied from bottomland drainage sites to upland sites. All sites were from the Brennan-McAllen Soil Association (USDA 1972) and represent the approximate percentage of sites within this association. No site had a slope greater than 10 percent. Land management choices consisted of stocking cattle alone and stocking goats in combination with cattle. Light stocking was set at 25 acres per animal unit and heavy at 12 acres per animal unit. When goats were grazed in combination with cattle the composition was a ratio of 80 cattle to 10 goats on an animal unit basis. Data parameters in the hydrology module that were varied based on land management choices were the modified universal soil loss equation cover parameter (FLDC), a mulch cover factor (GR), and the top two soil layer porosity (SMO) values (table 1). When adjusting parameters the trend was to make lower stocked range and combination grazed range have greater residue cover and soil porosity values.

Additionally, six generic plant groups were idealized for the simulation. These groups were: three groups of grasses based on association with good, fair, and poor range conditions, two woody species groups based on moderate and low palatability to goats, and last a group representing forbs. Actual input plant data for model parameterization requires 36 data per plant group. Validation parameterization of the plant and hydrology module was based on 15-year simulations. The method was to initially estimate parameter values from existing literature for each of the six plant groups. These values were then averaged across all plant groups to obtain one parameter value. In essence this created six identical plant groups. The average plant group was used to validate that the model could respond to wet and dry weather, absolute biomass production values, and litter decomposition rates.

After the model was validated to predict reasonable values of biomass production averaged over 15-year simulations, the unaveraged plant parameter data was used as a target to shift the averaged parameter data toward. This was done in an iterative process with the final result generating responses that suggested plant community compositions under light and heavy stocking. Indirect simulation of plant responses to stocking pressure was done through the plant and hydrology module rather than the animal module. Rather than using the animal module for simulating differences between cattle and goats on rangeland hydrology, the simulation results were also achieved by altering plant and hydrology module data parameters.

Three plant parameters played a key role in achieving the simulation results. These variable were biomass to leaf area conversion (P16), root respiration (P24), and maximum leaf area (CRIT1). The final community species compositions were sensitive to extremely small changes in these values

Table 1—Hydrology data parameters varied for alternate land management choices.

Sites	SPUR-91 variables	Land management choice[a]			
		Hsgt	Hsng	Lsng	Lsgt
1-4	FLDC (unit less)	0.13	0.11	0.07	0.08
1-4	GR (unit less)	0.60	0.50	0.40	0.30
1-2	SM0 (decimal fraction)	0.40	0.41	0.41	0.43
3-4	SM0 (decimal fraction)	0.42	0.45	0.50	0.52

[a]Land management choices: Hsgt, heavy stocking with goats and cattle; Hsng, heavy stocking with cattle only; Lsgt, light stocking with goats and cattle; Lsng, light stocking with cattle only. Sites: 1, Brennan Soil Series; 2, McAllen Soil Series; 3, Ramadero Soil Series; 4, Zapata Soil Series.

(for P24 ± 0.00002). Important, but not as sensitive were maximum and optimum plant activity temperatures (P3 and P4) and the Julian day that senescence begins (CRIT8).

Results

Simulated rainfall (all precipitation fell as rain) averaged 22.57 inches per year compared to an actual average of 22.59. The 15 year simulated weather pattern was dry the first 5 years, the next 4 years were approximately average, then there were 3 more wet years, and then the 15 years ended with 3 dry years. The general pattern is dry-average-wet-dry (fig. 1).

Patterns of vegetative composition under the four management treatments showed considerable variation. The general trend was for light stocking either with a combination or only cattle to show the greatest diversity of species groups (fig. 2). Also, plant composition under the light grazing showed a pattern of grasses dominating in biomass until the 1982 growing season (the 300th 15-day simulation interval). Hence, brush gained a competitive advantage from a wet rainfall cycle followed by an average rainfall cycle. Additionally, between any two management choices the least variation was shown when comparing light stocking with cattle—slightly more forb biomass in wet years—to light stocking with a combination of cattle and goats.

Heavy stocking with only cattle (fig. 3) when contrasted to light stocking with only cattle (fig. 2) shows a marked reduction in grass biomass from all condition groups. Essentially, the only species groups remaining are unpreferred browse, which dominates in biomass, followed by the preferred browse, and then forbs. Under the heavy stocking with above average rainfall at the peak of the growing season, live unpreferred browse comprises an average of near 1,800 pounds per acre and the forbs contribute an average of roughly 500 pounds per acre. Also, with the increased stocking pressure the resiliency of the vegetation is reduced.

Comparing results between light stocking with cattle only (fig. 2) and heavy stocking with goats and cattle (fig. 3) the vegetation takes almost an additional year longer (interval 127 versus interval 150) for the range to respond to wetter annual weather patterns. When comparing heavy stocking with cattle to the combination stocking management choices, the addition of goats essentially eliminated the forb biomass (figs. 3 and 4). Heavy stocking with cattle and goats created a virtually solid woody brush community that had an increased level of live biomass of unpreferred browse compared to other management choices.

Runoff was greatest averaging 3.204 inches per year under the heavy stocking with goats and least, 2.883 inches per year, under the light stocking with goats (table 2). Interestingly the light stocking with cattle alone had the highest standard deviation in runoff followed closely by the heavy stocking with a combination of livestock. Sediment rankings showed a similar influence based on stocking rate and livestock choices. Sediments averaged 0.111 tons per acre for heavy stocking with goats and had a low at 0.062 tons per acre with light stocking and a combination of livestock. Plant transpiration correlated with total biomass production and was highest with light stocking with goats averaging 11.563 inches and the lowest, 5.695 inches, with heavy stocking.

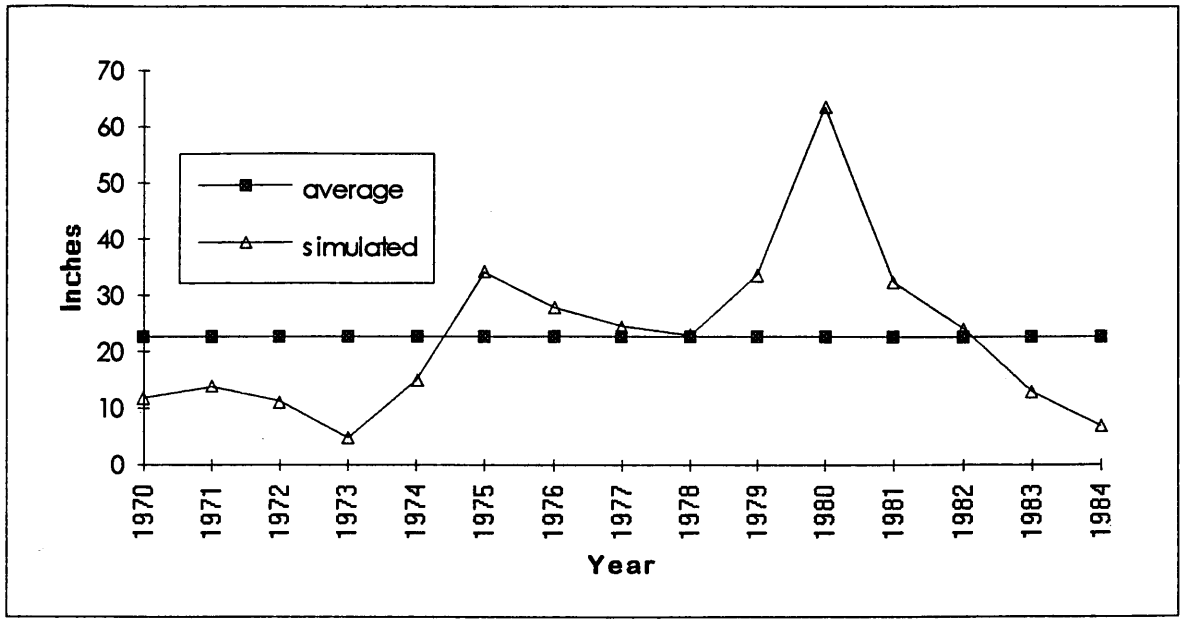

Figure 1—Simulated 15-year precipitation versus annual precipitation for Rio Grande City, Texas.

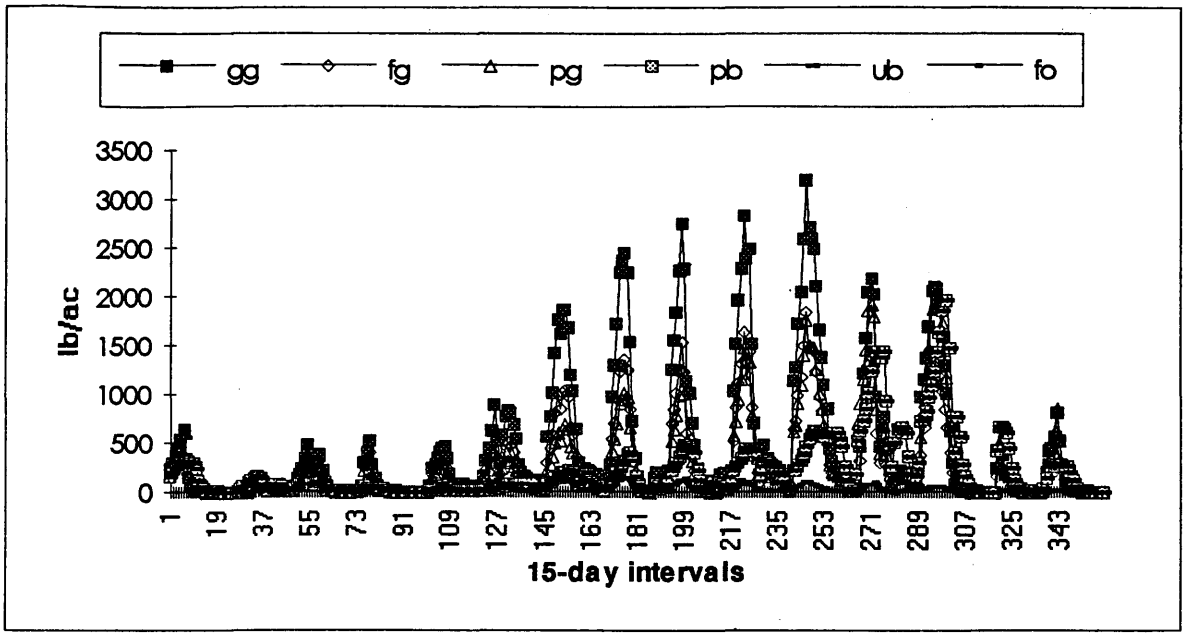

Figure 2—Simulated plant community compositions under light stocking with only cattle over a 15-year period measured in pounds per acre every 15-days for six idealized plant groups: grasses associated with good range condition (gg), grasses associated with fair range condition (fg), grasses associated with poor range condition (pg), browse preferred by goats (pb), browse not preferred by goats (ub) and forbs (fo).

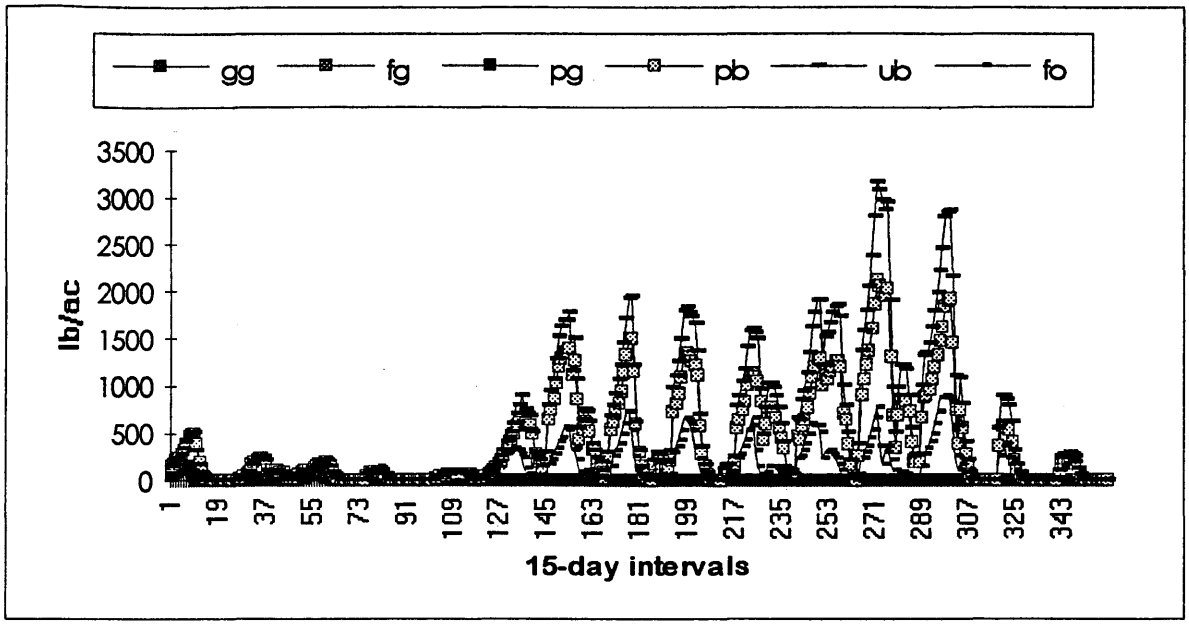

Figure 3—Simulated plant community compositions under heavy stocking with only cattle over a 15-year period measured in pounds per acre every 15-days for six idealized plant groups: grasses associated with good range condition (gg), grasses associated with fair range condition (fg), grasses associated with poor range condition (pg), browse preferred by goats (pb), browse not preferred by goats (ub) and forbs (fo).

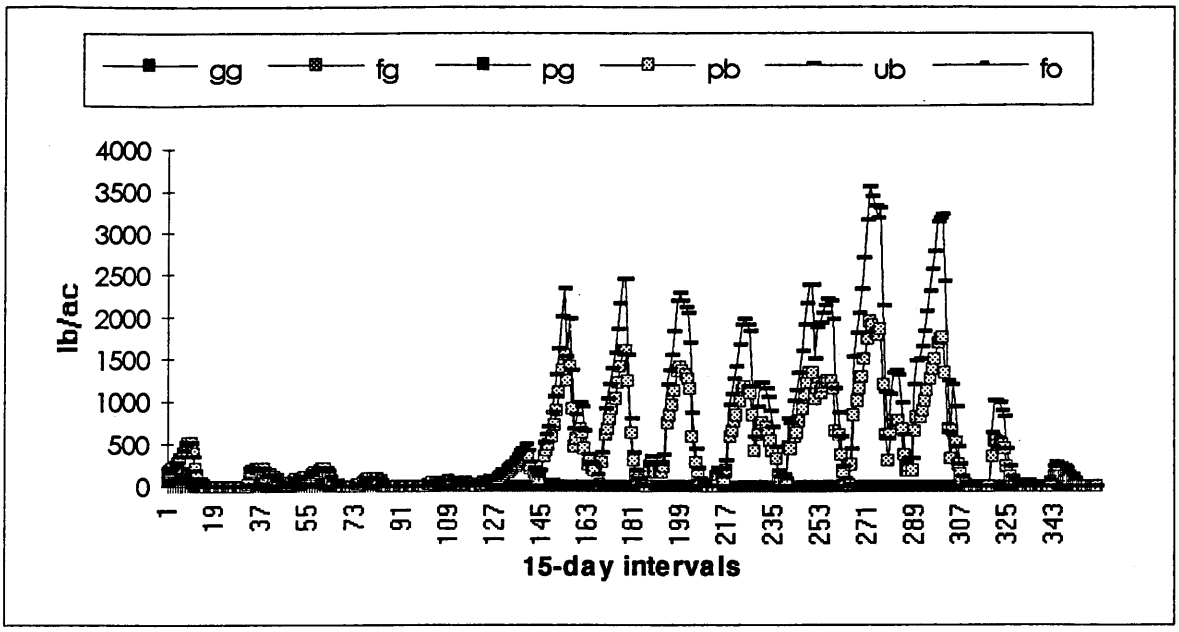

Figure 4—Simulated plant community compositions under heavy stocking with cattle and goats over a 15-year period measured in pounds per acre every 15-days for six idealized plant groups: grasses associated with good range condition (gg), grasses associated with fair range condition (fg), grasses associated with poor range condition (pg), browse preferred by goats (pb), browse not preferred by goats (ub) and forbs (fo).

Table 2—Effect of four land management choices on hydrologic characteristics for south Texas as modeled by SPUR-91.

Hydrologic effect	Land management choice[a]			
	Lsgt	Lsng	Hsng	Hsgt
Runoff (in.) avg.	2.883	3.079	3.007	3.204
Runoff std. dev.	4.579	4.897	4.639	4.868
Sediments (tons/ac.) avg.	0.062	0.063	0.088	0.111
Sediments std. dev.	0.102	0.104	0.142	0.175
Plant transpiration (in.) avg.	11.5631	1.329	8.463	5.695
Plant trans. std. dev.	10.307	9.925	8.044	5.263

[a]Hsgt, heavy stocking with goats and cattle; Hsng, heavy stocking with cattle only; Lsgt, light stocking with goats and cattle; Lsng, light stocking with cattle only.

Conclusions

Four objectives were established to assess the feasibility of SPUR-91 for providing input data into an economic study of range watershed management. The first objective was to determine if the model could accurately simulate plant compositional changes resulting from alternate land management choices. Four management choices were used to make this determination. Simulation experiments showed that the linkage between the plant and animal module was inadequate to predict directly plant community dynamics resulting from the type and amount of livestock grazing interactions. Nonetheless, plant compositional differences under alternate grazing and stocking pressures were modeled by altering input data parameters in the plant and hydrology modules.

The plant module has two limitations that require considerable modeling effort to circumvent. The first is often simply a lack of information about data parameterization. The range in reported data for any one parameter is often so large that it is difficult to select the appropriate value for the present conditions. Also, there is the issue of a limited capability to model plant-plant competition. SPUR-91 plant parameters are limited to the physiological parameters of the idealized plant groups. This has two repercussions. First, the parameter may be affecting outcomes in the model that would not be observed in reality. Hence, the actual parameters values used may not correspond directly to empirical values. Second, the lack of a coherent theory of plant community dynamics in the plant module or SPUR-91 model as a whole imposes constraints on what can be modeled.

Results from this study suggest efforts to include more detailed dynamics or greater plant diversity would require increasingly large amounts of modeling time and large doses of counter-empirical (and likely non-intuitive) parameterization. Both suggest SPUR-91 is at a limit on modeling both plant community diversity and dynamics until additional conceptual elements are incorporated into the model. These elements would be processes operating at an ecological scale larger than plant physiological processes.

The second objective was to verify decomposition rates of organic matter. These appear adequate as non-living organic matter quantities tend to cycle with seasons in response to overall weather conditions rather than accumulate or vanish altogether.

The third objective dealt with assessing the applicability of the animal and economic model. As noted earlier, the poor linkage between the animal and plant modules made it infeasible to reflect vegetation composition changes by altering stocking rates and livestock preferences in the model.

Due to this it was determined to be more accurate to determine appropriate stocking rates exogenous to SPUR-91 by using other data sources. This outcome yields the output from the economic module invalid for purposes in the larger economic study.

The fourth objective was to determine if hydrologic properties could be distinguished for rangeland under alternate land management. The model performs this task well if a commitment is made to learn how plant parameter changes will induce vegetation composition changes, which will act indirectly on rangeland hydrologic properties. Undoubtedly, there remains much work in refining SPUR-91 module linkages and the mathematical representation of bio-physical interactions on rangeland. Despite this, the differences in hydrologic results obtained in the study suggest SPUR-91 has a definite role to play in contributing input data into regional watershed studies.

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Juniper-Pinyon Population Dynamics Over 30 Years Following Anchor Chaining

Richard Stevens
Scott C. Walker

Abstract—Permanent marked trees and vegetative belt transects were established within five-way exclosures on five chained big game rehabilitation projects in Sanpete County, Utah. Resulting research focuses on changes in cover of trees, shrubs, grasses, and forbs; population dynamics of pinyon and juniper and other plants; forage production; herbivore effects; and interaction between native and introduced grasses.

A majority of the winter and spring-fall big game and livestock ranges in the Great Basin are in Utah juniper (*Juniperus osteosperma),* pinyon *(Pinus edulis),* and sagebrush *(Artemisa tridentata)* types. Within the Great Basin, prior to settlement, a majority of the juniper-pinyon stands were confined to selected areas where understory competition and fire controlled tree density and recruitment. From the late 1800's to the present, distribution and density of juniper and pinyon and accompanying understory have been significantly altered as an indirect response to livestock grazing. Livestock grazing reduced the density and vigor of perennial understory, which, in turn, regulated fire, the establishment of exotic annuals, and tree regeneration.

Adjoining semiarid grass and shrublands underwent similar changes as desirable species were eliminated or reduced in density and vigor by grazing. The absence of fire and the reduced competition, due to loss of dominant shrubs, grasses, and other forbs, allowed for an increase in juniper and pinyon trees, and substantial tree invasion into many adjoining grass and shrublands (Aro 1971; West 1984b; West and Van Pelt 1986; Woodbury 1947). The invasion of juniper and pinyon, and thickening of stands have resulted in loss of big game habitat and livestock forage, and have diminished watershed resources.

Considerable effort has been given to the development of practices and techniques to reduce tree density and reestablish desirable understory species. Most control measures do not result in complete tree eradication, nor completely suppress reinvasion. Many trees have remained or reestablished following fire (Barney and Frischknecht 1974), cabling and chaining (Stevens and others 1975; Van Pelt and others 1990; West 1984a), or construction activities (Kruse and others 1979).

Studies related to the recovery, invasion, and stand thickening process have contributed generalized schema or notions of succession and stand growth (Blackburn and Tueller 1970; Barney and Frischknecht 1974; Tausch and Tueller 1977; Severson 1986; Tausch and West 1988). Patterns of tree recruitment and ecology could be better explained if individual trees were studied over several decades. The few such investigations have focused on individual tree survival and growth following mechanical control or related treatments, or destructively sampled trees (Jameson 1965; Tausch 1980; Van Pelt and others 1990). In addition, few studies have been developed to evaluate the effects of grazing on pinyon-juniper survival, growth, and reproduction following control measures.

To obtain a better understanding of tree responses following anchor chaining of Utah juniper and pinyon and seeding, permanent marked trees and vegetative belt transects were established within five-way exclosures constructed on five chained big game range rehabilitation projects in Sanpete County, Utah. Resulting research on these five exclosures focus on: changes in percent cover of trees, shrubs, grasses, and forbs (Stevens and others 1977); population dynamics of pinyon and juniper (Stevens and others 1975) and basin big sagebrush, black sagebrush, and white rubber rabbitbrush (Stevens 1986); forage production (Plummer and others 1970a); herbivore effects on seeded alfalfa (Rosenstock and Stevens 1989); and interaction between native and introduced grasses (Walker and others 1995).

Areas and Methods

The five areas are known as Manti (1 mile south of Manti), south Mayfield (1 mile south of Mayfield), east Mayfield (2 miles east of Mayfield), South Hollow (5 miles southeast of Mayfield), and Fountain Green (8 miles east of Fountain Green). Areas treated and chained vary from 600 to 1,200 acres (1,480 to 2,960 ha) and occur at elevations of 5,750 to 7,000 feet (1,750 to 2,100 m). Long-term average precipitation range from 11.5 to 18 inches (29 to 46 cm). Soils at Manti, south Mayfield, east Mayfield, and South Hollow are limestone-derived, cobbly loams in the Frontreen series. Soils at Fountain Green are formed from alluvium and colluvium derived from sandstone, limestone, quartzite, and mixed igneous rocks in the Deer Creek series (USDA, SCS, USDI, and BLM 1981).

Prior to tree removal, the sites supported juniper and pinyon with a scattered understory of Wyoming and basin big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* and ssp. *tridentata*) 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

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nomenclature follows Plummer and others (1977b). All five sites were double-chained during October and November: Manti in 1959; south Mayfield in 1960; east Mayfield, South Hollow, and Fountain Green in 1961. Between chainings a seed mixture of native and introduced grasses, forbs, and shrubs was applied by fixed-wing aircraft. Downed trees were left in place to enhance seedling establishment and for watershed protection.

During the summer of 1962, a 300 by 300 foot (91 x 91 m) five-way exclosure was constructed on each of the five sites. Five grazing treatments were provided with each exclosure (fig. 1); (a) control-rabbits, deer, and livestock excluded (no use); (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.

At each exclosure a set of five permanent 100 foot (30 m) long transects were randomly located within each of the five grazing treatments (fig. 1). Ten end-to-end plots, 10 feet long by 1 foot wide (3 by 0.3 m), were centered over each 100 foot (30 m) long permanent transect to measure herbaceous plant numbers, production, and ground cover. Overlying these transects, 100 by 4.356 foot (30 by 1.33 m) transects were established to measure shrub and tree numbers, size, production, and cover. Every juniper and pinyon within each transect was marked, mapped, and measured for maximum crown canopy. Heights and weights were estimated and placed in a condition class. Measurements along these transects have been made at 1- to 7-year intervals for the past 30 years.

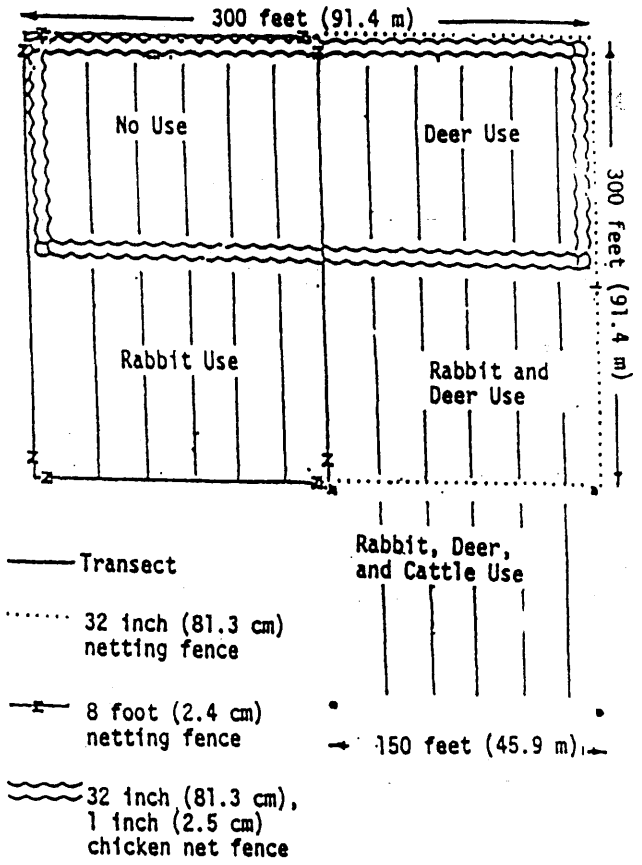

Figure 1—Four-way exclosures and comparable outside areas.

Trees were placed into four condition classes: (1) standing trees - live trees that had not been tipped over with chaining; (2) seedlings - young trees 1- to 3-years-old that were present and alive following chaining; (3) downed trees - live trees that had been tipped over but not completely uprooted by chaining; and (4) recruits - seedlings that appeared after 1964. The total number of reported recruits may not represent all seedlings that emerged along the transects over the 30 years. Some seedling recruits may have appeared and died between measurement years. Tree number data were exposed to general linear model analysis of variance by year, grazing treatment, area, and class. Significant differences were determined at the $P<0.05$ level. If differences were significant from the GLM - ANOVA, Fisher's LSD posthoc test was used to determine where the differences occurred (Fisher 1966).

Changes in tree numbers of residuals and recruits are reported in this paper. Tree size, growth rate, production, and cover data are on file at Great Basin Experiment Station, Utah Division of Wildlife Resources, Ephraim, Utah 84627.

Results

No significant difference in tree numbers occurred over time between grazing treatments and areas. There were, however, significant changes in total numbers of juniper and pinyon trees in all transects, treatments, and areas. In 1964 there were 61 live pinyon and 152 live juniper trees (table 1) along the five permanent transects in five grazing treatments on five areas.

Within all five study sites, there were 61 live pinyon in 1964 (table 1). Of these, 19 were trees that had been tipped over by chaining but were still rooted by at least one root. There were 31 live standing pinyon and 11 seedlings (young plants less than 3 years old). Thirty years later, in 1994, there were significantly less trees in all three tree classes. Only 31 of the original 61 (51 percent) trees present in 1964 were alive in 1994. Thirty-two percent of the standing trees, 74 percent of the downed trees, and over half (55 percent) of the seedlings had died between 1964 and 1994. Total loss was 49 percent. Four new recruit pinyon seedlings were found between 1964 and 1993. None of these were alive in 1994.

In 1964, there were 152 live juniper trees (table 1). Between 1964 and 1994, 43 percent (65) of these died. Fifteen (27 percent) of the original 55 standing trees died within the 30-year sampling period. Of the 21 seedlings that were present in 1964, 13 (62 percent) died by 1994. Forty-nine percent of the 76 trees that had been tipped over by chaining died before 1994. Between 1965 and 1994, 46 new recruit juniper seedlings were located along the permanent transects. Nineteen of these died by 1994. Thus, 27 new juniper trees were added to the population over the 30 years. Even with this addition of 27 additional trees there was a significant loss in numbers of juniper trees; 152 in 1964 and 87 in 1994, a 43 percent loss.

There were 213 juniper and pinyon trees within all transects in 1964. Of these original trees only 118 (55 percent) were alive in 1994. During this 30 years, 27 new

Table 1—Number of individual marked pinyon and juniper trees 1964 through 1994.

Tree type	Pinyon 1964	Pinyon 1994	Pinyon % Change	Juniper 1964	Juniper 1994	Juniper % Change
Standing[1]	31[A]	21[B]	–32	55[A]	40[B]	–27
Seedling[2]	11[A]	5[B]	–55	21[A]	8[B]	–62
Downed[3]	19[A]	5[B]	–74	76[A]	39[B]	–49
Total	61[A]	31[B]	–49	152[A]	87[B]	–43

Recruit seedlings[4]

Pinyon Total 1965 through 1993	Pinyon Alive in 1994	Pinyon % Change	Juniper Total 1965 through 1993	Juniper Alive in 1994	Juniper % Change
4	0	0	46	27	+57

Total trees	1964	1994	% Change
Pinyon	61[A]	31[B]	–49
Juniper	152[A]	141[A]	–8
Total	213[A]	172[B]	–20

Numbers within a row followed by the same letter are not significantly different ($P<0.05$).

[1]Mature vertical trees.
[2]Immature trees 1- to 3-years-old.
[3]Live trees that have been tipped over by the chaining process which have at least one major root still in the soil.
[4]Recruit seedlings, 1 to 3-years-old. Number may not represent total number of recruit seedlings in all years. Seedlings may have established and died between sampling years. Numbers represent seedlings encountered in the years counts were made. Fountain Green: 1965, 1967, 1972, 1977, 1982, 1987, 1994. Manti: 1966, 1967, 1969, 1971, 1972, 1975, 1977, 1982, 1987, 1994. South Mayfield, East Mayfield, and South Hollow: 1967, 1972, 1977, 1982, 1987, 1994.

juniper and no new pinyon seedlings were added to the population. The total number of trees in 1994 was 172, which is an overall 20 percent reduction of the 1964 number.

Discussion

Anchor chaining has been used on hundreds of thousands of acres to reduce juniper and pinyon density and facilitate seedlings, shrubs, forbs, and grasses. Percent tree kill from chaining has depended on size and age of trees in the community, soils, and chain type, weight, and chaining techniques (Stevens 1987).

A majority of trees on the five sites were uprooted and killed by chaining. Some of the trees that were tipped over but were still partially rooted initially survived. Among these, there was a considerable loss; 84 percent of the pinyon and 48 percent of the juniper. Some of the trees that remained upright and rooted were apparently injured, probably from cambial injuries or root exposure. Fifty-five percent of the pinyon, and 62 percent of the juniper that were left standing, died within the 30 years. Deer, rabbit, cattle, and sheep grazing use, or lack of use, over 30 years did not adversely affect number of juniper and pinyon trees.

Most trees that remain alive on a chained area will increase in size, become more visually apparent, and may even give the false impression of reinvasion. Some recruitment of new seedlings will occur. Total number of trees on the permanent lines in the five exclosures decreased by 20 percent over 30 years from 171 trees per acre in 1964 to 138 per acre (340 per ha) in 1994. There was no reinvasion or thickening of the stands. Recruit seedlings did appear. However, reproduction did not keep up with the number of deaths in the residual population.

Forty-six juniper and only four new pinyon seedlings were found on the transects in the 30 years. None of the pinyon and 27 (54 percent) of the juniper seedlings were alive in 1994. These numbers may not represent total number of recruitment seedling. Some may have established and died between years when sampling occurred.

The trees in the five communities did increase in size, which gave the impression of more trees. However, increase in tree density did not occur. There was, in reality, a decrease in number of trees. Similar results have also been reported by Dalen and Snyder (1987); Stevens (1987); and Van Pelt and others (1990). All four of these studies repudiate the concern of reinvasion or increase in tree numbers, and need for retreatment expressed by Evans (1988); Johnson (1987); Jameson (1987); and Tausch and Tueller (1977).

Acknowledgments

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Summer Establishment of Four Sonoran Desert Shrubs Using Line Source Sprinkler Irrigation

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Steven E. Smith
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Mark Pater

Abstract—A line source irrigation system was used to create a water application gradient and determine establishment requirements for native Sonoran desert shrubs and trees. Mesquite (*Prosopis juliflora* var. *veluntina*, catclaw acacia (*Acacia greggii*), blue palo verde (*Cercidium floridum*) and jojoba (*Simmondsia chinensis*) all established when 2 weeks of irrigation were followed by summer rainfall. Jojoba seedlings emerged about 2 weeks later than those of the other species. Because the soil profile was initially at field capacity, the line source system mainly created a difference in water availability between irrigated and unirrigated soils. This study suggests a possible strategy for using in-place irrigation systems to revegetate farmlands during the first year of abandonment. Soils could be heavily irrigated after sowing to fill the soil profile. Subsequent irrigation for about 2 weeks to keep the soil surface wet until seedlings emerge should result in high establishment. For the coarse-loamy soil in this study that would require about 5 to 10 cm of total irrigation. Establishment on drier areas sites with finer-textured soils would require more water.

Since the early 1950's, over 400,000 ha of once-irrigated farmland have been abandoned in Arizona (Charney and Woodward 1990). Abandonment is the result of variability in costs of production and also in demand and returns for agricultural products over the years. When Arizona's 1980 Groundwater Management Act restricted pumping in certain Active Management Areas, cities began purchasing farmlands for water sources (Gelt 1993). Future purchase of such so-called water farms has now been prohibited by the 1990 Groundwater Transportation Act but large tracts of grandfathered water farms still lie abandoned. Problems with abandoned farmlands include wind erosion and hazardous dust storms that have resulted in highway fatalities, expense of controlling weeds such as Russian thistle (*Salsola kali*), and loss of ecological and aesthetic value (Meitl and others 1983).

Much of the abandoned farmland in Arizona is in the south-central part of the state in the Santa Cruz Valley and along the Gila River between Phoenix and Yuma. These lands are characterized by fine-textured soils and annual rainfall often less than 250 mm (Jackson and others 1991; Gelt 1993). Reinvasion of these lands from native shrubs such as creosotebush (*Larrea tridentata*) and desert saltbush (*Atriplex polycarpa*) is limited by lack of dispersal vectors (Jackson 1992), as well as aridity and poor soil physical conditions. Some abandoned farmlands with comparatively coarser-textured soils and higher annual rainfall may be colonized by desert broom (*Baccharis* spp.) and burroweed (*Isocoma tenuisecta*), while others remain bare or dominated by Russian thistle over 25 years after abandonment (Karpiscak 1980).

Revegetation of abandoned farmland without irrigation requires some form of water harvesting and concentration. The Natural Resource Conservation Service and Jackson and others (1991) have successfully established native shrubs between runoff areas and catchment berms near Redrock and Eloy, Arizona, respectively.

Use of functioning irrigation systems to establish adapted plants the first year of abandonment is a promising approach to revegetating abandoned farmlands in arid areas with erratic precipitation (Cox and Thacker 1992). However, establishment and persistence of irrigation-established plants is highly dependent on site conditions and drought tolerance of the seeded species. For example, Cox and Madrigal (1988) failed to permanently establish forage grasses on a silty clay loam soil at the San Xavier Indian Reservation but Cox and Thacker (1992) succeeded in establishing grasses on sandy loam and clay loam soils in the Avra Valley in southeastern Arizona. In the latter study, plant establishment required sufficient irrigation to keep the soil surface moist until seedling roots were 5- to 15-cm long (4 to 6 weeks of irrigation). To successfully establish, many warm-season grasses may require rather extended periods of available soil moisture at the soil surface to develop adventitious roots (Roundy and others 1993).

If irrigation systems can be used to revegetate farmlands the first year after abandonment, we need to identify adapted plant materials and their associated water requirements for

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establishment. The line source sprinkler system (LSS) produces a gradient in applied water that has been used mainly to determine crop production response to irrigation (Sorenson and others 1980; Miller and Hang 1980). LSS has the advantage of providing a continuous gradient in irrigation from excess to no irrigation within a small area as distance increases from the line source (Hanks and others 1976; Fernandez 1991). The objective of our research was to use LSS to determine water requirements for establishment of adapted shrubs and trees in the Sonoran desert.

Methods

The study site was at the Tucson Plant Materials Center of the Natural Resources Conservation Service. Elevation is 773 m and mean annual precipitation is 294 mm with 54% (159 mm) falling between July and October (Sellers and others 1985). Soil is of the Anthony series, coarse-loamy, mixed, calcareous, thermic family of Typic Torrifluvents.

We seeded velvet mesquite (*Prosopis juliflora* var. *velutina*), catclaw acacia (*Acacia greggii*), jojoba (*Simmondsia chinensis*), and blue paloverde (*Cercidium floridum*) in 1992 and 1993 in July prior to the summer rainy season. Shrubs (catclaw and jojoba) and trees (mesquite and paloverde) were seeded at the rate of 33 and 16 pure live seeds per m of row, respectively, in rows 0.41-m apart using a no-till planter. Rows were seeded perpendicular and to a distance of 16.5 m on both sides of the line source sprinkler. The soil was preirrigated on both years prior to sowing to fill the soil profile and create similar antecedent soil moisture conditions throughout the field. An extra sacrifice row of each species was seeded next to each row in two of the six total replications for root measurements.

The LSS had nine sprinklers 6-m apart on 1.6-m high risers with each sprinkler producing an overall wetted radius of 13.5 m. Irrigation water was applied daily for 10 days after sowing to maintain available moisture in the upper 3 cm of soil nearest the line source.

Applied water was measured in catch cans after every irrigation and plants per m of row (PMR) were counted every 1 to 2 weeks until November at distances of 1.5, 4.5, 7.5, 10.5, 13.5, and 16.5 m from the line source. Soil matric potential was measured every minute and hourly averages recorded using gypsum blocks connected to electronic microloggers. Two blocks were placed at depths of 1-3, 8-10, and 18-20 cm, while one block was placed at depths of 38-40 and 58-60 cm in each of three replications at distances of 1.5, 6, 10.5, and 16.5 m from the line source.

Plant height was measured every 1 to 2 weeks on the same five plants of each species at distances of 1.5, 7.5, and 13.5 m from the line source. Tap root length of excavated plants was measured at the same distances as plant height.

Since irrigation treatments using LSS are not randomized, significance of distance from the line source and interactions of species x distance were based on Wilk's Lamda from multivariate repeated measures analysis of variance (Fernandez 1991; Torabi-Zadeh 1991). Means of species were compared by LSD at each distance from the line source for each sample date.

Results

Natural precipitation after sowing for July and August totalled 76.2 and 68.1 mm in 1992 and 1993, respectively (fig. 1). Total irrigation plus precipitation for July and August after sowing ranged from 356.7 to 106.9 mm in 1992 and from 285.2 to 106.6 mm in 1993 from 1.5 to 13.5 m from the line source. For both years, irrigation was most frequent right after sowing in July, while natural precipitation was most frequent in August (fig. 2). This pattern of water inputs, as well as the initially wet soil profile, mainly resulted in differences in soil water availability between irrigated and unirrigated soils, rather than differences within irrigation levels (figs. 3, 4). Surface soil water up to 10.5 m from the line source was highly available through mid August while unirrigated soils were dry at seed depth until natural precipitation fell in early August. Soil water was available below 18 cm through July and August for irrigated and unirrigated soils.

PMR differed significantly ($p > 0.05$) with distance from the line source for all dates measured in 1992 and 1993. Significance of species and the species x distance interaction varied for different dates of PMR measurement. Differences

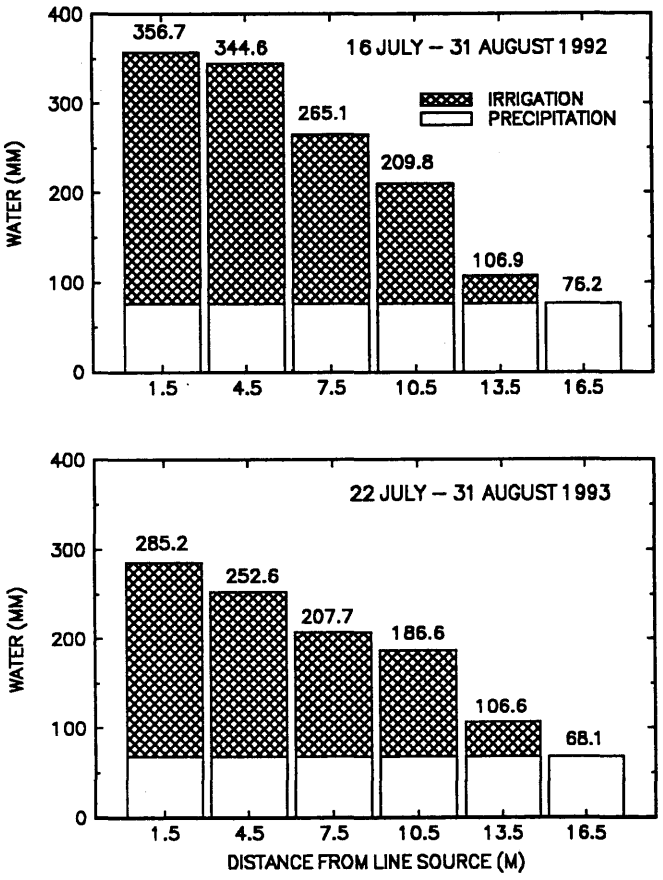

Figure 1—Irrigation and precipitation at six distances from a line source sprinkler in 1992, 1993.

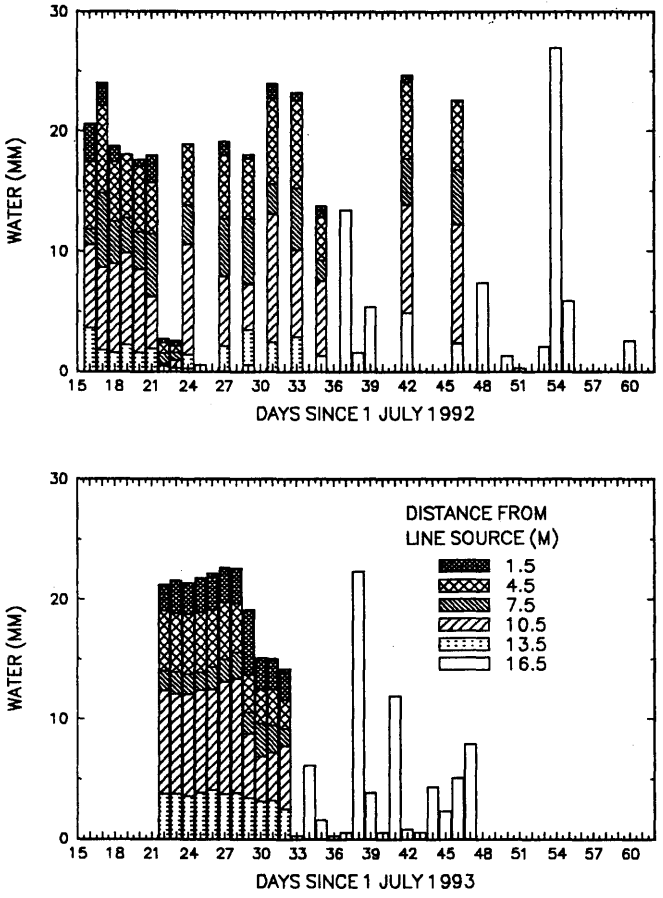

Figure 2—Date and amount of summer rainfall and irrigation from a line source sprinkler.

in PMR were mainly associated with differences in the pattern of surface soil water availability between irrigated and unirrigated soils (figs 5, 6). In 1992, acacia, mesquite, and paloverde had high initial emergence on all but the lowest and nonirrigated soils. Jojoba emerged about 2 weeks after the other species and eventually had high PMR at all but the lowest and nonirrigated soils. All other species eventually produced at least 4 PMR on the lowest and nonirrigated soils in response to August precipitation. A similar pattern of emergence occurred in 1993, except that acacia PMR was less than in 1992 (figs. 5, 6). Jojoba again emerged slower than the other species. Palo verde and jojoba eventually had higher PMR on unirrigated than lowest irrigated soils. Plant establishment was acceptable for all species for all irrigated and unirrigated treatments for both years, except for jojoba on unirrigated soils in 1992.

Although plants established at all irrigation levels, plant growth was less on lowest and unirrigated soils than on soils receiving higher irrigation (fig. 7). Tap root length was greatest for mesquite and least for jojoba (fig. 8). Tap root length of acacia, mesquite, and palo verde was over 60 cm by October or November.

Discussion

The initially wet soil profile and frequent irrigation resulted in long periods of soil water availability and excellent establishment of all four of these woody species at all but the lowest irrigation and on unirrigated soils. The LSS did not create a strong gradient in soil water availability in this study. Use of the LSS on initially dry soils would probably

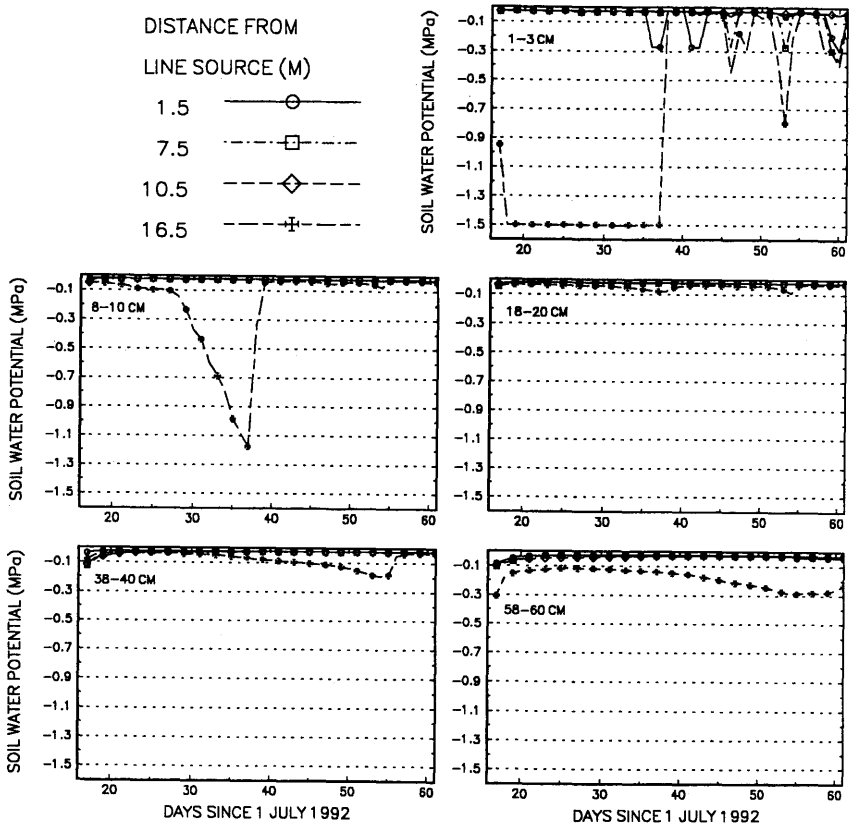

Figure 3—Soil matric potential at four distances from a line source sprinkler for five soil depths in summer 1992.

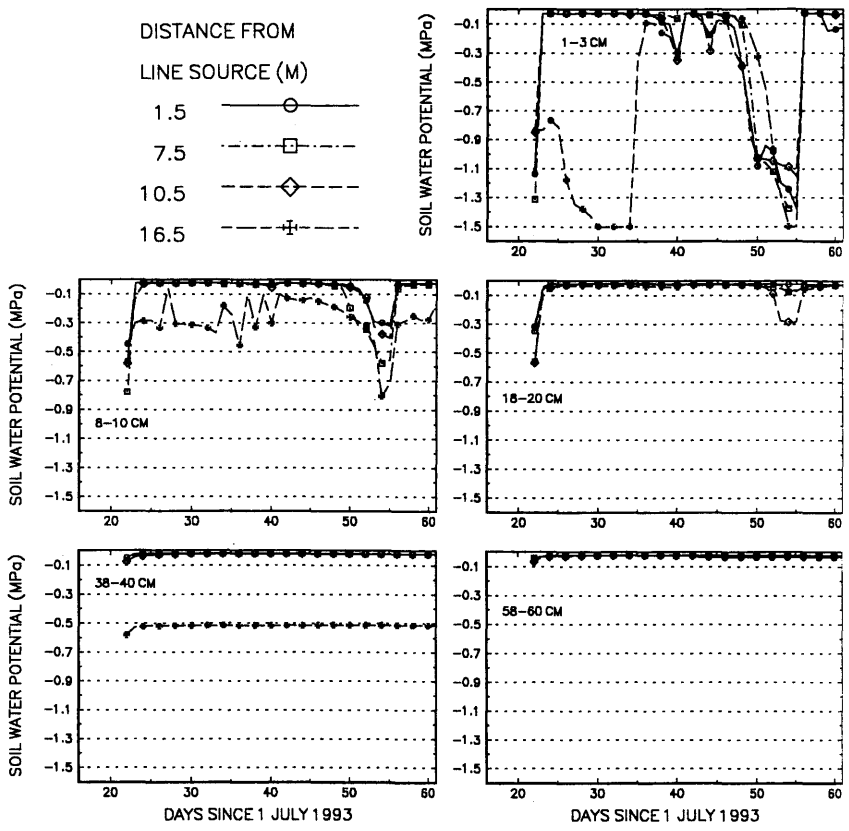

Figure 4—Soil matric potential at four distances from a line source sprinkler for five soil depths in summer 1993.

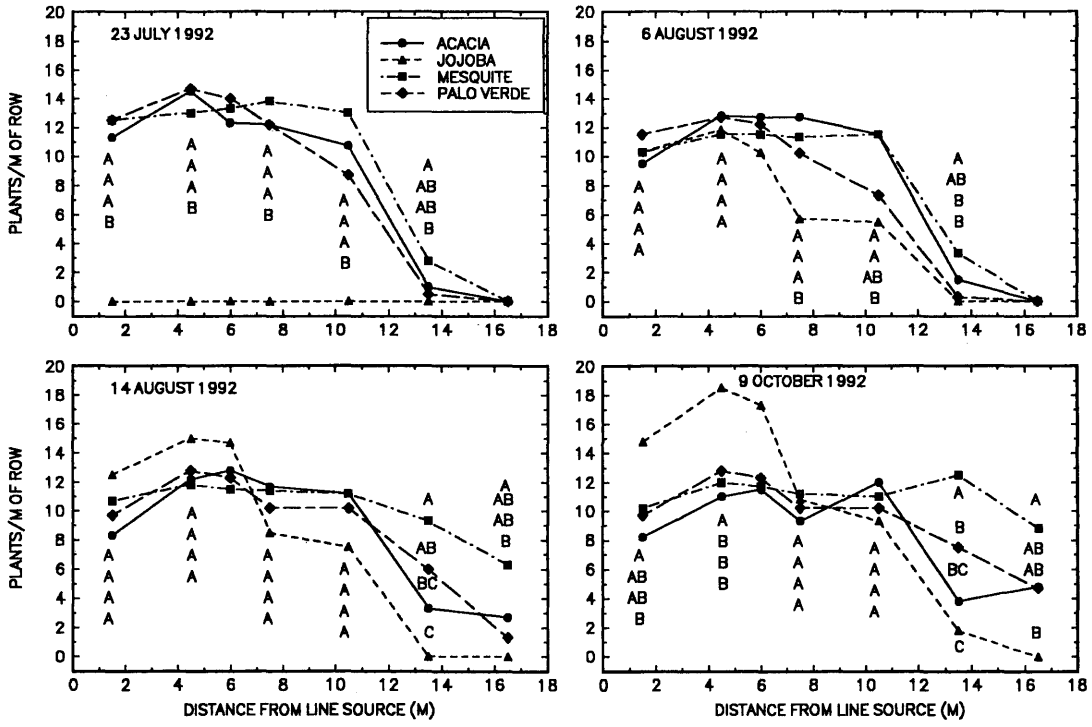

Figure 5—Plants per meter of row for four woody species at seven distances from a line source sprinkler on four dates in summer and fall 1992. Similar letters in vertical order indicate no differences for species at that distance and date by LSD ($p < 0.05$).

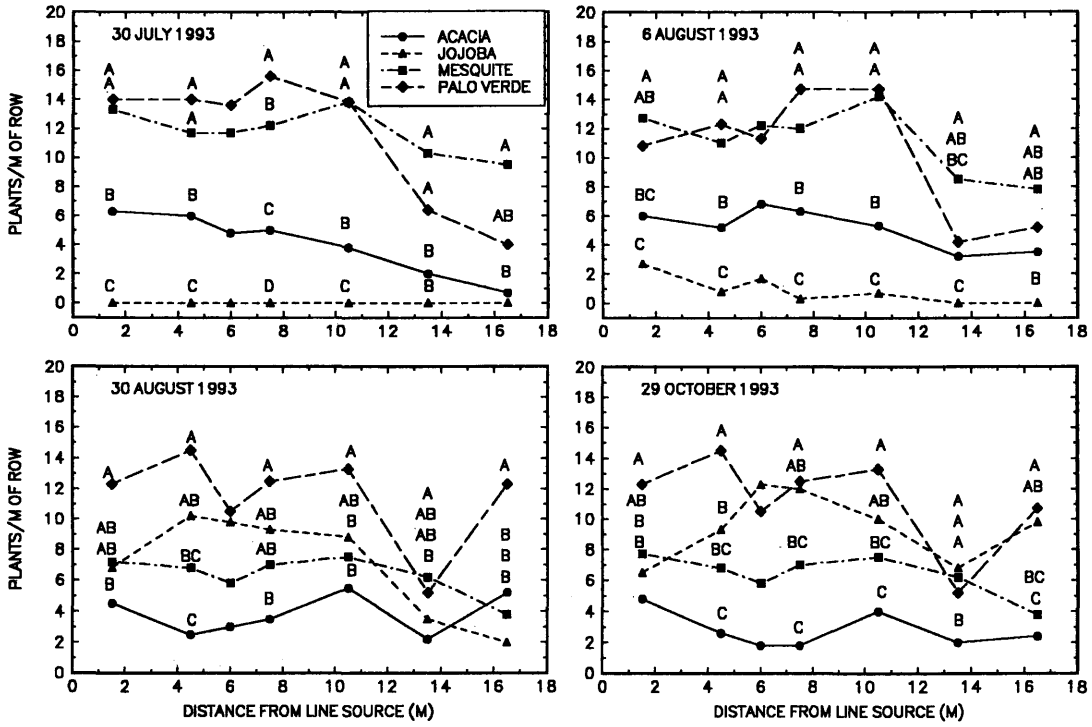

Figure 6—Plants per meter of row for four woody species at seven distances from a line source sprinkler on four dates in summer and fall 1993. Similar letters in vertical order indicate no differences for species at that distance and date by LSD ($p < 0.05$).

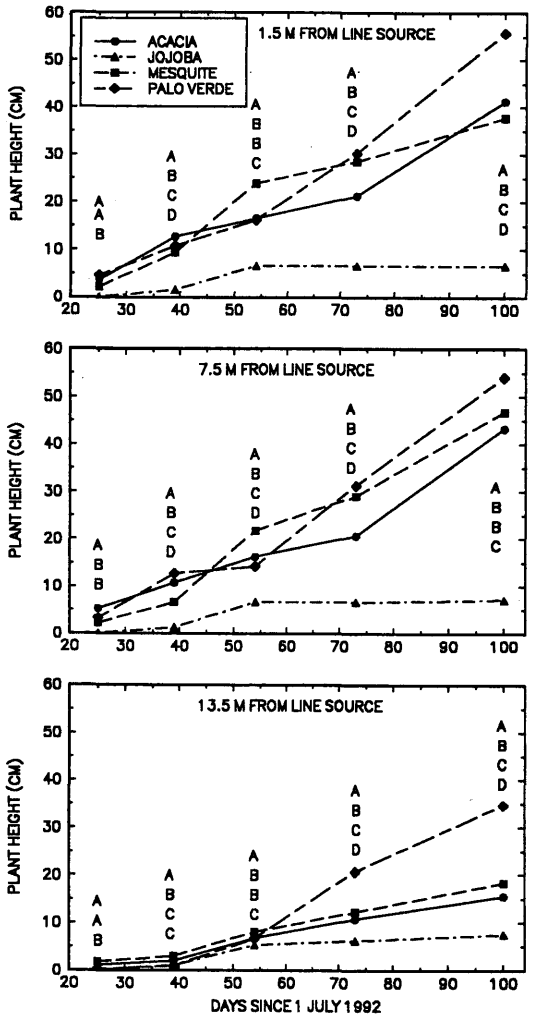

Figure 7—Plant height for four woody species at three distances from a line source sprinkler during summer 1992. Similar letters in vertical order indicate no differences for species at that date and distance by LSD ($p < 0.05$).

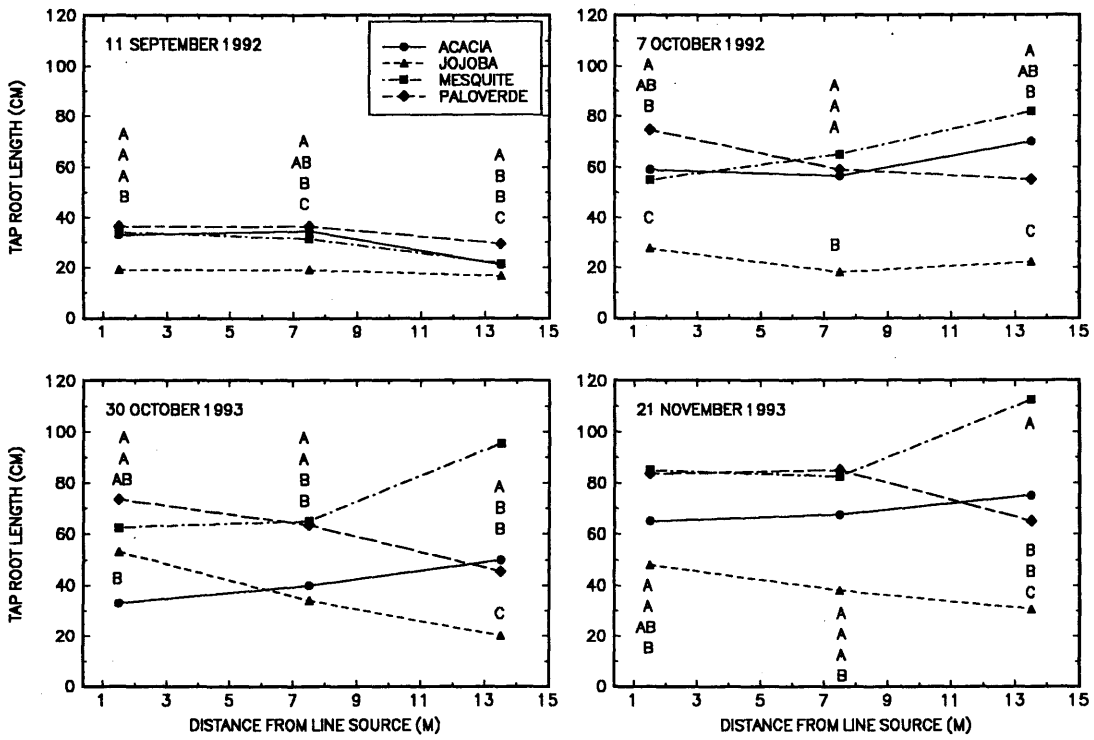

Figure 8—Tap root length for four woody species at three distances from a line source sprinkler in late summer and fall 1992 and 1993. Similar letters in vertical order indicate no differences for species at that distance by LSD ($p < 0.05$).

create a stronger gradient in soil water availability and better define water requirements for establishment of these species. The pattern of irrigation or precipitation influenced establishment of some of these species. Greater establishment of palo verde and jojoba on unirrigated than lowest irrigated soils in 1993 suggests that seeds on the latter soils germinated but died before August precipitation.

Rapid germination and fast root growth of most of these species suggests that they could be established by sowing, then irrigating sufficiently to fill the soil profile. Continued supplemental irrigation to keep the soil surface wet until seedlings emerge in about 2 weeks should result in high seedling establishment on similar soils. For the sandy soil of this study about 3 to 5 cm of water were needed to fill the upper 60 cm to field capacity and an additional 2 cm of water applied over a 1.5- to 3-week period resulted in high plant establishment. More frequent and longer duration irrigation would probably be necessary to establish these species on finer-textured soils. Use of an existing irrigation system to establish adapted woody species as well as grasses (Thacker and Cox 1992) should be considered to revegetate lands abandoned after farming. From a practical standpoint, this strategy will be most successful if done right after abandonment before the irrigation system falls into disrepair. Establishment of these woody species on similar soils without irrigation is possible, but highly dependent on rainfall pattern and amount. Abnormally high precipitation would be necessary for successful revegetation.

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A Simulation Model for Shrubland Ecosystem Dynamics in Arid Karoo, South Africa

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Abstract—We present a spatially explicit model that simulates shrubland dynamics over long timespans. The model, based on life history attributes of five dominant shrub species, explores the effects of natural weather patterns and grazing on their competition, survival, growth and abundance. Changing mean seed production in the model altered the dynamic state from one where five dominant species could coexist to states where some species became rare or locally extinct. Simulating heavy grazing (low seed production of palatable species), decreased overall plant densities but increased the abundance of unpalatable shrubs. The time scales for recovery were long compared with human lifespans. The probability of substantial increases in carrying capacity of overgrazed rangeland within 60 years was 7% with livestock withdrawal, and 64% when resting was combined with partial bush clearing.

An understanding of the dynamic behavior of arid shrubland plant communities is needed in order to manage them for sustained animal production and species conservation. On all continents, utilization of arid shrublands by domestic livestock has resulted in changes in plant species composition that reduce carrying capacity for these animals (Friedel and others 1990; Schlesinger and others 1990; Dean and Macdonald 1994). Rehabilitation of overgrazed shrublands on extensive sheep ranches in the South African Karoo and comparable Australian and American arid and semiarid shrublands has seldom been achieved by withdrawal of livestock (Westoby and others 1989; Bahre 1991; Milton and others 1994). Attempts at increasing densities of natural forage plants by reseeding rarely succeed. Inertia of this kind (Walker 1993) casts doubt on the widely used range succession concept (Clements 1916) which envisages that resting restores what grazing has removed.

Alternative conceptual models, for example the cup-and-ball (George and others 1992) and state-and-transition models (Westoby and others 1989), envisage that vegetation can exist in any one of a number of quasi-stable states (Westoby and others 1989; Milton and Hoffman 1994). Transitions between states may be initiated by either physical (fire, hail) or biotic forces (grazing, clearing, reseeding). Although models of this type are more appropriate for arid shrublands than the range succession model, they can do little more than suggest probable responses of a given state to a transition factor.

The development of computer techniques for simultaneously modelling the spatial and temporal responses of organisms to their environment (individual-based, cellular automata models), offers scope for quantitatively exploring vegetation dynamics (Jeltsch and Wissel 1994). Here we show how a model simulating the dynamics of a Karoo shrubland (Wiegand and others 1995) can be used to estimate time scales for change as well as to explore the effects of weather patterns and management (grazing) on the relative abundance of component plant species. More specifically, we show how our model can be used to investigate typical time scales of vegetation change and the long-term effects of modified seed production (through species-selective foraging by sheep) on the dynamics and composition of an arid shrubland.

Methods

Site Description

The arid shrubland ecosystem simulated in our model is typical of the southern Karoo, South Africa. Field data were collected at Tierberg Karoo Research Centre (TKRC) 33°10'S latitude, 22°17'E longitude, 800 m above sea level. Rainfall occurs mainly in autumn and spring but varies in timing and amount (mean 167 mm p.a., range 50-400 mm over 93 years). Folded sedimentary strata give rise to rocky outcrops and intervening plains with deep colluvial soils. Vegetation on the plains covers 15-25% of the soil surface and comprises dwarf succulent and nonsucculent shrubs (200-600 mm in height and canopy diameter), predominantly Asteraceae, Aizoaceae and Mesembryanthemaceae. The shrubs, which occur at a density of 3-7 plants m^2, are isolated or aggregated in small, mixed-species clumps interspersed with bare ground (Milton and others 1992). Grasses and forbs are largely restricted to drainage lines.

Five shrub species dominated the plains vegetation at TKRC. These were *Brownanthus ciliatus* (Mesembryanthemaceae), a mat-forming stem-and-leaf succulent,

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Ruschia spinosa (Mesembryanthemaceae) an evergreen leaf-succulent, and three nonsucculent species, namely semi-deciduous *Galenia fruticosa* (Aizoaceae), deciduous *Osteospermum sinuatum* (Asteraceae), and evergreen *Pteronia pallens* (Asteraceae). These shrubs differed in their life history attributes and in acceptability to domestic sheep. Information on longevity, seed production, seed dispersal distance, establishment sites, competitive abilities, rainfall thresholds for seed production, germination and survival and on palatability of these species to livestock at TKRC (table 1) has recently been published (Esler 1993; Milton 1992, 1994, 1995; Milton and Dean 1990, 1993; Yeaton and Esler 1990). We assumed that 34 less frequent species present at the study site played a relatively minor role in vegetation dynamics.

Carrying capacity of the vegetation for domestic livestock is low, approximately 6 ha being required to maintain one sheep (Vorster 1985). Browsing by sheep reduces the size and seed production of shrubs (Milton and Dean 1990; Milton 1992).

Model Description

The spatially explicit models we use may be called dynamic automata (Jeltsch and Wissel 1994; Wiegand and others 1995; Wissel 1992) and are an advanced form of the cellular automata (Wolfram 1986). Basic to the method is the division of the space (area) to be modelled into a cellular structure. The size of the cells and their ecological state depend on the local dynamics of the system, the available data and on the aim of the model. The quantitative and qualitative information, and even hypotheses, are then used to develop a set of rules which are used to generate local dynamics within cells.

The ecological state of a cell depends on (1) its present or previous state (or content), (2) external factors (weather, management), and (3), the ecological state of neighboring cells (competition, seed dispersal). Because automata models use rules instead of mathematical equations they are able to use qualitative as well as quantitative knowledge. Thus, they are especially suitable for working out ecological problems. Ecological knowledge can be translated directly into rules instead of being forced into mathematical equations.

There is little available field data on the dynamics of plant communities in arid regions. This is because changes may take decades to occur where lifespans of individuals are long and driving events rare. On the other hand, growth, reproduction, dispersal, natality, survival and interactions between individual species are relatively easy to observe.

Moreover, such information can be incorporated into individual-based, dynamic automata models in the form of simple rules. In order to investigate community dynamics, the model simulates life histories of individual plants (within the community) and interactions between species, the sum of which is community dynamics. In this way the model extrapolates from the behavior of individual plants to long-term community dynamics.

The five dominant species can be divided into two functional groups. Seedlings of "colonizer species" (*B. ciliatus*, *G. fruticosa* and *R. spinosa*) need large gaps in open vegetation to establish while seedlings of "successor species" (*P. pallens* and *O. sinuatum*) establish in shaded sites under the canopy of colonizer plants. Plants of the five dominant species reproduce only sexually (via seeds). We divide the space into a grid of cells which represent mature plant sites. The local dynamics (succession) within a cell is given by the sequences ("empty"→ "colonizer plant" →"successor plant"→ "empty"), or ("empty" → "colonizer plant" → "empty").

For a given cell, the pathway followed and the duration (in time steps) of each state, is determined (1) by the variables which characterize the state of a cell, and (2) the rule-set which determines how these variables change in the course of time depending upon the states of neighboring cells, and on such external factors as rainfall, disturbances or management actions.

Rules were developed for the five dominant species at TKRC. We considered less common species in the model only as occupiers of space, and termed them "fixed plants". Their life histories were not considered, and they remained at fixed densities throughout simulated time, their only function being to prevent colonization of cells by pioneers. The rules for the dominant species are summarized below (for a detailed description of the rules see Wiegand and others (1995)). Monthly rainfall data (93 years) from the nearest village was used to generate the realistic rainfall scenarios that determined the behavior of the component species.

Rule 1—Seed production of adult plants depends on the timing and amount of rainfall. Certain thresholds of rainfall during the growing season (which differ among species (table 1)) are required to stimulate seed production. The number of seeds produced is determined by the amount of rainfall during the growing season. Seed production of established plants that have not reached maximum size is calculated as being proportional to their surface area.

Rule 2—Germination of all species occurs during autumn (March to June). With the exception of *G. fruticosa* and *R. spinosa* in which 70% and 11.5% of seeds respectively remain dormant in a soil seedbank, all viable seeds germinate

Table 1—The standard parameter-set for the simulation model based on life history attributes of five common shrub species in ungrazed vegetation

Parameter	*B.cili.*	*G.frut.*	*O.sinu.*	*P.pall.*	*R.spin.*
Lifespan (years)	10	30	50	70	25
First reproduction (yrs)	1	2	1-9	1-9	3
Max seed dispersal (m)	2.5	2.5	50	30	2.5
Seeds production/plant	1309	2000	542	200	174
Safe gap size (m^2)	>3.25	>1.00	—	—	1.25
Seed viability (%)	50	4	5	30	90
Seed loss (%)	10	10	77	80	10
Rain-thresholds (mm)[2]					
Seed production Apl-Sept	20	50	20	20	70
Germination Mar-Jun	20	30	30	30	30
Seedling surviv. Jul-Oct	10	15	20	20	10
Relative palatability[3]	1	4	5	0	3

[1]Seed production measured in 1989.
[2]Total rain during months (stipulated) critical for seed production, germination and seedling survival.
[3]Where 0 is toxic and 5 most preferred by sheep.

after monthly rainfall totals that exceed a species-specific threshold during the germination season (table 1).

Rule 3—Seedling survival depends on a minimum amount of rain during the post-germination period (July to October). For seedlings in safe sites, survival is 70% in high rainfall years, 10% in average years and nil in dry years.

Rule 4—Seed dispersal of small-seeded colonizer species (*B. ciliatus*, *R. spinosa*, *G. fruticosa*) is by means of water. The seeds are trapped by soil particles and seldom move more than 2.5 m from the parent plant. Successor species have wind-dispersed tumble seeds that are assumed to roll 10-40 m from the parent plant before being trapped by a mat-forming succulent or plant debris. In the model, we distribute single seeds of each plant. We determine the direction of the seed-movement randomly and choose the dispersal distance (within limits of the maximum dispersal distance) in accordance with a weighted random distribution based on field experience. Seeds of colonizer species are deleted unless they are dispersed to open cells.

Rule 5—Safe sites for colonizers are those free of competition from other plants. The minimum size of a safe site (gap) differs among with colonizer species (table 1). Successor species can establish in cells that contain colonizers, but *P. pallens* is limited by the presence of four or more conspecifics in adjacent cells.

Rule 6—Competitive interactions are modelled by assuming that only one of many seedlings that germinate in a given cell can survive. If seedlings germinating within a cell are different species, survival will be determined by competitive ability, defined in our model as growth rate. The competitive ranks are (*B. ciliatus* > *G. fruticosa* > *R. spinosa)* and (*O. sinuatum* > *P. pallens*). In this way, the rule implicitly takes self-thinning into account.

Rule 7—Establishment is attainment of reproductive maturity and the time taken for establishment is considered to be species-specific (table 1).

Rule 8—Growth of a shrub canopy (C) is modelled for each annual time step (t+1) as its responses (A(a)) and (R(r)) to age (a) and rainfall (r) during the growing season respectively

$$C(t+1) = C(t)+A(a)R(r)$$

The functions (A and R) were determined by field experience.

Rule 9—Mortality occurs mainly during the seedling stage. Mortality factors for established plants include hail, drought and excavation by foraging mammals. We therefore model a low, age independent mortality rate for established plants until they reach 80% of their expected lifespans, and then increase the probability of mortality exponentially.

Sub-Model "SEED"—Before beginning a simulation run we fix the parameter set, the initial density and distribution of the plant species and a weather scenario that delivers monthly rainfall data for each time step (year). Although the output for the spatial and temporal simulations is in annual time steps, processes such as seed production, germination and survival depend on rainfall seasonality. For this purpose we developed a sub-model "SEED" that internally calculates on a monthly basis, the total number of seeds produced and dispersed, germinating and surviving (using Rules 1 to 4), and sums these values for one year. The cell dynamics for a single iteration (one year) then proceeds by determining effects of neighboring plants (Rule 5) and competition (Rule 6) on seedling survival, and deleting all dispersed, nonsurviving seeds other than those in the seed bank. The annual iteration is concluded once time, weather and disturbance effects on plant size, reproductive maturity and survival (Rules 7 and 8) have been considered. The cycle for one year is thus complete and the simulation of the next year begins.

Results

Weather and Event-Driven Dynamics

In our initial simulation run, we used the parameter set in table 1, 93 years of monthly rainfall data from the study area, and realistic densities and relative abundances of component shrub species. Seed production parameters were for ungrazed vegetation. Successor plants were randomly dispersed over the grid and colonizers and "fixed plants" were randomly assigned to remaining sites. The spatial and temporal dynamics of the shrubland community was then simulated for 1000 years. Figure 1 shows the outcome of a simulation run for the first 240 time steps.

We found that all five species could co-exist for the simulation period. However, relative densities of component

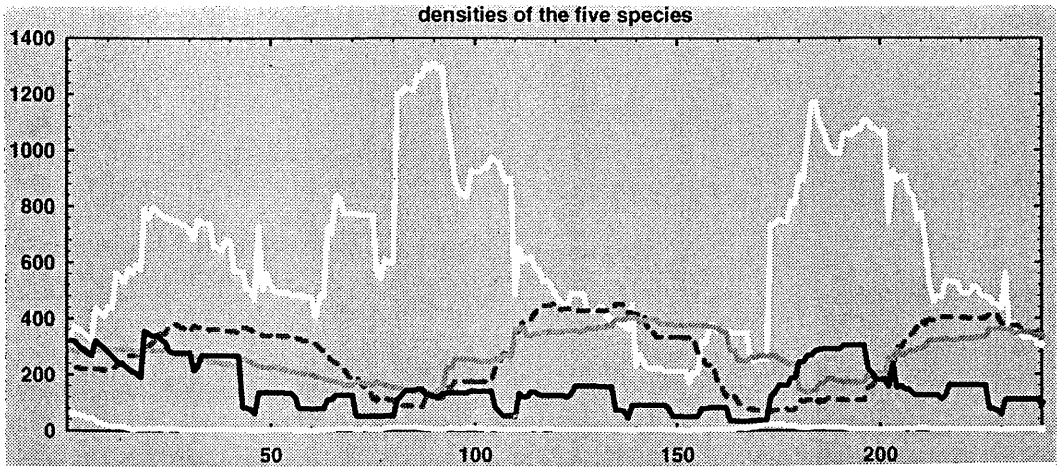

Figure 1—Time series (240 years) showing changes in the abundances of the five study species in a modelled area of 4048 cells. Key: white (upper): *Galenia fruticosa*; white (lower) *Brownanthus ciliatus*; grey: *Pteronia pallens*; black: *Ruschia spinosa*; broken line: *Osteospermum sinuatum*.

species did not reach a state of equilibrium. Instead, we found episodic, event-driven behavior, with quasi-stable periods interrupted by sudden, discontinuous changes in species composition. Sudden increases in density of colonizer species occur when rains, suitable for germination and recruitment, follow long periods with rainfall unfavorable for recruitment. Failure of plant populations to replace natural mortality during prolonged growing-season droughts leads to a decrease in the density of established plants, and consequently, to an increase in the size and abundance of gaps that serve as safe establishment sites for colonizers.

For example, figure 2 shows the time series for the abundance of the colonizer-species *R. spinosa* together with the number of its seedlings that can survive the post-germination period. We see that large recruitment events can occur only when two conditions are fulfilled. First, the timing and amount of rainfall over the year must be suitable for seed production, seed germination and survival (fig. 2a), and second, safe sites must be available to the dispersing seeds. Our model indicates that rainfall suitable for reproduction and recruitment occurs in only 22-44% of years, depending on species (fig. 2a). The coincidence of rainfall conditions suitable for reproduction and availability of safe recruitment sites is so rare that large recruitment events in these arid shrublands are likely to occur only 2-5 times per century.

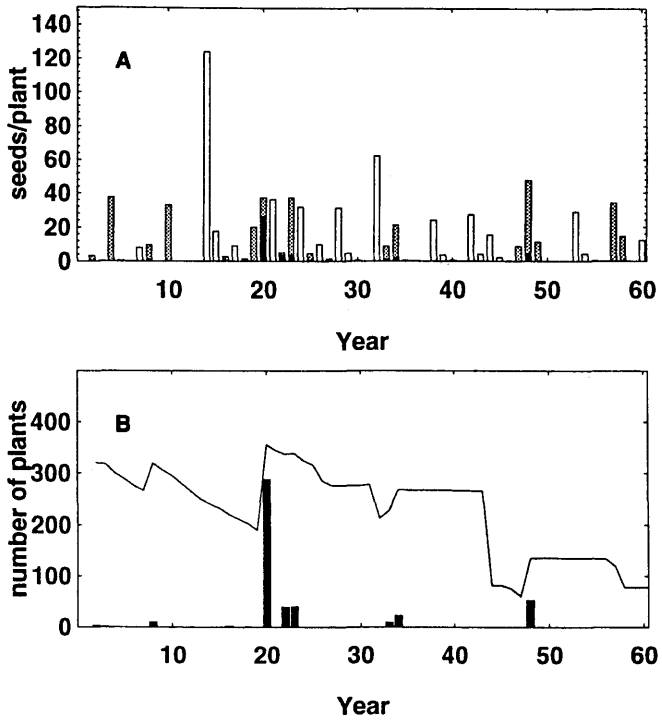

Figure 2—(A) Seed production, germination and number of seedlings which would survive in safe sites of *R. spinosa*, calculated with the sub-model (SEED) over the first 60 years of the local rainfall scenario. Bars show seeds that fail to germinate (white), seeds that germinate but die (hatched), and surviving seedlings (black). (B) Time series (60 years) for the colonizer species *R.spinosa* (solid line) and the number of seeds (bars) per adult plant which would survive as seedlings in safe sites.

Influence of Seed Production on Dynamics

In real shrubland ecosystems, weather patterns or livestock management practices can reduce the seed production of some plant species more than others. Our model gives us the opportunity of varying the parameter "seed production" in order to understand its effect on community dynamics. Such manipulations of seed production are difficult to perform in the field on a large scale, over long timespans. The dynamic behavior of the plant community is complicated by interactions between all species (Wiegand and others 1995). We therefore first investigate a simple case, without interspecific competition, where we model only one species in detail (see section on Single Species Simulation), treating all other individuals as fixed plants (see section on Model Description). In a second step we include the effect of interspecific competition, and analyze the influence of seed production on the relative abundance of component species and on community dynamics.

Single Species Simulations—We model only one species in detail and treat all plants of other species as "fixed plants". The number of fixed plants thus defines the availability of gaps (resource availability) for colonizer species. In order to explore the response of selected species to different resource availability and different values for mean seed production, we then ran 180 year simulations and determined its mean abundance. We define the mean percentage of available gaps occupied by a species (= mean abundance relative to available gaps) as its resource exploiting potential. This definition incorporates the ability of the species to reach available resources and to maintain a mean population of a certain size.

We found that both the availability of recruitment sites and seed production strongly influenced mean abundance of a colonizer species (fig. 3). Where gaps were abundant (fig. 3a, solid line), the resource exploiting potential rapidly reached saturation with increasing seed production; but when gaps were limited (fig. 3a, dashed line), the species exploited its resource less effectively. When we reduced the availability of gaps between simulation runs (increase in fixed plants), but kept mean seed production constant, the abundance of colonizer plants decreased (fig. 3b).

Full System Simulations—In the single species simulations we found that resource exploiting potential, in the absence of interspecific competition, was related to seed production and gap availability. In the full system, the competitive hierarchy among the seedlings of various species that reach gaps modifies the resource exploiting potential of a given species.

Safe sites for plants, particularly colonizers, are limited in our model system as they are in natural ecosystems. An advantage may therefore accrue to species that produce more seeds than potential competitors for safe sites, because the species with more seeds has a higher probability of reaching gaps (higher resource exploiting potential), especially where gaps are very limited (figure 3a, dashed line).

In order to observe the effects of varying the seed production of competing species on community dynamics, we ran a series of 200 year simulations and calculated the mean

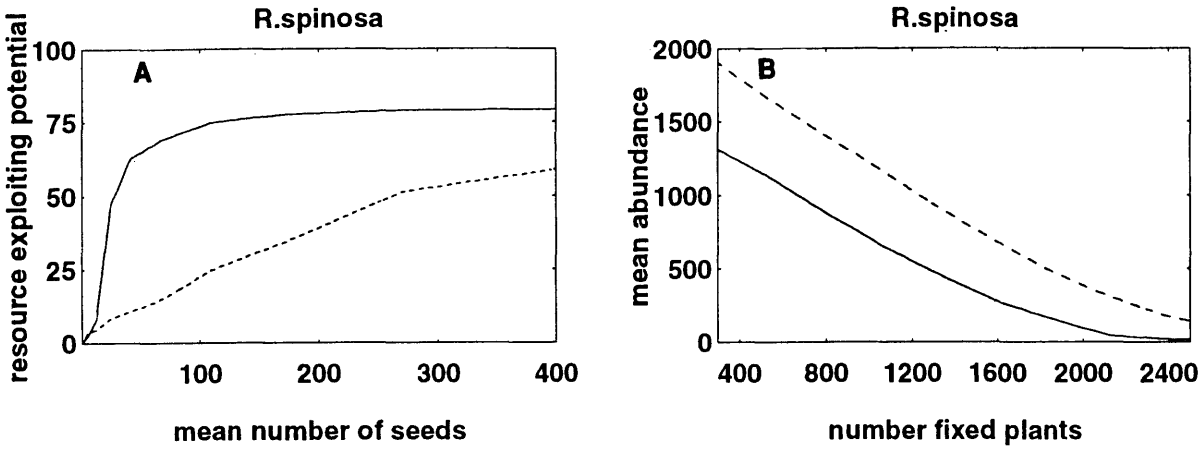

Figure 3—(A) Changes in the resource exploiting potential of *Ruschia spinosa* with an increase in the mean number of seeds produced per plant. Solid line: high availability of safe sites (density of fixed plants: 0.025 plants/cell), dashed line: low availability of safe sites (density of fixed plants: 0.25 plants/cell). (B) Changes in the resource exploiting potential of *Ruschia spinosa* with an increase in the number of fixed plants. Solid line: low seed production (170 seeds/plant), dashed line: high seed production (10,000 seeds/plant).

abundance of each species. In simulations where seed production of one of two colonizers (*G. fruticosa*, *R. spinosa*) was reduced, the other member of the pair filled most of the available establishment sites, because its resource exploiting potential was much greater than that of its competitor. For both species there were critical seed production values below which the populations decreased exponentially. Variation in seed production of colonizers had little effect on densities of successor species, except when seed production of both colonizers were very reduced.

When we varied the seed production of successor species (*O. sinuatum*, *P. pallens*), we again found that relatively low seed production by one of the pair could reduce its mean population size or lead to its extinction (fig. 4a), and that the competing species filled most of the available establishment sites (fig. 4b).

Seedlings of forage plant *O. sinuatum* are faster growing than those of the toxic shrub *P. pallens*, and can therefore out compete it. However, when seed production by the forage plant is less than half that of its competitor (intersections of the two curves in figure 4a,b), the abundance of the forage plant will be less than that of *P. pallens*. In addition to their influence on one another, the seed production, and thus the mean abundance of successor species influences the composition of the colonizer guild.

Thus, the resource exploiting potential (seed production and dispersal) of a species together with its competitive ability (growth rate) determines the composition and dynamics of the plant community. By varying seed production of component species in the model we found the following tendencies:

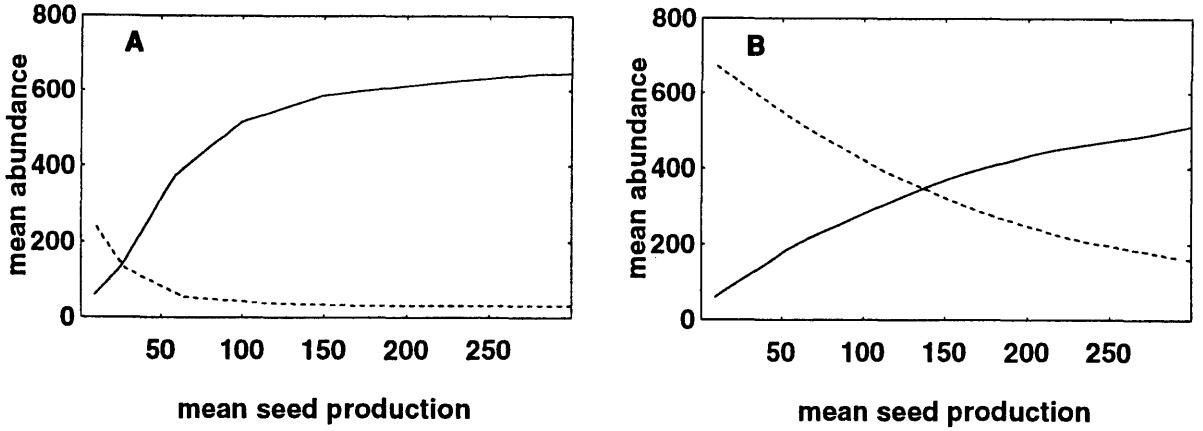

Figure 4—Mean abundances of the successor species *Osteospermum sinuatum* (solid lines, fast-growing forage shrub) and *Pteronia pallens* (broken lines, slow-growing, toxic shrub) as a function of the mean seed production of *O. sinuatum* relative to its competitor. (A) Seed production of *P. pallens* = 9. (B) Seed production of *P. pallens* = 272.

1. When their seed production is adequate, all five species coexist indefinitely and the dynamics of the community is typically episodic and event-driven.

2. When seed production for one species falls below a critical threshold relative to seed production of competitors, its population collapses, and the dynamics of the plant community changes from event-driven to oscillatory behavior caused by explosions, and subsequent crashes, in populations of species that lack competitors.

3. When seed production of a number of (palatable) species was considerably reduced (overgrazed scenario) the vegetation composition changes to a degraded state characterized by large gaps, high abundance of pioneers and non-palatable successor species.

Estimated Transition Times

One of the most urgent and unsolved questions for rangeland management and for the rehabilitation of degraded rangeland concerns the time scales of vegetation change. The major problems in this respect are the complex interactions of component species among themselves as well as with the unpredictable rainfall pattern. The uncertainty of rainfall makes the driving events unpredictable so that the development of the plant community over the next, say 60 years, can be described only in terms of probabilities.

To investigate transition times, we conducted two simulation experiments each comprising 100 sixty-year simulation runs, using different rainfall data for each run. We used the rainfall simulation program GENRAIN (Zucchini and others 1992) to generate 100 different rainfall sequences with the same monthly mean and variance as rainfall at our study site. The initial plant distribution differed in the two simulation experiments as follows:

1. A distribution where the relative abundances of the five dominant species and the fixed plants correspond to ungrazed rangeland in good condition (carrying capacity about six ha/sheep).

2. A distribution corresponding with overgrazed vegetation in poor condition (one third of the above carrying capacity).

Using seed production values that correspond to ungrazed plants (table 1) we simulate the dynamics of these two states of rangeland vegetation. Thus, in experiment (b) we simulate resting after overgrazing. To be able to categorize and compare the vegetation state we introduce a grazing potential index (P). This index sums up the densities of all species weighted with their sheep utilization index (s) (see table 2, Milton and Dean 1993):

$$P = s1\ D1 + s2\ D2 + s3\ D3 + s4\ D4 + s5\ D5$$

The (Di) are the relative densities of plants of species (i) in the simulation grid (ie. total plants of species i/total cells). A grazing potential index of 0 indicates a community without any palatable plants while a value of 1 indicates the opposite extreme where each cell is occupied by a 100% palatable species.

We found that during simulations of the ungrazed plant community (fig. 1) not more than half of all cells were occupied by plants. This restricts the biological range of the grazing potential index for such arid shrubland to values between 0 and 0.5. However, as natural rangelands comprise a mixture of species of differing palatability to sheep, P seldom exceeds 0.12 even in good rangeland. table 3 shows the abundances of the component species for (a) good rangeland and (b) overgrazed rangeland and the values of the grazing potential index for each case.

The grazing potential of rangeland in good condition (case a) cannot be expected to change much when livestock are withdrawn for 60 years (fig. 5a, left). The grazing potential of overgrazed shrubland (case b) is expected to show little change within 30 years of livestock withdrawal (fig. 5b left), but after 60 years (fig. 5b right), there is a 7% probability that its condition will improve three-fold (grazing potential of 3 x 0.038 = 0.114, see table 3).

Recovery of grazing potential may possibly be accelerated by partial clearing of long-lived, unpalatable shrubs. To test the impact of this management action in our model, we "cut" a fixed number of *P. pallens* (40% of the initial density) at random in simulation years 0, 10, 20, 30, 40, 50. After cutting an established plant in the model, we designated that 50% of the cells would be open and the remainder occupied by plant skeletons which could trap tumbleseeds with a probability of 80%. When partial clearing of this kind was combined with resting, overgrazed rangeland (case b) had a 13% probability of attaining a good condition within 30 years (fig. 5c left), and 64% after 60 years (fig. 5c right).

Table 2—Sheep utilization index: the proportion of the plants in a species population that are utilized by sheep.

B. ciliatus	*G. fruticosa*	*O. sinuatum*	*P. pallens*	*R.spinosa*
0.063	0.588	1.000	0.000	0.185

Discussion

Short-term field studies in the arid Karoo shrublands of South Africa suggested that community composition may be controlled by the quality of establishment sites (Esler 1993), by the relative abundance of seeds of species with similar site requirements (Milton 1995), and by hierarchical competition among neighboring plants for water or nutrients

Table 3—Initial abundances of the five shrub species and the grazing potential in the 4048 (0.14 m^2) cells of the approximately 1/18th hectare grid that comprises the spatial model (a) good condition, (b) overgrazed.

Experiment	*B. ciliatus*	*G. fruticosa*	*O. sinuatum*	*P. pallens*	*R. spinosa*	Total	Grazing potential
(a)	49	284	260	161	251	1509	0.117
(b)	115	75	97	367	37	1195	0.038

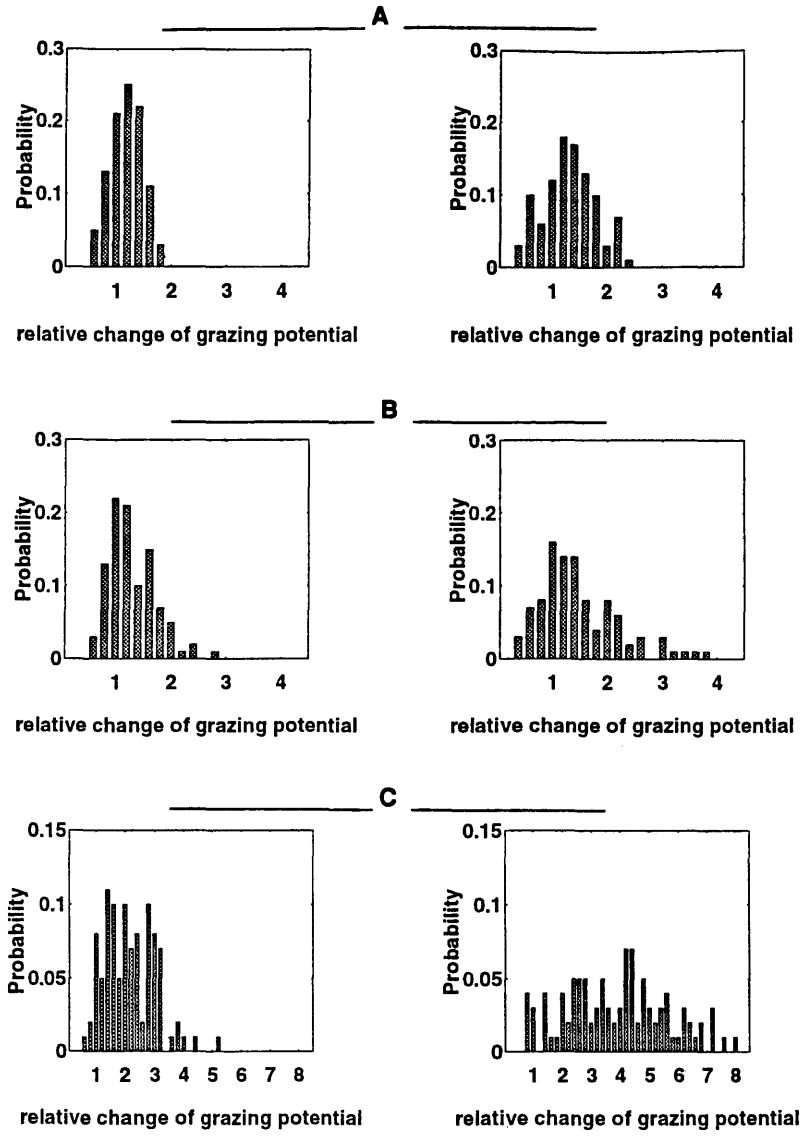

Figure 5—Probability that the grazing potential reaches a certain level, relative to the initial condition, after 30 and 60 years. (A) Resting of rangeland in good condition. (B) Resting of rangeland in poor condition. (C) Resting and selective clearing of rangeland in poor condition.

(Yeaton and Esler 1990). Our model, governed by rules based on field data from these studies, was able to generate realistic densities and spatial arrangements of species as well as to maintain coexistence of dominant species, without grazing, over one thousand simulated years.

In addition to reproducing spatial patterns observable in the field, the model indicated that community composition was unlikely to reach a stable equilibrium, but would fluctuate erratically in response to weather and/or disturbance-triggered mortality and recruitment events. Rapid changes in species composition can be expected only when establishment sites are readily available and the timing and quantity of rainfall is suitable for seed production, germination and seedling survival. Similar event-driven dynamics appear to be characteristic of arid Australian shrublands (Griffin and Friedel 1985).

On the basis of field observations, Milton (1992) and Milton and Hoffman (1994) hypothesized that forage plant populations, in species that were incapable of vegetative reproduction, were seed-limited on rangelands that had been heavily grazed for many decades. We tested this hypothesis by manipulating the seed-production parameter in our model, and found that the mean density that a species maintained over simulated time was related to its seed production. However, we also found that the initial hypothesis was simplistic because species were limited by the interaction of seed abundance with the availability of gaps. Lottery competition for limited safe sites occurs among species within an establishment guild, so that a species population is not limited by absolute seed production but by its contribution to the total seed pool of its establishment guild. The implications of this result for rehabilitation of overgrazed rangelands are that, in order to change rangeland composition, a manager would need to add more seeds of the desired species where seed availability of competing species was abundant, than where it was scarce.

In our simulation model, it generally took >60 years of resting and selective bush-clearing for 64% of overgrazed

vegetation samples to regain a grazing potential comparable with arid rangeland in good condition. This timespan is comparable with anecdotal accounts (Roux and Vorster 1983) and hypotheses (Milton and Hoffman 1994) about rates of recovery in arid rangelands. The variability in recovery time was, as predicted by Westoby and others (1989) and Walker (1993) the result of variation in the timing and seasonality of rainfall, a variable outside the control of a land manager.

Conclusions

The basic model for the Karoo can potentially be extended for investigations of effects of grazing intensity, frequency and seasonality on the spatial and temporal dynamics of this and other arid shrubland ecosystems. It could also be used to compare the effectiveness of active interventions (seed addition, micro-habitat modification, bush clearing) for rehabilitation of event-driven rangelands. We have shown that individual-based dynamic automata modelling technique is a powerful tool that allows the field biologist to explore the long-term and large-scale implications of temporally and financially constrained field studies.

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Sagebrush Restoration in the Shrub-Steppe of South-Central Washington

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L. Fitzner

Abstract—Fires over the past two decades eliminated an estimated 70 percent of the shrub cover on the Fitzner/Eberhardt Arid Lands Ecology (ALE) Reserve on the Hanford Site in south-central Washington State. Big sagebrush was planted to aid in the recovery of sage grouse on the Reserve. A Geographic Information System screening process was used to optimize planting site selection and reduce the time required in the field to identify suitable planting sites. Criteria for selection of planting sites were geographically defined and converted into a series of map layers. Overlapping map regions meeting all criteria became the basis for field reviews leading to final planting site selection. The process of using a GIS to screen for potential planting locations was effective in optimizing plant site selection and greatly decreased the time required to locate suitable planting sites. Preliminary surveys after the first growing season indicated a high rate of seedling survival.

Populations of western sage grouse (*Centrocercus urophasianus phaios*) have declined substantially in Washington State during the past several decades as a result of loss or conversion of big sagebrush-steppe habitat to agricultural and other uses. When a naturally caused range fire destroyed approximately 70 percent of the big sagebrush on the Department of Energy's (DOE) 31,000 ha Fitzner/Eberhardt Arid Lands Ecology (ALE) Reserve, a DOE research natural area, in south-central Washington State, a large block of sagegrouse habitat was further degraded. DOE and the Washington State Department of Fish and Wildlife implemented a plan to enhance natural big sagebrush recovery on the ALE Reserve by selectively planting burned areas that are devoid of big sagebrush. The intent was to plant seedlings of a local stock of Wyoming big sagebrush (*Artemesia tridentata* ssp. *wyomingensis*) in selected areas to provide seed sources for dispersion and natural recolonization of the shrubs. Only a small portion of the total burned area could be planted, so we established several planting criteria and used a Geographic Information System (GIS) to screen the landscape for potential planting sites. When that was complete, potential planting sites were inspected by ground survey, and final planting locations were selected. We describe here the GIS-based approach to selecting planting locations.

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Planting Criteria and GIS Map Layers

Five planting criteria were identified based on location of seed collection sites, the need to optimize establishment and growth conditions for sagebrush seedlings, known habitat requirements of sage grouse, and road/access constraints. GIS map layers were created for each criteria using the Geographical Resources Analysis Support System (GRASS) version 4.1, a raster-based GIS package developed by the Environmental Division of the U.S. Army Construction Engineering Research Laboratory (Champaign, Illinois) (fig. 1A-E). The 5 map layers were then overlaid to produce a new map layer depicting areas in which all criteria exist (fig. 1F).

To maintain the genetic integrity of the local big sagebrush on the ALE, collection and propagation of seed from onsite was preferred over the use of seed from outside the immediate area. Seeds were collected from sagebrush stands remaining on ALE at elevations of 335 m and 640 m in order to propagate plants from stocks derived from both upper and lower elevations of ALE. Seed collection was somewhat constrained by the location of remnant sagebrush plants after the 1984 burn and by climate. We decided to plant within a 100-m elevation band above and below the elevation from which seeds were collected to ensure that plants were well adapted for environmental conditions at planting locations. Therefore, areas lying at elevations from 235 m to 435 m and 540 m to 740 m were considered for planting (fig. 1A).

The second criteria for identifying planting areas regarded the current vegetation. Past fires had burned large stands of big sagebrush where few, if any, surviving shrubs were present. Available GIS-based land cover maps (Downs and others 1993) were used to pre-select the burned areas and thereby avoid the necessity of physically inspecting

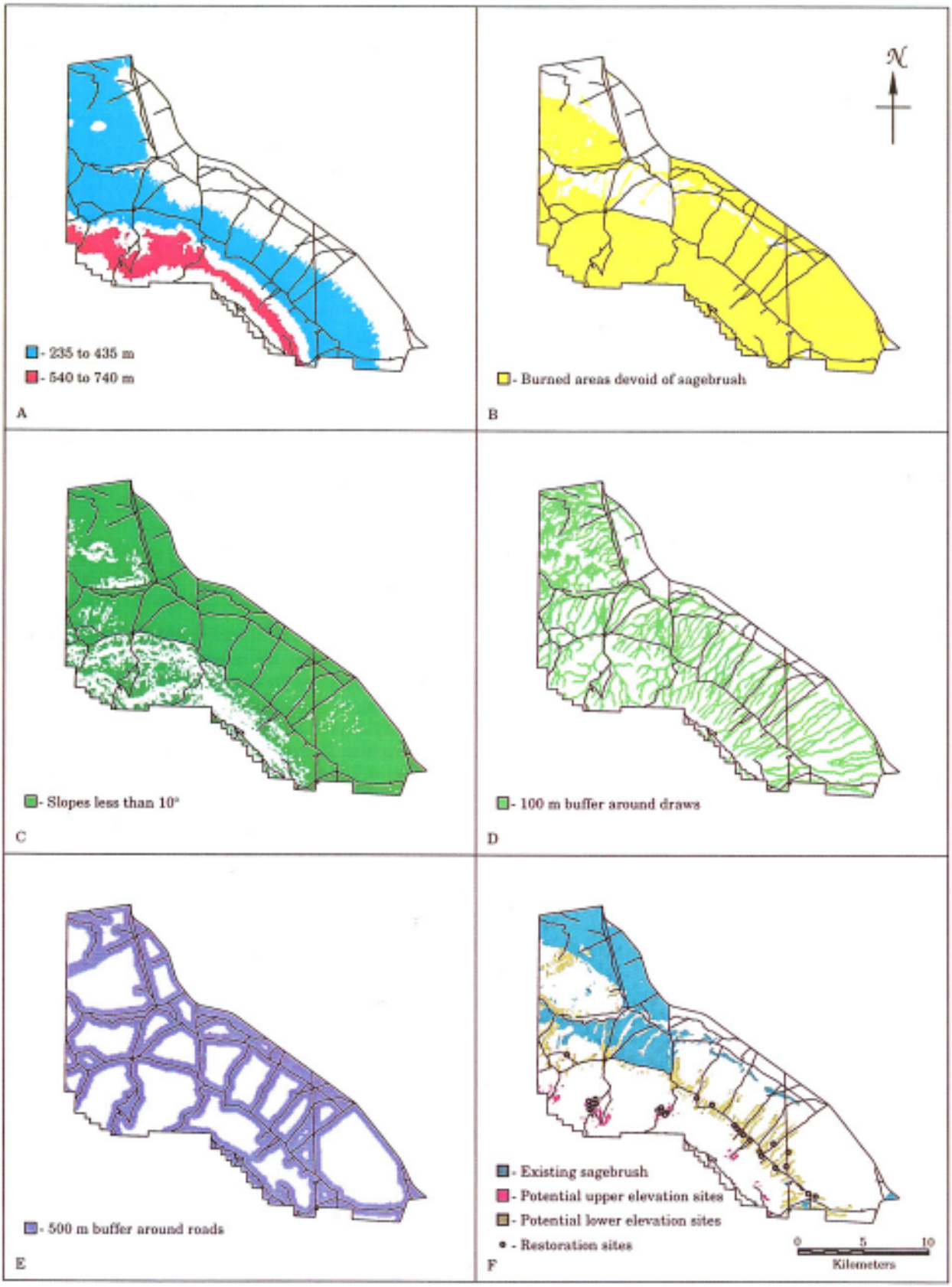

Figure 1—Map layers used in GIS analysis: (A) planting elevations; (B) burned areas; (C) slopes less than 10°; (D) 100 m buffer around draws; (E) 500 m buffer around roads; and (F) potential planting sites and actual selected planting locations.

large land areas to determine whether or not specific areas were devoid of big sagebrush. The total area considered for restoration of sagebrush habitat was 24,600 ha comprising the land areas burned by wildfires in 1981 and 1984 (fig. 1B).

Research on sage grouse inhabiting sagebrush habitat adjacent to ALE indicate that grouse prefer gently sloping hillsides (Cadwell and others 1994). Therefore, planting locations were constrained to areas having slopes <10° to maximize the potential benefit of increased habitat for sage grouse. Areas of the reserve where slopes were less than 10 ° are shown in figure 1C.

We further reasoned that seedling survival would likely be greatest in locations having the most available soil moisture. Thus, we decided to plant in or near draws where soil moisture may be most abundant, and established an additional planting criteria to limit planting sites to within 100 m of draws. Figure 1D indicates a 100-m buffer around the numerous draws and drainages across the northeast facing slopes on ALE where soil moisture conditions might be more conducive to sagebrush seedling establishment and survival.

The final planting criterion, one based not on biological constraints, but rather on cost and efficiency, was to restrict the planting operation to areas relatively near roads. Off-road driving is not allowed in the research natural area, and it was necessary to identify potential planting sites that could be conveniently accessed without hand-carrying planting tools and seedlings long distances. A 500-m buffer was developed for roadways on the reserve to indicate those areas where walking and carrying equipment and plants was most feasible (fig. 1E).

The common overlay area of the five map layers defined potential planting areas that met planting site selection criteria and consisted of approximately 2,990 ha (fig. 1F).

Final Sites and Planting

The GIS analysis allows identification of potential planting zones, but visual reconnaissance of individual areas is required to confirm and "ground truth" the map information in the GIS. Field surveys of the potential planting zones were conducted to verify the suitability of the area. A planting site was determined suitable according to whether the site exhibited the following characteristics:

- Soils deeper than 1 m with relatively few rocks on the surface
- Slope criteria (<10°) were met
- Plant community dominated by native forbs and grasses rather than invasive alien species
- Planting site large enough to plant 500 to 1,500 shrubs spaced several meters apart

At each planting site, a global positioning system was used to determine site coordinates for mapping, and the site was marked for location by planting crews. Planting was completed in March and April 1995.

Conclusions

The GIS-based approach to site selection proved to be both an effective and an efficient means to identify potential planting sites. Field surveys of the pre-selected sites confirmed that the screening criteria for site selection were adequately identified by the map-based screening process. Time spent in the field marking plots for the planting crews was minimized because preselected locations were usually judged suitable for planting, and there was no need to spend field time searching for locations that met the basic screening criteria. In a few locations, existing vegetation cover that consisted of alien weedy species or soils that were excessively stony caused the preselected sites to be disqualified during the ground survey process.

We have not yet completed surveys to determine survival of the planted seedling, but preliminary late winter counts suggest that survival through the first growing season was greater than 85 percent. Although we did not set out to "study" the relative efficiency of GIS-based screening for big sagebrush planting site selection, it is clear that the application of GIS-based analyses simplified the process, facilitated selection of planting sites that met several basic "geographic" criteria, and saved a considerable amount of time and money that would otherwise have been required to conduct field reconnaissance of potential planting locations.

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Ecotonal Dynamics of High-Bush Blackberry in Eastern Kansas

Thomas A. Eddy

Abstract—An aggressive and bothersome invader in Eastern Kansas is the high-bush blackberry (*Rubus ostryifolius* Rhbd.). This study investigated the rates and patterns of invasion of this thorny bramble from forest border areas into tallgrass prairie on a site in Elk County, Kansas, that has been unburned and ungrazed since 1978. Blackberry populations advanced a mean distance of 5.4 m on deep loam soil compared to 2.3 m on shallow loam and clay soils with exposed sandstone rock. Patterns of invasion were broadening bramble borders along woodland edges and stream's peninsulas of bramble growth into prairie, and expanding islands of brambles in open prairie.

The role of fire in maintaining the integrity of the tallgrass prairie ecosystem is well known (Weaver and Rowland 1952; Hulbert 1969; Bragg and Hulbert 1976). Ungrazed and unburned prairies along forest borders are especially vulnerable to change. Accumulated plant materials alter the microclimate which encourages retrogression of prairie grasses and forbs and their replacement by woody plants. An aggressive and bothersome invader in Southeast Kansas is the high-bush blackberry (*Rubus ostryifolius* Rhbd). This study investigated the rates and patterns of invasion of this thorny bramble from forest border areas into tallgrass prairie and cultivated fields on a 2,800 acre area in Elk County, Kansas.

Methods and Materials

The study site is located in the Chautaqua Hills, an undulating uplift extending from the Kansas-Oklahoma border to Woodson County, Kansas (Bare 1979). The hills are dissected by deep ravines with occasional sandstone bluffs along the major drainages. Soils are sandy clays and loams with sandstone outcrops of Pennsylvanian age. The tallgrass prairie vegetation is interspersed with groves of blackjack oak (*Quercus velutina* Lam.) and post oak (*Quercus stellata* Wang). A variety of shrubs are associated with the woodland borders. Fire and grazing have not occurred on the site for at least a decade. Disturbances include strip thinning of oak groves in 1978, introduction of milo feed patches for wildlife food and cover, and construction of roadways.

Natural propagation and expansion of high-bush blackberry populations occur by root suckers (primocanes) (Stephens 1973). Primocanes remain vegetative through the first growing season and become flower and fruit bearing (floricanes) the second year. Invading strategies of the high-bush blackberry were studied during the growing season of 1994. Thirty 5 m line transects were randomly established along 300 m of the advancing edge of high-bush blackberry populations on the study area in April. Quadrats (5 m x 10 m) were located perpendicular to the 5 m line transects in the direction of movement of the invading blackberries. Primocanes in the quadrats were counted in April and August.

High-bush blackberry stem and root dimensions related to population growth were examined. Two hundred floricanes and their associated root systems were randomly selected for measurements of cane length, height, depth to lateral roots, and root sprout intervals.

Patterns of expansion of invading shrubs and acres invaded were determined from aerial photographs and vegetation maps.

Two woody species accompanied the invasion of high-bush blackberries into prairies on the study site. The frequency of occurrence of coralberry (*Symphoricarpos orbiculatus* Moench) and dwarf sumac (*Rhus copillina* L.) was determined in 30 quadrats along the front of invasion.

Cultivated patches of grain and forage sorghum have been planted on scattered areas of the study site annually since 1978. Unplanted strips (2 m to 4 m wide) are frequently left between the rows of sorghum. High-bush blackberry plants have established in many of these strips. Twenty m^2 quadrats were established randomly along 100 m of invaded unplanted strips.

Results and Discussion

Primocane numbers in the 30 quadrats along the advancing edge of the bramble invasion ranged from 2/m to 9/m with a mean of 4/m. August readings in the 5 m x 10 m quadrats showed population extensions from 0.5 m to 6.3 m with a mean of 2.1 m. Populations advanced a mean distance of 5.4 m on deep loam soil compared to 2.3 m on shallow loam and clay soils with exposed sandstone rock.

Stem and root measurements indicated important aspects of the growth of the high-bush blackberry. Length of canes varied from 1.4 m to 0.11 m with a mean length of 0.82 m. The arching canes were 1.3 m to 0.2 m tall with a mean height of 0.7 m. Depth of lateral roots ranged from 0.5 cm to 25 cm with a mean depth of 6.2 cm. Primocanes sprouted from lateral roots at intervals of 6 cm to 53 cm with a mean distance between sprouts of 18 cm.

Two woody plant species were associated with the invading blackberries. Fourteen of the thirty 5 m x 10 m plots contained coralberry and 9 of the plots were occupied by

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dwarf sumac. These species competed with the grasses and forbs for light and moisture. Penfound (1964) determined that coralberry represented 15% of the foliage in ungrazed pastures in central Oklahoma as compared to 0.8% in ungrazed pastures.

Acres invaded and patterns of expansion by high-bush blackberry and associated woody species were estimated. Approximately 315 acres or 12% of the study site have been invaded since 1978. The three patterns of invasion identified and percent acreage in each type were: (1) broadening shrub borders along woodland edges and streams (75%), (2) peninsulas of shrub growth into open prairie (15%), and (3) expanding islands of woody vegetation (10%).

Intrusion of high-bush blackberry into unplanted wildlife food strips was measured. Density of canes ranged from $14/m^2$ to $43/m^2$ with a mean density of $35/m^2$. Primocanes frequently appeared in the planted strips. If food plantings are discontinued the cultivated areas will be invaded by high-bush blackberries in a few growing seasons.

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High Stocking Rate Potential for Controlling Wyoming Big Sagebrush

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Abstract—Our objective was to evaluate if excessively high cattle stocking rates over 3 years would mechanically control Wyoming big sagebrush (*Artemisia tridentata* spp. *wyomingensis*). The hypothesis tested was that high cattle stocking rates will first reduce Wyoming big sagebrush cover and second result in increased understory production. A Wyoming big sagebrush-bluebunch wheatgrass (*Agropyron spicatum*) habitat type in southwestern Montana was studied. A randomized complete block design with three blocks was used. Four stocking rates, from normal up to eight times normal, were applied for three consecutive years. Heavy stocking rates did reduce sagebrush cover primarily through mechanical damage, but some browsing was observed. The reduction in sagebrush canopy in the heavy stocking treatments did not result in increased understory production. We conclude that this treatment will not increase livestock forage but may reduce habitat quality for wildlife and other values.

The importance of big sagebrush (*Artemisia tridentata* Nutt.) is not surpassed by any species on rangelands in the western United States. Big sagebrush occupies nearly 60 million ha in this region (Beetle 1960). This taxon is often valuable in wildlife habitats as both cover and high quality forage (Welch and McArthur 1979). However, its aggressive nature as a climax dominant and low preference as forage by cattle are qualities responsible for it having been the subject of control projects (Welch and McArthur 1979).

Wambolt and Payne (1986) compared controlling Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young) on the same southwestern Montana site by burning, plowing, spraying with 2, 4-D, and rotocutting. Watts and Wambolt (1989) furnished an economic evaluation of these treatments. However, a potential opportunity to reduce sagebrush populations more biologically and economically efficiently was identified. The method had the potential to prove more environmentally acceptable than previously evaluated sagebrush control methods. It would avoid the negative aspects of herbicide use, the air pollution of burning, and the erosion potential associated with plowing, rotocutting, and often burning.

It was conjectured that cattle stocking rates normally considered excessive could be applied for short periods of time to mechanically reduce sagebrush cover. The idea was based on the undetermined premise that sagebrush is competitive with forage plants.

Our objective was to evaluate if cattle stocking rates normally considered excessively high could be used for a short period of time to mechanically control sagebrush cover and increase herbaceous production. The hypotheses tested were: 1) that high cattle stocking rates will reduce Wyoming big sagebrush cover, and 2) that any reduction in sagebrush cover from high stocking rates will increase understory production.

Methods

Study Area

The study area is located in southwestern Montana approximately 50 km north of Livingston at an elevation of 1800 m. It lies within the private holdings of the Grande family livestock operation and has been grazed by domestic livestock since the mid-1800's. The site is dominated by a Wyoming big sagebrush-bluebunch wheatgrass (*Agropyron spicatum* [Pursh] Scribn.) plant community. The average annual precipitation is approximately 380 mm with the peak received during May and June. The topography is very level with no prominent exposure. Clay loams predominate in surface and subsurface soils. The homogeneity of environmental parameters and community characteristics throughout the study area is great.

Experimental Design

The experiment utilized a randomized complete block design of three replicates. Four stocking rates (treatments) were tested: 1) normal stocking rate (as the experimental control) of 1.6 ha (4 ac)/AUM, 2) twice the normal stocking rate at 0.81 ha (2 ac)/AUM, 3) four times the normal stocking rate at 0.4 ha (1 ac) AUM, and 4) eight times the normal stocking rate at 0.2 ha (0.5 ac)/AUM. The treatments were first applied in August 1987 and again during August in 1988 and 1989. This timing allowed pre-treatment measurements of sagebrush canopy cover and herbaceous production to be taken. It also provided maximum forage production to be reached to sustain the unusually high stocking rates. Each block was stocked with 10 cow-calf pairs (AU's). This allowed treatment application to be accomplished in 15 days, thus avoiding complications that might have been encountered over a longer time with less cattle. Following the initial treatment in 1987, no additional grazing was allowed on the study area through the conclusion of the study after the summer of 1990.

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Before treatment application within each treatment replicate, 15.24 m (50 ft) transect lines (Canfield 1941) were randomly placed to determine Wyoming big sagebrush crown cover by line intercept. Data were taken in 3 cm units (0.1 ft). Openings in the line canopy larger than 3 cm were recorded as non-sagebrush intercepts.

In August 1990, one year after the last grazing treatments concluded, the study was photographed from the air. A Cessna 150 with a camera system utilizing a Hasselblad EL/M camera with 70 mm backs was used. Color infrared images were taken with Kodak Aero-Ektachrome film, type 2443, with the aid of a Kodak Wratten number 15 filter. Photo flights were made at 340 m above ground level, providing a scale of 1:6500. Thus, canopy coverage of Wyoming big sagebrush was measured one year after the final grazing treatment was applied by sampling each entire treatment plot with aerial infrared photographs. The photographs were projected to an image size of 2 m^2 and sampled with a dot grid. The number of sagebrush hits with the grid was divided by the total number of dots falling in the treatment to arrive at a percentage canopy coverage remaining following the three years of treatment.

Production data were obtained by clipping 0.5 m^2 circular plots (Wambolt and Payne 1986). They were randomly placed on diagonal lines beginning and ending no closer than 10 m from the treatment corners. The centers of the 0.5 m^2 plots were located no closer than 2 m apart to avoid disturbances of plants when clipping adjacent plots. In addition, records were kept to avoid reclipping the same 0.5 m^2 areas. Plant material was oven dried at 65 °C for 1 week before weighing. All measurements were taken as close to the peak of standing crop production as practical. Numbers of transects and plots were determined through adequacy of sample tests.

Analysis of variance was used to evaluate relationships among production means of perennial grasses, total herbaceous vegetation, and sagebrush canopy cover in the different stocking rate treatments. The Least Significant Difference (LSD) method ($P<0.05$) protected by a prior F-test ($P<0.05$) was used for comparing treatment means.

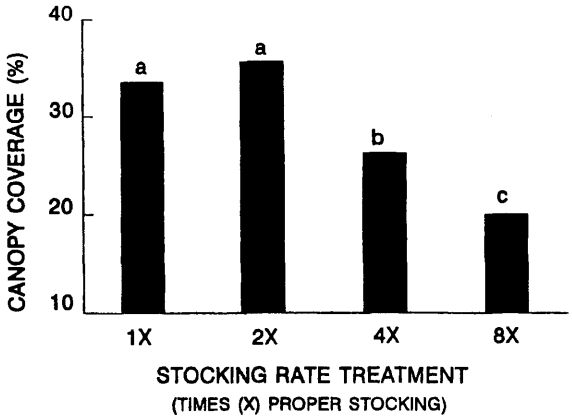

Figure 1—Wyoming big sagebrush percent canopy cover means by treatment (stocking rate) one year after the final treatments were applied. Means differ ($P<0.05$) when bars have a different letter.

Figure 2—Trampling effect on Wyoming big sagebrush stocked at eight times normal for one year on near side of portable electric fence.

Results and Discussion

We accepted our first hypothesis, that high stocking rates will reduce Wyoming big sagebrush cover. Sagebrush cover was equal throughout the study area before initiation of the grazing treatments. Over the three year study the heavier cattle stocking rates of four and eight times normal significantly ($P<0.05$) reduced sagebrush canopy cover (fig. 1). The eight times normal stocking rate was significantly ($P<0.05$) more effective than any other treatment. Most damage was from trampling (fig. 2), but some browsing was observed.

The second hypothesis, that any reduction in sagebrush cover from high stocking rates will increase understory production, was rejected. The reduction in sagebrush canopy with heavy stocking rates did not result in increased understory production that was equal throughout the study area before any treatments were applied. Perennial grasses were equal in all treatments one year after the third and final heavy stocking treatments were applied (fig. 3). The two, four, and eight times normal stocking rates resulted in less total herbaceous production than the normal stocking used as a treatment control (fig. 4).

Our results were not unexpected based on the experiences of others. Anderson and Holte (1981) in southeastern Idaho assessed changes in the big sagebrush type after 25 years of grazing exclusion. Cover of perennial grasses increased exponentially, from 0.28% to 5.8% in the 25-year period. However, during that period, shrub cover increased 154%, almost entirely due to changes in big sagebrush. The increase in grass cover was not at the expense of the big sagebrush dominated overstory. Mueggler and Blaisdell (1958) compared the sagebrush control techniques of burning, rotobeating, spraying, and railing. They found that regardless of treatment, total vegetal production three years after treatment was still considerably less than on untreated

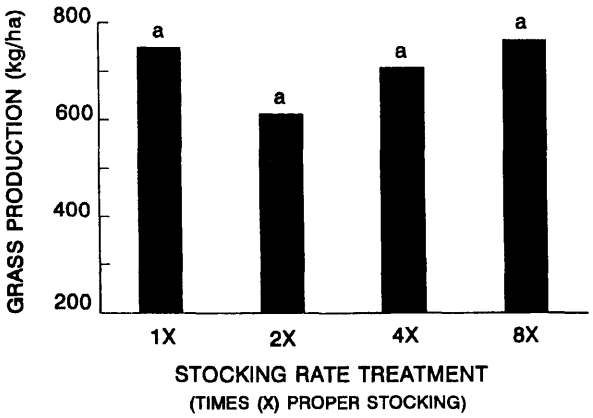

Figure 3—Production (kg/ha) means of perennial grasses by treatment (stocking rate) one year after the final treatments were applied. Means differ ($P<0.05$) when bars have a different letter.

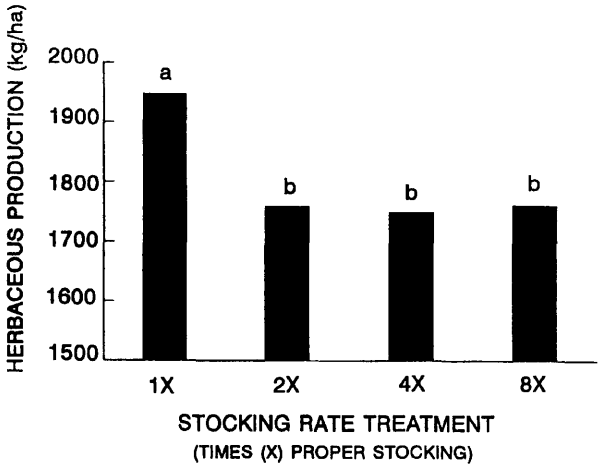

Figure 4—Production (kg/ha) means of total herbaceous vegetation by treatment (stocking rate) one year after the final treatments were applied. Means differ ($P<0.05$) when bars have a different letter.

areas. Harniss and Murray (1973) also concluded that sagebrush must utilize resources that are not available to other species because maximum vegetal production results when sagebrush is present. Harniss and Murray (1973) also noted the importance of post-treatment grazing practices.

Conclusions

Cattle stocking rates up to eight times normal will reduce Wyoming big sagebrush canopy cover, primarily through mechanical damage, with some browsing.

No increase in herbaceous forage species will result from reduced sagebrush canopy cover induced by heavy stocking.

Habitat quality is reduced for wildlife benefitted by sagebrush following heavy stocking.

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Management and Use of Browse in the Edwards Plateau of Texas

Stephan A. Nelle

Abstract—Range management in Texas has enjoyed a long and rich past with many noteworthy accomplishments. These efforts have been aimed primarily at improved management of grasslands and control of noxious woody plants. Desirable forage-producing woody plants are an unrecognized resource, and the management of shrublands as a valuable resource is a heretical concept to many range professionals. The lack of concern for and management of this resource has caused the higher quality forage plants to decline or disappear from many ranges and the lower quality forage plants to proliferate to problem levels. Basic range management principles adapted to woody plants can be used to help restore deteriorated shrublands and manage them as a renewable and sustainable resource.

The Edwards Plateau is one of the ten ecological regions of Texas. The 24 million acre region lies in the central and southwestern portion of the state and is dominated by shallow, rocky soils over fractured limestone. Average annual rainfall ranges from 12 inches in the west to 32 inches in the east. The region is mostly privately owned native rangeland. The rural agricultural economy is based on livestock ranching and lease hunting for white-tailed deer.

Ecologists are divided about the historic extent of trees and shrubs in the region prior to European settlement (Weniger 1984). Historical accounts can be found to support the notion that the region was a grassland with only scattered areas of woody vegetation. Other accounts are used to contend that the area was a shrubland-woodland with a herbaceous understory and scattered open prairies. Regardless of the composition of the historic landscape, the region has been dominated by woody plants for at least the past 50 years. Annual production of leaves and twigs of woody plants is commonly in the range of 500 to 2000 pounds per acre and often exceeds the production of grass and forbs.

Of the 200 native species of trees, shrubs and woody vines in the region, about 60 are common and comprise the bulk of the browse resource. The traditional simplistic view of land management in the region is that woody species have invaded productive grasslands and need to be controlled. A more realistic viewpoint is that all woody plants cannot be lumped together under the category of "noxious brush." Only about 10 species are invasive plants which cause problems and for which control may be justified. The others range from harmless to highly desirable from a ranching point of view.

Ungulates which rely upon browse for a significant part of their diet are the primary rangeland consumers of the region. Texas has more goats, sheep, deer and exotic wild ungulates than any other state. The majority of these animals within Texas are produced in the Edwards Plateau. With the combined population at about four million (Findley 1994; Traweek 1989; Karns 1993), the average density of these animals in the region is one per six acres. On many ranches their density equals or exceeds one per three acres. This region has the heaviest concentration of shrub-eating animals in the United States.

Principles of Browse Management

Despite the abundance of browse plants and browsing animals, little or no research has been conducted in the region which can be used as a basis for management. The management principles outlined here are based on observation, experience, studies from other regions, and the application of basic range ecology principles to browse.

Selectivity

Animals selectively browse some plant species in preference to others. Over a period of years, this uncontrolled selectivity will eliminate the best browse plants and favor the increase of less desirable browse plants. This is one important reason why some woody species such as junipers have developed into major brush problems, while other species have almost disappeared. This order of selection is somewhat predictable and enables managers to group woody plants into four categories of preference (table 1).

Class I plants are highly preferred. They often show heavy use and poor reproduction even with only moderate numbers of browsing animals. Although Class I plants are very nutritious and palatable, they are normally so scarce that they do not contribute significantly to animal diets.

Class II plants are moderately preferred. Under proper management, this class of plants can contribute significantly to animal diets. On ranches with excessive numbers of goats and/or deer, these plants will be heavily used, in poor vigor, and will not be successfully reproducing.

Class III plants are not preferred in relation to Class I and II plants. They are abundant on many ranches and often make up the bulk of the browse diet. The nutritional quality provided by these plants is frequently below optimum for browsing animals.

Class IV plants are aversive to browsing animals. They are the last to be used and will only be consumed in quantity

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when little else is available. When these plants show significant use, it is a sign of severe browse deterioration. These are the species that often become brush problems. Since they are not readily consumed, they have a competitive advantage and often reproduce with abundance.

Table 1—Common woody plants of the Edwards Plateau by class.

Class I	Kidneywood (*Eysenhardtia texana*)
	Littleleaf leadtree (*Leucaena retusa*)
	Texas sophora (*Sophora affinis*)
	Carolina buckthorn (*Rhamnus caroliniana*)
	Mountain mahogany (*Cercocarpus montanus*)
	Texas mulberry (*Morus microphylla*)
	White honeysuckle (*Lonicera albiflora*)
	Texas oak (*Quercus texana*)
	Black cherry (*Prunus serotina*)
	Hawthorne (*Crataegus crusgalli*)
	Rusty blackhaw (*Viburnum rufidulum*)
	Inland ceanothus (*Ceanothus herbacea*)
Class II	Hackberry (*Celtis reticulata*)
	Cedar elm (*Ulmus crassifolia*)
	Bumelia (*Bumelia languinosa*)
	Clematis (*Clematis drummondii*)
	Roemer acacia (*Acacia roemeriana*)
	Redbud (*Cercis canadensis*)
	Grapevine (*Vitis* sp.)
	Virginia creeper (*Parthenocissus quinquefolia*)
	Greenbriar (*Smilax bona-nox*)
	Carolina snailseed (*Cocculus carolinus*)
	Poison ivy (*Rhus toxicodendron*)
	Western soapberry (*Sapindus drummondii*)
	Elbowbush (*Forestiera pubescens*)
	Netleaf forestiera (*Forestiera reticulata*)
	Ephedra (*Ephedra antisyphyllitica*)
Class III	Live oak (*Quercus virginiana*)
	White shin oak (*Quercus durandii*)
	Vasey shin oak (*Quercus pungens*)
	Skunkbush sumac (*Rhus trilobata*)
	Evergreen sumac (*Rhus virens*)
	Flameleaf sumac (*Rhus copallina*)
	Littleleaf sumac (*Rhus microphylla*)
	Hogplum (*Colubrina texensis*)
	Feather dalea (*Dalea formosa*)
	Catclaw acacia (*Acacia greggii*)
	Peachbrush (*Prunus minutiflora*)
	Fourwing saltbush (*Atriplex canescens*)
Class IV	Blueberry cedar (*Juniperus ashei*)
	Redberry cedar (*Juniperus pinchotii*)
	Mesquite (*Prosopis glandulosa*)
	Mountain laurel (*Sophora secundiflora*)
	Catclaw mimosa (*Mimosa biuncifera*)
	Lotebush (*Zizyphus obtusifolia*)
	Condalia (*Condalia* sp.)
	Javelinabush (*Microrhamnus ericoides*)
	Agarita (*Berberis trifoliata*)
	Texas persimmon (*Diospyros texana*)
	Whitebrush (*Alloysia lycoides*)
	Wolfberry (*Lycium berlandieri*)
	Pricklyash (*Xanthoxylem clava-hercules*)
	Mexican buckeye (*Ungnadia speciosa*)

One important principle to apply to the concept of preference and selectivity is that availability dictates consumption. If there are no Class I or II plants available, then Class III plants become the most preferred class by default. Exceptions to the general order of preference do occur, especially seasonally. Preference also occurs within each class although much less predictably.

Degree of Use

Woody plants, like all other plants, respond to different levels of utilization or leaf removal. Browse plants remain healthy and productive when they are browsed moderately. The old range management principle "Take Half and Leave Half" is a good rule of thumb for browse. This ensures adequate photosynthetic leaf surface to convert sunlight to plant energy. At this moderate level of use, browse plants are a totally renewable and sustainable forage resource.

When browse plants are heavily used for prolonged periods, they will loose vigor, decline in productivity, and cease to successfully reproduce. With insufficient leaf surface to maintain itself, weakened plants are more vulnerable to drought and other stresses and will die prematurely.

Use of browse is expressed as the percentage of current years growth of available leaves and twigs removed by browsing animals. Browse use is divided into three categories:

Light use	0 - 40%
Moderate use	40 - 65%
Heavy use	65 - 100%

Light use does not allow for the most efficient use of the forge resource since much browse goes unused. Light use of Class I, II, or III plants is seldom seen on ranches with moderate numbers of goats or deer. Light use is recommended to allow formerly heavily used browse to recover, to maximize woody cover for wildlife, or to provide maximum selectivity and maximize animal nutrition.

Moderate use should be the management goal for sustained browse production and is compatible with good livestock production, good wildlife production and good ecosystem health.

Heavy use of browse will result in loss of vigor and production and will suppress reproduction. Heavy use is not compatible with good livestock or wildlife production or with ecosystem health.

Degree of use will vary within a pasture between plant species. With moderate use on Class III plants, most Class II plants will be heavily used and most Class IV plants lightly used. The manger must decide which group of plants he wishes to base management on.

Rest Periods

Periodic rest from livestock browsing is important for proper browse management. Rest periods allow the most preferred plants a time for recovery between browsing periods. This also allows flowering, seed maturation, and a better chance for seedling establishment than continuous browsing. Rest periods are best provided by some kind of

planned grazing system where a herd of livestock is rotated among two or more pastures.

The key to the success of a grazing system for browse is the frequency and length of rest periods. Rest should be provided at least once every one or two years. The length of rest should be four to six months. Since browse grows and responds slower than grass, rest periods must be longer than used for grass dominated grazing systems.

Even when goats or sheep are moved out of a pasture for a rest period, deer continue to browse and are in fact attracted to a rested pasture. So, rest periods are actually only a time of reduced browsing, not a complete rest. Where deer numbers are very high, rest from livestock browsing may not accomplish the desired results. Deer numbers must then be significantly reduced to allow proper management of the browse resource.

Figure 1—The natural growth form of live oak and most other woody species in the region.

Reading Browse Signs

The current condition of the browse resource is the result of how it was managed in the past. An accurate history of the management of shrublands can be determined by learning how to read several key browse signs. Managers must be able to recognize these signs of past use in order to assess the condition of the resource and determine needed management.

Hedging

Hedging is the growth form of woody plants that develops over a period of years when terminal twigs are browsed causing lateral twigs to develop. As the lateral twigs are browsed, a compound, multi-branched twig arrangement develops.

Moderate hedging is not harmful to a plant if adequate leaf surface is retained. Moderate hedging keeps more of the production within reach of animals.

Severe hedging creates a network of short stubby branches with limited leaf production. Severe hedging signifies poor plant vigor and greatly decreased browse production. Severely hedged shrubs often have dead or dying twigs and branches, limited flowering and fruiting, and greatly reduced leaf size.

Figure 2—Prolonged heavy use has greatly reduced the vigor and production of lower branches of live oak.

Browse Lines

The natural growth form of most woody species in the region is shrubby with branches, twigs and leaves near ground level as well as in the upper canopy (fig. 1). Browse lines develop on taller shrubs and trees subjected to heavy browsing by the removal of branch, twig and leaf production within reach of animals (fig. 2). The progressive pruning and reduction of low-growing branches is how browse lines begin. As they worsen, lower branches die and are broken off. Distinct browse lines signify long-term heavy use of the species and little or no production within reach of animals (fig. 3). The height of a browse line varies with the animal. White-tailed deer normally browse to only a three or four foot height. Goats can browse up to four or five feet in a bipedal position. Certain large exotics can browse to a six foot height or more.

Figure 3—Pronounced browse lines signify long-term heavy use of live oak with little or no available production.

Unlike severe hedging where the entire plant is threatened, browse lines only affect the lower part of the plant. The upper canopy and the shrub itself will remain healthy since much of it is above browsing height. Although the plant remains healthy, it is not producing browse which is available to animals. Furthermore, seedling recruitment is limited even though the plant may be producing abundant seed.

Reproduction

Adequate reproduction does not occur on heavily browsed species. A lack of seedlings and young plants signifies that the species may not be perpetuating itself and is therefore in decline even though there may be an abundance of mature plants. Fortunately, many species in the region are root sprouters, and vegetative reproduction is possible even if sexual reproduction is not. Excessive reproduction of Class IV plants and inadequate reproduction of Class I and II plants is the rule over most of the region.

Animal Condition

The physical condition of animals is another sign that can be used to assess browse condition. Since deer rely on browse more than any other animal and are seldom maintained with supplemental feed, deer performance is a good secondary indicator for managers. Average fall fawn crops below 50%, field dressed weights of mature does below 60 pounds, mature bucks below 100 pounds, and an abundance of spikes indicate poor nutrition and poor browse condition.

Putting Principles into Practice

The principles of browse management although not highly scientific nor proven by research can be used to improve shrubland ecosystems both ecologically and economically for both ranchers and society.

Recovery of Deteriorated Browse

When signs of past heavy browse use are evident, especially on Class III and IV species, and the manager desires improvement, drastic measures must be taken and a long term commitment made. If browse has been heavily used for many years, a long initial rest of one to three years from all goat grazing and a drastic reduction in deer numbers may be needed. Browse lines will begin to fill in with growth from basal sprouts or root sprouts (fig. 4). Following the extended rest, proper stocking rates to achieve moderate use must be established and a grazing system initiated to provide needed rest periods. In general goats should not make up more than 50% of the stocking rate.

Stimulating Browse Production

On ranges where the basic resource is stable and the manager desires to stimulate increased browse production, several options exist. The basis behind stimulating browse production is mostly a matter of changing its growth form to make it more accessible to animals. Physical damage to the top growth of most species will cause prolific basal or root sprouting. This damage can be caused mechanically (chaining, roller chopping, dozing or firewood harvest) or with fire (fig. 5). These practices often increase the availability of browse five to ten fold.

Another excellent way to increase browse production is to selectively remove competing Class IV brush species which can dominate a site to the detriment of better species. Selective dozing, individual plant treatment with herbicides or hand cutting of non-sprouting blueberry cedar are all used to control brush species and release better browse species. Periodic prescribed fire is needed to control cedar seedlings before they get too big and to keep sprouting species such as oaks within browsing height.

Figure 4—Deteriorated browse will recover with proper rest periods and moderate use. Root sprouts of live oak will fill the void below past browse lines.

Figure 5—Browse stimulation can be accomplished by firewood harvest or prescribed burning, which converts taller trees to shorter shrubs.

Biological Control of Shrubs

The intentional use of goats to control or suppress woody plants has been widely employed. Because of the notion that invasive shrubs destroy grasslands, the use of shrub eating animals is appealing to those who want to convert shrublands to grasslands. Goats are called by some "environmentally friendly" or "natures herbicide" with the perception that they control undesirable brush, help restore grasslands and reduce the use of herbicides. Heavy stocking rates of goats will control or suppress Class I, II and III plants very effectively. Control of Class IV brush species is much less effective and is difficult to achieve without abuse to the entire vegetative resource.

Conclusions

The Edwards Plateau is a region with a rich diversity of mostly desirable woody plants which can be managed for long-term sustainability. Ranching can remain profitable and ecologically sound when both the grass and shrub communities are properly managed. Both grazing and browsing animals belong in the region in proper numbers balanced to the forage resource. Woody plants, long considered a problem in need of control can also be considered an asset in need of wise management.

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Restoration of Native Shrubland in a Military Training Area Using Hand-Broadcasting of Seed

Dana L. Quinney
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Abstract—The Idaho Army National Guard trains on the Orchard Training Area, 55,848 hectares of BLM shrub-steppe in southwestern Idaho. Historically, grazing, wildfire, and military training have converted thousands of hectares of big sagebrush into stands of exotic annuals. Other areas remain in good condition. Hand-broadcasting of sagebrush seed can introduce "source islands" of shrubs into areas where sagebrush has been removed by fire.

In the Orchard Training Area, fires caused by lightning, railroad traffic, military training, and arson, have burned thousands of hectares of native shrub-steppe during the past fifteen years; most significant burns occurred in the early 1980s (Boise District, U.S.D.I. Bureau of Land Management unpublished fire data). To determine which species to plant at which sites, various sources are used, including A Grazing History of Southwestern Idaho (Yensen 1980) and a set of vegetation maps with an accompanying report and plant transect summaries, produced by Boise District Bureau of Land Management biologists in 1981. In this effort, vegetation polygons in the Snake River Birds of Prey Area greater than 16 hectares were mapped, ground-truthed, and sampled (Quinney and others, Boise District BLM, unpublished report, maps, and data). When possible, ecotypic seed is collected in the training area; otherwise, commercial seed is used. Since 1988, several thousand hectares have been planted to native shrub, grass, and wildflower species.

Vegetation restoration in the southwestern Idaho desert poses a challenge. Because of the fine, friable soils; low, irregular precipitation; multiple land uses; and exotic weeds; traditional seeding methods may fail.

Every land manager who has seeded into desert environments has encountered the problem of "good year for seed, bad year for planting." With sagebrush and some other Great Basin natives, seed must be planted before viability is lost, regardless of the precipitation. Also, in the authors' experience, mechanical disturbance of the soil surface by some seeding equipment may result in invasion of exotic annuals, and/or destruction of the cryptogamic soil crust and consequent wind erosion.

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The authors decided to try hand-broadcast seeding as a low-impact method of creating "source islands" of big sagebrush in large wildfire burns dominated by *Poa secunda*, *Poa secunda* and exotic annuals, or exotic annuals only. The seeding sites were areas where few or no native shrubs had been present for fifteen years or more (Quinney and others, unpublished report, maps, and data, Boise District BLM; personal observation), indicating that natural restoration was very slow or absent. Hand-broadcasting made it possible to seed into the most promising microsites present (drainage draws, snowdrifts, and the like), taking advantage of pockets of soil moisture, with little soil disturbance.

Methods

Twelve sites in Ada County, Idaho, were hand-broadcast with commercially obtained Wyoming big sagebrush seed during the winter of 1992-1993. These sites were small (six or fewer hectares). The sites were not exclosed from military training and are grazed in spring and fall by sheep and/or cattle. All sites supported Wyoming big sagebrush communities in 1979, according to the BLM maps and transect summaries identified above (Quinney and others, Boise District BLM unpublished report, maps, and data). Seeding of each site was accomplished in from one to three hours by one or two people. Seeding rates at each site are shown in figure 1. Rates are approximations derived from driving or walking the perimeter of the seeded sites with a global positioning system to determine the area, and dividing the number of pounds of seed (PLS) used at the site by the number of hectares; seed distribution within a site was not uniform.

SITE	CURLEW	VALLEY	LITHO	OBSIDIAN	PIT
LBS/HECTARE	1.98	2.69	3.29	2.96	1.65
PLANTS/METER^2	43	28	52	33	59

Figure 1—Seeding rates and densities of *Artemisia tridentata* for five sites in the Orchard Training Area, Idaho.

Hand broadcasting of seed creates irregular, ribbonlike bands of seedlings. These irregular bands are difficult to sample with straight-line transects. A modified Daubenmire (1979) method of canopy coverage sampling was used. An arc-azimuth method was used to lay out sampling transects on bands of seedlings, allowing for random placement of the measuring frame within a degree arc the width of the band at the distance where the next measurement was to be made. After the point of origin of each transect, a measuring frame was dropped and read at five-meter intervals. The location of the next measuring frame was five meters from the previous one, centered about a point perceived by using a sighting compass at the previous frame-center point and determining the arc of seedlings. Then, from a random-number table, the first number that fell within this degree-arc was chosen as the center point for the next frame. Frame center points were marked with 45-cm steel rods. At each site, four 20-frame transects were established, two in seedling bands and two control transects in unseeded interspaces. Five of the twelve sites, Curlew, Valley, Lithophragma, Obsidian, and Pit, were monitored in 1995.

Within each frame, the following percents canopy cover were estimated: cover for each vascular plant species, cryptogamic cover, grass litter, forb litter, shrub litter, cow/sheep litter. Stem ground cover was also estimated. Within each frame, big sagebrush individuals were counted and their heights recorded to the nearest half-centimeter. Two photographs were taken from a fixed height and location at the first frame of each transect, a frame vertical and a panorama. Annual monitoring of the sites is planned.

Four sites had an understory of *Poa secunda*. One site, Pit Road, had little grass, but an abundance of annual weeds, including *Ranunculus testiculatus* and *Lepidium perfoliatum*. Hand-broadcasting of sagebrush seed was successful on all sites, regardless of the presence, absence, or dominance of the site by native perennial *Poa* (fig. 2).

Results

Preliminary results indicate that hand-broadcasting of big sagebrush can be a viable restoration procedure in the southwestern Idaho desert. Sagebrush broadcast seedings can produce seedlings in areas dominated by weeds, and also in areas dominated by Sandberg's bluegrass (fig. 2). Hand-broadcasting of sagebrush into small sites is economical, does not disturb the soil, and can succeed in dry years because the most favorable microsites can be seeded.

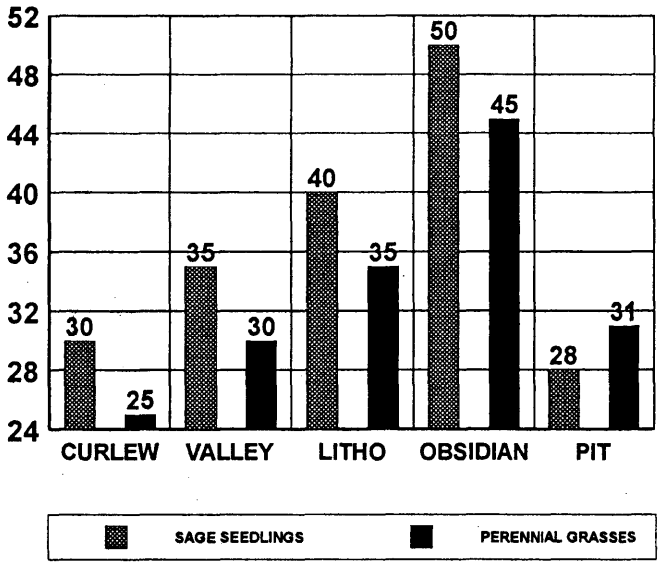

Figure 2—*Artemisia tridentata* seedling density and canopy cover of native perennial grasses for five sites in the Orchard Training Area, Idaho.

Since sagebrush transects were placed only within bands of seedlings, of course, only areas where seedlings appeared were sampled. Control transects characterize the sites' vegetation where no seedlings occurred. Preliminary results indicate only that big sagebrush seedlings did appear in the areas seeded. Subsequent annual monitoring will evaluate the success of this method of shrub restoration through time.

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Nurse Plant Associations in the Chihuahuan Desert Shrublands

Jamey Thompson
Laura F. Huenneke

Abstract—Spatial studies in the Chihuahuan Desert of associations with *Larrea* shrub islands found juveniles more often associated with shrub islands than unassociated. The spatial structure of the shrub islands points to Nurse Plant facilitation of seedlings. Experiments tested the effects of canopy, shrub islands, and understory on five perennials' germination. Longer survival times, but not higher germination, of *Zinnia acerosa* were found beneath artificial canopies in intershrub areas and cleared shrub islands as compared to intact shrub islands. Therefore, *Zinnia* may be a poor competitor, preferring germination microsites with few competitors, regardless of Nurse Plant effects.

It is often suggested in arid and semiarid environments, that adult plants facilitate germination and establishment. This idea is commonly called the Nurse Plant Hypothesis (Went 1942; Nabhan 1975; Nobel 1980; McAuliffe 1984a; Carlsson and Callaghan 1991; Cody 1993). Many seedlings in arid and other zones can be found associated either directly under (Nobel 1980) or near the canopy of adult plants (Carlsson and Callaghan 1991; Aguiar and Sala 1992; Belsky 1994). The mechanisms of these associations are often not known, but are usually credited to physical or biotic facilitation provided by the "safe sites" of the Nurse Plant as compared to other microsites (Fowler 1986a, 1986b; Huenneke and Sharitz 1986; Fowler 1988; Scherff and others 1994). These cited physical facilitations include: increased nutrient levels (Vetaas 1992; Belsky 1994), decreased soil temperatures (Nobel 1980), and increased soil moisture (Nobel 1980; Belsky 1994), all compared to areas outside of the Nurse Plant's influence.

On shrub islands in arid zones, the gradients of soil parameters such as carbon, nitrogen, and moisture shift dramatically across centimeters (Charley 1972; Charley and West 1975; Jackson and Caldwell 1993). The microsites provided by these putative Nurse Plants have higher nutrient levels (Vetaas 1992), translating into higher productivity for associated plants (Tiedemann and Klemmedson 1973; 1977; Kellman 1979; Escudero and others 1985; Georgiadis 1989). These nutrient differences are primarily limited to the top of the soil horizon where adult roots are rare (Charley and West 1975; Freckman and Virginia 1989; Franco and others 1994). The Nurse Plant's canopy also has a strong influence on the soil temperature beneath it (Miller and Stoner 1987). Evaporation and transpiration are decreased at lower soil temperatures by the ameliorating effect of the canopy (Tiedemann and Klemmedson 1973, 1977; Nobel 1980; Belsky 1994; Montaña 1994).

At best, though, Nurse Plant relationships are commensalistic for the seedling; at worst the seedlings compete with the adult plant for scarce resources. In arid zones, water stress can be the most limiting factor for plants, especially for seedlings' shallow roots (Leishmann and Westoby 1994). The shallow rooting structures of seedlings compete not only with other seedlings (Eldridge and others 1991; Aguiar and Sala 1994; Leishmann and Westoby 1994), but also with the shallow roots of the adult plant (Tiedemann and Klemmedson 1977; Aguiar and Sala 1992; Belsky 1994).

Larrea dominate creosote (*Larrea tridentata* [D.C.] Cov.) communities in southern New Mexico, complemented by a diverse, spatially associated mix of shrubs, succulents such as prickly pear cacti (*Opuntia* spp.), and annuals. Perennial grasses often sparsely populate large intershrub areas, which have lower soil nutrient moisture levels as compared to the shrub islands (Schlesinger and others 1990). The climate is typical of the Chihuahuan Desert, with irregular spring rains and seasonal storms in the summer (Conley and others 1992).

The spatial structure of the *Larrea* shrub islands points to possible Nurse Plant facilitation of seedlings. To test this possibility, germination trials were conducted under a split-plot design to test the effects of 1) canopies 2) shrub islands and 3) understory on germination. Main factors that influence germination include light, water, and nutrients. Light is generally not considered a limiting factor in the desert, especially under the open canopies of *Larrea*. If the main limitations to germination and establishment are soil temperatures and nutrient levels, then an artificial shrub canopy or increased nutrient loads respectively should stimulate seeds to germinate. However, if the main limitation to germination and establishment is soil moisture, then the absence of other seedlings should increase germination and establishment.

Materials and Methods

Site Description

The experiments were conducted on the New Mexico State University College Ranch near the Jornada Experimental Range, 37 km NNE of Las Cruces, New Mexico. Creosote (*Larrea tridentata* [D.C.] Cov.) and mesquite (*Prosopis glandulosa* Torr.) dominate the shrub community, with a mix of perennial shrubs, subshrubs, cacti, and herbaceous

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annuals making up the rest of the species. The site is on an alluvial wash of the Doña Ana Mountains, with alkaline soils and a shallow calcic horizon (Buffington and Herbel 1965).

Mean summer temperatures approach 40 C (Conley and others 1992), but during the study the June/July mean maximum temperature was near 43 C. Mean precipitation is 218 mm, with the bulk (> 120 mm) coming in strong thunderstorms in July, August and September, that begin July 4th ±14 days (Buffington and Herbel 1965). During the study summer the summer rains began on July 26th and brought 32 mm of rain at the germination site during July and August.

Shrub Island and Intershrub Area Criteria

The *Larrea* shrub islands that were chosen were mature enough to have few shallow roots (>1.5 meters tall) (Franco and others 1994), and at least 2 meters in diameter. Intershrub areas were paired with chosen shrub islands and were at least 4 meters in diameter and had all grass clumps and juvenile perennial plants removed. From the sample, we chose a random sub-sample of 48 intershrub areas and 48 shrub islands. The sample of randomly chosen shrub islands was nearly uniform in size and understory species composition.

Shelters and Seed Cages

Two experiments on seedling germination were conducted. The first experiment was a factorial of four treatments with eight replicates each testing the effects of shrub islands and intershrub areas on germination and establishment. In this factorial, all shrub islands were treated by removing all aboveground shrub and plant biomass on the shrub island. All intershrub areas were treated by removing all grasses and other plants within one meter of the center of the plot. Artificial canopies sheltered half of the shrub islands (SHR-Shade) and intershrub areas (ISA-Shade) while the other two treatments of the factorial were left uncovered (SHR-Open, ISA-Open). To simulate the shrub canopy, these shade canopies were constructed from 1 m^2 60% shade cloth (approximately the shade percentage of adult *Larrea;* V. Gutschick, pers. comm.) and held in place one meter above the plots. A second experiment of two treatments tested the effect of understory on germination. In the first treatment, the shrub canopy was left intact and all understory biomass was removed (No US); the other treatment was left entirely intact and served as the control for shrub islands in both experiments (SHR-Intact).

The experimental unit in both experiments was the seed cage. To test the differences in the microsites, seeds of five species (*Zinnia acerosa* (100 seeds), *Larrea tridentata* (50 seeds), *Prosopis glandulosa* (30 seeds), *Gutierrezia microcephala* (50 seeds), and *Opuntia imbricata* (50 seeds)) were dispersed on July 6th, 1994, in each 100 cm^2 seed cages. *Larrea*, *Prosopis*, and *Opuntia* were all scarified, either by acid or mechanically, before they were placed in plots.

Three major threats exist for seeds in the desert: ants, kangaroo rats, and wind or water movement. To exclude ants, an exclosure of 15 cm garden fencing formed a rectangle of 2000 cm^2 that was centered on the seed cage. The edging was coated with Tree Tanglefoot™, a commercial resin that traps insects. To exclude the kangaroo rats and bird predators, 50 cm high, 1-cm diameter chicken-wire exclosures surrounded the seed cages. Finally, to minimize seed movement due to water or wind, a 1 cm thick layer of common sand was spread over the plot after the seeds were dispersed.

The plots were monitored every three days from July 6th, 1994, until September 12th, 1994, and thereafter sampled every 21 days until early January 1995. A plastic overlay for each replicate allowed the location and survival of each seedling to be recorded. Data from these overlays were then translated into the survival curves for each species.

Microsite resource levels were measured for soil moisture and soil temperature. Soil moisture was measured gravimetrically once a week for 8 weeks from the time the seeds were sown on July 6, 1994 until late August 1994. Ten gram subsamples from the plots were dried until the weight varied less than 0.003 g from day to day. Soil temperature was measured using a thermocouple (Omega II) on six occasions (6 a.m. on July 14th, 1994, 12 p.m. on July 12th, 1994, 4 p.m. on July 6th, 1994, and 8 a.m., 12 p.m., and 4 p.m. on September 20th, 1994). Since the soil was variable across each plot, temperature readings were taken at a depth of 10 cm in the northwest and southeast corners in each plot and then averaged for the plot.

The temperature, moisture, and germination data were then compared with one-way GLM models using repeated measures analysis and contrasts (SAS 1994). Only *Zinnia* germinated, but had a non-normal distribution of germinants (but not survival of germinants). Tukey's transformation (sqrt[n + sqrt(n)]) shifted the data to normality. The analyses used one-way GLM models broken into three comparisons. First, the four treatment factorial was divided into presence/absence of shrub island and presence/absence of an artificial shade canopy and were then compared using repeated measures analyses. A second series of comparisons used one-way comparisons of artificial (ISA-Shade, SHR-Shade) and natural canopies (No US, SHR-Intact) and thirdly, understory (No US) and intact shrub islands (SHR-Intact).

Results

Resource Levels

Mean moisture content varied among treatments with the artificial shade treatments (ISA-Shade and SHR-Shade) having higher values than the naturally shaded treatments (table 1). These artificial shade treatments provided more soil moisture for potential germinants than these other treatments across the whole study. There was no difference in terms of soil moisture between intershrub areas and shrub islands or between artificial canopy and open treatments. Understory plants did increase soil moisture of shrub islands, but not significantly.

Time had a significant effect on soil moisture, most likely due to the lack of rainfall at the site. The only precipitation came during week four when the site received 32 mm of rain. The moisture means for week four show that there were higher levels of soil moisture with artificial shade canopies on week four compared to natural canopies (table 1, fig. 1).

Table 1—The effects of soil moisture on treatment. See text for details on comparison methods.

Time examined		Comparison	df	Mean square	F value	P<F
Entire study		Time	7	0.0441	216.35	0.0001****
		Time	7	0.0441	216.35	0.0001****
		Time*Shade	7	0.0009	4.43	0.0001****
		Time*Shrub	7	0.0001	0.16	0.9924
		Time*Shade*Shrub	7	0.0006	3.31	0.0023***
	Contrast:	Natural canopy/ Artificial canopy	1	0.0087	4.12	0.0435*
	Contrast:	No understory/ Intact shrub isl.	1	0.0018	1.15	0.2847
Week 4 only		Shade	1	0.0128	6.67	0.0155*
		Shrub	1	0.0004	0.28	0.6014
		Shade*Shrub	1	0.0078	4.42	0.0451*
	Contrast:	Natural canopy/ Artificial canopy	1	0.0155	7.38	0.0110*
	Contrast:	No understory/ Intact shrub isl.	1	0.0133	9.08	0.0093**

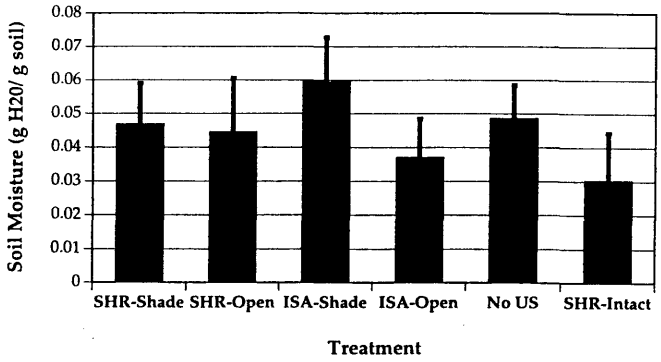

Figure 1—Soil moisture means after 32 mm of rain during the fourth week of the study.

Artificial shade treatments had higher soil moistures than unshaded treatments, but shrub islands were not different than intershrub areas, eliminating any retention effect by the higher levels of organic matter on the shrub islands. The interaction term of shade*shrub was significant, indicating that the combination of shade treatment with the absence of a shrub island (ISA-Shade) resulted in higher soil moisture than SHR-Open (fig. 1). There were positive effects on soil moisture of removing understory biomass, but overall, the artificial canopies produced the strongest effect on moisture levels.

Mean soil temperature did not vary among treatments as natural canopies and artificial canopies were not different, nor were there any effects of the understory on soil temperature (table 2). There were significant differences in soil temperature across time, primarily due to the inclusion of the July afternoon data. There was also an interaction of

Table 2—The effects of treatment on soil temperature. Comparisons follow method described in text.

Time examined		Comparison	df	Mean square	F value	P<F
Entire study		Time	5	42306.920	715.98	0.0001****
		Time*Shade	5	1076.718	18.22	0.0001****
		Time*Shrub	5	26.679	0.45	0.8117
		Time*Shade*Shrub	5	45.502	0.77	0.5726
	Contrast:	Natural canopy/ Artificial canopy	1	78.973	0.35	0.5529
	Contrast:	No understory/ Intact shrub isl.	1	2.870	0.01	0.9127
July afternoon		Shade	1	1278.443	46.59	0.0001****
		Shrub	1	37.719	1.37	0.2513
		Shade*Shrub	1	24.462	0.88	0.3554
	Contrast:	Natural canopy/ Artificial canopy	1	1178.032	40.71	0.0001****
	Contrast:	No understory/ Intact shrub isl.	1	11.390	1.19	0.2943

the artificial canopy treatments and time (shade*time) caused by the artificial canopy treatments were cooler over the whole study. Artificial canopy and open treatment did not differ, nor were there any differences between shrub islands and intershrub areas in terms of soil temperature across the whole study (table 2).

The average mean temperatures of each treatment through the different time periods show no difference except for the 4 p.m. readings in early July (fig. 2). The mean temperatures of the treatments on July 6th at 4 p.m. show higher values for the artificial shade treatments (ISA-Shade and SHR-Shade) as compared to both unshaded and natural canopy treatments (table 2). These two artificial canopy treatments were cooler than the rest of the treatments. The presence of an understory had no effect on soil temperature for shrub islands. Shrub islands were not different from intershrub areas, demonstrating that the results for soil temperature are the same as the results of the moisture data. The presence of an artificial canopy cooled the soil more than a natural canopy did.

Germination Trials

For *Zinnia*, the survival data were normal, but the number of germinants was not normal, so the number of germinants was transformed using Tukey's transformation (fig. 3). The results on the transformed germinant number show no differences (table 3). The Shrub/Shade comparison found an interaction of shrub*shade indicating that shrubs without canopies and intershrub areas with canopies had high germinant numbers. Survival was similar among treatments except for ISA-Shade (table 3, fig. 4). Germinants survived for a longer period of time in intershrub areas than on shrub islands, due primarily to the effects of the artificial canopy. This indicates that the lack of competition from juvenile and adult plants was the most important factor for survival and establishment.

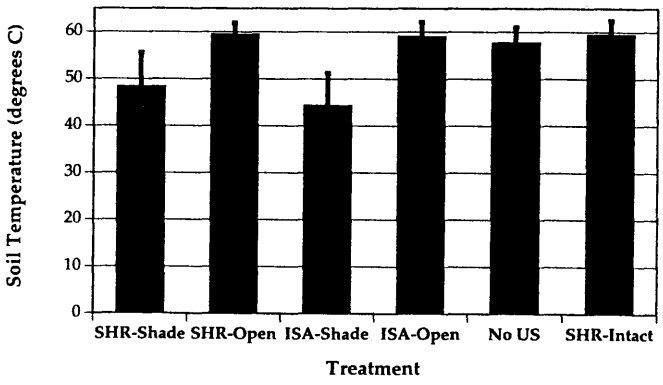

Figure 2—Soil temperature at 4 p.m. in early July. Note differences in shade treatments.

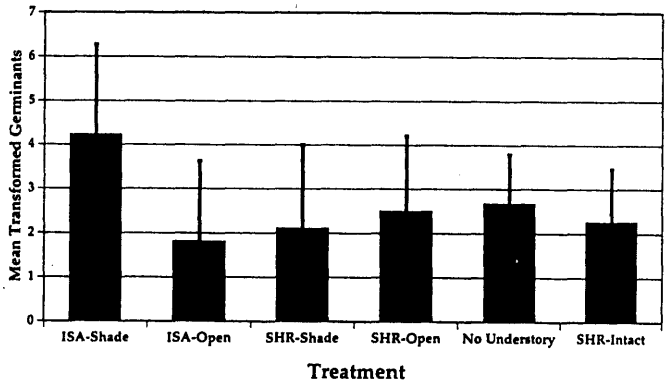

Figure 3—Mean number of germinants for each treatment.

Table 3—The effects of treatment on transformed germinant number and on survival. See text for details on comparison method.

Type	Comparison	Mean square	F value	P<F
Germinants	Shade	4.021	1.16	0.2918
	Shrub	7.934	2.28	0.1426
	Shade*Shrub	15.241	4.38	0.0458*
Contrasts:	Natural canopy/ Artificial canopy	4.673	0.96	0.3362
Contrast:	No understory/ Intact shrub isl.	0.676	0.50	0.4931
Survival	Shade	109.243	1.51	0.2847
	Shrub	1171.663	24.35	0.0001****
	Shade*Shrub	268.496	3.71	0.0552
Contrasts:	Natural canopy/ Artificial canopy	123.617	1.69	0.1946
Contrast:	No understory/ Intact shrub isl.	7.426	0.33	0.5675

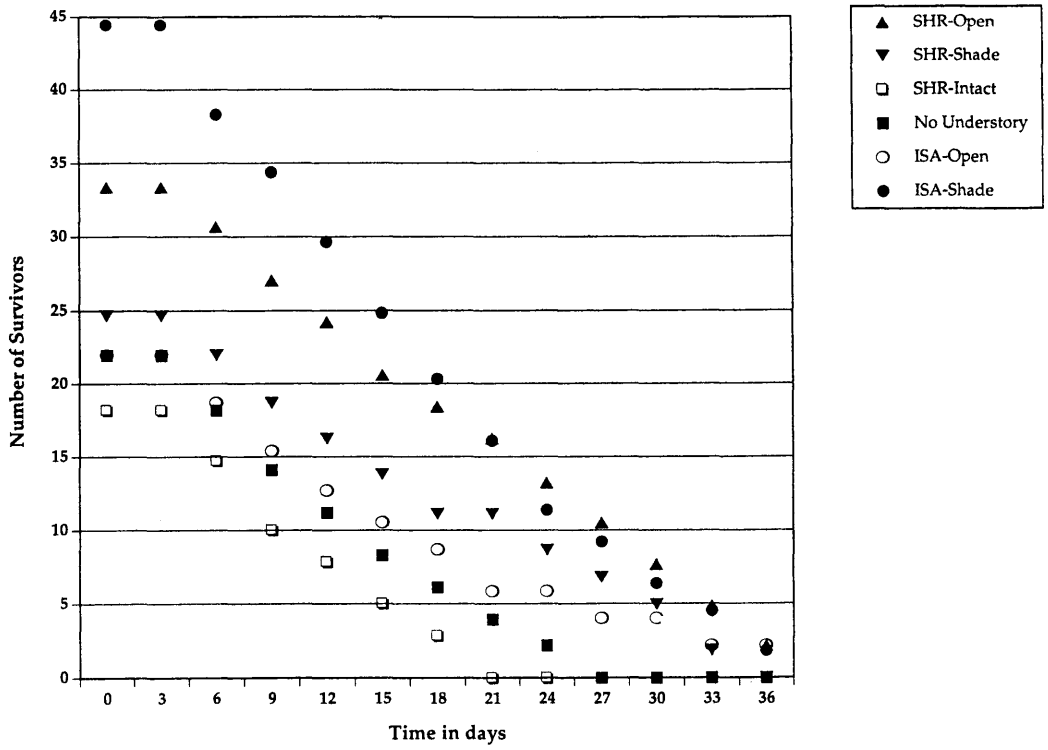

Figure 4—Survivorship curve for *Zinnia* germinants.

Discussion

Microsites and Resources

Subtle environmental differences in light and water strongly influence the germination of seeds in arid environments. Harper and others (1965) suggest that germination and early establishment may have the strictest requirements of all the lifestages of the plant in terms of nutrients and competition. The most important factors affecting soil moisture levels in deserts are root density (Fenner 1985; Franco and Nobel 1988) and soil temperature (Nobel 1984). Microsites that are exposed to direct solar input and those with shallowly rooted plants are less favorable to an arid environment seedling, since increased evaporation lowers soil moisture. Mesquite (*Prosopis*) and creosote (*Larrea*) are both dominant shrubs with strong shrub island associations in many Chihuahuan Desert communities, but both have relatively open canopies, limiting possible Nurse Plant facilitation (Bush and van Auken 1990).

Do Canopies Affect Soil Moisture and Temperature?

The artificial canopy treatments had higher levels of soil moisture compared to shrub canopies, since both ISA-Shade and SHR-Shade had significantly higher soil moisture levels over the whole study compared to the unshaded (ISA-Open and SHR-Open) and the naturally shaded treatments (No US and SHR-Intact). More moisture is available without competition for root uptake and without direct solar input evaporating the upper layers of the soil horizon. Previous work by Schlesinger and others (1990) measured soil moisture differences between *Larrea* shrub islands in intershrub areas and found a similar canopy shading effect on soil moisture. Belsky (1994) suggests that Nurse Plant effects should be more noticeable in more arid environments as the effects of shade on water relations become stronger.

The temperature data suggest that the most significant factor for soil temperature in different microsites could be the quality and density of the canopy shading the soil. For all time periods, both early and late in the summer growing season, the only difference in soil temperatures among treatments came at the daily high temperature early in the season (4 p.m. on July 6th). At this time, the artificial canopy treatments (ISA-Shade and SHR-Shade) were 10-15 C lower compared to the other treatments. This points to the possibility that the artificial canopies provided a different type of shading than did natural canopies. The open *Larrea* canopy permits larger amounts of direct sunlight compared to the more diffuse shadecloth, even at the same 60% total shading. This difference could eliminate comparison with a natural *Larrea* canopy, since the soil would receive alternate periods of direct sun and sharp shadow.

If the artificial canopy treatments provided more canopy shade than did natural ones, this points to a preferred microsite having the most canopy between the soil and the sun in times of peak temperatures. *Larrea* shrub canopies have never been studied for effects on germination, but some argue that *Larrea*'s canopy is too open to provide any substantive Nurse Plant effect on soil temperature. Juvenile columnar cacti in the Sonoran Desert associate with the nurse plant *Hilaria rigida*, a perennial grass which provides

a small, dense canopy (Nobel 1980; Franco and Nobel 1988; Cody 1993). The current data support McAuliffe, since the temperatures of the intact shrub (SHR-Intact) are not different than those of the intershrub areas (ISA-Open).

Do Shrub Islands Influence Germination?

There were no significant differences in germinant number among the treatments, but mean survival was lower for shrub islands compared to intershrub areas. In ISA-Shade, *Zinnia* survived longer with the higher moisture levels and lower temperatures than in the conditions of any other treatment. With the data for soil moisture and temperature included, this points to two possibilities: lower moisture and higher temperatures favor *Zinnia* germination or *Zinnia* is a poor competitor and favors more depauperate areas. The data refute the first possibility since none of the summer's germinants survived longer than 36 days in any treatment. As for the second possibility, *Zinnia* is a poor competitor for nutrients and water since ISA-Shade dominate the survival data compared to the shrub island treatments. Last summer, *Zinnia* survived longer in the more resource-limited, depauperate intershrub areas. It is possible that *Zinnia*'s preferred microsite is a young *Larrea* shrub island without a substantial understory. Thus, a *Larrea* shrub island would provide adequate shade for the germinants, lower soil temperatures through shading, but higher soil moistures in the absence of understory competitors.

Are There Nurse Plants in the Chihuahuan Desert?

There have been several studies of nurse plants in deserts of the Southwestern US and Mexico (Nabhan 1975; McAuliffe 1984b; Yeaton and Manzares 1986; Franco and Nobel 1988; Valiente-Banuet and Ezcurra 1991; Cody 1993), but all of them focused on succulents in the Sonoran and Mojave Desert. Shrubs and subshrubs in southern Mexico form shrub islands that structure the community spatially (Silvertown and Wilson 1994). Spatial studies in the Southwest US and Mexico have found that there is a significant focusing of productivity around shrub islands along with a range of interactions, from facilitation (nurse plants) to competitive inhibition (Charley and West 1975; Silvertown and Wilson 1994). Silvertown and Wilson (1994) concluded that *Larrea* served as a "focus shrub" with all other species occurring in association with *Larrea* in the southern Chihuahuan Desert. Other studies in the northern Chihuahuan Desert suggest that there are similar patterns for annuals focusing on *Larrea* and *Prosopis* in shrub communities (Lightfoot 1991).

Our results show a similar pattern of association. These results demonstrate only the shrub islands' effects impacting one species, *Zinnia*, and not surprisingly, suggest that it is a complex mechanism that determines the regeneration niche of that seedling (Grubb 1979). According to spatial studies, *Zinnia* associated with a *Larrea* shrub island more often than chance would allow. However, according to germination and resource data here, *Zinnia* seedlings survived longer in intershrub treatments with higher moisture, lower temperatures, and presumably fewer nutrients. This suggests that *Zinnia*'s survival may depend on a lack of competitors. Thus, the optimal association for establishment of a *Zinnia* is then a *Larrea* shrub island with few understory plants.

The germination study points to a variety of mechanisms that could account for the moisture and temperature data. The most obvious is a physical facilitation of soil factors. It is possible that there was some facilitation of soil factors by shrub islands such as more available moisture that gravimetric methods would not detect. It is also possible that any historic *Larrea* shrub islands' facilitation of *Zinnia* went undetected during the study due to unusual weather. Finally, it is possible that the observed *Zinnia-Larrea* spatial associations represent germination under different soil conditions (for example, higher moisture, lower soil temperatures) and consequent juvenile survival that is not dependent on shrub islands. A more complete picture of species' responses would involve examining the spatial association of *Zinnia* and understory plants around *Larrea* shrub islands during a summer with a more regular rainy season.

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Seed Germination Studies in *Atriplex confertifolia* (Torr. & Frem.) Wats.

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Abstract—Seed germination of *Atriplex confertifolia* (shadscale) has been studied sporadically since 1900, with little progress in understanding the mechanisms responsible for seed dormancy or in overcoming these obstacles for the purpose of successfully seeding shadscale in restoration projects. Most work has concentrated on the indurated bracteoles and their role in inhibiting germination, but no conclusive evidence has been presented to show that the bracts must disintegrate to allow germination. Experiments show that moist chilling of fresh seeds for 12 weeks allowed germination of up to 66 percent of fresh fruits and up to 85 percent of 3 year old fruits. No germination occurred in unchilled fruit. A preliminary trial showed increased germination with chill after 12 weeks afterripening at 50 °C. Retrieval experiments resulted in a mean germination (across all accessions) of 40 percent in the second spring after burial. No germination occurred in the first spring. After 4 years in the field, 40 percent of fruits were still alive but ungerminated. Germination in shadscale seeds appears to occur in a staggered fashion, suggesting the operation of multiple dormancy mechanisms.

Atriplex confertifolia (shadscale) is an important wildland shrub species in the Great Basin, on the Colorado Plateau, and in many arid parts of New Mexico, Arizona, and southern California (Sanderson and others 1990). Its range extends from Oregon south to Mexico and from California east to western Colorado and Wyoming. It grows in almost pure stands in many low-lying basins in Utah and Nevada, with sagebrush and winterfat at middle elevations and in mixed stands in pinyon-juniper woodlands. It is palatable to wildlife and livestock, even though spiny, but seems to be an increaser on moderately grazed rangelands (Blaisdell and Holmgren 1984). We have observed that intact shadscale stands seem to inhibit the encroachment of cheatgrass and other exotic annuals and are rarely able to carry wildfire. But shadscale stands are subject to dieoff, correlated with either extreme drought or extreme moisture (Nelson and others 1990), frequently resulting in the subsequent invasion of annual weeds such as halogeton and cheatgrass and a concomitant increase in fire frequency.

Shadscale is an important species for mine revegetation efforts. Efforts to regenerate this species by seeding in the Intermountain West have often met with failure due primarily to low or nonexistent seedling emergence (Bridges 1941; Stevens unpublished). Many laboratory germination tests confirm the failure of seed to germinate readily (Mikhiel and others 1992; Crofts 1977; Vest 1952). Utricle fill is often very low as well, which may contribute to these seeding failures. Therefore, it is important to understand seed dormancy mechanisms of shadscale before this species can be used successfully in revegetation or reclamation efforts.

Anatomy of the Shadscale Fruiting Structure

The fruit of shadscale, as in all chenopods, is known as a utricle. It is subtended by two bracteoles (hereafter referred to simply as bracts) that are derived from leaf tissue and fused almost completely around the fruit. Many species of *Atriplex* have utricles only loosely enclosed by the bracts. Some authors have mistakenly identified the bracts as the pericarp (Warren and Kay 1984; Lailhacar-Kind and Laude 1975; Fernandez 1978); in fact the pericarp is the wall of the utricle and is membranous and thin (fig.1). The seed is composed of the testa, the embryo, and the perisperm and is found inside the utricle; the seed coat (also known as the testa) is almost indistinguishable from the utricle wall (Munz 1974). The entire diaspore has been referred to as a fruit (Burbidge 1945; Firestone 1980), a false fruit (Vest 1952), a utricle (Crofts 1977; Lailhacar-Kind and Laude 1975; Warren and Kay 1984), or a seed (Vest 1952). Hereafter for simplicity we will refer to the utricle within its bracts as the fruit. The excised utricle will be referred to as the seed or excised seed.

Mechanisms of Dormancy in Shadscale

Several levels of dormancy should be considered when discussing seed germination in shadscale. If the bracts of *A. confertifolia* are removed, varying degrees of germination of the excised seed occur (see section on dormancy at the seed level). Sanderson and others (1990) found that cold desert collections had a mean germination of excised seeds of 26.6 percent, and warm desert collections a mean germination of 64.3 percent. Firestone (1980) reported a germination percentage of 68 percent for excised seeds from Mojave, California. Warren and Kay (1984) germinated 72 percent of 5 year old excised seed from Lone Pine Creek, California. Crofts (1977) reported only 19 percent germination of excised seeds

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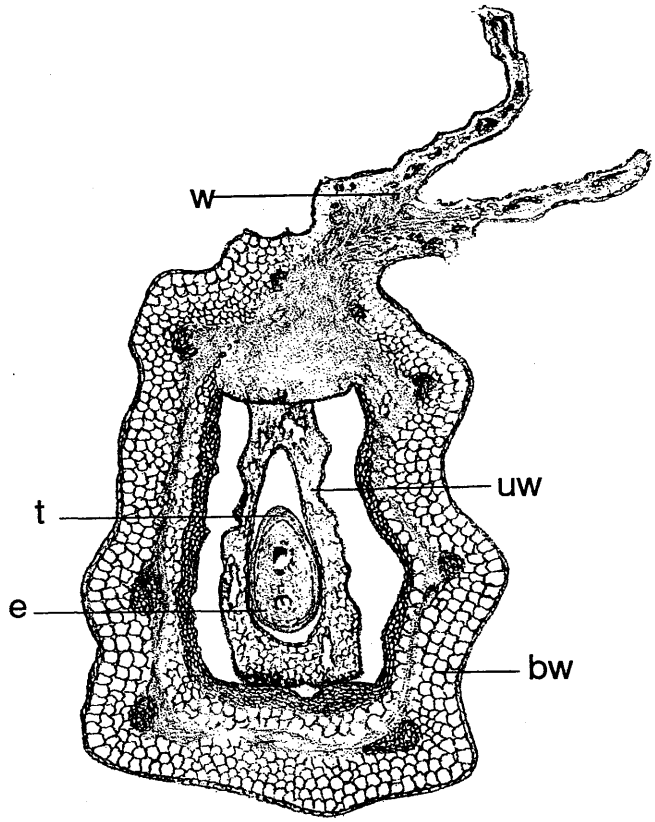

Figure 1—Oblique transverse section of immature shadscale fruit. Embryo is curled around the perisperm. Symbols: w–wing; bw–bract wall; uw–utricle wall; t–testa (seed coat); e–embryo.

from Bonanza, Utah, after 14 days, and all germination was abnormal, with only shoots or only roots appearing. Vest (1952) found a range of germination between 2.5 and 75 percent in excised seeds from northwestern Utah. Warren and Kay (1984) clipped the bracts without removing them, thus removing the physical restraint effected by the bracts, and still obtained no germination, suggesting that other mechanisms were inhibiting germination as well. Lailhacar-Kind and Laude (1975) and Fernandez (1978) found that only by removing the "pericarp" (bracts) could they obtain significant amounts of germination in fresh seed of the highly dormant South American species *A. repanda*. The 3 to 5 year old seed germinated somewhat better. These results argue that there can be dormancy at the seed level as well as at the bract level.

Dormancy at the Bract Level

Physical Effects of the Bract—The physical obstruction to germination imposed by the bracts has been noted in several studies. Vest (1952) and Vest and Cotton (1953) described the false fruit when sectioned with a microtome: "The ventral (inner) faces of the mature bracteoles are completely fused at the base and form a dome-like covering over the upper part of the enclosed utricle while the receptacles form the basal enclosure." Vest observed that the ventral tissues surrounding the utricle are impregnated with calcium oxalate crystals "forming a hard, shell-like inner layer continuous in the adjacent part of the receptacle." He described the inner portion to be so hard that fruits were soaked in dilute HCl for a week to avoid shattering the microtome blade.

Warren and Kay (1984) measured the amount of water imbibed by shadscale utricles within the bracts and found that utricle weight only increased by about 8 percent; excised utricles increased weight by 48 percent upon imbibition. They also observed that the seed is extremely tightly held within the bracts. This evidence suggests that the seed may not be able to imbibe fully and exert enough force to germinate when held within the intact bracts; if so, some mechanism of softening or weakening of the bract wall must occur before germination events can proceed. They also measured the ability of the seed to swell in sucrose solutions and calculated that the seed could exert about 8.5 bars of pressure to break through its various coverings; they estimated that about 116 bars would be necessary to penetrate the wet bracts.

Work in progress (Nelson and others unpublished) at the Shrub Sciences Laboratory in Provo, UT, verifies the lignification of the bracts and notes that despite the close proximity of the two bracts and fusion around most of the utricle, there remains a small opening between the wings of the bracts. This calls into confusion the idea that the bracts must disintegrate before seed germination can occur (Vest 1952), and suggests that some other mechanism besides physical inhibition is occurring.

Burton and others (1984) investigated the chemical and structural composition of the bracts of another highly dormant species, *A. gardneri*, and found large amounts of lignin and pectic substances contributing to the inflexibility of the bract. They attempted to break down the bracts with acidic sodium chlorite, but germination was less than in untreated seeds. Several researchers have attempted to break down the bracts of several Atriplex species with chemical or mechanical scarification (H_2SO_4, hammermilling, drum sanding). In some species these procedures have increased germination significantly; however, in *A. repanda* and *A. confertifolia* such attempts have damaged so many seeds that germination has remained near zero in most cases (Crofts 1977; Lailhacar-Kind and Laude 1975; Warren and Kay 1984).

A few exceptions to this notable lack of success have been recorded. Dumas and Sanders (1990) reported that several shadscale seed collections were scarified in a drum sander and then germinated in a growth chamber. Germination was improved by a mean of 15 percent over germination of unscarified fruit. Different periods of scarifying produced only random increases in germination. Crofts (1977) reported that thickness of the bracts increases with size of fruit and recommended that fruits should be sized before scarification to obtain optimum results. Sabo and others (1979) alternately scarified the bracts of fruits from New Mexico with a commercial seed scarifier for 2 minutes, cleaned them with a blower, and repeated the process until all seeds had most of the bract material removed. They reported a range

of 6 to 100 percent germination of scarified seed, occurring in 7.5 to 22 days, with optimum germination occurring at 12 °C in laboratory germination tests. Lehrer and Tisdale (1956) reported that 1.1 percent of intact fruiting structures recovered after 2 to 8 days in the rumen of a sheep germinated, compared with 0 percent germination of control fruits. They treated fresh fruits with 10 percent HCl for 5 minutes, and 5 percent of seeds germinated. More work needs to be done to verify and expand upon these results.

Several researchers have noted that fungi appearing naturally on the bracts may have a role in the scarification and softening of the bracts. Vest (1952) described the deterioration of shadscale fruit in the field and found no field germination until the bracts became blackened and had disintegrated vascular tissue. He attributed the breakdown to a fungus appearing to be an *Alternaria* species, particularly noting the multiseptate spores and dark brown hyphae. He found that a temperature of 35 °F does not stop the fungal growth.

Crofts (1977) identified three fungal species isolated from the bracts of shadscale: *Alternaria humicola*, a *Hyaldendron* spp., and *Phoma humicola*.

Firestone (1980) isolated and described two fungi from soil and litter around shadscale plants in Rush Valley, Utah. She observed that fungi will grow on leachate concentrated 17.5 times more than a 1:10 extract.

Research by Nelson and others (unpublished) has identified at least 10 genera of fungi occurring in and on the surface of the bracts. Further study is needed to identify the range of fungi occurring on the bracts over the course of several years and to determine the effect of inoculating likely fungi on sterilized bracts of shadscale seeds to ascertain if fungi do indeed break down the bracts. Perhaps some of these fungi can be shown to increase germination in shadscale seeds.

Preliminary research by Nelson and others (unpublished) indicates that significant numbers of intact shadscale seeds can germinate after being treated with 11 percent NaOCl (commercial strength bleach) when seeds are chilled for 8 to 30 weeks. In this study most of the germinated seeds remained free of fungal growth and none of them were visibly disintegrated. The degree of oxidation and softening of the bracts or other chemical effects on the seed itself after such harsh treatment is not yet known. These results on surface-sterilized fruits indicate that germination can proceed without fungal breakdown of the bracts.

Chemical Effects of the Bracts—It is likely that chemical inhibition of germination also occurs at the bract level. Many species of *Atriplex* have been shown to contain a water-soluble substance or substances in the bract tissue that inhibit seed germination in *Atriplex* spp. and other seeds (Firestone 1980; Fernandez and Johnston 1980). Vest (1952) compared the rate of leaching in fruits left in the field with artificial leaching in the lab and found that no inhibitory effect remained after 6 months in the field or 24 hours washing in the lab, measured by germination of excised shadscale, radish, and redtop seed.

Firestone (1980) ascertained that some factor in the leachate of *A. confertifolia* was inhibiting germination and causing root damage (absence of root hairs, browning of root tissue, reduced root/shoot ratio) in excised shadscale seeds to a greater extent and in different ways than inhibition by osmotic pressure alone. Attempts to isolate and identify the inhibiting substances were inconclusive, but it was found that fractions displaying low osmotic pressure were able to inhibit germination to the same extent as fractions with high osmotic pressure, indicating that some inhibiting substance besides salt was present. Molecular weight of the inhibitor(s) was less than 25,000. The root effects described have been reported in other *Atriplex* species as due to the presence of saponins (Nord and van Atta 1960; Askham and Cornelius 1971; Fernandez and Johnston 1980), but the presence of saponins has not been shown in seeds of this species (Stutz and Sanderson unpublished).

Crofts (1977) found a higher salt level in *A. confertifolia* fruits than in *A. cuneata* or *A. canescens* fruits and also observed, contrary to Vest, that the salt level was still quite high in fruits collected as late as March. Neither Vest nor Crofts recorded precipitation for the winter in question; it could be that Vest's fruits were leached more than those studied by Crofts, and this factor may prove to be a critical one in the establishment of shadscale plantings. Leachate from leaf tissue as well as from bract tissue could contribute to the osmotic and chemical environment of shadscale fruits in litter beneath mature plants.

Dormancy at the Utricle or Seed Level

Work by Warren and Kay (1984) suggested that some mechanism of dormancy beyond that of bract restriction or chemical inhibition may be operating in shadscale seeds. Work in progress at the Shrub Sciences Laboratory (Meyer and others in preparation) has shown germination of 0 to 66 percent (mean 11 percent) in 15 collections of shadscale

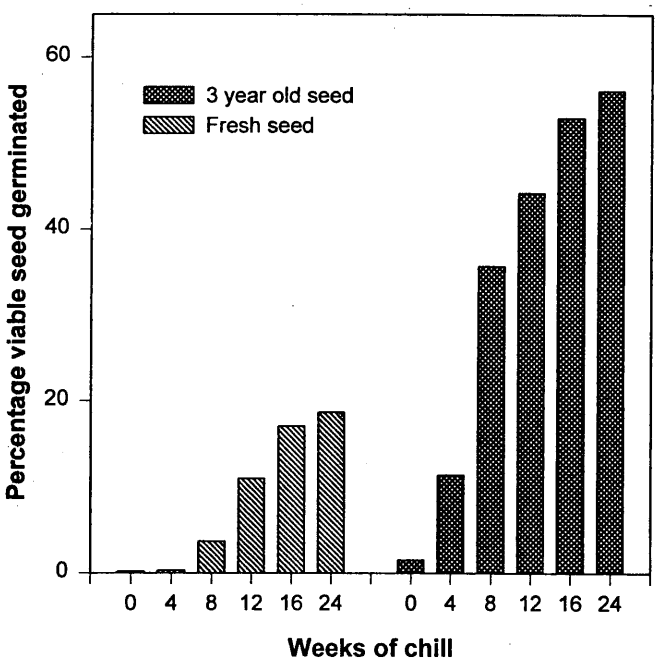

Figure 2—Mean germination response of 15 collections of recently harvested versus 3 year laboratory stored shadscale fruits to chilling for 0 to 12 weeks at 1 °C followed by 4 weeks at 5/15 °C.

seeds from Utah and Nevada if fruits are chilled moist at 1 °C for 12 weeks (fig. 2). No significant number of fresh seed germinated from any collection without at least 12 weeks of chill. Seeds stored dry in the laboratory for 3 years were tested again, and most collections began germinating after 4 weeks of chill and germinated 4 to 85 percent (mean 44 percent) after 12 weeks chill (fig. 2). In general, aging and chill affected seeds collected from warm-climate areas more than those collected from cold sites. The seeds in this study were not leached, other than the minute amount of solute wicking into the moistened blotters. Only small amounts of bract disintegration were visually observed. These observations suggest that adequate amounts of moist chill may overcome dormancy and that time spent in dry storage renders the seeds more chill-responsive.

Firestone (1980) noted that seeds planted in flats and left outside one winter showed some germination, ranging from 1 to 74 percent. The age and storage conditions for these seeds are not known.

The effect of time in dry storage has been noted in other *Atriplex* species. Olivares and Johnston (1978) found much higher germination in 5 year old fruits of *A. repanda* than in either fresh fruits or 3 year old fruits. *A. gardneri* also became more easily germinable after storage (Ansley and Abernethy 1985). It is not known how aging affects either the bract or the seed itself.

A preliminary trial at the Shrub Sciences Laboratory found that afterripening dry fruits at 50 °C for up to 12 weeks accelerated germination in chill conditions; afterripening at lower temperatures had little or no effect. More work on this effect is in progress.

A brief report from New Mexico (Smith 1980) indicates that shadscale seed germinated "in an oxygen atmosphere" after a 24 hour water soak, suggesting that there may be an inhibitor in the seed coverings that consumes oxygen, thus depriving the seed itself of oxygen necessary for germination events to proceed. If this is the case, it is doubtful that the bract itself would be responsible because it is porous and allows fairly free exchange of water and presumably air.

Careful studies on excised seeds of *A. repanda* report that the seed coat (utricle wall) in that species apparently retards but does not prohibit the passage of oxygen; a similar pattern is seen with regard to water uptake (Johnston and Fernandez 1978; Fernandez and Johnston 1978). Possibly aging or moist chilling or both break down the resistance of the testa to the passage of air and water.

The effect of moist chill was noted by Ansley and Abernethy (1984, 1985) in their studies on *A. gardneri*. They found that stratification for 4 weeks at 2 °C enhanced the effect of scarifying and leaching fresh fruit, but in year-old fruit, only 2 weeks stratification was necessary. They also noted that leachate from scarified fruits was much darker than that obtained from intact fruits. They hypothesized that inhibiting substances may have been leached from scarified fruits that could not easily escape from intact fruits. These substances may be associated with the seed coat or the embryo rather than with the bracts and could contribute to seed-level dormancy.

Meyer and others (in preparation; fig. 3) followed the fate of eight collections of shadscale seed, some from southern Utah, in field seed bank experiments in a northwestern Utah valley near Dugway. The experiment consisted of burying fruits enclosed in mesh bags 1 cm under soil or a mulch of shadscale litter. Results from this study indicate that under simulated seed bank conditions, seeds do not germinate in the first spring after fruiting. After the first winter in the seedbank, there was no germination in the field, but a few seeds germinated in the lab after 12 weeks of artificial chill. By November, a year after burial, approximately 60 percent of the seeds responded to chill, and by March of the following spring, approximately 25 to 75 percent of viable seeds germinated. Viable seeds were determined at each retrieval after chilling and germination testing by cutting to determine percent filled seeds. A few more seeds germinated in each of the following springs, and by spring of 1995, after four winters in the ground, approximately 40 percent of seeds were still alive but not yet germinated. Seeds from warm desert populations became germinable and disappeared from the seed bank sooner than those from cold desert sites.

These results suggest that the natural germination pattern for shadscale is staggered, resulting in an increased probability of survival under uncertain germination conditions. It is not yet known which dormancy mechanisms are

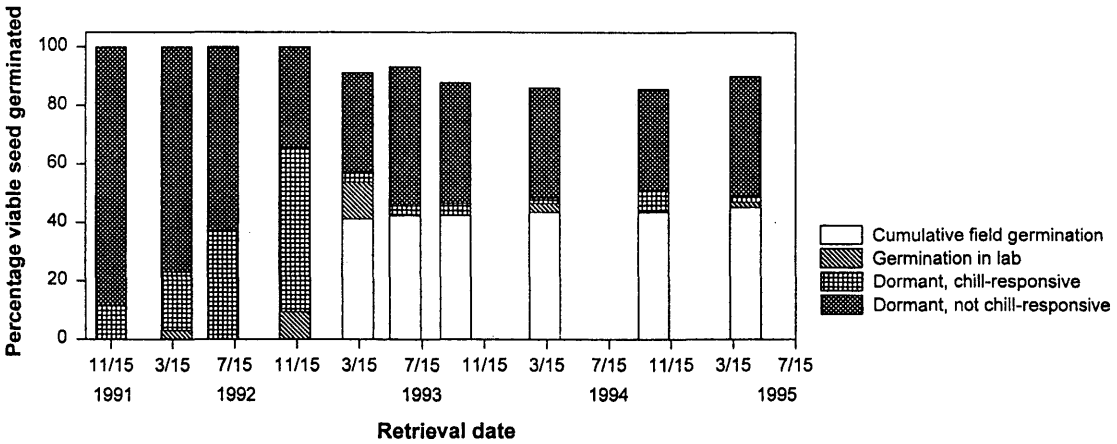

Figure 3—Fate of fresh shadscale fruits from eight collections in a retrieval experiment.

controlling this pattern, nor how to overcome them to obtain synchronous germination in an agronomic fashion. But enough information is available to give range managers some recommendations for improved emergence in artificial seedings.

Recommendations for Range Plantings

1. Select seed source from sites similar to planting sites.
2. Use only seed lots with high fill (50 percent or better) or consider the fill percentage when calculating planting rate.
3. If first season germination is critical, plant 3 to 5 year old seeds. Fresh seed probably will not germinate until the second spring.
4. Plant seeds early in the fall to take advantage of natural leaching action and oxidative processes in the soil as well as winter chill.
5. Do not assess the success of the planting until the second season, or even later if moisture is low during the second winter and spring. The dormancy of shadscale allows the seeds to germinate when chances of survival are the best.

Acknowledgments

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Developmental Instability as a Bioindicator of Ecosystem Health

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Abstract—Ecologically important parameters such as species diversity, productivity, survivorship or fecundity are often used as indicators of a population's or community's well being (or, conversely, stress). However, ecological indicators are lagging indicators of stress, documenting problems that have already occurred. Here, we advocate the use of developmental instability as a leading indicator of stress and illustrate its use with a variety of examples. The use of leading indicators provides managers with the time necessary to head off problems before costly restoration or remediation efforts are required.

Land managers have, since the 1960's, become increasingly concerned with the perpetuation and preservation of plant communities, and thus must assess the well being of natural plant populations. Classical ecological parameters are often used to indicate stress e.g. species diversity, productivity, biomass, yield, population density, survivorship, and various life history and reproductive parameters (Maltby and Calow 1989; Moriarty 1990; Mhatre 1991; Schroder and others 1991; Cairns and Niederlehner 1992). Unfortunately, ecological indicators are lagging indicators of stress. By the time declines in diversity, survivorship, or fecundity show a community or population to be stressed, managers have few options as the resource has already been, at least partially, degraded. At that point, managers can modify human use, engage in costly remediation and restoration projects, or watch as the situation worsens. Here, we advocate the use of developmental instability as a leading indicator of stress, and illustrate a variety of developmentally invariant features that may be used.

Ecological indicators are difficult to measure, particularly for long lived species such as most shrubs. Furthermore, ecological indicators respond to variations in climate and natural population cycles. Thus, long term studies might be needed to evaluate potential problems. Even studies spanning a decade might be misleading for species that live for decades to centuries, or that have persistent seed banks. Furthermore, the responses to climatic or other changes need not be proportional to the change itself. Ecologists are only beginning to come to grips with the nonlinear aspects of species and climatic interactions that can lead to complex cycles, thresholds, multiple equilibria (see Logan and Hain 1991), and vegetation inertia (see Tausch this volume).

Nonlinear responses may also occur in measures of fitness, i.e. survivorship and reproduction. These parameters, however, are for obvious evolutionary reasons highly buffered, and hence may not respond demonstrably, or consistently to stressors. Stephen Hendrix, in his review of the effects of herbivory on plant reproduction, documented a number of cases where 30 to 50% defoliation did not influence seed production. In other cases, similar amounts of defoliation were devastating. Ecologists are only beginning to study these differing buffering abilities, but such differences greatly complicate the use of life history features as measures of stress.

Despite these obvious defects in ecological indicators, managers must make decisions in a timely fashion. The era of 50 year grazing studies (Clary and Holmgren 1982) is past. How can we determine if populations, and thus communities and ecosystems, are being subjected to undue stress? How can we evaluate the efficacy of management without resorting to long term ecological studies? The temptation is to say that if management cannot afford to understand the dynamics of a given system, then the next best thing is to conduct comparative ecological studies. However, Robin Tausch (this volume), has argued that temporal or spatial comparisons of communities are virtually meaningless because it is impossible to determine if the control and experimental communities share a common history, potential, or equilibrium (if any). Indeed, the notion that there is a magic composition that communities should attain belies both climatic and ecological dynamics, and is, in any case, normally beyond our ability to objectively determine.

We suggest that ecologists and land managers need to adopt a new strategy. The old strategy of range improvement, i.e. remediation and restoration, using the aforementioned ecologically important but lagging indicators of stress, is costly, time consuming, and perhaps self-deceiving. A more sensitive, surrogate measure for fitness, is needed. Such a measure would provide time to correct or ameliorate

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the problem before costly restoration measures had to be implemented.

Measures of stress, based upon genetic or physiological parameters are generally not efficacious for routine monitoring of populations, because, while valuable in their own right, they are expensive, time consuming, restricted in their application to a few species, and unresponsive to a wide range of stressors. Genetic measures of stress, such as the rates of mutation, sister chromatid exchange, micronuclei formation, unscheduled DNA synthesis, adduct formation, or chromosomal aberrations, have been shown to respond to various stressors and ionizing radiation (see Carrano and others 1978; Kantor and Schwartz 1979; Poirier 1984; Shugart and Kao 1985; Shapiro 1992; and Ali and others 1993, for an introduction to this literature), but it is unlikely that such indicators respond to grazing, parasites, and other biotic stressors.

In our experience, physiological measures of stress, such as water potential, and the rates of photosynthesis, respiration, and stomatal conductance are extremely sensitive. These measures, however, may respond to a gust of wind or a passing cloud. This extreme sensitivity to transitory events makes it difficult to conduct comparative studies, or to assess integrated effects over time, particularly in environments that are spatially or temporally heterogeneous. Thus, while they yield valuable insights by establishing cause and effect relationships, we do not, however, advocate their use as a routine first stage monitor.

Developmental Stability

Here, we advocate the use of developmental instability as a means of assessing the well being of natural populations. Developmental instability is more sensitive than traditional measures of stress (Graham and others 1993a,b; Clarke 1993, 1995); applicable to virtually any multicellular organism; based upon the responses of indigenous organisms, in situ, rather than a transplanted lab pet, and thus is relevant to the population under consideration; it is responsive to a wide range of stressors including grazing (Alados and others in review), heat/cold (Siegel and Doyle 1975; Siegel and others 1977; Beecham 1990), chemical stressors (Valentine and Soulé 1973; Jagoe and Haines 1985; Kieser 1992; Graham and others 1993b), electromagnetic radiation (Turner and others in review), parasites (Polak 1994; Mara 1995; Escos and others in press), aneuploidy (Shapiro 1992), inbreeding (Markow and Martin 1993), and hybridization between disparate taxa (Graham and Felley 1985; Graham 1992). Virtually all of these are known sources of stress that can befall shrubs. Developmental instability is evident only when the buffering capacity of the organism has been exceeded (thus the organism integrates the information); it is inexpensive to use (calipers are sufficient), and requires a limited sample size (40 individuals per species per site).

Developmental instability is ideally suited for detecting stress in the field. The use of developmental instability is similar to taking one's temperature. If body temperature deviates from 98.6 °F, a person is presumed ill. We do not, however, know the cause of the illness; further investigation is required. Neither can the cause of stress be identified by examining developmental instability. A cursory glance at the list of stressors known to influence developmental instability (above) shows that all yield the same result—greater instability. Thus, developmental instability is used to determine if populations are healthy or if the situation is improving (management is working) or worsening.

Developmental instability is the failure of a genotype to consistently produce the same phenotype in a given environment (Zakharov 1992; Graham and others 1993a). To determine the phenotype that would have been produced in the absence of stress we use developmentally invariant traits, i.e. traits that do not normally change during the course of development (see Graham and others 1993a and in review for a discussion of developmental invariance). Such invariance defines one or more forms of symmetry. Thus, the degree of asymmetry, for normally symmetrical traits, is a measure of developmental instability; the symmetrical state is the idealized phenotype expected in the absence of stress. Deviations away from this idealized phenotype indicate that development has been disturbed.

Measuring asymmetry, in principle, amounts to examining the within individual variance for a given trait (Graham and others 1993a), i.e., the repeated parts within the individual required to compute a variance. Repeated parts share the same genotype and developmental history, and to the extent that they experienced the same environment, should be identical. Not all repeated parts are equally well suited for estimating developmental instability. Clearly, sun and shade leaves (on the same plant) are repeated parts, yet they differ because they experienced different environments. Thus, examining size related differences among such leaves would be inappropriate, but the left and right sides of each leaf should still be fairly similar as the two sides of the same leaf can reasonably be expected to have experienced similar environments.

Types of Symmetry

Plants exhibit a variety of symmetries that can be used to assess developmental instability; the pinnate leaves of most plants are bilaterally symmetrical. Palmate leaves, such as those of maples, can display both bilateral and radial symmetry. Flowers are commonly categorized based upon symmetry as being either bilaterally or radially symmetrical. How well the flowers fit these idealized phenotypes is rarely ascertained, but potentially could be quite informative. Leaves on many species change size as one moves up the stem. This is a form of translational symmetry with scaling. In some species the relationship between leaf size and node number is simple, but in others it may follow complex patterns. Finally, the branching of stems, roots, and leaf veins often exhibit a symmetry across scale. Thus, if one removes a branch from a tree, the branch resembles a young tree. Similarly, part of a root may resemble the whole. This type of symmetry is known as self symmetry. We illustrate the use of each of these symmetries in estimating developmental instability.

Bilateral Symmetry

Bilateral symmetry usually varies in one of three ways. In fluctuating asymmetry, one side may be slightly larger than

the other, but which side is larger fluctuates between the left and right side. In this case, symmetry is the normal condition. In directional asymmetry one side is consistently larger than the other. This is the case with the two sides of the human heart, and the two sides of a lateral soy bean leaflet. Antisymmetry occurs when one side is normally larger than the other, but which side is larger varies among individuals, as with fiddler crab claws.

Fluctuating asymmetry is estimated as the variance in a measure on the left and right sides, or as the absolute value of the difference between measures on the left and right side. Where the difference between the sides increases, with, say, leaf size, it may be necessary to scale the difference to the mean, i.e. var [(R–L)/(R+L)] (see Palmer and Strobeck 1986; Graham and others 1993a for a complete discussion).

We have examined fluctuating asymmetry of leaves of *Epilobium angustifolium* growing at various distances from a chemical production facility in northern Russia (fig. 1). We similarly examined the fluctuating asymmetry of lateral leaf lobes of morning glory (*Convolvulus arvensis*), and of the location of leaflets on black locust leaves (*Robinia pseudoacacia*) growing at various distances from a chemical production facility in Ukraine (figs. 2-4). In all three cases, leaves became more symmetrical as one moved away from the chemical production facility.

Traits that are directionally asymmetric or antisymmetric also may be used. However, one must first specify the relationship between the sides before examining the asymmetry (Graham and others in review). For example, in their

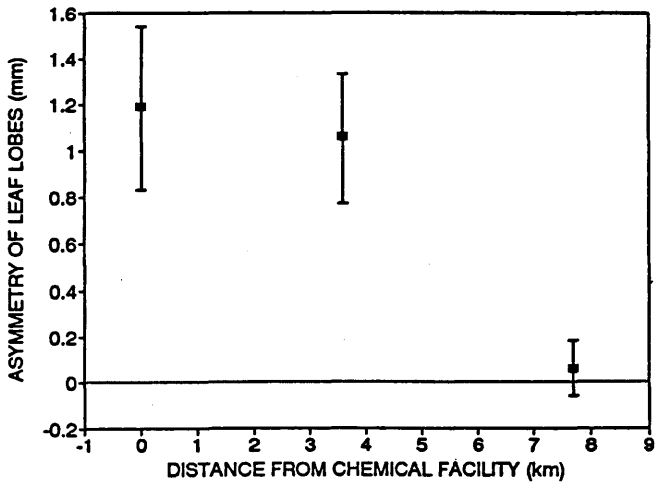


Figure 2—The fluctuating asymmetry of the length of the lateral leaf lobes of *Convolvulus arvensis* was compared among plants growing at various distances away from a chemical production facility in Ukraine. Twenty plants were examined per site (means and 95% confidence intervals are shown) and the degree of fluctuating asymmetry varied significantly among sites $F_{2,27} = 16.69$, $P < 0.001$.

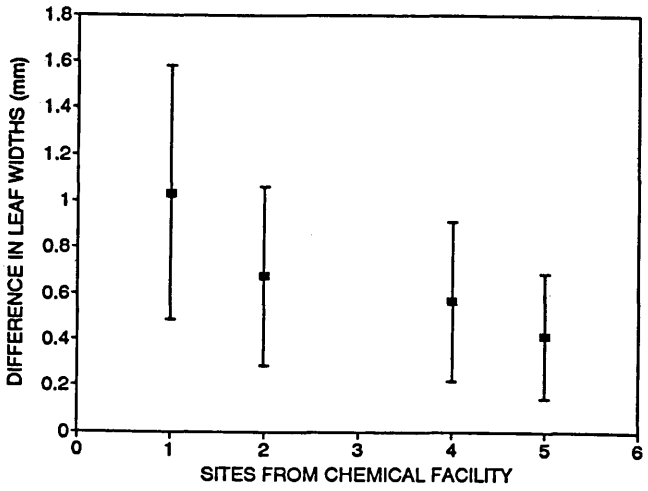


Figure 1—The left and right leaf blade widths of *Epilobium angustifolium* were measured to the nearest 0.01 mm. Measurements were made at the midlength of each leaf. The sites sampled were at various distances from a chemical production facility in Northern Russia. Site 1 is on the facility premises. Sites 2, 4, and 5 are 2, 9, and 20 km from the facility, respectively. Twenty plants were sampled per site. Means and 95% confidence intervals are shown. The degree of fluctuating asymmetry differed significantly among the sites, $F_{3,76} = 4.83$, $P < 0.01$.

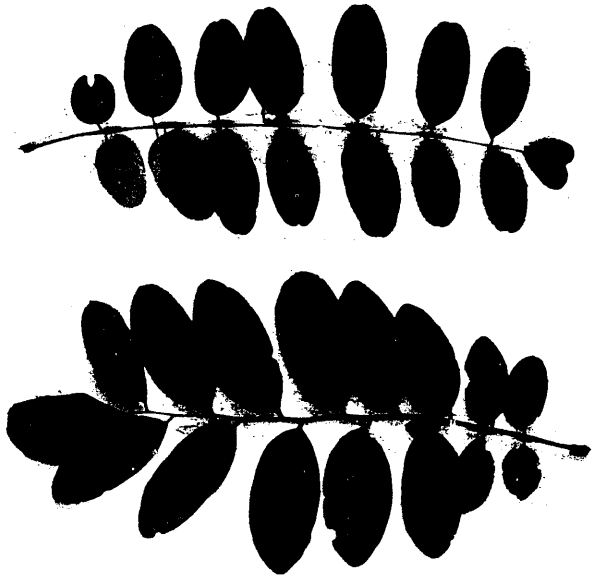


Figure 3—The fluctuating asymmetry in the origin of the lateral leaflets of *Robinia pseudoacacia* was compared for plants growing at various distances away from a chemical production facility in Ukraine. Ten plants were examined per site. The top leaf is from the control site, and the bottom is a leaf from the facility premises.

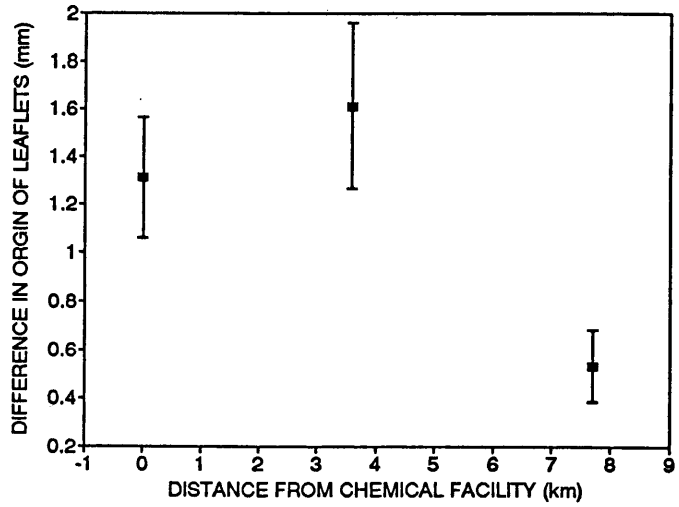
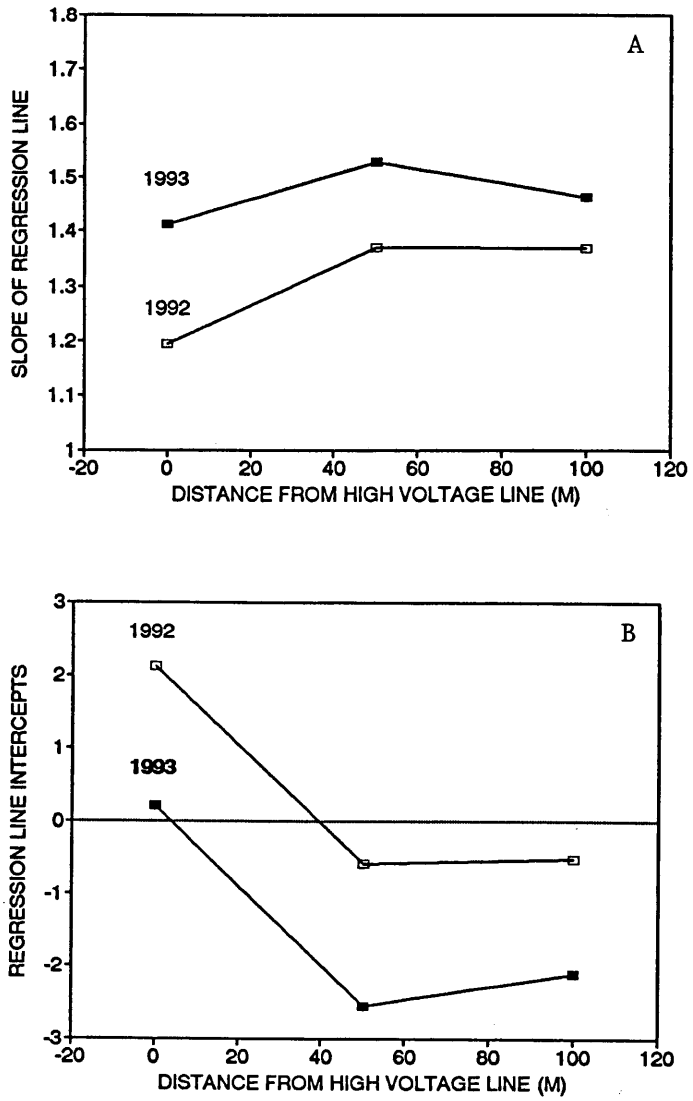


Figure 4—The degree of asymmetry in the origin of lateral leaflets of *Robinia* leaves differed significantly among the sites ($F_{2,872} = 16.56$, $p < 0.001$). Means and 95% confidence intervals are shown.

study of the effects of electromagnetic fields on soy beans, Turner and others (in review) found that the lateral leaflets of soy beans are normally strongly directionally asymmetric. The distal side of each lateral leaflet is smaller (fig. 5) than the proximal side. However, the relationship clearly changes as one moves away from the high voltage power line (fig. 5). In fact, the asymmetry in the widths of the two sides of the lateral leaflet was least under the power line. The change in the regression coefficients as well as the residual about the regression line indicate that development has been disrupted (Graham and others in review).

Rotational Symmetry

Rotational asymmetry can be used in three ways to assess developmental instability. First, one can examine the degree to which a full circle is occupied, this amounts to examining the sum of all of the angles. Secondly, one can examine the variance in the angles between structures. And finally one can examine the variance in measures of the structures themselves. Mara (1995) has shown that the



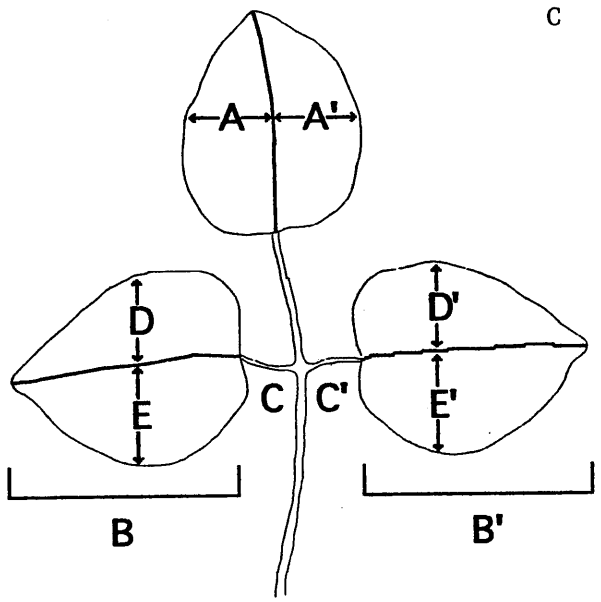


Figure 5—The width of the distal side, "D" of the lateral leaflets of soy beans (*Glycine max*) is normally smaller than the proximal side "E". Here we have regressed the width of the proximal side against that of the distal side for soy beans growing at three different distances (0, 50, and 100 M) from a 765kv electric transmission line. Two different fields were sampled in two different years. Here we have plotted the slopes and intercepts as a function of the distance. Note the consistent change in these parameters as one moves away from the high voltage line.

leaves of red maples infected with gall forming mites—(*Vascates quadripedes*) occupied less of a complete circle, regardless of whether or not the leaf itself was infected, than leaves of trees that were not infected (fig. 6). We have shown elsewhere (Freeman and others 1994) that angles between the veins in the leaves of Norway maple were more acute and variable for trees growing near a chemical production facility in northern Russia, than those growing some 20 km from the facility. Finally, lupines have compound palmate leaves.

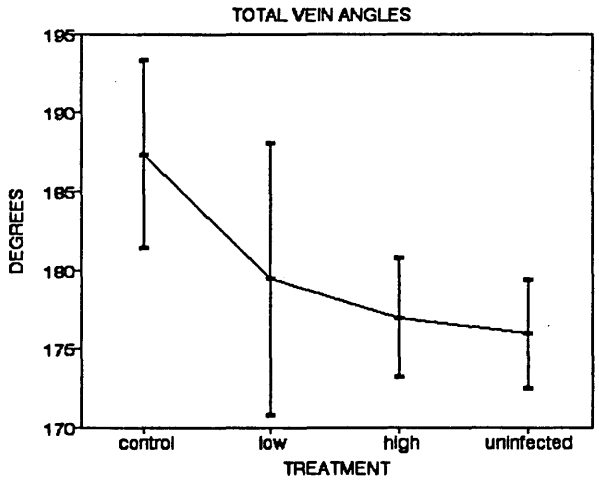


Figure 6—Leaves of red maples infected with gall forming mites exhibited less complete circles in terms of total vein angles, than did uninfected leaves.

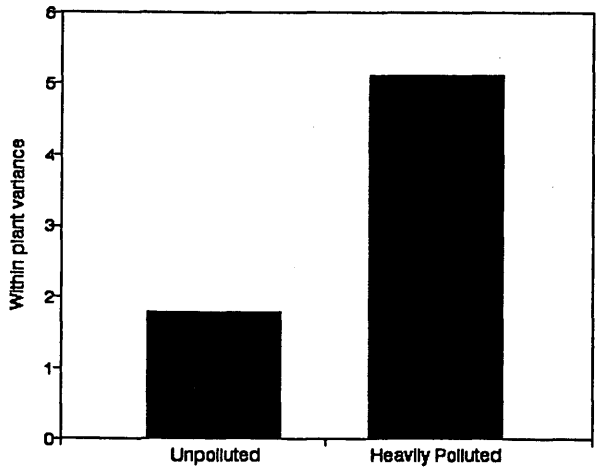


Figure 7—Translational asymmetry of internode lengths in *Elodea canadensis* was compared among sites in southeastern Michigan. Plants from the polluted site showed a significantly greater within plant variance than plants collected from the control site ($F = 20.764$, $p < 0.001$). Seventy-five plants were examined per site.

Lupines exposed to the drift of herbicides and pesticides from orchards exhibited more than four times the within leaf variance for leaflet length than did plants far removed from agriculture ($F_{1,68} = 6.21$, $P < 0.02$, Freeman unpublished data).

Translational Symmetry

Translational symmetry implies that something stays the same as one moves from place to place. In some plants such as *Elodea* (Tracy and others 1995), the size of mature leaves and internodes does not vary with node number, and thus shows true translational symmetry. In this case, the appropriate measure of developmental instability is the within individual variance, which was found to increase as a result of pollution (fig. 7). In other species, internode lengths, and diameters, or measures of leaf size change in predictable ways with node number as one moves up the stem; this is translational symmetry with scaling. Scaling relationships may be linear, parabolic or more complex. Alados and others (in review) examined the developmental instability of internode lengths in *Chrysothamnus greenii* across a gradient of grazing intensity, and found the internode lengths to fit the following equation:

$$\ln(\text{internode length}) = a \ln(\text{node number}) - b(\text{node number}).$$

Developmental instability, estimated as the standard error of the regression, was found to decrease with increased grazing intensity (fig. 8). These results appear counterintuitive. However, the results make sense when one realizes that *Chrysothamnus* itself is not often grazed, while its

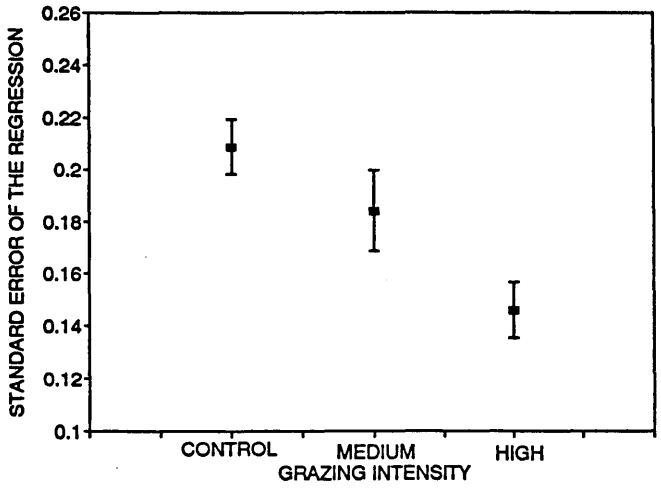


Figure 8—The standard error of the regression of internode length on node number for *Chrysothamnus greenii* (see text for the allometric formula) decreases as grazing intensity increases.

competitors are heavily grazed (Hutching and Stewart 1953). Thus, in the highest grazing treatment, *Chryothamnus* experiences the least competition, while in the ungrazed control treatment, *Chrysothamnus* is stressed by competition.

Self Symmetry

Self symmetry is symmetry across scale, and is common in branching structures. Here, we illustrate the use of self symmetry to estimate developmental instability using the brown alga *Fucus* (fig. 9; Tracy and others 1995). *Fucus* exhibits dichotomous branching, and each branch resembles the whole alga; this species exhibits symmetry across scale. Notice also that the individuals in figure 9A and 9B do not completely fill the planes defined by their thalli. The alga clearly fills more space than a straight line (dimension one) connecting any two points on its body, but less space than the whole plane (dimension 2). The alga, in fact, has a fractional dimension, and approximates a fractal (see Emlen and others 1994; Freeman and others 1994; Graham and others 1993a,c for a discussion of developmental instability and fractals; Peitgen and others 1992 is an excellent introductory text on fractals, chaos and related phenomena).

To estimate the dimension filled by *Fucus* individuals, we employ a box counting procedure (fig. 10). To do this, overlay the individual with grids of different size boxes and count the number of boxes in which at least part of the *Fucus* occurs. We then regress the natural log of number of occupied boxes against the natural log of the length of the box. The absolute value of the slope of the line is the fractal dimension. This is a measure of the space filled by the individual. Developmental instability is the degree to which the individual failed to fit the idealized phenotype, and is measured as the standard error of the regression. Under nonstressful conditions all points should lie on the regression line. In the case of *Fucus* growing off the coast of Washington, Tracy and others (1995) found that the standard error of the regression increased significantly with pollution (fig. 10).

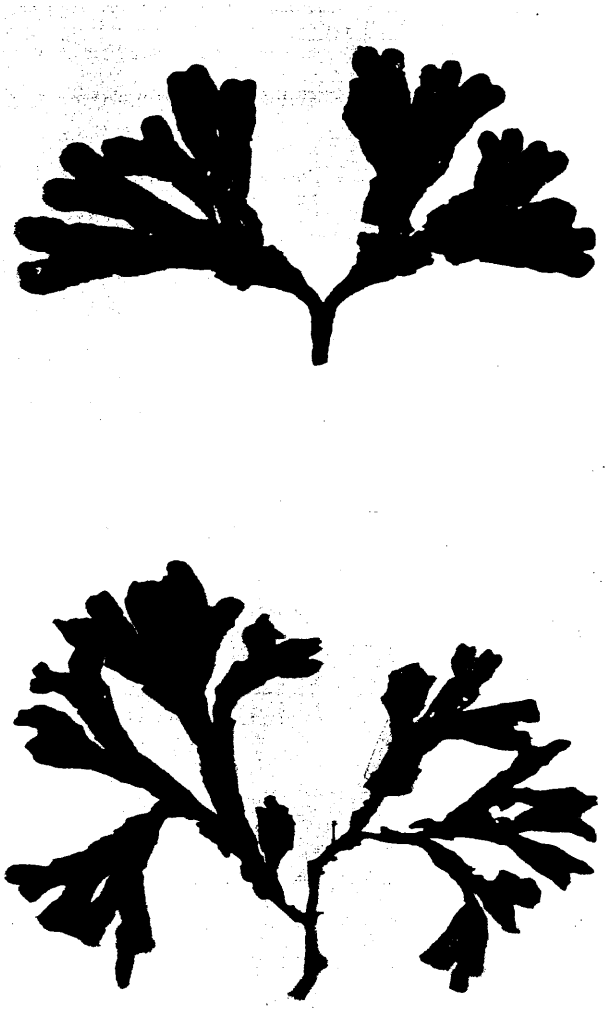


Figure 9—Top: *Fucus furcatus latifrons* collected from a relatively unpolluted site in Puget Sound, Washington, appears to have a normal thallus. Bottom: *Fucus furcatus latifrons* collected from a heavily polluted site in Puget Sound, Washington shows a breakdown in self symmetry.

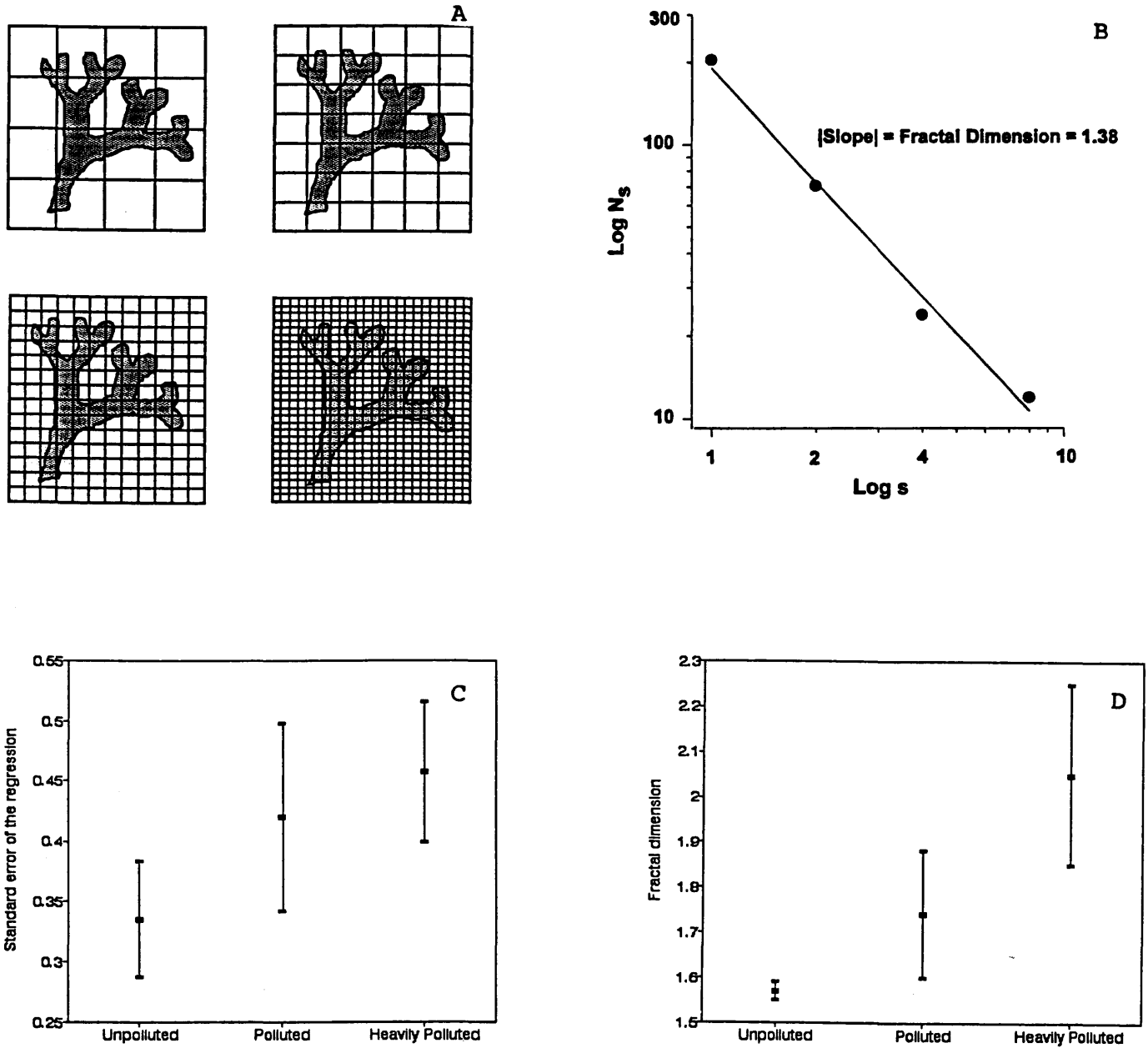


Figure 10—(A) Grid overlays are used to calculate a fractal dimension using the box counting method. In this hypothetical example, the relative box sizes (s) are 1, 2, 4, and 8. The number of occupied boxes in each grid N(s) are: 205 in size 1, 71 in size 2, 24 in size 4, and 12 in size 8.

(B) The double log plot is computed from the hypothetical box counting example. The fractal dimension = absolute value of the slope of the line defined by the log of total boxes occupied versus the log of box size.

(C) Variability about the regression line used to determine the fractal dimension of *Fucus* at each collection site is assessed using the standard error of the regression. The mean and 95% confidence interval is shown. A significant difference occurs among sites ($X^2 = 11.157$, $p < 0.001$).

(D) The fractal dimension of *Fucus* differed significantly among sites ($X^2 = 37.03$, $p < 0.01$). Data is shown as the mean and 95% confidence intervals.

Conclusions

Most ecological parameters are lagging indicators of stress; indicating problems only after they have already occurred. By using such indicators, managers cannot catch early symptoms of deterioration, and must instead continually play catchup, trying to restore already damaged lands. Developmental instability, as a leading indicator, can signal trouble before it reaches the point of apparent demographic consequences. By using such a leading indicator of stress, managers should be able to better manage lands at lower economic costs.

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Interaction Assessment: Predicting the Impact of Alternate Range Management Actions

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J. M. Escos
C. L. Alados

Abstract—Interaction Assessment, or "INTASS," is an analytic tool used to quantitatively describe the effects of species interactions and local environmental variables on the per-capita population growth of a species, either plant or animal. Data from a farm on the Iberian Peninsula in Spain was analyzed for 19 variables. Using INTASS, the plant community dominated by *Anthyllis* was shown to be most changed by grazing pressure. Work continues on developing user-friendly software for INTASS applications.

Good rangeland management requires that the likely impacts of alternative management options be assessed on both plants and animals, including livestock, before any specific action is taken. Such assessments are not easily made. Because grazers exhibit food preferences, different plant species will be differentially affected by grazing. Some plants may benefit from grazing, at least light grazing, while others are harmed. Plant growth and reproductive output may be impacted quite differently by grazing. Further, even knowledge of grazing preferences and impacts on the individual species is insufficient to predict the response of the plant community, for the temporal and spatial dynamics of that community are affected also by competitive and facilitative interactions that occur among the plant species. To make the picture still more complex, grazer consumptive patterns and spatial distribution are likely to change with shifts in plant community composition and grazer density.

Perhaps the most reliable means of assessing the likely consequences of management options is to consult one of those grizzled guru naturalists who somehow hold in their heads a gestalt of all the system's complexities. Unfortunately, grizzled guru naturalists are a dying breed. Deprived of this resource, we are destined to fall back on either educated guesses, based on past experience, or on modelling. The first option may work in some circumstances, but will likely fail in many others, and must inevitably leave one feeling a bit uncertain. Modeling may require lengthy and costly experimentation to parameterize the model. Consequently, predictions may become available only well after decisions have to be made. The bottom line, of course, is that decisions must be made, even if extensive, reliable data are not available. This does not, however, imply that decisions must be made in a vacuum. What is needed is a rapid field based approach for assessing the impacts of management decisions and species interactions on the population growth rates of all species in the community.

One promising candidate for such a method is Interaction Assessment, or "INTASS" (Emlen and others 1989, 1993; Freeman and Emlen 1995). INTASS is an analytic tool that can be used quantitatively to describe the effects of species interactions and local environmental variables on the per-capita population growth parameter of any species of interest. Such expressions, derived for all major species in a community, comprise a set of simultaneous equations which, by subsuming the web of biotic-abiotic interactions, can be utilized to predict how the impacts of various management actions might ramify throughout the system. In this paper, we present the rationale behind INTASS, then illustrate its use in the context of a grazing management situation.

Interaction Assessment

INTASS is based on the assertion that fitness (sensu the number of individuals produced per individual per unit time, such as an individual's contribution to the per-capita population growth rate) is, on average, the same for individuals in all occupied microhabitats. Microhabitat is defined with respect to the values of all physical and biotic variables affecting fitness in the immediate vicinity of the individual in question; immediate vicinity is defined as that area around an individual within which environmental variables (soil features, slope and aspect, water availability, facilitative or competitive effects of plants of all species, grazers, etc.) are likely to effect the individual's growth, survival and reproduction. The assertion is based on the following lines of reasoning.

Regarding animals, a critical aspect of behavioral adaptation is that individuals have the ability to assess the impact of their immediate surroundings on their survival and health. If food is in short supply, predators are leering from every corner and cover is scarce (all local variables affecting fitness), the adaptive response will be to leave the immediate area. Where conditions are more benign, the animal should

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be more likely to remain. Whether the response to move or stay results from guided search behavior or some sort of kinesis is immaterial. The consequence is that individuals will accumulate in patches of the "best" microhabitats until the increased pressures of their density counteract the microhabitat qualities. Net movement ceases when individuals can no longer increase their fitness by moving somewhere else, resulting in equal average fitnesses across the entire occupied habitat. Support for this assertion as it applies to animals can be found in Emlen and others 1989.

On the other hand, plants cannot move as animals do, but they possess tremendous plasticity with respect to growth, flowering, and seed set. Thus the number of viable seeds produced by a plant reflects not only the size of the plant, but also the local microhabitat of the plant and, thereby, indirectly (and loosely, depending on the distance of seed dispersal), the environment in which the seedlings will grow. Now, because seedling survival falls with density feedback (produced by competition from the parent plants and from other seedlings), the number of seedlings that survive their first year must rise and then fall with the number of seeds produced per unit area by a parent plant. That is, there is an optimal seed production for every plant in any given year, which is a function of microenvironmental conditions, including cover of the parent plant and any other conspecifics in the immediate vicinity. If we presume that natural selection has shaped a plant's capacity to "do the right thing," we should find seed production to be heavier (after correction for size of parent plant) in microhabitats where each seed, on average, is more likely to survive, and lighter in overcrowded microhabitats where seedling survival is less likely. That is, we expect an equilibrium to be approached in which the average number of surviving seedlings per seed produced is the same in all occupied microhabitats (Emlen and others 1989). Inasmuch as the vast proportion of fitness variance in plants is accounted for by early survival, the above implies, to a good approximation, that average fitness of seeds will converge across all occupied microhabitats.

If this equilibrium is reached only slowly, then the assertion of equal average fitness applies only loosely unless population sizes are at equilibrium. There is good evidence, however, that these adaptive changes in seed production occur extraordinarily quickly. Palmblad (1968) conducted experiments in which seeds from seven weed species were sown in densities ranging from 55 to 11,000 seeds per square meter. Despite the enormous discrepancy in density of seeds sown, the number of seeds produced per unit area by the resulting adults one year later varied by less than a factor of 2.0 in six of the seven species. Thus, within a single generation, the differential was reduced from 200 (11,000/55) to less than 2.0. Harper (1977) cites another study in which a 300-fold seed sowing density range resulted in only a threefold difference in seed output per unit area for *Digitalis purpurea*. In pure stands of *Agrostemma githago*, seed output per unit area was nearly independent of seed input (Harper and Gajic 1961). Finally, *Bromus rubens*, both in pure stands and in mixtures with *Lepidium densiflorum*, exhibits similar behavior (Freeman, unpublished data). While the above argument treats all seeds of a species as identical, there is evidence also that suggests fitness is essentially invariant with seed size (Stephenson and Winsor 1986). Studies by Wulff (1986) indicate possible adaptive advantages to observed seed size variation. If, as an evolutionist would suspect, this is generally true, seed size polymorphisms also suggest equal expected fitness contributions per seed.

The per-capita population growth rate of any species can be modelled as a function of local environmental variables, including the densities of conspecifics and other interacting species. Reasonable forms for such models can be gleaned from the extensive literature on population dynamics; they range from simple Lotka-Volterra type to any level of complexity desired. The difficulties of constructing and using such models lie not in adequately approximating their forms, but in assigning reasonable values to their various coefficients or parameters. Extremely detailed models are, of course, the most reliable, but only if the parameter values used are known to be accurate. If not, errors may compound, cascading through the calculations to generate utterly unreliable predictions. Sacrificing too much detail for exigency, on the other hand, leads to inaccuracies for quite a different reason; the models are too simplistic to reasonably describe the system of interest. The INTASS methodology can, at least in theory, be used to parameterize either model extreme, but too detailed models require unrealistically large data sets (and may suffer from other statistical complications, for example, a multitude of local solutions). Models of intermediate complexity, tailored to the local situation and problem, are the most practical alternative.

Once a model (or a series of models, one for each species to be analyzed) has been chosen, INTASS may be applied to parameterize it as follows. Gather data on a quadrat-by-quadrat basis on all environmental variables deemed pertinent to fitness of a species of interest. Quadrat size reflects "immediate vicinity" which, in the case of plants, will generally be an area just slightly larger than the root mass/crown of the species of concern. These quadrats are centered around randomly chosen individuals of the species of interest. The data for all individuals are then entered into a software routine that finds those model parameters/coefficients that most accurately reflect the assertion of equal average fitness, for example, that result in minimal across-microhabitat (across quadrat, in effect) variance in fitness. In the case of plants, there is no contribution to fitness by individuals that produce no seeds; indeed, the contribution is proportional to seed number. Thus, for plants, the routine is applied over all seeds rather than over individual parent plants.

If a linear model is utilized, confidence intervals on the derived parameter values are calculated as in standard multiple regressions (see Emlen and others 1989, 1993). Where nonlinear models are used, confidence intervals can be found with the use of the inverted Hessian matrix (matrix of second derivatives of the variance with respect to all parameters).

Methods

Data were collected during the summers of 1993 and 1994 on the Pajares Livestock Farm in the Filabres Mountains (elevation 850 m) in Almeria Province, Iberian Peninsula, in Spain. The plant community there is shrub-steppe, with

600 mm annual rainfall, dominated by *Anthyllis cytisoides*, *Artemisia tridentata*, *Retama spaerocarpa*, *Stipa tenacissima*, and various other grasses. Grazing (by goats) is light or absent over much of the area, heavier on the rest. Variables measured in each quadrat included:

1. Age of plant
2. Plant canopy area
3. Plant volume
4. Area occupied by other conspecifics within the quadrat
5. Total number of seeds on each sampled plant (in 1993)
6. Mean seed weight for each sampled plant
7. Number of seedlings under each plant in 1994
8. Percent cover of *Artemisia*
9. Percent cover of *Stipa*
10. Percent cover of *Retama*
11. Percent cover of other grasses
12. Slope (level ground = 1, slight = 2, high = 3)
13. Soil stone structure (few or no mid-sized stones = 1, intermediate = 2, high = 3)
14. Soil pH
15. Soil conductivity
16. Soil organic content
17. Soil texture (percent soil consisting of particles greater than 2 mm diameter)
18. Grazing (no = 1, yes = 2)
19. Soil moisture at 10 cm depth

Preliminary analyses included regressions of *Anthyllis* cover values on the various measured variables (8 through 19), and plots of estimated fitness (no. seedlings in 1994/no. seeds in 1993) against these variables. On the basis of the results, the final INTASS analysis was simplified by deleting variable 13. In addition, we reasoned that the soil moisture measure would be highly variable over time and might, therefore, be misleading as a reflection of effective moisture availability to *Anthyllis*. Rather, it seemed likely that available moisture would be a global variable modified by the other variables. Consequently, variable 19 also was deleted from the final analysis.

The Model

In this semi-desert habitat, moisture is likely to be the primary factor limiting plant fitness. Other variables, nevertheless, might be important in their own right, as well as mediators of local differences in moisture availability. Consequently, we constructed an extremely general function to describe "environmental quality per unit plant cover," Q, and presumed that the probability of early plant survival (P) would rise and then asymptote with Q:

$$P \propto \frac{Q^2}{\alpha+Q^2} : Q = (x_{16}^{\delta 1} x_{14}^{\delta 2} x_{12}^{\delta 3} x_{15}^{\delta 4} x_{17}^{\delta 5})/(N+\delta_6 x_8+\delta_7 x_9+\delta_8 x_{10}+\delta_9 x_{11})$$

The subscripts on {x} refer to the list of variables, above; Alpha and {δ} are the model parameters to be found by fitting the model to observed data.

Survival must fall off (roughly) exponentially with grazing rate. Thus, also:

$$P \propto \exp\{-\delta_{10} x_{18}\} .$$

Finally,

$$P = \frac{Q^2}{\alpha+Q^2} \exp\{-\delta_{10} x_{18}\}$$

Parameter values (α,{δ}) were found using a minimization routine where the objective function was mean $(\log P - \log P^*)^2$, with P^* the true early survival. The latter was estimated for each quadrat from the ratio "seedlings in 1994/seeds in 1993."

The study for which these data were gathered was conceived for purposes other than those discussed in this paper. Only *Anthyllis* was considered from the perspective of INTASS. While this, unfortunately, precludes a full analysis of potential grazing management effects, the following analysis nevertheless provides a partial illustration of how INTASS can be used for assessing such effects. Suppose, for example, that grazing were to be doubled. What would such a change do to the plant community, and ultimately to the well being of the grazers and to the consequent economic costs and benefits?

To address this question, we make use of the variable values gathered from random quadrats, but double the number of grazers in each quadrat. Then, using the derived parameter values for all plant species and a computer routine to figuratively add or subtract plant cover for all plant species, quadrat-by-quadrat, in such manner as to maintain minimum variance in fitness (keeping with the basic INTASS assertion) until average fitness returns to a value indicating population equilibrium (this will be the P^* value used in the analysis in most cases). Of course a doubling in grazer number will not necessarily result in a doubling of grazers, equally, in all quadrats; the grazers may shift their dispersion pattern as a function of social factors and/or increased competition for food. Certainly grazer dispersion will change as plant dispersion and codispersion change consequent to the increased grazing pressure. Thus, once a new, first estimate for plant abundance and distribution pattern has been calculated, the INTASS expression derived for the grazer must be used to calculate a next estimate for grazer dispersion pattern. This, in turn, is used to calculate a second estimate for plant dispersion and codispersion. The process is continued until convergence occurs in the values obtained.

In the present instance, we have an INTASS expression for *Anthyllis* only, so the full process cannot be demonstrated. Suppose, however, purely for the purposes of illustration, that we suppose the grazers don't redistribute themselves as their density changes and as plant distributions change, and that plant interactions have minimal effect on the response of *Anthyllis* to grazing. Then we can at least calculate the impact of a change in grazing intensity on the cover of *Anthyllis*. To do so we applied the model with the parameter values in table 1 (we used those for $P^* = 0.03$), incrementing or decrementing *Anthyllis* cover in each quadrat individually in such manner as to minimize Var(logP-logP*) until mean of logP equalled logP*.

Table 1—Derived parameter values for the *Anthyllis* model, with 95% confidence range for the case of P* = 0.03.

Parameter	δ Value P* = 0.01	0.03	0.10	95% confidence range for P*= 0.03
Soil organics	0.027	0.027	0.029	0.012 to 0.048
Soil pH	1.044	1.074	1.075	1.064 to 1.081
Conductivity	−0.179	−0.235	−0.221	−0.210 to −0.264
Texture	−0.070	−0.079	−0.103	−0.035 to −0.132
Slope	−0.058	−0.058	−0.057	−0.045 to −0.071
Grazing	0.187	0.181	0.162	0.147to 0.216
Anthyllis cover	1.0000 by definition			---
Artemisia cover	0.113	0.113	0.113	0.061 to 0.165
Stipa cover	0.432	0.432	0.432	0.252 to 1.116
Retama cover	0.902	0.902	0.902	0.010 to 1.794
Other grasses	0.824	0.824	0.824	0.734 to 0.914
α	0.354	0.107	0.032	0.088 to 0.127

$$Q = \frac{(\text{organics})^{.027}(\text{pH})^{1.044}(\text{slope})^{-.058}(\text{conduct})^{-.179}(\text{texture})^{-.070}}{(\textit{Anthyllis})+.113(\textit{Artemisia})+.432(\textit{Stipa})+.902(\textit{Retama})+.824(\text{grasses})}$$

$$P = \frac{Q^2 \exp\{-.181(\text{grazing})\}}{.107+Q^2}$$

Results

Early survival based on data from 1993 and 1994 (number of seedlings in 1994/number of seeds in 1993) is about 0.03. Of course, this can be expected to vary year-to-year. Accordingly, analyses were run for P* values ranging from 0.01 to 0.10. Except for the value of α, results varied only slightly (table 1). Confidence intervals, based on the inverted Hessian matrix approach were calculated using a P* value of 0.03.

The impact of various putative management schemes (doubling grazing pressure, eliminating grazing pressure, raising soil organic content by 20%, doubling soil organic content, raising pH by 0.1) are given in table 2. As might be expected in a situation where moisture, primarily a global, not locally varying variable, is undoubtedly the major factor influencing fitness, the only variable that appears to make much difference to *Anthyllis* is grazing pressure. Furthermore, even the effect of grazing is modest, a fifty percent change in grazing intensity resulting in a change in *Anthyllis* cover of only about 14 to 15%.

Table 2—Impact on *Anthyllis* cover of various habitat alterations.

Management action	Change in *Anthyllis* cover
	Percent
Double number of grazers	−13.4
Eliminate grazers	+15.4
Raise soil organic content by 20%	+0.5
Double soil organic content	+2.0
Raise pH by 0.1	+1.4

Discussion and Conclusions

Accurate and exhaustive data, gathered over time to reflect seasonal and annual variation in climate, form the most reliable basis for predictive models for resource management. The number of factors that must be considered, however, make prediction a risky practice because of the tendency for cascading errors in complex models. In addition, the time required to obtain parameter values sufficiently accurate to guard against such output errors is often much longer than managers have before management decisions have to be made. The INTASS approach, used to parameterize models of intermediate complexity, using rapidly and inexpensively acquired quadrat-type data, represents a practical compromise between simplistic approaches and unreliably unrealistic insistence on completeness. It represents a viable approach to addressing management problems where time and money are limited.

Work continues on protocols for modeling and on the development of user-friendly software for INTASS applications. We are still in a fairly early stage of our work, but would be delighted to share our ideas and existing software with interested parties. In particular, we welcome input, suggestions, research collaborations, questions from those who might start their own investigations into this methodology.

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Spacing Patterns in Mojave Desert Trees and Shrubs

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Abstract—Planting shrubs at an excessive density or planting incompatible species together may reduce desert revegetation success. As part of the revegetation program at a Mojave Desert mine, a study was initiated to determine spacing patterns among the woody perennial species in areas not disturbed by the current mining activity. Shrub density ranged from approximately 9,000-14,000 individuals/ha. Most shrubs were found to be randomly dispersed; however, larger shrubs such as creosote bush (*Larrea tridentata*), and Joshua tree (*Yucca brevifolia*), were regularly dispersed and widely spaced. Plants were found to often associate with conspecific neighbors. Data on species composition, density, dispersion, and neighbor preferences will be used in mine site revegetation.

Climatic conditions favorable for germination and establishment of native perennials are infrequent and unpredictable in the Mojave Desert (Barbour 1968), limiting the value of direct seeding for desert revegetation (Bainbridge and Virginia 1990; Lippitt and others 1994). Fortunately, nursery stock can be successfully transplanted in hot deserts (Bainbridge and Virginia 1990; Fidelibus and Bainbridge 1994; Romney and others 1989), facilitating recovery and speeding visual relief. Factors such as poor substrate quality, lack of plant protection and drought have been found to limit initial survival of transplants on bare areas (Bainbridge and Virginia 1990; Bainbridge and Fidelibus 1994). Plant interactions occurring several years after planting, however, may ultimately determine transplant success.

Previous studies have shown that competition in the desert is limited to belowground interactions (Cody 1986; Rundel and Nobel 1991). Fonteyn and Mahall (1981) have documented competition for soil moisture between creosote bush (*Larrea tridentata*) and bursage (*Ambrosia dumosa*). Chew and Chew (1965) found that creosote bush density is correlated with mean annual rainfall suggesting intra-specific competition. Furthermore, Cody (1986) has shown that some Mojave Desert shrub species may "prefer" or "avoid" specific species as neighbors, possibly because of competitive interactions between plants with similar root structure. Mine spoils and other disturbed substrates are often deficient in nutrients, organic matter, and microsymbionts, and may have poor moisture holding capacity (Fidelibus, unpublished data). As a result, belowground interactions may be different in revegetation sites than in native systems. At Viceroy Gold Corporation's Castle Mountain Mine, revegetation success will be determined by comparing plant diversity and density of revegetated lands to undisturbed sites 10 years after revegetation is completed. If transplants are placed too close together or in antagonistic relationships, revegetation goals may not be met.

To facilitate selection and placement of transplants at the mine site, a study was initiated to determine inter- and intra-specific shrub spacing patterns in areas not disturbed by current mining. Point to plant and nearest neighbor methods were used to determine species density and dispersion patterns, and examine inter- and intra-specific neighbor preferences. This data will be used to determine species composition, juxtaposition and distancing when replanting disturbed areas.

Methods

Current mining operations will disturb approximately 343 ha (at an average elevation of 1,300 m). Vegetation was classified into three major communities by Everett (1991), based upon the descriptions of Holland (1986). The communities in order of decreasing acreage are: Joshua tree (*Yucca brevifolia*) woodland (JTW), blackbrush (*Coleogyne ramosissima*) scrub (BBS), and Mojave mixed steppe (MMS). An on-going study is determining substrate qualities, elevation, slope, and aspect of undisturbed communities in order to determine which assemblages of native plants will be best suited for the modified substrates and new topography created by mining operations. It is expected that each community type will be recreated within the mine site. Sites for vegetation sampling were chosen to include each major community and were coordinated with the soil study.

Seventeen 50 m by 50 m quadrats were established within areas which were judged to be representative of the community sampled; 11 quadrats in JTW, 4 quadrats in BBS, and 2 quadrats in MMS. The JTW and BBS quadrats were established on relatively flat substrates of similar (within community type) elevation and substrate to insure that slope, aspect, elevation, or substrate differences were not responsible for observed vegetation patterns. The MMS community occurs on steep, rocky, slopes. For these sites, quadrats were established on slopes of similar aspect, elevation, and grade.

In each quadrat, twenty sampling points were selected using stratified random coordinates. At each point, the distance to the nearest perennial shrub was measured, and

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distances from this shrub to its first and second nearest neighbor and its nearest conspecific (if the nearest neighbor was a different species) were also recorded. For each species, the average point to plant distance (m) was calculated, and this value was used to estimate species density (# individuals/ha) following the methods of Cottam and Curtis (1956).

The observed mean distance between conspecifics was compared to the expected mean distance (generated by assuming a random distribution of each species at their measured density). Departure from randomness was then determined by the ratio of the observed mean distance to the expected mean distance as described by Clark and Evans (1954).

To determine if a specific species was a nearest or second nearest neighbor more or less frequently than would be expected based upon their density, chi-square analyses were performed (Cody 1986). Species are described as "preferred" neighbors if they occur as neighbors more often than would be expected by chance ($p < 0.05$), and "avoided" if they occur as neighbors less often than expected by chance. If species were found to be neighbors as often as would be expected by chance alone ($p > 0.05$), then their relationship is described as "neutral." The mechanisms behind preferred, avoided or neutral relations were not investigated.

Revegetation of Joshua trees is an important goal at the mine, and because the species is present in lower densities than other perennials, the distance from each random point to the nearest Joshua tree, and the distance to the nearest neighbor Joshua tree, were also recorded (if Joshua trees were within 10 m of a point) to insure an adequate data set for this species.

Results

Density

Shrub density varied among community type (table 1). The BBS community had the highest shrub density (14,800 shrubs/ha), but the lowest diversity (9 species). The JTW community had the lowest shrub density (8,900 shrubs/ha) but the highest species diversity (26 species). The MMS had intermediate shrub density (12,500 shrubs/ha) and diversity values (12 species). Relative shrub densities often differed dramatically among communities, and some species were characteristic of, or limited to, specific communities. The density of blackbrush, for instance, was nearly 9,000 individuals/ha in the BBS community; a density greater than the overall shrub density in the JTW community (table 1). By contrast, blackbrush occurred only infrequently in JTW, and was absent from the MMS sites.

Few species (other than blackbrush) were found in their highest relative densities in the BBS community (table 1); however, Mormon tea (*Ephedra nevadensis*), Pima rhatany (*Krameria erecta*) and Anderson's thornbush (*Lycium andersonii*) were equally abundant in BBS and MMS, occurring in JTW at lower relative densities (table 1). The arborescent monocots, Mojave yucca (*Yucca schidigera*) and Joshua tree, were found to occur at identical densities across the BBS and JTW communities. Cooper's goldenbush (*Ericameria cooperi*), a very abundant species in JTW (2,952/ha), was much less common in BBS (561/ha).

Table 1—The density (# of individuals/ha) of selected shrub species in three different plant communities surrounding Castle Mountain Mine, in the east Mojave Desert.

Common name	Species name	BBS[1]	JTW[2]	MMS[3]
Anderson's thornbush	*Lycium andersonii*	1,684	1,011	1,562
Beavertail cactus	*Opuntia basilaris*	0	202	0
Blackbrush	*Coleogyne ramosissima*	8,984	647	0
Buckhorn cholla	*Opuntia acanthocarpa*	0	121	0
California barrel cactus	*Ferocactus cylindraceus*	0	40	1,562
California buckwheat	*Eriogonum fasciculatum*	187	40	2,500
Cooper's goldenbush	*Ericameria cooperi*	561	2,952	625
Creosote bush	*Larrea tridentata*	936	1,051	1,875
Joshua tree	*Yucca brevifolia*	374	364	0
Mojave prickly pear	*Opuntia erinacea*	0	243	0
Mojave yucca	*Yucca schidigera*	374	364	625
Mormon tea	*Ephedra nevadensis*	1,123	647	1,250
Pima rhatany	*Krameria erecta*	749	566	0
Total shrub density[4]		14,800	8,900	12,500

[1]BBS = Blackbrush Scrub.
[2]JTW = Joshua Tree Woodland.
[3]MMS = Mojave Mixed Steppe.
[4]The calculation of total shrub density is based upon all observed species, including several less common shrubs not displayed in this table.

Table 2—Average distance (m) and standard error between the nearest neighbor (NN) and the nearest conspecific (NCSP) of several species of shrubs surrounding Castle Mountain Mine.

Species	BBS		JTW		MMS	
	NN	NCSP	NN	NCSP	NN	NCSP
Anderson's thornbush	0.40 ± 0.06	1.24 ± 0.46	0.79 ± 0.13	1.79 ± 0.29	0.50 ± 0.11	1.04 ± 0.31
Beavertail cactus			0.50 ± 0.22	5.39 ± 1.88		
Blackbrush	0.61 ± 0.03	1.39 ± 0.60	0.62 ± 0.07	1.05 ± 0.17		
Buckhorn cholla			1.83 ± 1.00	6.48 ± 2.79		
California barrel cactus					0.72 ± 0.17	2.01 ± 0.73
California buckwheat					0.53 ± 0.08	0.59 ± 0.09
Cooper's goldenbush	0.77 ± 0.09	1.1 ± 0.3	0.70 ± 0.06	1.05 ± 0.16	1.02 ± 0.78	2.17 ± 0.61
Creosote bush	1.02 ± 0.30	3.40 ± 0.98	1.07 ± 0.13	1.83 ± 0.29	0.69 ± 0.10	1.64 ± 0.29
Joshua tree		6.97 ± 0.69		6.97 ± 0.69		
Mojave prickly pear			0.74 ± 0.19	3.55 ± 0.77		
Mojave yucca	0.47 ± 0.22	5.67 ± 0.03	0.45 ± 0.17	10.31 ± 1.96	1.10 ± 0.76	7.27 ± 2.13
Mormon tea	0.72 ± 0.30	1.03 ± 0.49	0.79 ± 0.16	2.72 ± 0.70	0.62 ± 0.29	1.15 ± 0.55
Pima rhatany	0.38 ± 0.13	0.98 ± 0.31	0.51 ± 0.11	1.50 ± 0.34		

The density data indicates that Joshua tree woodland is primarily composed of a variety of small shrub species (table 1), with Joshua trees occurring at relatively low densities (374/ha, nearly the same density as in BBS). Cooper's goldenbush was the most abundant species, occurring at a density nearly three times that of the two next most abundant species in JTW; Anderson's thornbush and creosote bush (*Larrea tridentata*).

In the MMS community Joshua trees were absent, while Mojave yucca occurred at a density nearly equal to the combined density of both Yucca species in BBS or JTW. There were few species of cacti in MMS, aside from the California barrel cactus, (*Ferocactus cylindraceus*), a dominant plant on rocky slopes surrounding the mine (table 1).

Distance Between Plants

The average distance between shrubs and their nearest neighbors was found to be similar among communities (table 2). Most shrub species were found to grow within 0.5-1.0 m of another shrub. The average distance between conspecifics was typically much higher than the average distance to a nearest neighbor.

Dispersion

Most shrubs were found to be randomly dispersed (table 3). A regular dispersion pattern was observed for some large shrubs for example, blackbrush, California barrel cactus, creosote bush, Joshua tree, and Mojave yucca; table 3). California buckwheat (*Eriogonum fasciculatum*) was the only species tested which showed a clumped distribution.

Neighbor Preference or Avoidance

Neighbor preference or avoidance was only observed with a few species, and positive interactions (neighbor preferences) were more common than negative interactions (neighbor avoidances). Conspecific preferences were observed for Anderson's thornbush, blackbrush, California buckwheat, Cooper's goldenbush, creosote bush, Mormon tea, and pima rhatany. Avoidance was observed between Anderson's thornbush and creosote bush, Cooper's goldenbush, and pima rhatany. The significant neighbor preferences and avoidances for Cooper's goldenbush are displayed as an example (table 4).

Table 3—Dispersion pattern of common shrubs in three plant communities near Castle Mountain Mine, in the East Mojave Desert ($p < 0.05$).

Species	BBS	JTW	MMS
Anderson's thornbush	random	random	random
Beavertail cactus		random	
Blackbrush	regular	random	
Buckhorn cholla		random	
California barrel cactus			regular
California buckwheat			clumped
Cooper's goldenbush		random	
Creosote bush	regular	random	random
Joshua tree	regular	regular	
Mojave prickly pear		random	
Mojave yucca		regular	
Mormon tea	random	random	random
Pima rhatany	random	random	

Table 4—Selected results of chi square analysis of first and second nearest neighbor data for Cooper's goldenbush. Results with a Chi square value greater than 3.88 indicate significance at $p < 0.05$. Insignificant results are not displayed.

Cooper's goldenbush	NN1			NN2		
Neighbors	Expected	Observed	X^2	Expected	Observed	X^2
Cooper's goldenbush	24.88	42	11.77	27.54	49	16.72
Creosote bush	8.86	3	3.88	9.8	0	9.8

Discussion

Density

High shrub densities were found in BBS and MMS communities (12,500-14,800 individuals/ha; table 1). These findings agree with Lei and Walker (1994) who reported that blackbrush were "extremely abundant" within BBS communities (in southern Nevada), and Holland (1986) who characterized MMS as being a "fairly dense" plant assemblage. Everett (1991) also noted that density and diversity increase in MMS sites with increased grade and rockiness, and these sites were rocky and relatively steep grade. Cody (1986) noted that species diversity and density is related to sampling area. Consequently, more species may have been noted in BBS and MMS communities if sampling intensity were higher.

Although less abundant than BBS or MMS, plant density in JTW (table 1) was similar to, but higher, than values reported by Cody (1986); 8,900 plants/ha vs. 7,000 to 8,000 plants/ha. However, much of the desert surrounding the mine is free range, and JTW suffers the most intense grazing pressure. Evidence of grazing is expressed as heavily browsed grasses and shrubs and well marked cattle trails. Thus, plant density may be reduced in JTW because of herbivory.

If the 900 acres of disturbance were revegetated at a density similar to that of an undisturbed community (approximately 1 plant/m^2), more than 3.6 million shrubs would be required. Producing and planting this many shrubs would be impossible; however, plant spacing and neighbor interactions are still important.

Diversity

The low species diversity found in BBS was also noted by Lei and Walker (1995) who attributed the low diversity in BBS to blackbrush abundance. Species diversity in JTW (26 species) was similar to Cody's (1986) findings (35 species); although Cody's study, unlike ours, included perennial grass species. Much of the diversity in JTW comes from small shrubs. Larger shrubs such as creosote bush, Mojave yucca, and Joshua tree are visually important, however, they were found to grow in low densities (table 1). The revegetation program's emphasis on species diversity appears to be an ecologically sound management criteria.

Distance

Distance to nearest neighbor data (table 2) show that many shrubs grow closer together (0.5-1.0 m) than might be expected based upon mean density (approximately 1 plant/m^2). We also observed that the nearest conspecific was usually much further away (1.0-7.0 m) than the nearest neighbor (of any species). These findings are consistent with the observations that shrubs may form small groups or "islands" where plants are more densely packed, and that these islands may often be composed of several shrub species. Shrub islands are common in the deserts of the Southwest, and they play an important role in the ecology of desert shrubs (Goodall and Perry 1979). Thus, planting inter-specific assemblages of shrubs may be an effective revegetation strategy.

Dispersion and Neighbor Preference

The results of the dispersion and neighbor preference data analysis indicates that shrubs are generally randomly dispersed (in relation to other individuals of the same species), with a few larger shrub species being regularly dispersed (table 3). A random dispersion may simplify revegetation at the mine provided that shrubs are not planted near incompatible neighbors. The mechanism(s) creating a regular dispersion of trees, such as Joshua trees, is unknown but using the wide spacing observed in nature may be important for revegetation success. The clumped dispersion of California buckwheat is probably the result of the rocky terrain where sites for plant establishment are not uniformly distributed across the quadrat.

The results of the nearest neighbor analysis are less clear. Conspecific preferences were noted for several species including blackbrush, and Cooper's goldenbush (table 4), although these interactions are less common for second nearest neighbors than they are for first nearest neighbors. It is possible that observed conspecific preferences are the result of clonal growth forms, however, this hypothesis is not supported by distances to nearest conspecifics (which are typically longer than distances to the nearest neighbor).

Conclusions

Species composition and patterns in vegetation are often difficult to distinguish without performing systematic sampling. Vegetation sampling should be conducted to improve the chance of revegetation success by detecting spacing patterns and neighbor interactions, and to avoid focusing on charismatic mega-flora. Natural plant assemblages in desert systems may be slope, aspect, or substrate dependent, and belowground relations may be altered on disturbed substrates. However, belowground competition has been documented and should be considered when planning revegetation projects.

Acknowledgments

We thank John Tiszler, Robert MacAller, and Debbie Waldecker for field assistance and helpful editorial suggestions.

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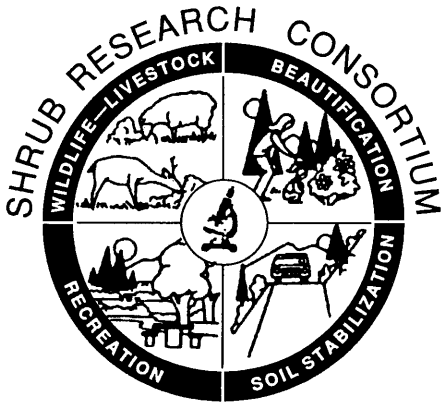

Ecophysiology

Impacts of Rising CO_2 Concentration on Water Use Efficiency of Woody Grassland Invaders

H. Wayne Polley
Hyrum B. Johnson
Herman S. Mayeux
Charles R. Tischler

Abstract—Water availability controls plant productivity and the abundance of shrubs on many rangelands. That control is mediated by factors like atmospheric CO_2 concentration that influence plant water use efficiency. Increasing CO_2 over past and projected levels elicited a similar (mesquite, *Prosopis glandulosa*; huisache, *Acacia smallii*) or possibly greater (threadleaf snakeweed, *Gutierrezia microcephala*) relative increase in intrinsic water use efficiency (photosynthesis/conductance) of shrubs that recently have proliferated on southwestern rangelands. The contribution of higher photosynthesis to the increase differed among species, however. By increasing productivity and competition for light, higher water use efficiency may favor taller woody plants over grasses on some rangelands. Rising CO_2 may benefit shrubs that realize much of the increase in water use efficiency as higher photosynthesis.

Because plant uptake of CO_2 (carbon dioxide) through stomata unavoidably is associated with water loss, plant growth is intimately coupled to water use. It is not surprising, therefore, that the distribution (Stephenson 1990; Whittaker 1975; Woodward 1987) and productivities of woody and other species (Rosenzweig 1968; Sala and others 1988; Webb and others 1978) often are strongly correlated with water availability and soil water balance. On grasslands and savannas where plant productivity is particularly closely coupled to precipitation (Pandey and Singh 1992; Sala and others 1988; Webb and others 1978), water availability in space and time exerts a dominant climatic control on the balance between grasses and woody species (Polley and others 1996). Water availability in these systems and other arid regions may be especially important during the critical period of woody establishment when seedlings often succumb to dehydration (Donovan and others 1993; Harrington 1991; Williams and Hobbs 1989).

Important to plant performance in arid and seasonally-dry environments is the efficiency with which water is used during growth. In water-limited systems, an increase in water use efficiency resulting from the global rise in atmospheric CO_2 concentration or other factors should increase plant productivity and may contribute to changes in the species and growth form composition of vegetation by favoring taller woody plants at the expense of grasses (Polley and others 1996). Changes caused by rising CO_2 in the coupling of vegetation and climate have, however, largely been overlooked in discussions of vegetation change in these systems. Most prior treatments of species change on arid and seasonally-dry grasslands implicate climate change, fire suppresion, and overgrazing or other effects of livestock (Archer 1994; Bahre and Shelton 1993; Grover and Musick 1990; Neilson 1986).

Atmospheric CO_2 concentration has increased 25% to 30% during the last two centuries from the preindustrial level of 270 to 280 μmol CO_2/mol air (parts per million, mole fraction basis) to the current 350 μmol/mol (Neftel and others 1985; Raynaud and Barnola 1985) and perhaps 100% since the last ice age 18,000 to 20,000 years ago (Delmas and others 1980; Neftel and others 1988). Recent changes largely reflect fossil fuel combustion and accelerated changes in land use. These changes are projected to contribute to atmospheric CO_2 levels during the next century that are at least double those of the preindustrial period.

We report effects of experimentally increasing CO_2 from near Ice Age levels to the current concentration and from the current concentration to levels possible in the future on a measure of water use efficiency of seedlings of woody species that recently have increased in abundance on grazing lands in the southwestern U.S. We studied these effects on the legumes honey mesquite (*Prosopis glandulosa*) and huisache (*Acacia smallii*) and half-shrub threadleaf snakeweed (*Gutierrezia microcephala*) using stable carbon isotope signatures of leaves and leaf gas exchange measurements. Each of the species possesses the C_3 photosynthetic pathway.

Threadleaf snakeweed is found in western Texas, New Mexico, Arizona, Utah, and northern Mexico (Pieper and McDaniel 1990). This short-lived half-shrub and the morphologically-similar broom snakeweed (*G. sarothrae*) were present on rangelands 100 years ago, but increased in number following droughts in the 1950s, 1970s, and 1980s. Abundance of mesquite on southwestern rangelands has increased greatly during the last 150 years. The increase reflects expansion of the legume within its historical range or an increase in the stature and visibility of suppressed populations (Bogusch 1952; Johnston 1963). Huisache is a aggressive invader of rangeland in southern Texas and

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northern Mexico. Vegetation surveys of Texas, for example, indicate an increase in the woody legume of over 20% per decade or 48% during the interval from 1964 to 1982 (USDA 1985).

Theory

Water use efficiency often is assessed at the leaf level as transpiration efficiency, the ratio of net photosynthesis or assimilation (A) to transpiration (E). In most C_3 plants, A usually is positively related to leaf intercellular CO_2 concentration (ci) over the physiological range and thus depends both on external CO_2 concentration (ca) and on the rate at which CO_2 diffuses through stomata into leaves as:

$$A = \frac{(ca-ci)g}{1.6} \quad (1)$$

where g is stomatal (leaf) conductance to water vapor and 1.6 is the ratio of the diffusivities of water vapor and CO_2 in air. Transpiration also is regulated by g and by v, the mole fraction water vapor gradient from leaves to bulk air as,

$$E = vg \quad (2)$$

Instantaneous water use efficiency, A/E, and the closely-related intrinsic water use efficiency, A/g (A/E calculated without v), thus are directly affected by changes in both A and g, each of which is sensitive to atmospheric CO_2 concentration.

On combination and rearrangement of eq. 1 and 2, it becomes evident that A/E and A/g are positively related to ca and negatively related to ci/ca, the latter of which reflects the balance between the supply of CO_2 to the leaf and consumption of CO_2 in photosynthesis,

$$\frac{A}{E} = \frac{1}{v} \times \frac{A}{g} = \frac{1}{v} \times \frac{ca(1-ci/ca)}{1.6} \quad (3)$$

A temporally-integrated measure of ci/ca conveniently is reflected in the difference between the stable C isotope (^{13}C, ^{12}C) compositions of photosynthesizing leaves of C_3 plants and the CO_2 present in the air in which leaves were grown (Farquhar and others 1982). Carbon fixed by plants is enriched in ^{12}C relative to the CO_2 in air and thus reflects a positive discrimination (Δ) against the heavier ^{13}C isotope where:

$$\Delta = \frac{\delta_a - \delta_p}{1 + \delta_p} \quad (4)$$

and δ_p and δ_a are the carbon isotope compositions of plant tissues and CO_2 in air expressed in "delta" units (per mil, ‰) relative to a standard. Carbon isotope discrimination by C_3 plants can be positively related to ci/ca by

$$\Delta = a + (b-a)ci/ca \quad (5)$$

where a and b are treated as constants that describe isotopic fractionation resulting from the diffusion of CO_2 in air and during carboxylation, respectively (Farquhar and others 1982).

Effects of Rising CO_2 Concentration on Intrinsic Water Use Efficiency

Measurements of CO_2 concentration and of the stable C isotope compositions of air and leaves were used to calculate ci/ca (eq. 5) and intrinsic water use efficiency, A/g, (eq. 3) of seedlings of honey mesquite, threadleaf snakeweed, and huisache that were grown in atmospheres with different CO_2 concentrations. Threadleaf snakeweed and the legume mesquite were grown in separate experiments over a continuous daytime gradient in atmospheric CO_2 concentration that ranged from near that of the last glaciation (200 µmol/mol) to the present level (350 µmol/mol). Plants were grown within an elongated controlled-environment chamber located within a ventilated glasshouse (Mayeux and others 1993). Aerial parts of plants were enclosed in a tunnel-like polyethylene cover attached to the top of a 0.76 m (30 inch) deep, 0.45 m (18 inch) wide, and 38 m (125 foot) long soil container. Air was moved unidirectionally through the chamber. The dewpoint and dry-bulb temperatures of air were automatically reset to conditions within the glasshouse at five equally-spaced points along the chamber. Huisache was grown in a separate experiment at nominal CO_2 levels of 350, 700, and 1,000 ppm in air-conditioned glasshouse bays. Water was added weekly during all experiments to bring soils to field capacity.

The $\delta^{13}C$ values of air and of leaves of mesquite, snakeweed, and the concurrently-grown C_4 grass maize (*Zea mays*) increased linearly (became more enriched in ^{13}C) as plants depleted CO_2 from the present concentration to atmospheric levels near those of the last glaciation (figs. 1, 2). The difference between the $\delta^{13}C$ values of atmospheric CO_2 and

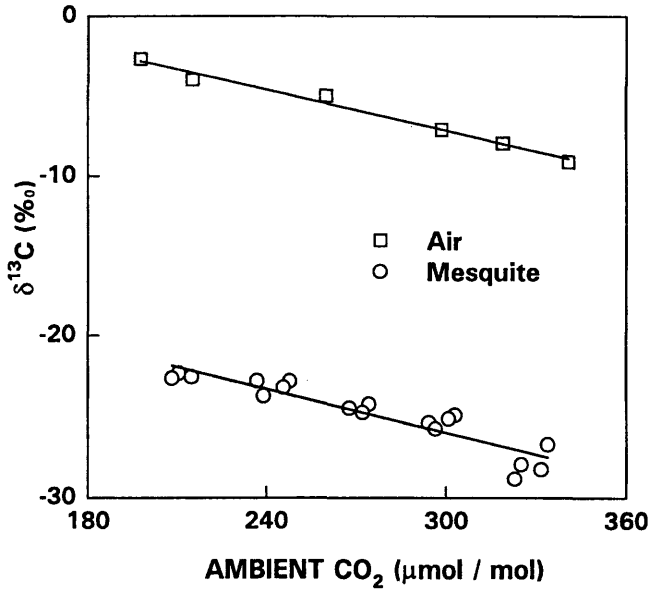

Figure 1—The stable carbon isotope composition ($\delta^{13}C$) of air and upper leaves from 1-year-old mesquite plants grown along a daytime gradient of subambient CO_2 concentration. Lines are linear regressions of $\delta^{13}C$ on instantaneous (air) or mean daytime CO_2 concentration (leaves). The figure is reproduced from Polley and others (1994).

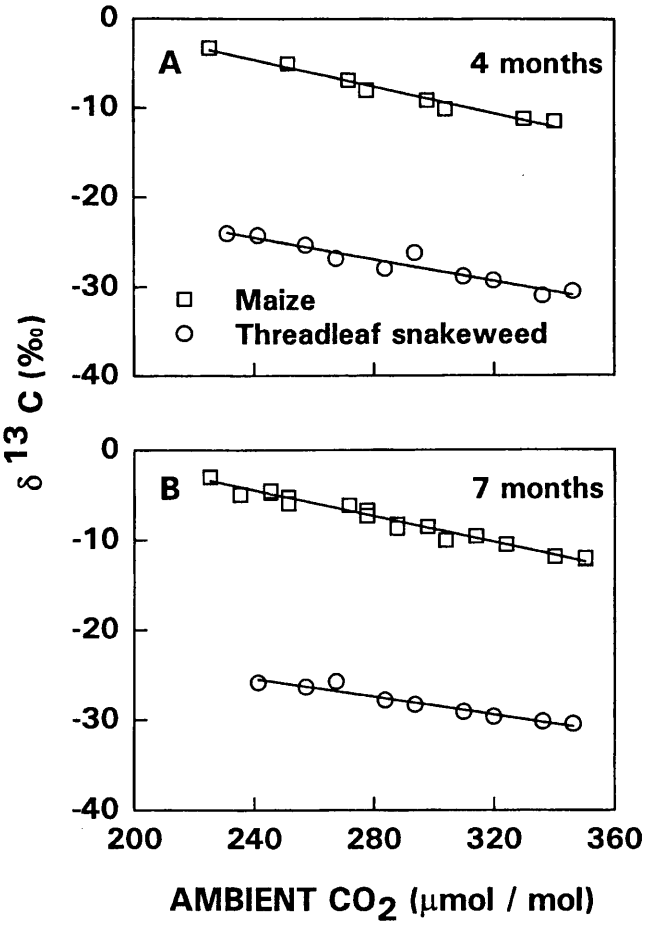

Figure 2—The stable carbon isotope composition ($\delta^{13}C$) of upper leaves from C_3 threadleaf snakeweed and C_4 maize plants grown along a daytime gradient of subambient CO_2 concentration. Snakeweed had been grown at the different CO_2 concentrations for (A) 4 and (B) 7 months when samples were collected. Data points for maize represent single measurements per plant. A single measurement at each CO_2 level was taken on a composite of leaves collected from five to six plants of 4-month-old threadleaf snakeweed (A). Values for 7-month-old snakeweed are means of $\delta^{13}C$ measurements on leaves from each of six plants per CO_2 level (B). Lines are linear regressions of $\delta^{13}C$ on mean daytime CO_2 concentration. Slopes of linear regressions differed significantly between maize and 4-($P<0.05$) and 7-month-old plants of threadleaf snakeweed ($P<0.001$).

leaf carbon of maize was found be conservative at 3.1‰ (Polley and others 1993), allowing us to use the $\delta^{13}C$ value of maize leaves grown in the same air as shrubs to calculate the isotope composition of air along the CO_2 gradient. Slopes of linear regressions of $\delta^{13}C$ on CO_2 concentration did not differ significantly between the air and leaves from 1-year-old mesquite plants (fig. 1; $P > 0.50$). As a result, Δ (eq. 4) and ci/ca (eq. 5) remained nearly constant across CO_2 concent rations, and A/g of mesquite increased by about the same relative amount as did CO_2 concentration (fig. 3).

Leaf $\delta^{13}C$ increased slightly more rapidly in maize than in 4- and 7-month-old plants of threadleaf snakeweed as CO_2 was depleted below the current concentration (fig. 2). Assuming that Δ of well-watered maize remained constant across CO_2 levels at 3.1‰, Δ of the shrub decreased from about 23.7 to 22.1‰ and from 24.6 to 22.3‰ as CO_2 rose from about 240 to 345 μmol/mol, in 4- and 7-month-old plants, respectively. The decline in carbon isotope discrimination of snakeweed as CO_2 increased suggests that ci/ca also declined at higher CO_2 concentrations (eq. 5), and that leaf A/g of the shrub rose by a greater relative amount than did CO_2 concentration (about 98% and 125% in 4- and 7-month-old plants with the 44% increase in CO_2 concentration from 240 to 345 μmol/mol).

Temporally-integrated values of ci/ca for huisache were calculated from the carbon isotope signatures of huisache and maize leaves grown at the current and elevated CO_2 concentrations. The ci/ca of 8-month-old huisache seedlings differed little among CO_2 treatments (mean = 0.66, 0.69, 0.71 for plants grown near 360, 700, and 1000 μmol/mol), indicating that as CO_2 increased, leaf A/g of the legume increased by a similar relative amount.

Instantaneous measurements of leaf gas exchange confirmed that A/g of the two legumes, mesquite and huisache, increased by a similar relative amount as did CO_2 concentration. In neither species did ci/ca vary with CO_2 treatment (mean = 0.65 for mesquite, $n = 17$; 0.74 for huisache, $n = 72$). Contrary to results from isotope analyses, however, gas exchange measurements on leaves and photosynthetic stems of threadleaf snakeweed indicated that ci increased linearly and proportionally (by the same ratio) with ambient CO_2 (fig. 4). The ci/ca calculated from gas exchange measurements also did not differ with tissue type (mean = 0.87).

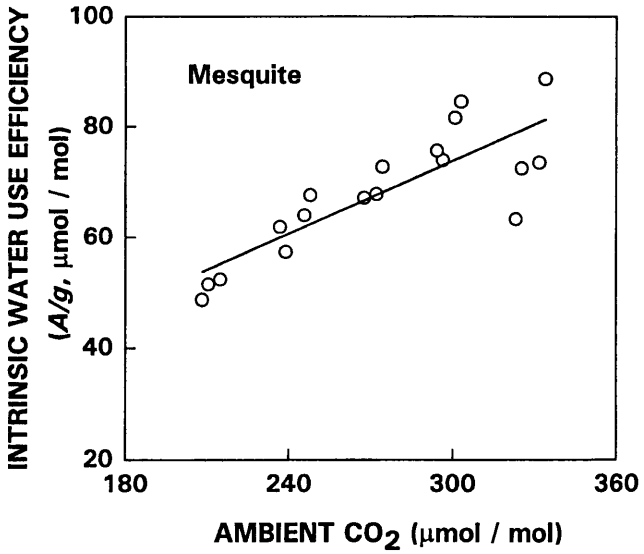

Figure 3—Relationship betwen intrinsic water use efficiency (net photosynthesis (A)/stomatal conductance to water (g)) of mesquite plants derived from the $\delta^{13}C$ of leaves and the daytime CO_2 concentration at which plants were grown. The line is a linear regression of A/g on CO_2 concentration.

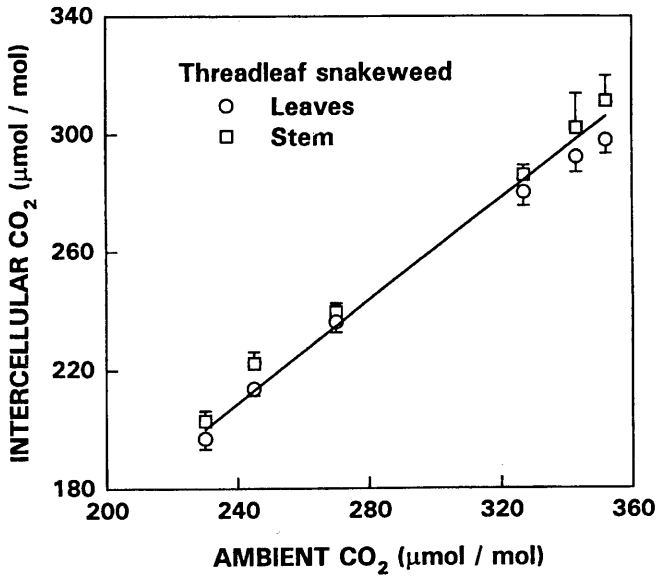

Figure 4—Intercellular CO_2 concentration (*ci*) of leaves and photosynthetic stems of threadleaf snakeweed plants as a function of the CO_2 concentration at which plants were grown and measured. Vertical bars denote 1 standard error of the mean of three gas exchange measurements per CO_2 level. The line is a linear regression that was fit through the origin to all data.

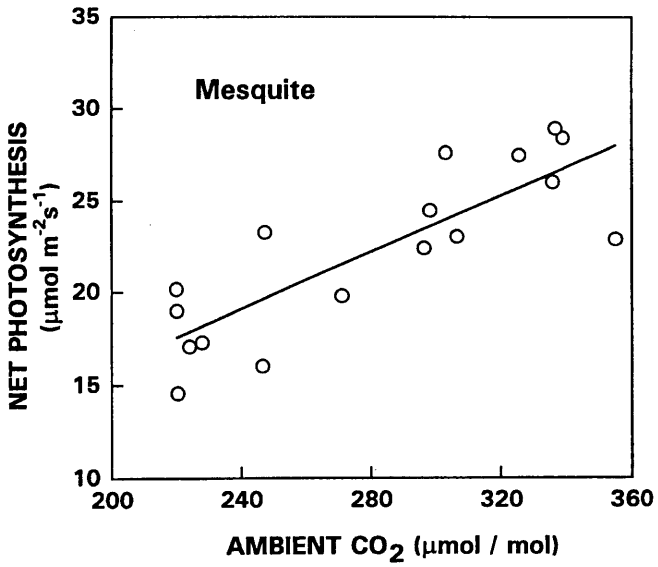

Figure 5—Leaf net photosynthetic rates of mesquite as a function of the CO_2 concentration at which plants were grown and measured. The line is a linear regression of single measurements per plant on CO_2 concentration. The figure is reproduced from Polley and others (1994).

Effects of Rising CO_2 on Net Photosynthesis and Stomatal Conductance

Gas exchange measurements also provided an indication of the extent to which changes in *g* and *A* contributed to higher water use efficiency as CO_2 rose. It was in this respect that species differed most markedly. Stomatal conductance measured at high light was not significantly altered by CO_2 from 225 to 345 μmol/mol in mesquite (Polley and others 1994). Net photosynthesis of this legume, however, increased linearly by about the same relative amount as did CO_2 concentration (fig. 5). Higher photosynthesis consequently accounted for all of the CO_2-mediated increase in A/g in mesquite. By contrast, the response of net photosynthesis to CO_2 in both leaves and photosynthetic stems of threadleaf snakeweed was strongly curvilinear (fig. 6). Photosynthesis increased markedly from about 230 μmol/mol CO_2 to near the preindustrial level of 275 μmol/mol (74 to 133%), but changed little as CO_2 was raised to the current concentration. In this species, much of any increase in water use efficiency during the last two centuries may therefore have resulted largely from a decline in conductance.

Both greater photosynthesis and lower stomatal conductance contributed to the increase in A/g of huisache from 350 to 1000 μmol/mol. Leaf net photosynthesis of huisache was not significantly ($P > 0.05$) greater in plants grown for a year near 700 μmol/mol than in those grown at 350 μmol/mol (fig. 7), but was stimulated by a further increase in CO_2 to

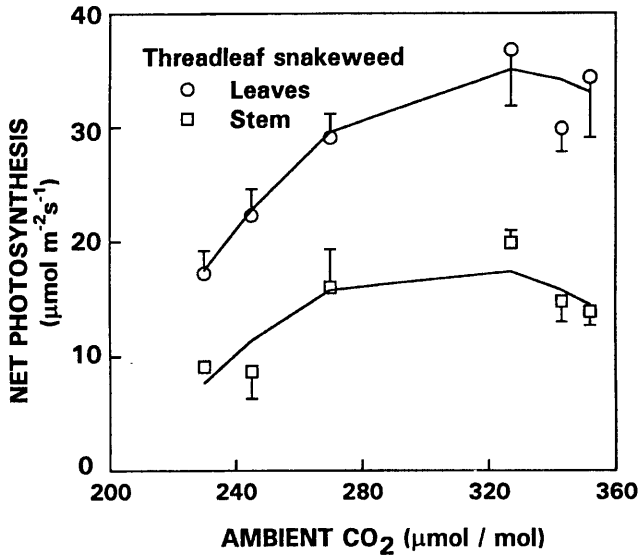

Figure 6—Net photosynthetic rates of leaves and photosynthetic stems of threadleaf snakeweed as a function of the CO_2 concentration at which plants were grown and measured. Vertical bars denote 1 standard error of the mean of three measurements on each tissue type per CO_2 level. Cubic polynomial regressions were fit to measurements on each tissue type.

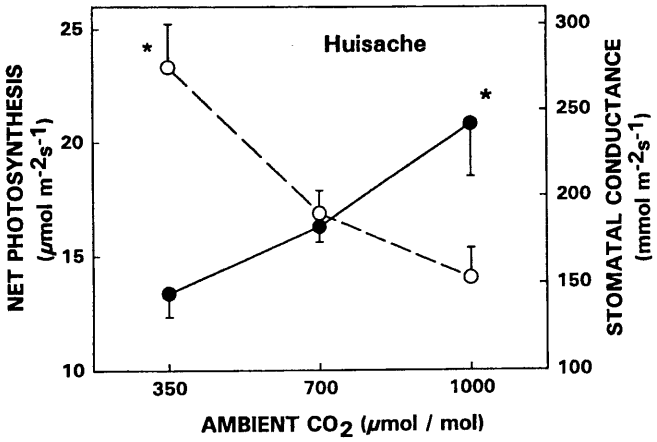

Figure 7—Leaf net photosynthesis (closed symbols and solid line) and stomatal conductance to water vapor (open symbols and broken line) of huisache measured near the CO_2 concentration that prevailed during growth. Vertical bars denote 1 standard error of the mean (n = 26, 25, and 18 leaves at 350, 700, and 1000 μmol/mol, respectively). Within measurement type, means differed significantly ($P < 0.05$) if labelled with an asterisk.

1000 μmol/mol. Conversely, stomatal conductance declined significantly from 350 to 700 μmol/mol, but did not differ at 700 and 1000 μmol/mol.

Rising CO_2, Water Use Efficiency, and Vegetation Dynamics

Increasing CO_2 dramatically increased potential water use efficiency of three shrubs that recently have become more abundant on rangelands in the southwestern U.S. A given relative increase in CO_2 concentration between 200 and 1000 μmol/mol elicited a similar (mesquite, huisache) or possibly even greater (threadleaf snakeweed) relative increase in potential water use efficiency of the shrubs. If manifested in nature, an increase in water use efficiency of the magnitude suggested during the last two centuries alone likely has increased primary productivity in water-limited ecosystems. The increase in water use efficiency may also have contributed to vegetation change. On average, for example, A/g of mesquite increased about 16.5 μmol CO_2/(mol water) with the increase in CO_2 from 275 to 350 μmol/mol that has occurred during the last two centuries. That increase is similar in magnitude to the approximately 22 μmol/mol increase in A/g that was associated with a change in C_3 composition along a soil moisture gradient in the Sonoran desert (Ehleringer and Cooper 1988). Importantly, data from huisache suggest that proportional effects of CO_2 on water use efficiency should continue unabatted to CO_2 concentrations exceeding those forecast for the foreseeable future. These changes almost certainly have contributed and will continue to contribute to species change on arid and semiarid rangelands by altering competitive relations among species or increasing plant survival during drought.

Given the differing contributions of increased photosynthesis versus decreased conductance to higher A/g that were observed among species and over different CO_2 concentrations, it is unlikely that the three shrubs would be favored similarly by a given increase in water use efficiency. Higher water use efficiency that derives primarily from lower g and transpiration may not always be competitively advantageous in water-limited environments (Cohen 1970; Delucia and Heckathorn 1989; DeLucia and Schlesinger 1991). Water that is not used by one plant may be lost to competing vegetation, evaporation, or drainage through the soil profile. Potential water savings resulting from lower g can be reduced if leaf temperature or the leaf-to-air vapor pressure gradient increase because energy is dissipated more slowly by transpiration. Further, when water is available, little or no benefit of higher CO_2 may accrue to the growth of plants that derive most of their increase in water use efficiency from a decrease in g and transpiration (Gifford and Morison 1985).

It appears from studies within and among species at the current CO_2 concentration that the opposite strategy of rapid photosynthesis and growth may be more conducive to seedling survival in a competitive environment when water is limited (DeLucia and Heckathorn 1989; Donovan and Ehleringer 1994; Donovan and others 1993). By virtue of more extensive or deeply-placed root systems, for example, larger seedlings are more competitive for surficial soil water and better able to access moisture in deeper soil layers. The greatest benefit of an increase in water use efficiency as CO_2 rises may accrue over concentrations where photosynthesis is most sensitive to CO_2 or to species which realize most of the increase as higher photosynthetic rates. We suggest, therefore, that species differences in the sensitivity of g and A to CO_2 may prove important in understanding likely consequences of an increase in water use efficiency to the success of woody and other seedlings on arid and semiarid rangelands.

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Morphological Variation in Creosotebush, *Larrea tridentata*: Effects on Ecosystem Properties

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Abstract—Morphological characteristics of creosotebush canopies (angle of exterior stems), size of litter layer and sub-canopy soil chemistry were measured on several sites on the Jornada Experimental Range. Soils under canopies of inverted cone shaped shrubs had little or no litter layer and significantly lower total soil nitrogen and soil carbon than soils under canopies of hemispherically shaped shrubs. In Death Valley, creosotebushes growing in braided washes were predominately hemispherical in shape and those growing on a dry bajada were predominately inverted cone shaped. The morphological characteristics of creosotebushes appear to vary with soil type and with mean annual rainfall. The proportional distribution of different morphotypes of creosotebush affects the heterogeneity of creosotebush dominated ecosystems.

Creosotebush, *Larrea tridentata*, is the most widely distributed and most abundant shrub in the hot deserts of North America (Shreve 1942; Mabry and others 1977). *L. tridentata* is a small leafed, C3, evergreen shrub that dominates many desert ecosystems and determines the characteristics of those ecosystems. Several studies have focused on the physiological characteristics of this plant that contribute to its success (Lajtha and Whitford 1989; Fisher and others 1988; Oechel and others 1972).

Morphological characteristics of creosotebush have received less attention. The orientation of the branches of *L. tridentata* maximizes light interception in the early morning when moderate temperatures allow maximum photosynthesis (Neufeld and others 1988). The variation in canopy structure and foliage characteristics has been shown to affect the abundance and structure of the arthropod community living on the shrubs (Lightfoot and Whitford 1989).

Physiological studies have demonstrated that *L. tridentata* is limited both by water and by nutrients, especially nitrogen (Fisher and others 1988). Water availability is generally the most important factor limiting growth in arid ecosystems. The growth of an evergreen C3 shrub like *L. tridentata* is dependent upon water that is available for growth at the beginning of the growing season when temperatures are suitable for a plant with C3 physiology. In a summer rainfall desert such as the Chihuahuan Desert, winter and spring are frequently very dry. The early season growth of *L. tridentata* is therefore dependent upon water stored deep in the soil profile during the previous wet season. Stemflow and root channelization are potentially the primary source of that water (Martinez-Meza and Whitford 1995). These studies showed that stem angle was a significant factor in stemflow generation in *L. tridentata*. We hypothesized that creosotebushes growing in sites where rainfall is limited or on sites where most rainfall runs off would be characterized by an inverted cone canopy morphology.

In the northern Chihuahuan Desert, annual rainfall is between 200 mm and 250 mm with 60% of that rainfall as summer convectional storms. In this desert creosotebush morphology should be a compromise between optimization of water channelization to the root systems via stemflow and a canopy shape that enhances litter deposition under the canopy. In the driest part of the range, virtually all of the creosotebush should have conical shapes that optimize stem flow. Death Valley, at the northern edge of the Mojave Desert, is the driest area within the range of *L. tridentata* (average annual rainfall <50 mm). We hypothesized that a larger proportion of *L. tridentata* in Death Valley would have exterior stem angles greater than 45° than creosotebushes from habitats in the northern Chihuahuan Desert.

Nitrogen content, mineralization and nitrogen availability varies with the organic matter content of the soil and is related to the litter layer (Fisher and others 1990). The under shrub nutrient patches are characterized by horizontal and vertical gradients that are greatest under the shrub canopy near the stem and that decrease toward inter-shrub spaces (West and Klemmedson 1978; Crawford and Gosz 1982; Whitford 1986). In desert soils, nutrient concentrations, especially nitrogen, are correlated with soil organic matter content (Skujins 1981; Whitford and others 1987). The decomposition of organic litter accumulated under creosotebushes increases the nitrogen content of the under-shrub soil as suggested by Parker and others (1982). Two factors affect the size of the litter accumulation layer under shrub canopies: (1) size of shrub and (2) the morphology of the shrub. Size and shape affect litter accumulation by affecting the wind turbulences that develop over and around canopies (Reichman 1984). In a landscape with scattered small shrubs, turbulence and the circular movement of dust and debris (eddy currents) result in fine particulate deposition under shrubs in addition to the deposition of dead

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leaves and other organic debris. The effectiveness of this deposition should be a function of shrub morphology. We hypothesize that hemispherically shaped creosotebushes should accumulate larger litter layers than those with a more conical shape.

Materials and Methods

Exterior branch stem angles were measured at three creosotebush sites on a piedmont slope on the Jornada Long Term Ecological Research Site 40 Km NNE of Las Cruces, NM. The caliche site is an erosional surface where more than 90 percent of soil surface has accumulations of calcium carbonate-coarse fragments in a discontinuous layer. The slope gradient is >4%, and creosotebush plants are mostly small with a sparse canopy. The sand site is a middle piedmont-slope with a 3-4% gradient. The surface layer of soil is an alluvial mantle composed primarily of sandy and pebbly or gravelly sediments. Most creosotebush plants grow in clumps of 4-5 shrubs. The gravel site is on a lower piedmont slope with a gradient <3% and soil texture of sandy loam. The creosotebushes form a stand with few clumps.

Measurements of stem-angle were also made at two sites in Death Valley, California, one at the base of the valley in an area of braided washes, and the other on a bajada at 1200 m elevation on the east side of the valley, 10 km from Furnace Creek, CA.

At the Jornada, three 50 m transects were randomly located at each site. All plants along transects were divided into one of two groups, those with all stem-angles greater than 45° and those with most (90%) of stem-angles less than 45°. The selection of 45° as a separation was based on the data on stemflow in Martinez-Meza and Whitford (1995). The average number of plants falling into these two groups were transformed into percentages and compared.

Stem-angles from the horizontal were measured with an inclinometer (1 square meter frame). This frame constructed with PVC was subdivided by placing several inclined strings crossing from one side to the right angle corner opposite that side. The strings were placed at angles of 75, 60, 45, 30, and 15 degrees. An estimate of exterior stem-angles of plants was obtained by placing the frame vertically on the ground and moving it around the plant to align stems with strings angles on the frame (Martinez-Meza and Whitford, 1985).

The stem-angles of plants sampled at two sites in Death Valley, California, were estimated by calculating stem-angles of exterior branches using the following:

$$\text{stem-angle} = \text{arctangent}\,\frac{d1}{d2}$$

where: d1 = Vertical distance from the top exterior edge of the branch to the soil surface.
d2 = Horizontal distance from the base of the trunk to the point where it intersects the line of vertical distance.

Litter area under the canopy of each shrub at the Jornada site was from two diameters through the center of the soil surface area covered with litter. To estimate the nitrogen concentrations both under shrub canopies and in the intershrub spaces, soil samples were collected from under mid-canopy and at the midpoint between the canopies of adjacent shrubs. These soil samples were placed in plastic bags and sent to the New Mexico State University Soil and Water Testing Laboratory for total N measurement.

Results and Discussion

The variability in morphology of *L. tridentata* in various topographic locations and soil types may be related to the importance of stemflow water to the shrub in any particular site. The highest percentage of *L. tridentata* plants with stem-angles greater than 45° was at the sand site, with the lowest percentage at the caliche site (fig. 1). Plants growing on the sand site were mostly large and well developed, whereas those growing on the caliche site usually were small and poorly developed. These results suggest the influence of characteristics of each site, such as slope and soil texture, on shrub morphology and distribution, which in turn affects the distribution of resources, for example, water and nutrient supplies.

The steeper slope gradient and a high accumulation of calcium carbonate-coarse fragments which may contribute to high erosional runoff at the caliche site, may explain the presence of the highest percentage of poorly developed plants with stem-angles less than 45° in that site. Creosotebushes at this site are characterized by shallow, lateral root systems (Brisson and Reynolds 1994). In contrast, the favorable conditions of topography and surface soil texture on the sand site results in creosotebushes with deep root systems (Virginia and others 1989). There is a wide size distribution of plants at this site and evidence that creosotebush has only recently established (unpublished data). The sand site is dominated by plants with stem-angles greater than 45°.

In Death Valley at the braided wash site, ten of the largest shrubs were adjacent to channels in the stream bed that exhibited evidence of recent flows. Those plants all had stem angels less than 35°. The average stem angle of the smallest shrubs (canopy radius <25 cm) was 59°. On the bajada site in Death Valley, there were no shrubs with stem angles <23°

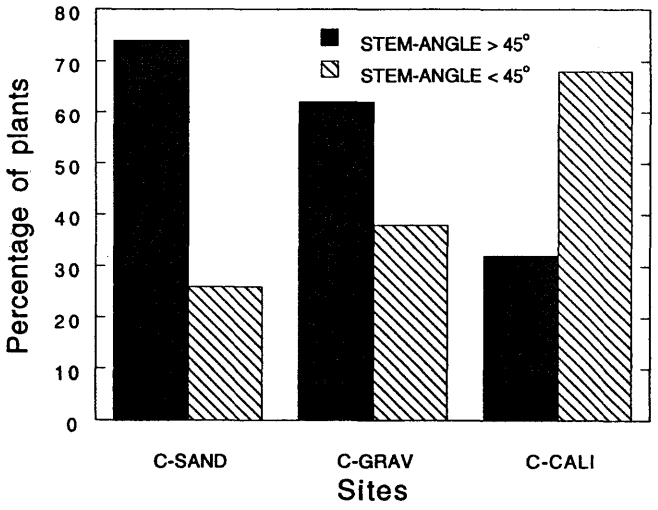

Figure 1—Percentage of *Larrea tridentata* plants with all stem angles greater than 45° and plants with exterior stem angles less than 45° at three sites in the Jornada Basin, New Mexico.

(table 1). A larger proportion of the shrubs in the Death Valley sites had exterior stem angles >45° than the creosotebushes from the Jornada sites in the Chihuahuan Desert (table 1).

The distribution of stem angles in *L. tridentata* appears to be related to the predominant limiting factor for the shrubs in a given location or to soil limitation of root depth. Obviously *L. tridentata* shrubs growing at the edge of active wash channels have access to more water (transmission loss water stored in stream bed sediments) than plants growing at a distance from a run-off channel. For shrubs with access to stream bed sediments, enhanced stem flow is less critical for growth than is availability of soil nutrients. Growth of *L. tridentata* that have adequate available water is rapidly limited by nitrogen availability (Fisher and others 1988). Plants with low stem angles trap and retain litter under the canopy which results in nutrient enhancement of soil beneath the canopy. Virtually all of the *L. tridentata* growing on the bajada in Death Valley had stem angles greater than 45°. Only 12% of the creosotebushes at this site had stem angles less than 45°.

These data suggest that the morphology of creosotebushes varies considerably among sites within a region and among regions. Creosotebushes growing in microsites with enhanced water (run-on sites and edges of arroyos) tend to be more hemispherical in shape. This facilitates retention and accumulation of litter and nutrient enrichment of soils under the canopy.

At sites where water is limited by climate and topography (Death Valley piedmont) or dry microsites (run off sites), creosotebushes tend to be conical in shape. This shape enhances stemflow which is channelized to the deep roots (Martinez-Meza and Whitford In Press). The distribution of morphologies of creosotebush within a region or site therefore probably reflects the spatial pattern of redistribution of water at that location.

The aerodynamics of shrubs of different shapes and the effect of those shapes on litter retention or litter deposition was examined by correlating air stream flow lines around a hemispherical object and a conical object (Blevins 1984). These object shapes approximate the shapes of *L. tridentata* shrubs with exterior stem angles > and <45°. For shrubs approximating a hemispherical shape, wind flows around and above the canopy causing small local turbulances (primarily under the canopy) and deposition on the downwind side of the canopy (fig. 2). This local turbulence may result in some mixing of litter but will not reduce the litter layer under the shrub. For shrubs of a conical shape, the wind flows around the base of the cone with no reduction in velocity or turbulence. Also some of the lateral flow has a down flow component which accelerates the wind speed at ground level (fig. 2).

Table 1—Morphological characteristics of *L. tridentata* from two sites in Death Valley, California.

	Braided wash 0 m elevation	Bajada 1230 m elevation
Average stem angle	48°	51°
Percent >45°	63%	88%
Percent >60°	33%	23.5%
Percent <23°	6%	0%

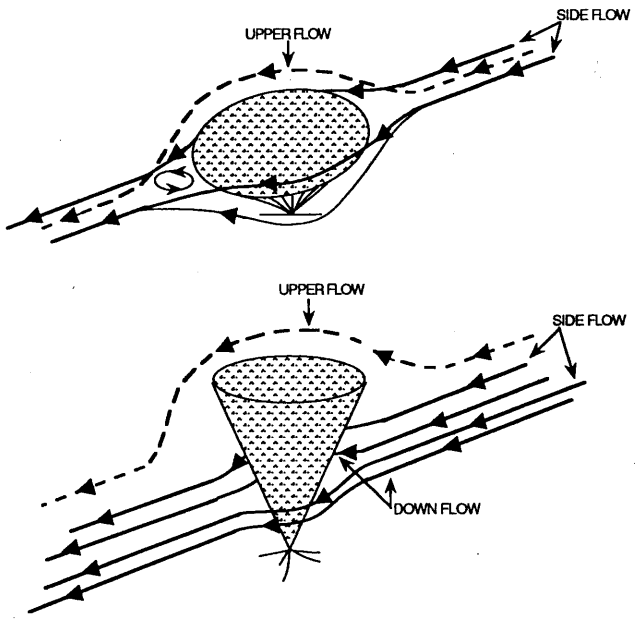

Figure 2—The movement of wind and development of eddy currents around shrubs with a hemispherical shape (top panel) and shrubs with a conical shape (bottom panel).

Threshold velocities required to entrain the litter components of *L. tridentata* in an air stream and transport that litter to another location were calculated based on mass-surface area relationships measured on 50 leaves, 50 stem segments, and 50 fruits. The threshold velocity for leaves was calculated using the aerodynamic equation:

$F_L = C_L (1/2\ Y\ V^2\ A_L$, where:
F_L = lifting force (kg),
C_L = lifting coefficient (dimensionless),
Y = air density (kg/m^3),
V = wind velocity (m/s),
and A_L = lift projected area (m^2).

The threshold velocity for rolling fruits was calculated from:

$V^2 (9.97 \times 10^{-7}) - (w \times f)/r = 0$, where:
V = wind velocity (m/s),
w = average mass,
f = rolling resistance coefficient,
r = radius (m).

The threshold velocity for stem segments was calculated from:

$C_D (1/2\ Y\ V^2\ A_D) - (w \times f) = 0$, where:
C_D is the drag coefficient,
Y = air density,
V = wind velocity,
A_D = drag projected area,
w = average mass/length (kg/m)
f = friction coefficient.

For leaves, the threshold velocity was calculated to be 3.9 km/h, for seed - 6.12 km/h and for a 25 mm length stem segment - 3.3 km/h. These low threshold velocities demonstrate that creosotebush litter can be moved on a large fraction of days in a year. Average daily wind velocities

exceed 10 km/hr 150 days per year (unpublished data, Jornada Long Term Ecological Research Program).

The data on threshold wind velocities and on air streams and shrub shapes lead to the prediction that there will be little or no litter accumulation under shrubs with a conical shape if there is no other vegetation in the immediate vicinity that affects the turbulence and velocity of the wind.

The canopy characteristics of the *L. tridentata* shrubs of conical and hemispherical shapes under which litter accumulations differed in average canopy diameter and exterior stem angles. The conical shrubs had an average canopy diameter of 132 ± 24 cm, average height of 111 ± 20 cm and average exterior stem-angle of 59 ± 4°. The hemispherical shrubs had an average canopy diameter of 209 ± 47 cm, average height of 116 24 cm and average exterior stem angle of 24 ± 6°. The average area of litter accumulation under the conical shrubs was 126 ± 427 cm^2. Only 2 of the 20 shrubs with stem angles of 45° or larger had a measurable accumulation of litter. The average area of litter accumulation under the hemispherical shrubs was 16473 ± 8263 cm^2 with a range of 2971 –30481 cm^2. All of the hemispherical shrubs had measurable litter accumulations.

The difference in litter accumulations under shrubs that differed in exterior stem angles was reflected in the soil chemistry under the shrub canopy (table 2). The most obvious difference in soil nutrients was total nitrogen. Nitrogen may enter the system via rainfall or dry-fall that is subsequently washed into the soil via stemflow and throughfall and from the decomposition of dead leaves and other detritus that accumulates under the canopy of the shrub. The differences in soil nitrogen are probably the result of the differences in quantities of organic material available for decomposition and subsequent mineralization. Differences in concentrations of other nutrients were not as consistent. Elements like calcium enter the system as dust (dryfall) and are washed from the leaf surfaces via stemflow and throughfall. While most throughfall infiltrates into the soil, much of the rainfall that hits the intershrub space is lost in runoff. This probably accounts for most of the differences in table 2.

Considering the data presented herein, it is evident that the morphology of creosotebush based on exterior stem angles has important effects on the redistribution of rainfall (Martinez-Meza and Whitford 1995) and on the accumulation and retention of litter under the canopy. The accumulation and retention of litter plus the transport of adhering dust from the stems and leaves during rain events produces the "fertile islands" that have been described for desert shrubs. The relative abundance and spatial distribution of the morphotypes of creosotebush therefore affects the spatial heterogeneity of *Larrea tridentata* dominated ecosystems. The health of a shrubland ecosystem is in part determined by the ability of that system to retain and efficiently use scarce resources such as water and soil nutrients. The distribution of morphologies of the shrubs within an ecosystem provides information about the use and retention of critical resources within a site.

Table 2—Comparisons of concentrations of nutrients in soils from under mid-canopy of *Larrea tridentata* (creosotebush) shrubs with exterior stem angles >45° and exterior stem angles <45° and soils open, unvegetated, intershrub spaces. Numbers in a row followed by different letters are significantly different ($p < 0.05$).

	Exterior stem angles		
	<45°	>45°	Open
N_{total} ppm	571.1a	416.7b	350.8c
P ppm	10.4a	9.8a	8.5b
K ppm	46.6a	43.4a	26.2b
$C_{organic}$ %	0.5a	0.4b	0.3c
Mg meq/l	1.2a	1.0a	0.85b
Ca meq/l	5.5a	5.1a	3.0b

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Evapotranspiration from a Saltcedar-Dominated Desert Floodplain: a Scaling Approach

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Abstract—The purpose of this study was to investigate evapotranspiration (ET) from a variety of scales (leaf to landscape) in saltcedar-dominated floodplain vegetation along the lower Virgin River of southern Nevada. Leaf-level gas exchange indicated that saltcedar exhibits similar stomatal conductance as the sympatric phreatophytes arrowweed, mesquite, and willow. However, sap flow in saltcedar was higher per unit sapwood area than the other species, suggesting that it maintains higher leaf area per unit sapwood area. At the stand level, saltcedar ET was found to exceed potential ET early in the summer when soils were moist and the water table was near the surface, but by late summer, after floodplain soils had dried and the water table had dropped, saltcedar ET was well below potential rates. Summer irrigation did not result in increased conductance of saltcedar for at least four weeks, suggesting that saltcedar does not utilize summer rainfall under normal conditions in the arid Mojave Desert.

The importance of riparian zones in the arid Southwest as wildlife habitat and as recreational resources has recently led to a considerable amount of research and management efforts that seek to determine the instream flow requirements of riparian vegetation (Stromberg and Patten 1990). There have been numerous ecological studies of the floodplain vegetation of many riverine systems in the West. Much of the literature consists of little more than inventories of dominant plant and wildlife communities, although recent studies have linked ecological processes with various hydrogeological variables. For example, studies of the relationships between the population biology of riparian plants and stream discharge dynamics (Everitt 1968; Stromberg and others 1991) have helped to clarify the essential role of flooding in the recruitment of trees in riparian forest communities. Studies of diverted streams in the western U.S. have shown that curtailment of annual flooding may result in a long-term senescence of riparian vegetation (Smith and others 1991; Stromberg and Patten 1990).

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The riparian communities of the arid Southwest are dominated by saltcedar (*Tamarix ramosissima*), a naturalized thicket-forming shrub that is reputed to be capable of losing vast quantities of water through evapotranspiration (ET). From a very localized distribution in the 1920's, saltcedar has spread across the floodplains of rivers in the West, and is continuing to expand its dominance of floodplains and of isolated springs and wetlands today. Most of the large river systems of the Southwest were historically dominated by gallery cottonwood-willow (*Populus-Salix*) forests, only a small percentage of which are left today. In a study of the distribution of saltcedar, Everitt (1980) concluded that the invasion of saltcedar along southwestern watercourses was related to seed becoming increasingly available as changing physical and hydrological factors associated with development (dam-building, levee construction, etc.) was changing the flow regimes that native forests were historically adapted to. At the same time, the lack of annual flooding was resulting in the senescence of the former cottonwood-willow dominants due to increased water and salinity stresses along aridland floodplains (Busch and Smith 1995).

A number of studies have attempted to quantify "consumptive use" (i.e., ET) from southwestern riparian zones. Researchers have tended to conduct these studies in floodplains that have been invaded by saltcedar due to the widespread belief that it is a "water spender" relative to native phreatophytes such as cottonwood, willow, and mesquite. Most of these studies have used lysimeters or vertical micrometeorological masts (e.g., Bowen ratio) to estimate ET from individual plants or whole stands. Estimates on the order of 150-210 cm (ca. 60-80 inches) annually, based largely on lysimeter studies in Arizona and New Mexico (van Hylckama 1970; Horton 1972) have been reported and used in management programs throughout the Southwest. Robinson (1965) used such data to estimate that over 1.2 x 10^9 m^3 of water are consumed in the Southwest by saltcedar each year. Unfortunately, some of the early water consumptive studies were conducted in open areas, rather than in characteristic dense vegetation, leading to potentially large overestimates of ET due to advective water loss (Anderson and Idso 1987). Potential extrapolation problems from lysimeter studies led to attempts to predict the ET of saltcedar communities from meteorological data and vegetation structural characteristics (Gay and Fritschen 1979). However, such estimates were often obtained without accurate knowledge of the effects of environmental factors on stomatal resistance of the plant surfaces in question.

Other investigators have attempted to predict stand ET based on transpiration measurements of individual leaf surfaces, but these estimates are criticized due to the inherent problem of "scaling up" from individual leaves to the entire canopy (McNaughton and Jarvis 1991). However, these latter studies do not support the characterization of saltcedar as a profligate water spender, relative to other floodplain phreatophytes, at least at the level of the individual leaf (Anderson 1982; Busch and Smith 1995). Therefore, high ET rates of saltcedar stands must be more related to the maintenance of very high leaf area index (LAI; leaf area per unit ground area) during the growing season, although LAI estimates have yet to be made in southwestern riparian vegetation.

In this study, we examined evapotranspiration from saltcedar stands using multiple scales (leaf to watershed) at two study sites along the lower Virgin River floodplain in southern Nevada. We examined water flux estimates of saltcedar and co-occurring native phreatophytes using conventional gas exchange techniques and sap flow analysis, and we also examined stand-level ET in saltcedar-dominated vegetation with sap flow and Bowen ratio techniques. We hypothesized (1) saltcedar would have comparable water loss rates as co-occurring phreatophytes at the leaf/branch levels, (2) stand density would influence stomatal conductance in saltcedar, but (3) saltcedar stands would exhibit very high ET rates due to the maintenance of high LAI.

Study Sites

Two sites were established within the lower Virgin River floodplain in southern Nevada prior to the river entering Lake Mead. These sites were (1) the Halfway Wash site, near the location where Half-Way Wash enters the Virgin River (36° 40′ N, 114° 20′ W) and (2) the Duck Club site, located along the lower watershed (36° 35′ N, 114° 20′ W). Both sites occur at an elevation of ca. 380 m. These sites were selected because they are representative of the overall geomorphology and vegetation structure of the Virgin River floodplain. For example, the upstream Halfway Wash site was characterized by a relatively open, recently burned successional floodplain community with a mixture of saltcedar, arrowweed (*Pluchea sericea*), screwbean mesquite (*Prosopis pubescens*), and other shrubs, with a fairly dense groundcover of saltgrass (*Distichlis spicata*) in the open spaces between thickets. In contrast, the downstream Duck Club site was characterized by a dense thicket of tall saltcedar vegetation (up to 7 m tall) with essentially no subordinate woody species or herbaceous groundcover present.

Methods

Stand Structure

At each site, density of rooted woody stems was measured in fifteen 20 m^2 (2 x 10 m) plots distributed in a systematic random fashion along three parallel transects placed perpendicular to the river channel. In each plot, all rooted woody stems larger than 5 mm diameter were measured just above ground level with calipers. At the Halfway Wash site (floodplain width = 750 m), average stem densities of arrowweed and saltcedar were 23,500 and 23,000 stems ha^{-1}, respectively, with willow and mesquite each having stem densities below 1,000 stems ha^{-1}. At the Duck Club site (floodplain width = 1,200 m), average rooted stem density of saltcedar plants was ca. 65,000 stems ha^{-1}, or over 6 stems per m^{-2} ground surface area.

At each study site, four 20 m^2 circular plots were laid out in four cardinal directions from each of three permanent masts used to set up instrumentation. The center of each plot was 10 m from the central mast location. Stem diameter of all woody species present in the plot (with a stem diameter greater than 5 mm were measured at a height of 0.2 m from the ground surface. Total leaf area of saltcedar in each plot was then estimated from stem diameter-leaf area relationships obtained by destructive sampling of individual stems used to measure sap flow. Leaf-area Index (LAI) was then calculated by dividing total leaf area by the plot area.

Gas Exchange

During several days in the summer of 1994, comparative gas exchange was measured on saltcedar, arrowweed, screwbean mesquite, and coyote willow (*Salix exigua*) on a two-year-old sandbar near the bank of the Virgin River (Halfway Wash site). All plants were young thickets or tree saplings. Commencing near dawn and continuing until early afternoon, photosynthetic gas exchange was measured for terminal shoots using a LI-COR 6200 portable photosynthesis system (Li-Cor, Inc., Lincoln, NE). After obtaining a steady-state measurement of photosynthesis and leaf conductance, the shoot was detached and its water potential was determined immediately using a pressure chamber (Soil Moisture Equip. Corp., Santa Barbara, CA). The shoot was then placed in a sealed bag and stored on ice for transport back to the laboratory where the leaf area of each sample was determined with a leaf area meter (Decagon Devices, Pullman, WA).

Sap Flow

Sap flow (transpirational flux) was estimated in the four study species, and in different densities of saltcedar stands, in both 1993 and 1994 using the stem heat balance method (Baker and van Bavel 1987). Devitt and others (1993) successfully applied the sap flow method in woody ornamental trees under a similar climate. The sap flow system consisted of a DNX10 data logger (Dynamax Inc., Houston, TX) attached to three 8-channel multiplexers, which were mounted on three permanent posts set up at 50 m intervals from the river channel edge into the floodplain. Groups of eight sap flow gauges (Dynagage, Dynamax Inc.) were connected at each multiplexer and operated at constant power.

Global shortwave radiation, air temperature, relative humidity, wind velocity and rainfall were measured simultaneously with sap flow during each measurement period with a Campbell Scientific Weather Station (Campbell Scientific, Logan, UT). At each study site, weather sensors were mounted on a 5 m mast located in an open area. Weather and gauge outputs were measured every minute and stored every 30 minutes in a Campbell SM716 storage module. Potential evapotranspiration was estimated from standard hourly weather data using the Penman-Monteith equation, as modified by van Bavel (1966).

Sap flow was calculated according to gauge output signals, gauge characteristics, and stem diameter. Stem diameters ranged from 10 to 40 mm to accommodate intra- and interspecific variability. Whenever possible gauges were installed on main stems at a distance greater than 0.3 m from the ground. Gauges were covered with insulating foam and several layers of aluminum foil to avoid direct insolation and naturally induced temperature gradients (Gutierrez and others 1995; Shackel and others 1992). The sheath thermal conductance (K_{sh}; see Baker and van Bavel 1987) was determined from the average minimum apparent values calculated at night when transpiration was assumed to be near zero (this was later confirmed by severing the branch above the stemflow gauge at the end of the run, thus forcing flow to zero).

Bowen Ratio

Evapotranspiration can be estimated via an energy balance which takes into account the vapor pressure and temperature gradient above a soil-plant system. However, in the field, it is often difficult to measure the transfer coefficient, h, which is a function of wind velocity, surface roughness, and height. Furthermore, this coefficient cannot be directly measured but must be inferred from a transfer model. One alternative method to get around the difficulty of measuring this coefficient is called the Bowen Ratio. The Bowen Ratio makes the assumption that the ratio of H (sensible heat flux away from the surface) to LE (latent heat flux away from the surface) is the same at a height above the surface as it is at the surface. This ratio can be expressed by the equation:

$$B = V * (T_2 - T_1)/(e_2 - e_1)$$

where T (temperature) and e (vapor pressure) are measured at two heights above the vegetated surface and V is the psychrometric constant. ET then becomes:

$$LE = (R_n - G)/(1 + B)$$

where R_n is the net radiation at the surface and G is the conductive soil heat flux away from the surface. When carefully measured and properly averaged, this method has been shown to yield good estimates of ET under a variety of circumstances (Tanner 1968).

A ca. 13 m (40') Bowen Ratio mast was placed near the center of the floodplain at the Duck Club site, assuring that there was at least 100 m of "fetch" in uniform vegetation (i.e., dense saltcedar vegetation) in all directions. Mast arms were placed at 1 m and 3 m above the canopy to measure temperature and vapor pressure at two heights above the canopy.

Potential evapotranspiration (ET_o) was estimated with the Penman combination equation:

$$ET_o = W * R_n + (1 - W) * f(u) * (e_a - e_d)$$

where W is a temperature related weighting factor, f(u) is a wind related function, and (e_a–e_d) is the difference between saturation vapor pressure at air temperature and the mean actual vapor pressure of the air. Meteorological data (solar radiation, wind run, maximum and minimum temperature, maximum and minimum relative humidity, and rainfall) were collected with an automated weather station (Campbell Scientific) at a central location on the site. ET_o estimates were then used to assess environmental demand and to determine the extent to which plant water status was directly coupled to changes in environmental demand.

The response of saltcedar thickets to summer rainfall was assessed by irrigating six thickets at 100% of ET_o and six at 50% of ET_o. Plants were watered weekly from during June and July. The amount of water applied to each group of plants (water was applied by hand with buckets in bermed depressions around each thicket) was based on the ET_o predicted from the previous weeks weather data (see previous equation). Plants were instrumented with sap flow gauges and were monitored one day per week for stomatal conductance and plant water potential, as described previously.

Results and Discussion

Gas exchange of saltcedar, arrowweed, mesquite and willow was investigated on June 9, 1994, at the Halfway Wash site. Environmental conditions during that time were indicative of early in the growing season on the Virgin River floodplain. Due to below average flows in late spring, water tables were starting to seasonally decline (but were still less than 1 m) and soils were dry at the surface but still moist in the subsurface. Air temperatures were very warm (>42°C) and relative humidity was low (<10%) around midday. Comparative results (table 1) showed that saltcedar maintained the lowest daily plant water potentials whereas willow maintained the highest water potentials. Willow had significantly higher stomatal conductance (g_s) than saltcedar or mesquite, and arrowweed had the lowest conductance. CO_2 assimilation rate (A) was highest in mesquite, intermediate in willow and saltcedar, and lowest in arrowweed. Finally, the slope of the A:g_s relationship (A as the dependent variable), which is an indication of intrinsic water use efficiency, was highest in mesquite and saltcedar (table 1). In other words, per unit decrease in conductance as the day progressed, carbon dioxide assimilation decreased more slowly in mesquite and saltcedar than in arrowweed and willow.

Comparative gas exchange of these four species on the same site in August 1994 provided similar results. Some of these gas exchange results obtained from plants in the Virgin River floodplain support previous findings for saltcedar. Anderson (1982) found saltcedar stomata to be extremely sensitive to changes in light intensity, but they were less sensitive to changes in humidity. Busch and Smith (1995) found saltcedar to exhibit midday declines in stomatal conductance during the hot summer months, but these declines were often less pronounced than were midday declines in conductance of sympatric cottonwood and willow trees. Busch and Smith (1995) also found saltcedar to operate at lower plant water potentials and to exhibit higher water use efficiency than did cottonwood and willow along the lower Colorado River, in agreement with our findings from the Virgin River.

Rates of sap flow in the four species during the same time period that gas exchange was measured (June 8-13, 1994) showed that saltcedar maintained significantly higher daily accumulated sap flow per unit sapwood area than did the other three species (fig. 1). Averaged over the six day period, saltcedar exhibited a 1.9-fold higher sapflow rate than did

Table 1—Mean daily values of plant water potential (Plant WP), stomatal conductance (g_s), CO_2 assimilation (A) and the slope of the CO_2 assimilation:conductance relationship (A:g) for four species of floodplain phreatophytes. For the two regression relationships, the slope is based on the latter variable in each case being the independent variable and the first listed variable being the dependent variable. Data were taken from a whole, sunny day (June 9, 1994) at the Halfway Wash site on the lower Virgin River, Nevada. Data points in the same row that are followed by different letters are significantly different at p = 0.05 (one-way ANOVA).

	Species			
Parameter (unit)	**Saltcedar**	**Arrowweed**	**Mesquite**	**Willow**
Plant WP (MPa)	−2.20a	−1.66b	−1.78b	−0.98c
g_s (mol m^{-2} s^{-1})	0.340a	0.198b	0.354a	0.550c
A (mmol CO_2 m^{-2} s^{-1})	8.4a	4.3b	12.1c	14.7c
A:g slope	26.5	18.5	30.6	15.3

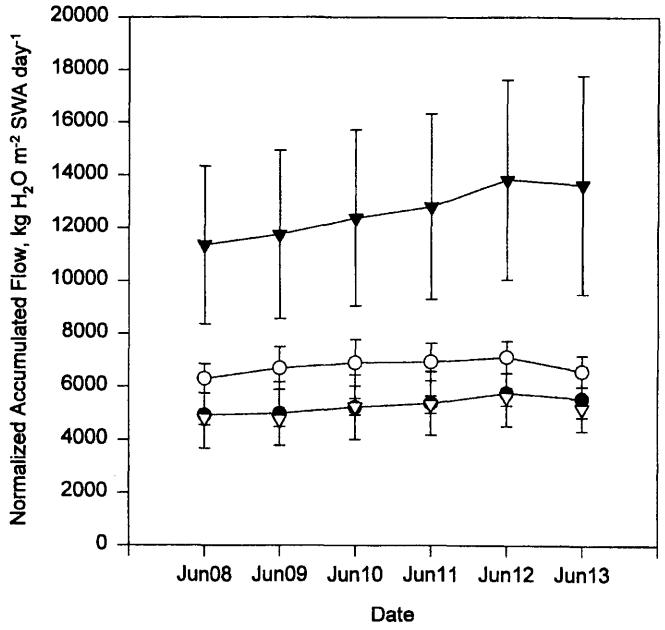

Figure 1—Normalized daily accumulated sap flow in saltcedar from June 8 to June 13, 1994, at the Halfway Wash site, lower Virgin River, Nevada. Symbols represent saltcedar (closed triangles), coyote willow (open circles), screwbean mesquite (closed circles), and arrowweed (closed triangles). Vertical bars represent one standard error.

willow, 2.4-fold higher than mesquite, and 2.5-fold higher than arrowweed. Interestingly, saltcedar does not exhibit higher sap flow per unit leaf area than do arrowweed, mesquite, or willow (Sala and others 1996), which must indicate that saltcedar maintains greater leaf area per unit sapwood area than do the other species.

Observations from the Virgin River suggest that saltcedar exhibits a curvilinear increase in leaf area as stems age (data not shown), and so for mature thickets saltcedar may be able to maintain very high leaf area. Our estimates of LAI (leaf area index) for mature saltcedar on the lower Virgin River is between 3.0 and 4.0 for most mature stands (Sala and others 1996). Under those LAI's, Sala and others (1996) used sap flow data to calculate that actual evapotranspiration (ET) from mature saltcedar stands can exceed predicted potential evapotranspiration (ET_o), at least when conditions are favorable for high ET rates (i.e., moist soils and/or high water tables).

Given these results, we were interested in determining what may regulate ET under natural conditions. Results from a number of sap flow runs during the 1993 growing season indicated that daily accumulated flow in individual saltcedar plants was linearly related to leaf area of that plant (fig. 2) under conditions when subsurface water was not limiting (1993 was a high flow year). This relationship does not preclude the fact that ET of saltcedar stands may decline as the floodplain environment seasonally desiccates, but does indicate a strong influence of total leaf area on ET rates under mesic conditions. Therefore, environmental

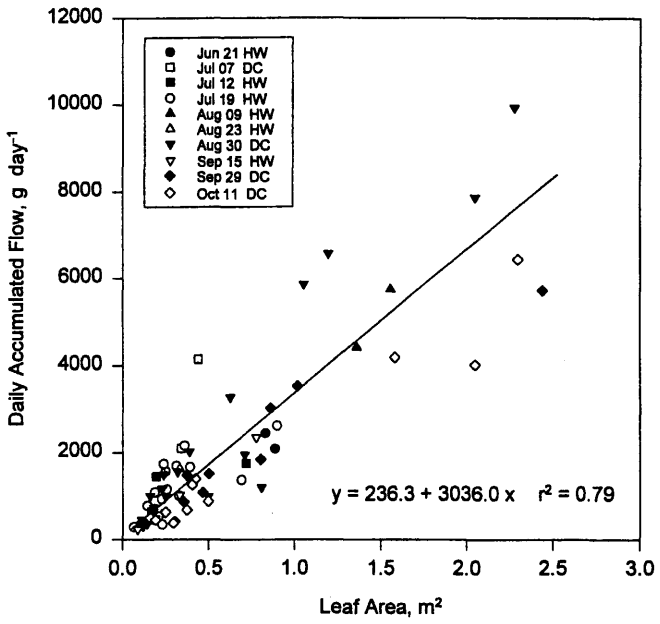

Figure 2—Daily accumulated sap flow as a function of total leaf area in saltcedar at two sites (Duck Club = DW; Halfway Wash = HW) over nine days from June 21 to October 11, 1993.

influences on maintenance of leaf area in saltcedar stands may have far greater influence on seasonal ET rates than do short-term influences on stomata.

One factor that can influence both stomatal conductance and leaf area maintenance is the density of saltcedar canopies. We were particularly interested in understanding how the ET process may change as open, successional saltcedar stands develop into closed, mature stands in which individual saltcedar thickets show considerable overlap of individual canopies. A comparison of mean stomatal conductance at midcanopy level during the summer growing season in 1994 showed that g_s was consistently higher in dense stands than it was in more open stands (fig. 3), which were characterized by individual thickets with non-overlapping canopies and open ground between the thickets. We attributed this difference to a boundary layer effect, in which canopy transpiration in dense stands has a positive feedback effect on stomatal conductance. A large boundary layer would tend to reduce transpiration in comparison to an open thicket exhibiting equal g_s, so that dense stands may be able to operate at higher g_s without exhibiting higher transpiration per unit leaf area. We are continuing experiments to elucidate these types of relationships.

Bowen ratio estimates of ET from mature saltcedar stands from the Duck Club site on the lower Virgin River indicate that latent heat flux (LE) actually exceeded net radiation (R_n) early in the growing season (May and June) when channel flow and the water table were both high (table 2). In fact, on June 17, LE was almost twofold higher than R_n during the middle of the day. Because LE exceeded R_n, the energy to drive such a process must come from other sources besides incoming radiant energy. The source of that energy was apparently the advection (i.e., horizontal transport) of sensible heat from the surrounding dry desert, causing a net influx (-H) of sensible heat into the canopy. By late June, LE was still slightly higher than R_n, but in early July LE began dropping and quickly became lower than R_n, becoming only 35% of R_n on July 21 and 29% of R_n on October 21. On these dates, the dominant flux of sensible heat was upward from the canopy (+H) rather than into the canopy. Therefore, LE

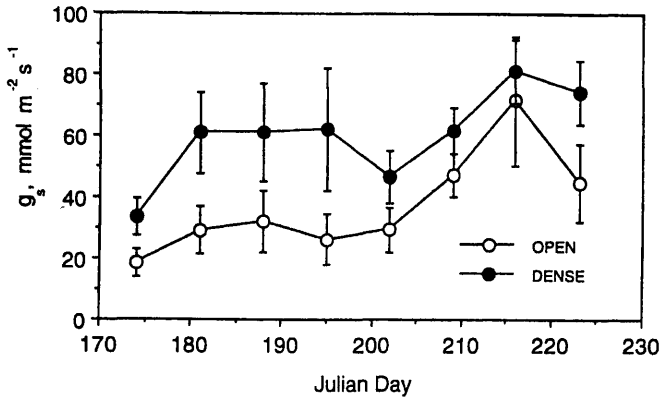

Figure 3—Mean daily stomatal conductance (g_s) of saltcedar in dense stands (closed circles) and open stands (open circles) from mid-June (Day 175) to August (Day 225) at the Duck Club site, lower Virgin River, Nevada. Vertical bars represent one standard error.

Table 2—Bowen ratio analysis of mean daily net radiation (R_n), latent heat flux (LE), sensible heat flux (H) and soil heat flux (G) for a mature saltcedar stand at six times during the growing season in 1994 for the lower Virgin River, Nevada. Means were calculated between 0900 and 1500 h each day. Positive values for net radiation denote net downward flux; positive values for latent heat denote upward flux; for sensible heat, positive values denote upward flux and negative values denote downward flux; and for soil heat flux positive values denote downward flux from the surface into the soil.

Date	Parameter			
	R_n	LE	H	G
	$W m^{-2}$			
May 5	509	654	−168	23
June 17	586	1047	−474	13
June 25	616	660	−63	19
July 3	590	431	109	50
July 21	571	204	337	30
October 21	394	114	241	39

appeared to be very high during the first half of the growing season due to sensible heat advection adding considerably more energy to the stand than was provided by net radiation alone. Although we placed the Bowen ratio tower in a location where it had at least 150 m of fetch in each direction, it was apparent that such fetch was not adequate to buffer the tower from horizontal exchange with the surrounding hot, dry desert. That reality, plus the fact that soils were moist and the water table was high, acted to produce extremely high ET rates for these intact saltcedar stands.

A second aspect related to annual ET from saltcedar stands is the effect that the summer dry season has on stomatal conductance and resultant transpiration rates. Although a phreatophyte, saltcedar appears to be a facultative phreatophyte that can take up water from both groundwater and the unsaturated soil profile, whereas cottonwood and willow trees are obligate phreatophytes that only take up water from the water table (Busch and others 1993). Because of their ability to take up water from multiple sources, and because hydraulic resistance to water transport increases as the water table becomes deeper, we tested what the response of saltcedar is to summer rainfall by irrigating saltcedar thickets after the 1994 summer dry season was well under way (1994 was a dry year).

All plants exhibited low stomatal conductance at the start of the experiment in June; plants irrigated at 100% ET_o took four weeks and plants irrigated at 50% ET_o took six weeks to exhibit stomatal conductance that was significantly elevated over unwatered controls (fig. 4). Sap flow data showed similar lags before increased sap flows were observed in irrigated plants (data not shown).

This irrigation experiment suggests that saltcedar does not normally respond to summer rainfall in the arid Mojave Desert, unless that rainfall is unusually heavy. This conclusion is based on the observation that plants did not physiologically respond to increased surface water for a full month, and then the response was not dramatic even though the irrigated plants had received the equivalent of potential ET for four to six weeks. Such levels of summer rainfall never occur in the Mojave Desert, although summer flash floods may result in substantial recharge of the soil profile. Even

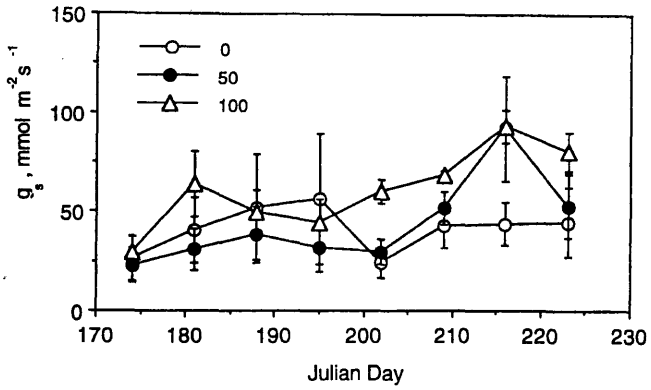

Figure 4—Mean daily stomatal conductance (g_s) of saltcedar plants irrigated weekly at 50 and 100% potential evapotranspiration (closed circles and open triangles, respectively) versus unwatered controls (open circles) at the Duck Club site, lower Virgin River, Nevada. Irrigations commenced in mid-June (Day 175) and continued through August (Day 225). Vertical bars represent one standard error.

so, the potentially rapid response to soil water addition that we thought may occur did not materialize.

We also did not observe a significant increase in root length per unit soil volume, even after four to six weeks of irrigation, leading us to conclude that saltcedar does not normally respond to summer rainfall, except under extremely wet conditions or after repeated flood events.

Conclusions

The results of these experiments, collected at various scales, indicate that saltcedar appears to have similar gas exchange behavior as sympatric woody phreatophytes such as mesquite and willow, but at the whole plant level it exhibits higher sap flow (and therefore transpirational flux) per unit sapwood area. Perhaps due to its ability to support higher ET per unit sapwood area, saltcedar exhibits high ET at the landscape level due to its ability to maintain very high leaf area as stands mature. In such dense stands with high LAI, ET can dramatically exceed net radiation (and thus predicted ET_0) under conditions of moist soils and a high water table, and particularly under advective conditions which result in sensible heat flux into the canopy.

However, even though saltcedar is phreatophytic, it still exhibits reduced ET during the dry summer months when surface soils dry and the water table drops, thus increasing hydraulic resistance for water transport to the leaf canopy. During this time of the year, ET is significantly lower than net radiation. Therefore, the notion that saltcedar stands lose vast quantities of water is only partially true. Under moist, advective conditions we observed extremely high ET from saltcedar stands, but these high ET rates did not continue into the dry summer months. During the dry season, stand-level ET actually dropped to well below predicted ET_0 and stayed at those reduced levels for the rest of the summer and fall.

Therefore, we conclude that dense saltcedar stands can lose large quantities of water during high runoff years or in habitats where the water table is perennially high, but on sites like the Virgin River floodplain where flooding is restricted to late spring snowmelt runoff but then water tables drop as the dry season progresses, saltcedar stands may show dramatic differences in ET between wet and dry times of the year even though it maintains perennial contact with subsurface water.

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Do Soil Factors Determine the Distribution of Spineless Hopsage (*Grayia brandegei*)?

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Abstract—Spineless hopsage (*Grayia brandegei*) sites are distinguished from adjacent non-hopsage sites by high levels of soluble salts and by factors relating to small soil particle size and clay minerology. Spineless hopsage most likely represents a stress-tolerant species capable of establishing on steep eroded sites where the combination of salinity, aridity, and fine soil texture makes establishment of other species difficult.

Spineless hopsage (*Grayia brandegei*) is a small chenopod shrub endemic to the Colorado River drainage. Also known as *Zuckia brandegei* var. *brandegei* (Welsh and others 1987), spineless hopsage is unusual both in its reproductive system (Pendleton and others 1988) and in the type of habitat where it is found. Spineless hopsage typically occurs in monotypic stands on steep outcrops of weathering and eroded shale (Stutz and others 1987). These sites are often visually distinct from surrounding areas in the amount of exposed or eroded material and lack of other vegetation, appearing as "mini-badlands."

Because of its ability to persist on such apparently inhospitable slopes where other species cannot, spineless hopsage may have value in the revegetation of similarly environmentally challenging sites. However, more must be known about factors affecting the distribution of this species before this potential can be explored. This study was undertaken for the purpose of documenting soil properties of sites where spineless hopsage naturally occurs and determining factors that distinguish these sites from adjacent areas.

Methods

Soil and vegetation samples were collected in June 1986 from nine populations of spineless hopsage growing in Utah, Colorado, and Arizona (fig. 1). Population locations are given as follows: Rifle, 12 km nw. of Rifle, Garfield Co., CO; Rabbit Valley, 16 km w. of Mack, Mesa Co., CO; Round Rock, 16 km n. of Many Farms, Apache Co., AZ; Moab, 8 km nw. of Moab, Grand Co., UT; Blue Notch, 20 km se. of Hites Crossing, San Juan Co., UT; Montezuma Creek, 6 km n. of Montezuma Creek, San Juan Co., UT; Bottle Hollow, 18 km e. of Roosevelt, Uintah Co., UT; Capitol Reef, 3 km e. of Notom Exit 24, Wayne Co., UT; and Henry Mountains, 33 km s. of Hanksville, Garfield Co., UT. Both tetraploid and diploid populations were included in the study (see Stutz and others 1987).

At each location, on-site and off-site collection areas were established. On-site samples were taken from within the hopsage community; off-site samples were collected from the nearest adjacent community devoid of hopsage, keeping slope and aspect constant whenever possible. On-site characteristics and off-site vegetation are recorded in table 1. At each collection site, a soil profile was exposed to three feet. Profiles were described and samples for physical and chemical analysis collected from the surface horizon, in which the majority of hopsage roots were concentrated. Site slope and aspect were also recorded. Hopsage leaf tissue was collected from the on-sites and returned to the laboratory for nutrient analysis.

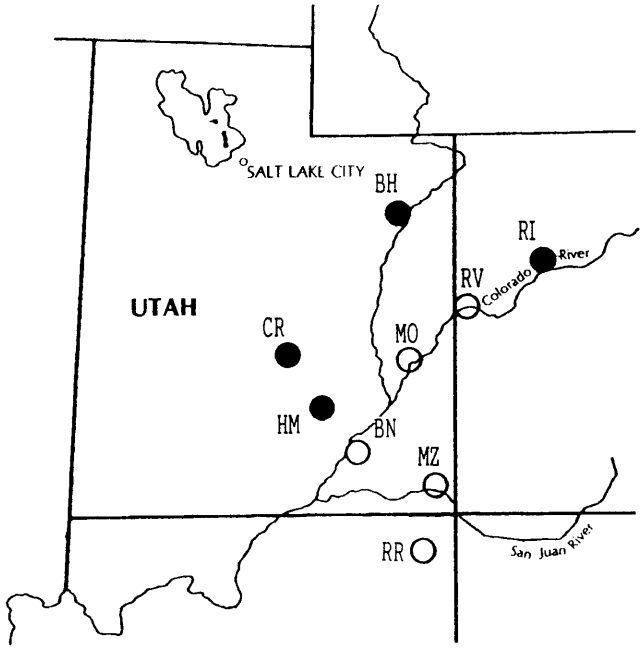

Figure 1—Locations of nine study populations of spineless hopsage. ● = tetraploid populations; ○ = diploid populations. Population locations are: Bottle Hollow (BH), Moab (MO), Henry Mountains (HM), Round Rock (RR), Rifle (RI), Montezuma Creek (MZ), Rabbit Valley (RV), Blue Notch (BN), and Capitol Reef (CR).

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Table 1—Characteristics of nine population locations used in the study.

Population location	Ploidy level[1]	Elevation (m)	Slope %	Aspect	Off-site vegetation
Rifle	4X	2,130	70	W	Pinyon, Gambel oak, rose, big sagebrush, ricegrass, rabbitbrush
Rabbit Valley	2X	1,445	53	E	Shadscale, snakeweed, groundsel
Round Rock	2X	1,645	28	NW	Shadscale, ricegrass, silver orach, galleta grass
Bottle Hollow	4X	1,565	52	NNE	Black sagebrush groundsel, phlox, buckwheat, snakeweed, western wheatgrass
Moab	2X	1,415	40	SW	Yucca, blackbrush, ephedra, silver orach, ricegrass, galleta grass, rabbitbrush
Blue Notch	2X	1,675	70	NE	Blackbrush, galleta grass, pinyon, ephedra, snakeweed, ricegrass, rabbitbrush
Montezuma Creek	2X	1,400	40	W	Snakeweed, rabbitbrush, milkvetch, needlegrass, goldenbush
Capitol Reef	4X	1,585	62	N	Rabbitbrush, horsebrush, ephedra, Bigelow sagebrush, ricegrass, winterfat, snakeweed
Henry Mountains	4X	1,725	30	E	Big sagebrush, juniper, needlegrass, ricegrass, shadscale, Oregon grape, ricegrass, snakeweed

[1]Determined by Stutz and others 1987.

The following laboratory analyses were performed on each soil sample: soil texture, pH, percent organic matter (%OM), cation exchange capacity (CEC), electrical conductivity (EC); plant available No_3–N, P, K; DPTA extractable Zn, Fe, Mn, Cu; soluble Ca, Mg, Na, K; –0.33 bar moisture, and –15 bar moisture (Black, part 1 & 2, 1965). Sodium absorption ratio (SAR) and available water holding capacity (AWHC) were calculated from the above information. Soil tests were done by the Plant and Soil Testing Laboratory, Brigham Young University. The selenium concentration of soil and plant samples and total Kjeldahl nitrogen of plant samples was determined by the Analytical Laboratories at Utah State University. All other analyses of spineless hopsage leaf material were conducted at the Laboratory of Biomedical and Environmental Sciences, UCLA, using a mass spectrophotometer.

Statistical analyses were performed using the PC version of SAS (SAS Institute Inc. 1989). Univariate comparisons of on- and off-sites used the paired-comparison t test. Two multivariate analyses, principal components analysis (PROC FACTOR) and discriminant analysis (PROC CANDISC), were also used. Variable reduction was accomplished using stepwise forward regression (PROC STEPDISC).

Results

Soil Analyses

Spineless hopsage sites differed significantly ($p \leq 0.05$) from adjacent sites in having higher levels of available K and soluble Ca, higher EC values, and proportionately less sand and more clay (table 2). A number of other variables were marginally significant ($0.05 \leq p \leq 0.10$), suggesting that a suite of interrelated variables distinguish hopsage sites from non-hopsage sites.

A multivariate approach for evaluating overall soil chemistry of on- and off-sites was subsequently performed using principal components analysis (PCA). Percent silt, AWHC, and extractable Zn, Fe, Mn, Cu were omitted from the analysis in order to satisfy underlying assumptions of PCA (no variable can be a linear combination of other variables, and the number of variables used must be less than the number of cases). Percent silt and AWHC are linear combinations of other variables. Of the remaining variables, extractable Fe, Mn, and Cu were considered least likely to be of biological significance.

Table 2—Univariate results from paired-comparison t tests on 22 soil variables. Values that differ significantly ($p \leq 0.05$) between sites dominated by spineless hopsage and adjacent non-hopsage sites are marked with an asterisk.

Variable	On-site mean	Off-site mean	t	Prob>|t|
PH	7.9	7.7	1.9124	0.0922
CEC (me/100g)	23.3	15.5	2.1507	0.0637
%OM	0.35	0.38	–0.4407	0.6711
NO3-N_{av} (ppm)	8.4	3.31	2.0683	0.0724
P_{av} (ppm)	4.8	5.4	–1.1995	0.2647
K_{av} (ppm)	274.8	171.0	3.4558	0.0086*
EC (dS/m)	3.5	0.6	3.9175	0.0044*
ZN (ppm)	0.35	0.28	2.1953	0.0594
FE (ppm)	27.7	28.3	–0.0350	0.9729
MN (ppm)	7.8	13.0	–0.8410	0.4248
CU (ppm)	0.67	0.52	1.0504	0.3242
K_s (ppm)	131.8	7.1	1.3104	0.2264
CA_s (ppm)	161.3	46.3	2.3219	0.0488*
MG_s (ppm)	44.3	11.1	2.0765	0.0715
NA_s (ppm)	1136.4	68.2	1.9482	0.0872
SAR	302.2	53.0	1.7427	0.1196
%SAND	29.1	39.7	–2.6018	0.0315*
%SILT	32.7	28.2	1.2803	0.2363
%CLAY	38.2	32.0	2.6789	0.0280*
–0.33 bar (%)	20.7	15.8	2.0695	0.0723
–15 bar (%)	15.0	10.7	1.9021	0.0937
AWHC (%)	5.7	5.1	0.3658	0.7240

Table 3—Principal components analysis of surface horizon characteristics collected from 18 spineless hopsage and non-hopsage sites. Variable units are given in table 1.

	Factor 1	Factor 2	Factor 3
Eigenvalue	**6.2944**	**3.5333**	**2.5057**
cumulative variance (%)	**37.0**	**57.8**	**72.6**
Character	*Factor pattern*		
PH	0.40121	–0.21301	–0.64383
CEC	0.73322	–0.44744	–0.38672
%OM	–0.01717	–0.41205	0.74781
$NO3–N_{av}$	0.42378	–0.47472	–0.33662
P_{av}	0.11563	–0.11384	0.62648
K_{av}	0.23178	–0.21547	0.07780
EC	0.88439	–0.10680	–0.28413
Zn	0.58412	0.36730	0.66578
K_s	0.66291	0.71359	0.02896
CA_s	0.46705	–0.41120	0.32557
MG_s	0.73408	0.44978	0.18830
NA_s	0.75957	0.61927	0.06328
SAR	0.73664	0.61502	–0.01720
%SAND	–0.32603	0.75227	–0.22998
%CLAY	0.62493	–0.62525	0.35190
–0.33 bar	0.83919	–0.23816	–0.13796
015 bar	0.84163	–0.17597	0.06501

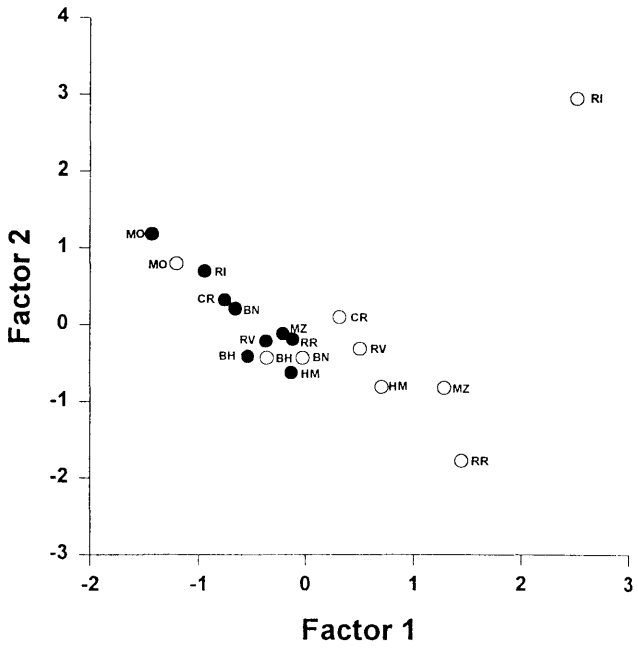

Figure 2—Principal component analysis of soil characters from nine locations. Open symbols represent hopsage on-sites; filled symbols represent values from adjacent off-sites. Population locations are: Bottle Hollow (BH), Moab (MO), Henry Mountains (HM), Round Rock (RR), Rifle (RI), Montezuma Creek (MZ), Rabbit Valley (RV), Blue Notch (BN), and Capitol Reef (CR).

Results from principal components analysis are given in table 3. Only the first three components (factors), representing over 70% of the variance, are reported. Factor one relates both to high overall salt content and to a high percentage of clay in the soil. High loadings (standardized regression coefficients for each variable) were obtained for EC, SAR, and soluble K, Mg, and Na. –0.33 bar moisture, CEC, and –15 bar moisture are positively correlated with clay content. Factor 2 relates to soluble salt chemistry, having high loading values for soluble Na and K, as well as SAR. Factor three is not readily interpretable but may relate to soil fertility, being positively correlated with %OM, P, and Zn concentrations and negatively correlated with pH.

A graph of site values for factors one and two reveals that spineless hopsage sites tend to have higher values for factor one and lower values for factor two than do non-hopsage sites (fig. 2). Hopsage sites, therefore, tend to be higher in total salt content and heavier in texture than adjacent areas. The Moab on-site is somewhat atypical, having more silt than clay. However, even at this location, the move from on- to off-site is accompanied by a decrease in factor one and an increase in factor two. Factor three was not useful in distinguishing between on- and off-sites.

The forward selection procedure of STEPDISC was used to select the subset of soil variables best revealing differences between on- and off-sites while retaining the maximum amount of information. Seven variables were selected, all of which contributed significantly in distinguishing hopsage sites from adjacent areas (table 4). Multivariate tests using these seven variables found highly significant differences between on- and off-sites (table 5).

A discriminant function based on the selected variables was obtained using the CANDISC procedure. This procedure derives a linear combination of variables that best

Table 4—Partial R^2 values and probability levels for seven variables selected using forward stepwise discriminant analysis. Variable units are given in table 1.

Variable	Partial R**2	F	Prob > F
K_{av}	0.3503	5.391	0.0426
EC	0.6507	18.630	0.0015
ZN	0.3542	5.485	0.0412
K_s	0.6294	16.984	0.0021
NA_s	0.6174	16.136	0.0025
%SAND	0.7403	28.512	0.0003
%CLAY	0.7529	30.476	0.0003

Table 5—Multivariate statistics and exact F statistics from discriminant analysis using a subset of seven selected soil variables. Num and Den refer to the numerator and denominator degrees of freedom, respectively.

			Num DF	Den DF	
Statistic	**Value**	**F**			**Pr > F**
Wilks' Lambda	0.08087744	16.2348	7	10	0.0001
Pillai's Trace	0.91912256	16.2348	7	10	0.0001
Hotelling-Lawley Trace	11.36438669	16.2348	7	10	0.0001
Roy's Greatest Root	11.36438669	16.2348	7	10	0.0001

Table 6—Total canonical structure of the discriminant function separating spineless hopsage sites from adjacent vegetation. Variable units are given in table 1.

Variable	Coefficient
K_{av}	0.602867
EC	0.684130
%SAND	–0.392774
%CLAY	0.317005
Na_s	0.461758
K_s	0.325935
ZN	0.301164

distinguishes among groups. The squared canonical correlation between the resulting discriminant function and the classification variable of on- or off-site was extremely high (R^2= 0.919). The structure of the discriminant function is given in table 6. Available K and EC had the highest positive coefficients or loadings, followed by water soluble Na and K, % clay, and extractable Zn. Percent sand was negatively correlated with a moderate loading value.

Individual site scores for the discriminant function are plotted in figure 3. Separation of hopsage on- and off-sites is complete, confirming that the discriminant function obtained from this analysis can successfully identify/classify these particular sites accurately. However, before it could be used on a more universal basis, additional testing using data obtained from other locations would be necessary. The equation was used on soil data from one additional hopsage site located in Antelope Valley, 4 km nw. of Sterling, UT. The resultant canonical score of 3.49 correctly identified this location as a hopsage site.

Plant Tissue Analyses

Mineral element concentrations in leaf tissue samples of spineless hopsage are reported in table 7. Kjeldahl N concentration corresponds to a crude protein value of 11.5 percent, a value consistent with those of other shrub species (Welch and Monsen 1981). Na concentrations are fairly high compared with most other desert shrubs, but similar or even lower than those reported for *Lycium* and some *Atriplex* species, (Wallace and Romney 1972; Romney and Wallace 1980; Romney and others 1980; Wallace and others 1980a,b). Mg and Mn concentrations are also high, similar to levels

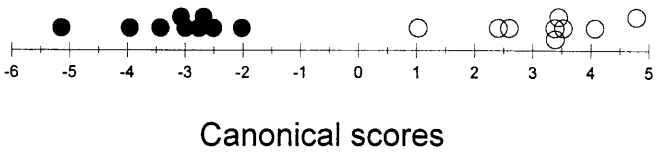

Figure 3—Site scores from discriminant analysis using seven selected soil variables. Open symbols represent hopsage on-sites; filled symbols represent values from adjacent off-sites.

Table 7—Mineral element concentrations in leaf tissue of spineless hopsage collected from nine locations.

Variable	N	Mean	Standard deviation	Range
N (%)	9	1.85	0.49	1.36 - 2.94
P (%)	9	0.17	0.09	0.09 - 0.40
Na (%)	9	1.31	0.59	0.76 - 2.56
K (%)	9	1.19	0.30	0.85 - 1.68
Ca (%)	9	1.40	0.50	0.84 - 2.47
Mg (%)	9	1.54	0.71	0.69 - 2.85
Si (%)	9	0.14*	0.14	0.05 - 0.50
Zn (ppm)	9	22.1	11.9	9.2 - 43.1
Cu (ppm)	9	6.1	3.7	2.4 - 13.8
Fe (ppm)	9	463.1*	431.0	214.3 -1503.0
Mn (ppm)	9	234.3	131.6	89.8 - 473.7
B (ppm)	9	28.9	16.1	9.1 - 53.4
Al (ppm)	9	304.1*	235.8	120.2 - 848.3
Ti (ppm)	9	18.3*	25.6	1.4 - 79.7
Mo (ppm)	9	0.8	0.4	0.1 - 1.5
Cr (ppm)	9	0.2	0.3	0.03 - 0.98
Sr (ppm)	9	190.4	123.5	41.6 - 413.7
Ba (ppm)	9	13.4	10.0	1.8 - 29.3
Li (ppm)	9	8.4	10.9	1.1 - 36.8
Se (ppm)	9	11.8	26.9	0.1 - 83.0

*Relatively high levels may indicate dust contamination.

reported for *Grayia spinosa*. Mg concentrations in *Grayia spinosa* plants growing at the Nevada Test Site were consistently higher than those of other shrub species (E. M. Romney, letter dated August 26, 1987). *Grayia spinosa* also accumulates high concentrations of K (Wallace and Romney 1972). In contrast, P and K concentrations in spineless hopsage were relatively low when compared with other desert shrubs growing at the Nevada Test Site. B, Mo, and Cr concentrations are also somewhat low.

Spineless hopsage has been identified as a facultative selenium absorber (Kingsbury 1964). Selenium concentrations in plant samples collected from the nine study populations ranged, for the most part, from 0.1 to 8.2 ppm. However, one plant sample obtained from Capital Reef had a selenium concentration of 83.0 ppm, a value consistent with those of other secondary absorbers (Mayland 1985). The relatively low concentration of selenium in hopsage leaf tissue is consistent with soil selenium concentrations. Selenium concentrations in the five soils submitted for analysis were beneath detectable levels (<0.5 ppm). Unfortunately, due to insufficient sample material, the soil sample from Capital Reef was not included.

Discussion

In arid portions of the western United States, soil development often proceeds at a very slow rate (Buol and others 1980). Plant distribution is largely affected by soil parent material. This is particularly true for the Colorado drainage system, where geologic strata are exposed essentially unmodified over vast areas (Welsh and others 1987). Many endemics present on the Colorado Plateau are edaphically restricted specialists occurring on specific outcrops of raw parent material (Welsh 1978).

Spineless hopsage follows a similar pattern, occurring exclusively on fine clay and clay loam soils derived from exposed and eroding shales in the Colorado River drainage. Parent formations on which it is found include the Duchesne River, Uinta, Kaiparowits, Summerville, Morrison, Chinle, Moenkopi, Colton, and Green River formations (Welsh and others 1987; Pendleton and others 1988), and probably others as well. These shales are Triassic to early Tertiary in origin. Many are highly colored due to copper, iron, cobalt, nickel, and vanadium compounds that coat particle surfaces and whose colors reflect various oxidation states.

Shales in arid environments generally weather to fine textured soils containing illite or montmorillonite clay minerals, and are frequently highly alkaline, saline, and sodic (Buol and others 1980). High concentrations of sodium, selenium, potassium, and micronutrients are common (Tisdale and others 1993). The soils in our spineless hopsage study sites showed little evidence of horizonation, and largely consisted of slightly weathered shales that were relatively unleached. Our soils data show sites occupied by spineless hopsage to have moderate levels of soluble salts, but high levels of exchangable sodium and potassium. SAR values for many of the sites were sufficiently high (81-1286) to preclude growth of most plant species. With the exception of zinc, these soils also have high micronutrient levels. It can be concluded that these sites are typical of the majority of recently exposed soils developed from the afore-mentioned geologic formations, and do not reflect the extreme soil chemical and physical properties of formations such as Mancos shale (Potter and others 1985).

Our tissue data show that spineless hopsage can accumulate selenium, and tends also to selectively accumulate magnesium and sodium, properties it shares with related chenopod shrubs including species of the genus *Atriplex* and *Grayia spinosa*. Calcium and magnesium levels in spineless hopsage leaf tissue were essentially equal in our study, while most desert shrubs tend to have much larger Ca:Mg ratios (Wallace and Romney 1972). One curious paradox is potassium leaf tissue concentrations are low despite high soil test values, which may reflect low root absorption of tightly bound potassium. However, this is in contrast to what other investigators have observed, particularly with the congener *Grayia spinosa* (Wallace and Romney 1972).

Spineless hopsage represents a highly stress-tolerant species (Grime and others 1988) able to survive and reproduce on steep outcrops of eroding and weathered shale where the combination of aridity (exacerbated by steepness of the slope), salinity (particularly Na), and high expandable-clay content makes establishment of other species difficult. Where geologic parent material changes or is covered by alluvium, or where soils are more developed, other plant species are able to establish and grow. Principal component analysis of soils data reveals that the transition to other vegetation is accompanied by a decrease in soluble salt and clay content of the soil (Factor 1) as well as a change in cation composition (Factor 2).

Grime's model of ecological strategies predicts that a highly stress-tolerant species would be correspondingly poor in competitive ability (Grime and others 1988). The lack of spineless hopsage on immediately adjacent areas suggests that it is indeed unable to establish in the presence of other vegetation despite the presence of a nearby seed source, and that its restriction to such inhospitable sites is therefore a reflection of poor competitive ability as well as tolerance of extreme growing conditions.

The usefulness of spineless hopsage for revegetation will likely be limited to specialized situations where the above-mentioned suite of conditions are met. However, in certain problem areas or degraded sites where other species cannot establish, spineless hopsage could prove a useful candidate for slope stabilization projects. A discriminant function such as was generated in this study may prove useful in identifying such sites. Further testing of this function will be required, however, before its usefulness as a predictive equation can be determined.

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Dark Respiration Comparisons of Forbs and Grasses from Common Gardens

Tom Monaco
Bruce N. Smith
Dan Hemming
Lee D. Hansen
Stephen B. Monsen
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Abstract—Dark respiration rate can predict accessional differences in plant growth ability under drought and temperature stress. Selection based on dark respiration may lead to competitive success of native species against foreign weeds such as cheatgrass. Western yarrow (*Achillea millifolium*) has attributes desirable for both fire suppression and greenstripping. Sandberg bluegrass (*Poa secunda*) is a native perennial grass that occurs over a variety of habitats in the Intermountain West and has the capability to withstand cheatgrass invasion. This study compares dark respiration measured as CO_2 production rates of closely related accessions of western yarrow and Sandberg bluegrass originating from both dry and moist sites to determine whether these species have significant intraspecific physiological differences. Dark respiration rates were measured in common garden plots at the Orchard ranch near Boise, ID, and near Nephi, UT. Measurements were made with an infrared gas analyzer in July and August of 1994 and May and June of 1995 to compare plant responses to seasonal changes. The results indicate that accessions originating from dry sites are able to maintain growth later in the season and show greater adaptation to high summer temperatures, while those originating from moist sites show high rates of respiration earlier in the season at cooler temperatures. The differences in metabolic and growth rates of accessions in common gardens are correlated with sites of origin and ability to withstand extremes of temperature and drought. This simple metabolic test enables rapid choices to be made as to which accession might be more vigorous and successful for revegetating a given location.

Disturbed plant communities can be restored with native grasses and forbs for fire and cheatgrass suppression, fulfilling land management goals of replacing flammable annual vegetation with fire resistant and tolerant perennial species (native and introduced) (Pellent 1990). To be successful, tolerant species must demonstrate seedling vigor enabling them to compete well with annual weeds such as cheatgrass.

Replacing cheatgrass with other species is extremely difficult. Much research has demonstrated the competitive attributes of cheatgrass. Harris (1967) and Harris and Wilson (1970) found that cheatgrass continues root growth in cold temperatures and thus reduces bluebunch wheatgrass subsequent root growth and survival by exhausting available soil water. Cheatgrass seedlings generally develop faster than vigorous cultivars of crested ('Hycrest') and bluebunch ('Whitmar') wheatgrasses, regardless of temperature (Aguirre and Johnson 1991a). Cheatgrass roots elongate and initiate branching of adventitious roots about 1 week earlier than 'Hycrest' and 'Whitmar' (Aguirre and Johnson 1991b). These studies show that perennial seedling survival is ultimately influenced by reduced root growth either due to temperature extremes or cheatgrass competition for soil moisture.

Biological control of cheatgrass by seeding grasses that can competitively suppress cheatgrass without additional control has received much attention. Mountain rye (*Secale montanum*), an introduced perennial grass, exhibits both little post harvest dormancy and high germination at cool/widely fluctuating temperatures, suggesting the ability to fall germinate concurrent with cheatgrass (Anderson and others 1990; Buman and Abernethy 1988). Buman and others (1988) relate the necessity for successful cheatgrass competitors to germinate and have extremely vigorous seedling growth to establish simultaneously with cheatgrass. They conclude that root growth and development of cheatgrass may be inhibited by the ability of mountain rye to establish vigorous seedlings and deplete soil moisture. However, more attention should be given to the selection of key native species. Despite the availability of exotic perennial species that compete well with cheatgrass, these species rarely allow recovery of the native community (Monsen 1994a,b). To avoid this situation, native species possessing features for fire and cheatgrass suppression would be most desirable in restoration.

There is need for more effective and less expensive plant selection techniques that will improve the success of selection (Roberts 1990; Monsen 1994b). Few techniques that evaluate morphological and physiological characteristics have been successful in plant breeding programs, thus, reliable screening procedures to assess integrated plant responses to stress are needed (Johnson and Asay 1993).

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Johnson (1980) and Johnson and others (1981) explain that plant screening techniques should (1) enable researchers to assess plant performance at the critical developmental stage, (2) be completed in a relatively short time, (3) use small quantities of plant material, and (4) be capable of screening large populations. This paper is a preliminary report of our attempt to select plants in such a manner. Recent studies of dark respiration rates of plants (Hansen and others 1995; Criddle and others 1991) show that this property is positively correlated with plant growth rates and may be useful in predicting growth rates. When properly interpreted, dark respiration rates measured under controlled conditions accurately predict relative specific growth rates and stress responses of individual genotypes of plants. The purpose of this study is to make a preliminary evaluation of dark respiration rate as a predictor of plant performance in a given location.

Materials and Methods

Plant material used in this study is in common gardens in Nephi, UT, and at the Orchard ranch near Boise, ID. Western yarrow and Sandberg bluegrass were monitored at the Nephi site. Sandberg bluegrass was monitored at both the Orchard ranch and the Nephi site. Data were collected in spring/summer of 1994 and 1995. Gas exchange measurements were evaluated in the field by placing leaf material in a dark 7cm^3 glass cell in a closed system. Airflow passed through a Li-Cor 2600 infrared gas analyzer for determinations. Measurements were recorded for three successive one minute intervals per sample. Respiration rates were calculated from the increase in CO_2 concentration. Samples from three different plants of the same accession were measured. All respiration rate results are given as μg CO_2/min/g dry weight. Leaf material was saved and oven dried at 65°C for mass determination. Estimation of percent dryness of yarrow plants in the common garden at Nephi was done by visual evaluation of basal leaf material. Dark respiration measurements and dryness ratings were made on the same plots but not on the same individual plants.

Results

Yarrow is a perennial herb in many plant communities located between 1,070 and 3,750 m elevation in Utah. The accessions of yarrow in the common garden in Nephi, UT, originated over a gradient of habitats, and although plants were grown together under similar environmental conditions, respiration rates varied among the accessions (table 1). For example, plots containing *Achillea* spp. (B-4) had respiration rates nearly seven times greater in 1994 and three times greater in 1995 than rates from *Achillea sulfurea*, a species introduced from Iran. For both years, the sequence of rates was the same for the accessions presented. Dark respiration rates also varied with season, those measured in July (1994) were generally lower than those measured in May (1995). This decrease in metabolic rate was expected since drought and high temperature stress increase as summer weather progresses. Figure 1 shows the correlation between dark respiration rates and tissue percent dryness. Respiration and dryness ratings were made on the same plots but not on the same individual plants.

Table 1—Dark respiration rate (CO_2 production) in leaves from yarrow in July 1994 and May 1995, near Nephi, UT. The "B" numbers identify seed collection sites.

Accession	μg CO_2/min/g dry weight 1994 (July)	1995 (May)
B-4 *A.* spp.	+1004.4	+1159.0
B-1 *A. conferta*	+729.0	+1047.0
B-1 *A. santolina*	+373.8	+808.1
B-2 *A. santolina*	+354.8	+699.6
B-1 *A. sulfurea*	+148.0	+460.3
B-28 *A. millifolium*	+764.8	+450.5
B-31 "	+609.7	+456.7
B-34 "	+401.1	+458.3

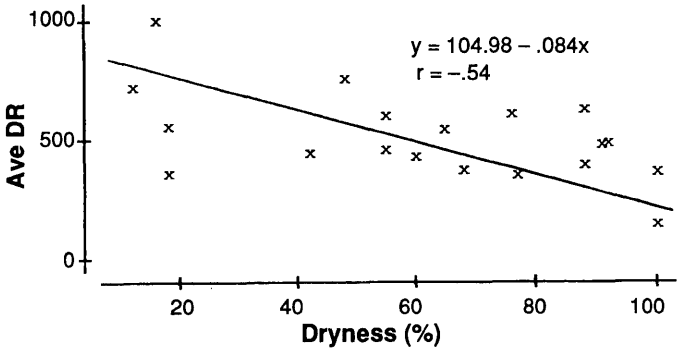

Figure 1—Correlation between dark respiration rates and tissue percent dryness of yarrow accessions.

Respiration rates measured in early May and late July allow rapid screening to predict growth performance at two stages in plant development. Accessions that perform poorly under a certain degree of stress may not be suited for revegetation or restoration purposes on sites with similar environmental limits. On the other hand, those accessions showing excellent adaptation by being able to maintain high respiration rates during temperatures in excess of 40°C, as was observed during the July 1994 data collection, may be very useful in extreme environments. Native western yarrow (*A. millifolium*) accessions had very similar respiration rates in May, but in July significant differences were found between the accessions. In May, native western yarrow had lower respiration rates than the other species, but in July tended to have higher respiration rates than the introduced species.

Sandberg bluegrass (*Poa secunda*), a native perennial grass occurs over a wide variety of habitats in the Intermountain West and varies greatly in morphological and phenological characteristics, offering numerous ecotypes. These different ecotypes occur in distinctive habitat types. In response to differences in elevation, annual precipitation, disturbances, and other site characteristics, physiological functions such as dark respiration should also show considerable variation within this species.

Table 2—Accessions and habitat types of seed collection sites. "B" numbers identify different sites where Sandberg bluegrass occurs.

Accessions	Habitat type
Dry Sites	
B-36	Arid, cold desert occupied by scattered stands of bluebunch wheatgrass and squirreltail, occurring with Wyoming sagebrush.
B-5	Considerably dry site occupied by Sandberg bluegrass and Wyoming sagebrush, site with average annual precipitation below 9.5 inches.
B-12	Site is dryer than B-5, salt desert, occupied by Wyoming sagebrush, shadscale, winterfat, and squirreltail. Soils are windblown, calcareous.
B-33	Sandberg bluegrass grows with Wyoming sagebrush. Located on the Snake River plains, soils are deep. Site receives <8 inches annual precipitation.
Moist sites	
B-8	Upland bench. Summers are short and cool. Average annual precipitation is 12-14 inches. Soils are calcareous. Mountain brush community.
B-20	Boise foothills bench. Moist site with considerable winter snow. Bluebunch wheatgrass and stable vaseyana x Wyoming sagebrush hybrid plant community. Soils on site are granitic.
B-4	Orchard, ID, site. Average annual precipitation around 8.5 inches. Wyoming sagebrush, Thurber needlegrass community.
B-25	Greatly disturbed site. Moist with 14 inches annual precipitation. South facing slope, cool summers. Antelope bitterbrush and Idaho fescue community.
B-14	Cooler, moist site, with 12 inches annual precipitation. Soils are colluvial loams, slightly basic. Mixed Wyoming and vaseyana sagebrush, and bluebunch wheatgrass community.

Accessions originating from dry and moist sites were chosen to evaluate whether dark respiration rates vary systematically with the conditions prevailing at the seed origin. Table 2 describes the habitat and site characteristics where seed was collected. Seed was used to establish common garden plots in Orchard, ID, and Nephi, UT. Four accessions from dry (<10 inches annual precipitation) sites and five from moist (>10 inches annual precipitation) sites were chosen and dark respiration measurements were made in the field in May and June of 1995.

In both common gardens, accessions from dry sites consistently had higher respiration rates than those from moist sites (table 3). In addition, accessions with the lowest respiration rates were those from higher elevation benchland sites receiving greater annual precipitation. Rates of dark respiration among the accessions varied by nearly a factor of two in both gardens at both times. Accessions from the dry sites generally increased respiration rates from May to June, while accessions not adapted to arid environments decreased respiration rates between May and June at Orchard, but increased rates in the garden at Nephi.

Table 3—Dark respiration rate (CO_2 production) in leaves from Sandberg bluegrass (*Poa secunda*) measured at the Orchard Ranch near Boise, ID, and near Nephi, UT, in May and June of 1995. The "B" numbers identify seed collection sites for accessions.

	μg CO_2/min/g dry weight			
	Orchard		Nephi	
Access	May	June	May	June
Dry				
B-36	+584.0	+987.2	+422.0	+544.1
B-5	+561.8	+1227.7	+495.8	+618.7
B-12	+531.7	+621.5	+468.6	+526.8
B-33	+554.3	+1028.5	+392.2	+512.4
Moist				
B-8	+402.6	+379.2	+276.9	+356.6
B-20	+375.8	+356.0	+286.2	+385.5
B-4	+363.7	+219.5	+145.2	+452.6
B-25	+339.4	+208.5	+117.0	+402.9
B-14	+260.8	+205.5	+139.5	—

Table 4—Dark respiration rate (CO_2 production) from native stands of Sandberg bluegrass (*Poa secunda*), squirreltail (*Sitanion hystrix*), and needle-and-thread grass (*Stipa comata*) in May and June of 1995 at Orchard ranch near Boise, ID and at the UT-ID border rest stop (I-84).

	μg CO_2/min/g dry weight			
	Orchard		UT-ID border	
Grasses	May	June	May	June
Sandberg bluegrass	318.6	—	—	491.7
Squirreltail	237.8	538.2	—	—
Needle-and-thread grass	—	—	—	457.3

Dark respiration rates of Sandberg bluegrass and two other native grasses; squirreltail (*Sitanion hystrix*) and needle-and-thread grass (*Stipa comata*) were measured in native stands at the Orchard site and at another site near the Utah-Idaho border. Results are shown in table 4. Squirreltail respiration rates more than doubled from May to June. Sandberg bluegrass was completely dried-out at the Orchard site in June, but at the Utah-Idaho border was quite green and vigorous as was needle-and-thread grass. Data collected at native stands further emphasize the effect that considerable microclimate variability due to geographic, annual precipitation, and elevational differences has on dark respiration rates (Criddle and others 1994).

Discussion

The results of this study suggest that measurement of metabolic parameters can be used to select native cultivars that have promise in specific site restoration. This technique

monitors the rate and efficiency of carbon use at critical developmental stages while plants are balancing trade-offs between growth rate and stress tolerance (Tilman 1993). At these stages, respiratory CO_2 measurements reveal much about competitive ability differences between cultivars. Instantaneous respiratory measurements can be obtained throughout the life-cycle of the plant, allowing for thorough comparisons.

We measured metabolic differences among accessions of the same species and related taxa of western yarrow (*Achillea millifolium*) and Sandberg bluegrass (*Poa secunda*). Collections of western yarrow are widespread with many ecotypic variations. Sandberg bluegrass is a widespread native grass with characteristics to compete with cheatgrass. Significant metabolic differences between accessions depending on site characteristics were observed. Differences in respiratory CO_2 rates between accessions of the same species explain why some are more competitive and will establish better at specific sites. This simple metabolic measurement enables rapid choices to be made as to which accession might be more vigorous and successful for revegetating a given location.

Cheatgrass, like many annuals, germinates in the fall and overwinters as a small seedling. Germination rate is very high for mature seed (Beckstead and others 1995). In the Great Basin, most of the precipitation comes as winter snow with summer rains very rare events. Thus while water is normally the limiting factor for desert plants, it is readily available for seedlings such as cheatgrass that can grow at the low soil temperatures of early spring. Such plants will mature and grow much earlier than plants requiring warmer growth temperatures. This is a tremendous competitive advantage. The success of cheatgrass appears to involve high rates of metabolism and growth at lower temperatures than many native species. Based on this premise, selection for vigor at the critical seedling or establishment stage for accessions of native species or species adequately adapted to a particular site may result in predicting those that will compete successfully with cheatgrass.

Conclusions

Dark respiration rates provide important quantitative information about habitat preferences and also help define physiological tolerances to various environmental conditions. Results from comparing dark respiration rates of many accessions from the same or related species show that rates differ greatly in wide ranging species from a variety of different habitats with dissimilar site characteristics. Results from this study emphasize the physiological variation present in the grasses and forb observed. Dark respiration characteristics may be used as one criteria in the selection of species for particular restoration and reclamation purposes.

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Physiological Control of Evapotranspiration by Shrubs: Scaling Measurements from Leaf to Stand with the Aid of Comprehensive Models

Vincent P. Gutschick

Abstract—Plants exert major control over the hydrologic budget—and, thus, over their own community stability—by their own transpiration and by their partial control over soil evaporation via soil shading. Furthermore, they exert a major control over atmospheric humidity and consequent radiation balance in climate. Predicting future plant status and future climate will require predicting evapotranspiration (ET) over large regions and under varied climates. Models that are useful for diverse sites and species will require understanding of ET control at the process level, physiologically and micrometeorologically. ET prediction also presents significant challenges in quantifying vegetation and its spatial and physiological heterogeneity. We review how process-level understanding can be gained and tested by scaling down from satellite data and scaling up from leaf gas exchange. We have synthesized a model of leaf conductance and fitted its parameters to data on *Larrea tridentata* and *Prosopis glandulosa*. To scale up to whole-shrub and whole-stand evapotranspiration, we must sum over all leaves, accounting for (1) their different current microclimates and (2) their physiological states of acclimation to long-term histories of temperature and irradiance. We have developed models for each of these phenomena and are fitting them to data on many individual leaves. Our model can be integrated to predict whole-plant and whole-stand ET. We outline tests that will be performed on a 1000 m x 300 m transect of mixed shrubland on the Jornada Experimental Range.

Hydrologic and Climatic Role of Plants

On a worldwide average, plants are estimated to transpire about ⅔ of total evapotranspiration (ET) on land (Brutsaert 1982). Plants also intercept sunlight, affecting the soil radiative balance and thus exerting some control over soil surface evaporation, as well (Rosenberg and others 1983). In more arid areas, the proportion of ET accounted for by plants is reduced but still significant. Even in arid areas, plants have important effects on local topography generation (notably as forming "resource islands:" see Schlesinger and others 1990) and the associated hydrologic characteristics of runon/runoff and infiltration dynamics.

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Atmospheric humidity is an important determinant of regional and global climate (Rind and others 1991). Plants contribute the major portion of atmospheric water balance away from continental margins (see extreme case: Salati and Vose 1984), and plants both respond to climatic change (in ET and other ways) and modify climatic change. On regional scales, alteration of vegetation density and activity does affect regional climate (Anthes 1984; Lyons and others 1993; Pielke and others 1992). On the global scale, there is a growing body of evidence that plant control of ET, as well as contribution to surface roughness for momentum exchange in wind, has modified past climatic shifts (Bonan and others 1992) and, by extension, that plants will act so in future climatic change.

It is important in climate modelling to account for plant control of ET, as argued well by Dickinson (1984) and now by many others. In general circulation models of future climate, the atmospheric water balance is one of the major uncertainties, leading to uncertainties in atmospheric radiative balance and surface temperature, in mean cloudiness, and in precipitation patterns (Slingo and Slingo 1988; Soden 1992). Given that plants respond to humidity in controlling their own ET in a regional feedback loop, will they help maintain relative humidity levels, or amplify fluctuations in humidity? In addition to climatic responses of intact vegetation, conversion of native plant communities will affect ET and water balance regionally. Crop plants on the average have more than twice the stomatal conductance of native vegetation (Schulze and others 1994).

Prospects for Predicting ET Over Large Regions

Vegetation has long been sampled for quantitative measures of cover and of physiological activity, including transpiration. It remains extremely challenging to make estimates of transpiration and carbon gain on the scale of watersheds (see Hatton and others 1993) or grid cells in general circulation models for assessing effects of climate change (for example, Hunt and others 1991). Four major problems are:

First, quantifying the vegetation, either from the ground (where the sampling problem is virtually insuperable) or from satellite imagery. While a number of vegetation indices are in use for remote sensing (Myneni and Asrar 1994), their use is compromised by atmospheric interference in the images (Kaufman 1991; Myneni and Asrar 1994), and by variation in calibration according to soil background (Myneni and others 1995).

Second, inadequacies in process-level understanding of transpiration. It is certainly possible to monitor ET over moderate scales (hundreds of meters) with Bowen-ratio or eddy-flux correlation systems (Dabberdt and others 1993). However, these measurements do not directly clarify the role of vegetation in determining ET. Especially, they do not indicate how vegetation, and thus ET, will behave at different sites, under new climates, or with human- or climate-induced alteration of vegetation. Predictive understanding for global change requires that the plant physiological and biophysical controls be explicitly resolved. There are simple models that treat vegetation as one or two layers of uniform leaf matter (Choudhury and others 1991). They may be reasonably accurate when calibrated for a single type of vegetation and soil, for predicting ET under different weather conditions. However, they leave the following two problems:

Third, accounting for heterogeneity of vegetation on all spatial scales. Most obviously, plants with the C_4 photosynthetic pathway differ from those with the C_3 pathway two-fold in water-use efficiency and variously in absolute water-use rates. Even within one pathway, plant species vary markedly in stomatal conductance (Schulze and others 1994). It is not yet possible to distinguish plant species or functional types simply from remote sensing of their spectral signatures, and it may never be, even with new satellite sensors that resolve very many spectral bands (Price 1994). Spectral signatures must be abetted by ground-truthing. Even then, it is not routine to estimate the spectral radiances leaving the vegetative canopy, which are diagnostic for vegetation type, from the radiances received by the satellite. The corrections for atmospheric absorption and emission can be very large (Kaufman 1991). Consider that everything looks rather blue from an airliner cruising above the troposphere, and variably so according to aerosol loads that cannot be independently estimated from satellite measurements.

And fourth, accounting for stress effects on ET, particularly water stress. Different species, especially, downregulate their stomatal conductance and ET at very different soil water status (Turner and others 1984). This amplifies the spatial heterogeneity in ET. Detection of water stress by remote sensing of spectral changes in light reflected from vegetation (the "red edge" and xanthophyll absorptions, or features sensitive to the water content of leaves) has yet to prove practical (Gamon and others 1992). There is some promise in sensing the temperature difference between air (with ground-based measurements) and the surface (vegetation plus soil) (Moran and others 1994). However, there are some important limitations on the accuracy of temperature-based inferences for ET, given that atmospheric corrections are often large (Twomey and others 1977; Price 1983). More robust inferences can be made when the atmospheric humidity content is known or estimated from ground-level measurements and standard height profiles (Price 1983). Such methods apply well over rangeland. Also limiting accuracy of ET estimates, the surface emissivity varies enough to confound the estimation of kinetic temperature from radiative or brightness temperature (Norman and others 1995). A reasonably dense sampling of emissivity on the ground is needed.

These challenges may be addressed either by scaling up ET estimates from leaf to region, or downward from region to leaf (wherein the purpose is to verify process-level understanding). Both prospects are actively under discussion (Carlson 1991).

Scaling Down from Satellite Data

Evapotranspiration is not directly sensible by optical or microwave techniques, despite some innovative and massively data-intensive attempts to image the transport of water vapor in atmospheric eddies (Barnes and others 1990). Some empirical relations have been exploited but, in not being process-based, are not transferable between sites and climates. Most generally, remote estimation of ET must be formulated rigorously in terms of energy balance. The air carries away both the latent heat of evapotranspiration (LE below) and sensible heat (H) embodied in changed air temperature from air contacting the vegetation and soil. The source of these energy fluxes is the net input of radiation (R_n, equalling the difference between downward and upward fluxes of the sum of shortwave and thermal radiation), debited for heat flux into the soil (G):

$$LE - H = R_n - G.$$

Volumes have been written about various ways to estimate each term (see, for example, Rosenberg and others 1983; Brutsaert 1982; Asrar 1991; and many journal articles) The most general and reliable methods require that satellite measurements of radiative fluxes (down and up), vegetative cover (and type, if possible), and surface temperature be augmented by ground-based measurements at least of windspeed, air humidity, and air temperature at several heights. The radiative measurements yield estimates of R_n, though ground-based measurements to augment satellite measurements are widely gaining favor (Sellers and others 1995). If G is not measured on the ground, then it may be estimated in long-term average as a fraction of R_n (Clothier and others 1986; Daughtry and others 1990).

Several methods exist to partition the net energy flow between LE and H. One way is to estimate H from the surface-air temperature difference and the eddy diffusivity of the air, K, in turn estimated from the ground-measured profile of windspeed versus height. In sparse canopies such as in shrubland, estimation of K requires careful consideration of how plants and soil combine to set atmospheric drag and transfer characteristics (Kustas and others 1992).

For process understanding, it is required to relate estimated LE or ET to vegetation amount, type, and physiological status (developmental stage and stress degree). Vegetation amount is typically quantified by spectral indices, such as the normalized difference of infrared and red radiances, NDVI = (IR – R)/ (IR + R). Without local calibration of this index to biomass or leaf area index, its quantitative meaning is somewhat weak (Myneni and others 1994). This is particularly true in sparse canopies such as of shrubs, where spectral noise or soil color differences are equivalent to large relative changes in vegetative cover fraction (Price 1995). An alternative to simple indices is interpretation of radiances in as a mixture of spectra of pure components or "end members" (soil, vegetation, and sunlit and shaded portions of both); see Huete (1988). This method requires local calibration for soil

and vegetation color, as well as for the angles of solar illumination and of view, which affect shadow fractions.

Overall, then, scaling down from remote sensing to plant processes offers the ability to consider large scales, up to global. However, it runs into some significant challenges that can be met as yet only by: (1) Extensive use of ground-based measurements. This is not to be regretted, in that it assures contact with reality. The expense of ground work, while high, should be compared with the expense of satellite imagery. With proper design of protocols to measure ET with mixed satellite and ground information, the types of information multiply each other's value considerably and minimize the total cost. (2) Extensive local calibration of methods. We lack the power to generalize most things, such as how fractional cover by vegetation relates to ET. Escaping this limitation as much as possible is our research focus.

Scaling Up from Leaf and Plant Scales

Leaf conductance (g_s) and transpiration must be predicted under arbitrary conditions. Then, conditions on each leaf (or class of leaf) must be estimated from a knowledge of plant and community structure, including soil water status. Our knowledge of physiological control of g_s and leaf transpiration, $E_{L,a}$, is well advanced (Carlson 1991). Among a variety of formulations, we employ in our research an effective and concise one based on the empirical Ball-Berry relationship (Ball and others 1987):

$$g_s = mAh_s/C_s + b.$$

This expresses the close scaling of g_s to CO_2 assimilation rate, A, in a very specific way. It also embodies the scaling of g_s to humidity, specifically to the relative humidity at the leaf surface, h_s, below the leaf boundary layer. Finally, it incorporates short-term responses to varying leaf-surface CO_2 concentration, C_s. The factors m (slope) and b are constants, presumably permanent developmental characteristics of a leaf. Remarkably, well-watered plants from almost any habitat show very similar values of m, close to 10.0 (Gutschick and others, in preparation, studies of xeric shrubs, mesic crops, Eastern trees; fig. 1).

To complete the description of how leaf microenvironment determines $E_{L,a}$, we need process equations for (1) how A responds to light level (PAR irradiance), leaf temperature (TL), and CO_2 concentration as provided by the models of Farquhar and others (1980), and (2) how leaf temperature is determined by the balance between radiative gain, radiative loss, and cooling by transpiration and convective-conductive transfer (for example, Nobel 1992). When scattered radiation is prevalent, as within a canopy, the radiative transfers are tedious, if straightforward, to calculate (Gutschick and Wiegel 1984 and many others).

Thermal radiative transfers are likewise rather involved (Kimes and others 1981; Paw U and others 1989; Huband

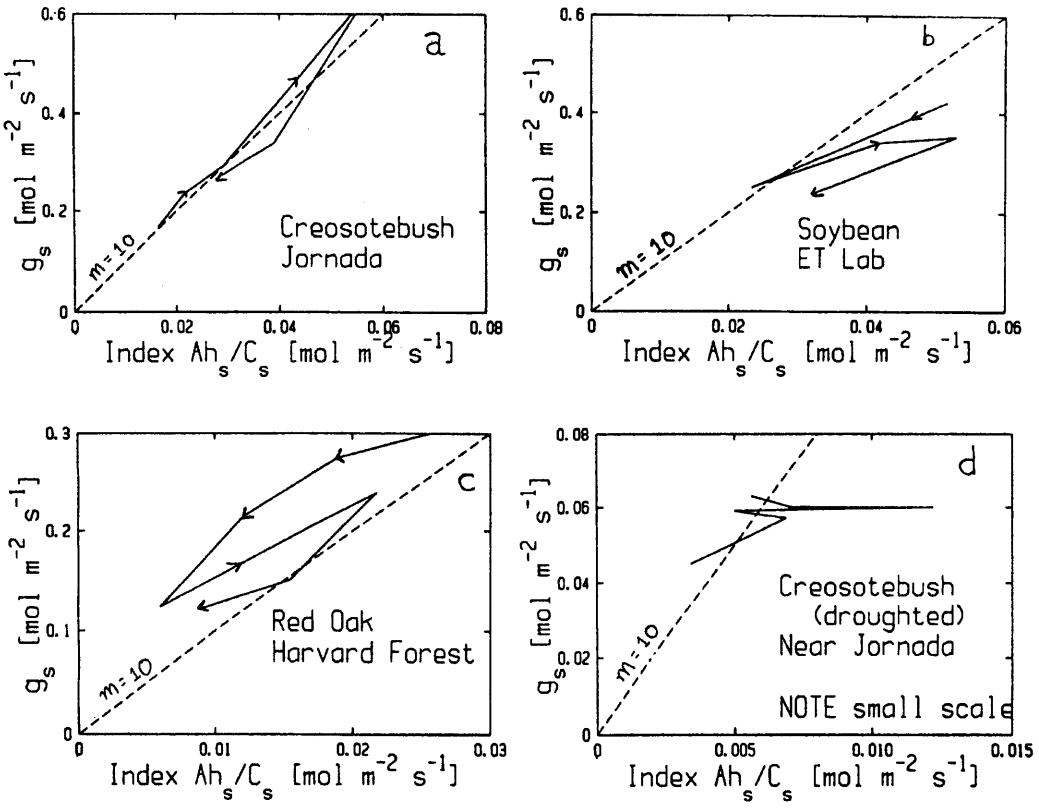

Figure 1—Similarity of Ball-Berry slope, m_{BB}, for several plant species when well-watered (a-c), and divergence from common slope for stressed plant (d). Measurements were made with open-mode gas-exchange system by the author's research group as noted in Acknowledgments.

and Monteith 1986). In any event, simultaneous solution of all three major equations for single leaves is possible (Collatz and others 1991). Computationally efficient solutions (Gutschick, in preparation, and fig. 2) are demanded to describe whole plant canopies with reasonable effort.

The microenvironment on each leaf is determined by the interplay of the microenvironment at the canopy boundary (PAR flux density, windspeed, temperature, and humidity at the top of the canopy) and the canopy structure. Once we know the light flux, windspeed, temperature, and such at a leaf location within the canopy, the leaf's temperature, too, is determined. The profile of humidity is affected rather little by the vegetation itself, especially in sparse shrubs. However, the profile of air temperature is notably affected by vegetation; the solution must be determined interactively (Gutschick 1988, 1994, and many others).

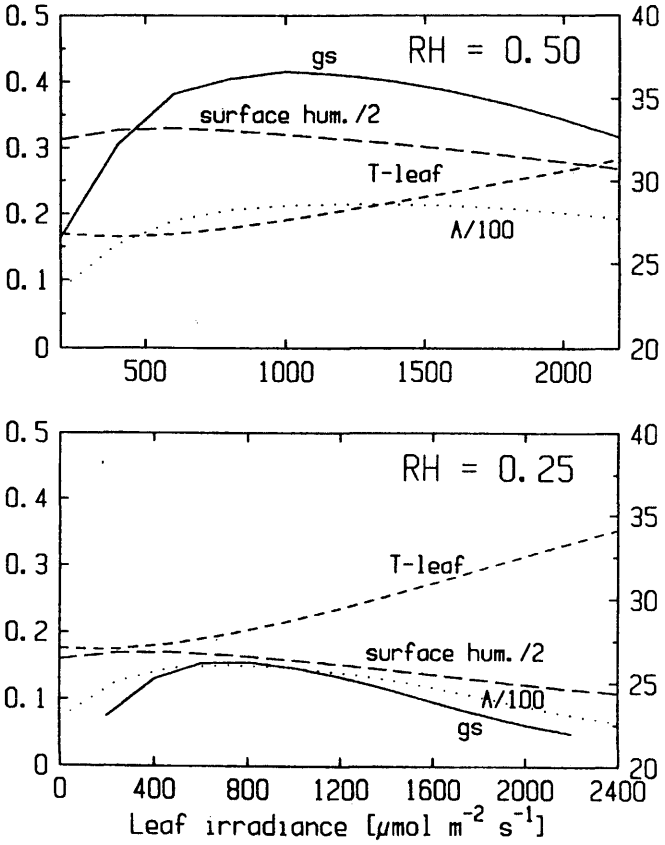

Figure 2—Model calculations of gas-exchange performance of single leaves in a cluster, operating at various leaf irradiances because they have various leaf angles. Results are presented for two different relative humidities (RH) in free air. Curves are given for stomatal conductance (g_s; as mol $m^{-2}s^{-1}$), CO_2 assimilation rate (A; as μmol $m^{-2}s^{-1}$, divided by 100), leaf surface humidity (h_s; divided by 2), and leaf temperature (T-leaf; degrees C, read on right-hand axis scale). Note the predicted falloff of performance at high irradiance, resulting from leaf heating and consequent drop in surface humidity. The drop is relatively much less significant at high RH. Leaves share the same Ball-Berry parameters (slope m = 10, intercept b = 0.008 mol $m^{-2}s^{-1}$) and maximal carboxylation capacity (81 μmol $m^{-2}s^{-1}$ at 25 °C). They share the same microenvironment of air temperature (30 °C), sky radiative temperature (0 °C), ambient CO_2 partial pressure (35 Pa), and windspeed and hence boundary-layer conductance (2 mol m^{-2} s^{-1}). Calculations were made with the authors model described in text.

The structure of the vegetation community is very complex but can often be approximated very well by simple functions to describe leaf positions and orientations (Campbell and Norman 1989). Sparse, irregular canopies, as in shrub land, are quite challenging to describe. The penetration of light into canopies is a very well developed topic. It remains more challenging to describe wind penetration into arbitrary structures (Raupach 1988), though some relatively simple ideas may apply (Goudriaan 1989; Massman 1987). By simple, I mean not computationally simple, but having a small demand for descriptors of the canopy structure. Computing power is easy to get; data on field vegetation never is. For any canopy, after its geometric arrangement is described, it is necessary to describe how leaf maximal g_s or, equivalently, maximal A, varies with position. Fortunately, canopy development is under genetic control, closely maximizing net assimilation (Sellers and others 1992; Myneni and others 1992). Thus, we can estimate maximal A of each leaf from the local microenvironment (seasonally averaged irradiance, temperature).

Water stress reduces g_s and E and introduces considerable diversity in plant control of g_s (Turner and others 1984). Using the Ball-Berry description, we may ask if stress alters slope m, assimilation capacity A, or both. We find that the answer is "both," and the stress level at which changes occur varies markedly with species. Acting to reduce the diversity is the generalization that g_s responds to soil water status primarily, not to more derived leaf water status (Tardieu and others 1993 and refs. therein), and in particular to soil mechanical strength (Masle and Passioura 1987). We seek to reduce the complication of diversity further. We postulate that stress responses diverge about a mean that is conservative among different communities in the same climatic zone. We are testing this empirically.

We are also attempting to explain such patterns with models of plant coexistence with competitive resource use (see Tilman 1994 and refs. therein; Maynard and others 1973). There are two additional stresses that alter A and thus g_s: thermal stress (Björkman and others 1980) and photoinhibition (Baker and Bowyer 1994; Ball and others 1991). These too, are potentially predictable from the leaf's microenvironmental history (Ögren and Sjöström 1990); we are developing general models in collaboration with M. Ball of the Australian National University (see Ball and others 1991).

Transect Study

ET has been measured on shrubland in the past. On the Jornada, W. A. Dugas, H. Mayeux, R. E. Gibbens, and their associates performed long-term monitoring of 4 different communities in 1991-1992, using the Bowen ratio method. We are constructing estimates of ET scaled up from our leaf-level gas exchange, to compare with these data. We further propose an intensive, one-day field campaign, tentatively set for September 1995, for two purposes:

The first is to test our ability to predict ET from microenvironment and vegetation structure in diverse plant communities. We will sample areas (covered by Landsat TM pixels) variously dominated by different, single shrub species and also intermixed. A 1000 m x 300 m transect in pasture 15 has been selected and given preliminary characterization for soils and vegetation. We will use our body of data on physiological control of g_s and $E_{L,a}$ in the plant species on this transect.

We will scale up from leaf gas exchange done on the campaign data, to whole branch or plant E as measured with novel sapflow gauges (Senock and Ham 1993). We will also scale down from Landsat TM data reduced to (a) estimates of vegetation leaf area, compared with aerial photos reduced by our methods of digital image analysis and (b) predictions of E as described earlier. We will measure vegetation water-stress level with time-domain reflectometry. If we find systematic discrepancies between the scaled-up and scaled-down estimates of ET, we will seek to assign them quantitatively to description approximations both in measurements and in usage of simple models, both in canopy structure and in physiological models of g_s control.

The second purpose is to test our ability to measure and use compact descriptions of vegetation, including its diversity in stomatal control. We have been developing image-analysis techniques for quantifying leaf area and angle distribution on a number of spatial scales, from branch to plant to community. In addition to testing the compact description of vegetation per se, we will test the use of simple transport models to predict irradiance and temperature on leaves. We will compare these to irradiance measurements made with compact, leaf-mounted light sensors (Gutschick and others 1985) and to leaf temperatures measured by contact and by imaging thermal infrared.

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Effects of Summer Drought on the Water Relations, Physiology, and Growth of Large and Small Plants of *Prosopis glandulosa* and *Larrea tridentata*

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Ross A. Virginia
James F. Reynolds

Abstract—Large and small plants of creosotebush and mesquite were subjected to drought during summer 1993. Large and small plants responded to drought with lowered xylem water potential and lowered photosynthetic gas exchange. Large plants appear to maintain a reduced but constant photosynthetic rate during drought, and responded to precipitation with increased photosynthesis. However, small plants attempted to maintain a high photosynthetic rate throughout the season, responding less strongly to precipitation events, but probably depleting reserves more and causing photosynthesis to decline more when droughted. Our results suggest that large, established plants are better able to withstand drought than are small, establishing shrubs.

Mesquite (*Prosopis glandulosa* (Torr.) var. *glandulosa* Torr.) and Creosotebush (*Larrea tridentata* D.C. (Cov.)) are two shrub species that have greatly increased in abundance during the last century, in valleys and basins throughout the southwestern U.S. where perennial grasses previously dominated. The replacement of perennial bunch grasses by shrubs may be due to many interacting factors including drought, grazing, climate shifts, and fire (Buffington and Herbel 1965; Schlesinger and others 1990). In light of continued climate change and environmental perturbation, the ability to predict fluxes in life-form (shrub versus grass) composition will depend on understanding how they respond to the various factors. Here, we consider the responses of the two shrub species to artificially induced drought, particularly in the context of the degree of establishment of a shrub. Small, establishing shrubs with underdeveloped, shallow root systems may be functionally similar to the perennial bunch grasses they displace. The root systems of larger established shrubs probably exploit a larger volume of soil and access moisture from deeper soil, which is not normally available to grasses (for example, Nilsen and others 1983). Larger, established plants simultaneously sequester increasing water and nutrient resources and effectively "focus" these resources into soil regions under their crowns. Establishment and the relative abundance of water and nutrient resources may also translate into morphological differences such as differences in stem angle (Whitford and others 1996).

Here we ask whether these morphological, size-related changes in the shrubs are accompanied by physiological changes that would allow them to make more effective use of the changing resource structure of the environment. In some species, for example, *Hedera helix*, some physiological characters such as stomatal aperture and photosynthesis exhibit age-dependent sensitivity to environmental factors (Bauer and Bauer 1980). Perhaps more simply, this sensitivity may occur as a result of size-dependent responses to shrub water, nutrient and osmotic reserves. Size-dependent differences in photosynthesis and stomatal conductance have been reported in mesquite (Brown and Archer 1990), and size-dependent differences in water-use efficiency have been found in the desert shrub *Crysothamnus nauseosus* (Donovan and Ehleringer 1992). Franco and others (1994) found some indication that large plants of creosotebush may access deeper soil water reserves even when not artificially droughted.

We hypothesize that mesquite and creosotebush shrubs of different sizes would have different physiological responses to artificially induced drought. Under drought, large established shrubs with greater access to, or greater "stored", nutrients and water should exhibit only a slow decline in photosynthesis until resource reserves are depleted. Drought should induce a greater decline of photosynthesis in small shrubs, which probably do not have a substantial store of nutrients or water. This leads to the corollary hypothesis that the physiological responses of small shrubs are more closely coupled to variation in soil moisture than are the physiological responses of large shrubs.

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To investigate these hypotheses we examined the relationships among plant and soil water contents and photosynthesis of small and large plants of mesquite and creosotebush growing in two mutually exclusive habitats in the Jornada Basin of the Chihuahuan Desert. Plants growing in this stressful, hot desert environment should show the clearest evidence of size-dependent coupling of physiological response with the availability of soil moisture.

Materials and Methods

Study Sites

Both study sites were in the Jornada del Muerto Basin in southern New Mexico, USA. The area has an elevation of 1,200 to 2,000 m, and is close to the northern limit of the Chihuahuan Desert. The climate is semiarid, with a mean annual precipitation of 233 mm (Conley and others 1992), of which 64% occurs as summer (July-October) rainfall from brief convectional storms. Summer mean maximum and minimum temperatures are 31°C and 10°C (Conley and others 1992). Freezing temperatures may occur from late October to mid April (data from the Jornada LTER Weather Station).

The mesquite study site was near Waggoner Well, in the northwest flank of the United States Department of Agriculture (USDA) Jornada Experimental Range. This is a sand dune area, which began forming about 80 years ago, following intensive grazing and drought (Buffington and Herbel 1965; Hennessy and others 1983).

The creosotebush study site was on the coarse-loamy soils of the northeast-facing piedmont slope of Mt. Summerford, the northernmost peak of the Doña Ana Mountain range.

Experimental Plots and Shrub Size Classes

While small creosotebush may have a single primary stem, both creosotebush and mesquite commonly occur in multi-stemmed clumps, and clumps having a discrete canopy were considered to represent a single shrub. From these we selected sixteen large (established) and sixteen small (establishing) shrubs of each species on the basis of height, diameter, and litter accumulation under the shrubs. The root systems of selected shrubs were isolated from the surrounding soil by digging a trench 0.6 m from the edge of the shrub's crown to a depth of approximately 1.5 m, lining the trench with black plastic sheeting, and returning the soil to the trench. All trenching was done between January and February 1991.

Open-sided rain-exclusion shelters, constructed of metal two-by-fours, with a greenhouse quality transparent plastic (CT Film, Harrington, DE) pitched roof, having a minimum vertical clearance of 1.5 m from the top of the plant and extending approximately 0.6 m beyond the edge of the trench, were placed over half the plants of each size class of mesquite and creosotebush. The architecture of these shelters allowed free movement of air through the shelter, and minimized light exclusion, while effectively excluding meteoric water.

Water Relations and Gas Exchange

Net photosynthetic rate was measured on leaf clusters on marked terminal stem segments (creosotebush) or leaves (mesquite) with an LI 6200 Portable Photosynthesis System (LI-Cor Inc., Lincoln, NE) on seven days for each species during the summer of 1993. Volumetric water content of soil (VWC) and plant water potential (Ψ_L) were also measured on these days. Photosynthesis measurements were repeated at approximately 1.5 hour intervals, from approximately 0700 to 1700 Mountain Daylight Savings Time. These measurements were used to obtain an integrated daily value for photosynthesis (A_i) over a standard time period for all measurement days. Soil water content was measured at 0.3, 0.6, and 0.9 m through an aluminum tube permanently installed in each plot, with a 503 DR hydroprobe (CPN Corp., Santa Barbara, CA). Plant water potential was measured on stem segments (creosotebush) or leaves (mesquite) with a model 3005-1422 Plant Water Status Console (Soil Moisture Corp., Santa Barbara, CA).

Results

Volumetric Water Content of Soil

At the beginning of summer 1993 VWC of creosotebush plots at 0.3 m was similar in large control (0.11 ± 0.01 m^3H_2O m^{-3} soil) and large droughted (0.14 ± 0.05 m^3H_2O m^{-3} soil) plant plots, and in small control (0.18 ± 0.02 m^3H_2O m^{-3} soil) and small droughted (0.17 ± 0.01 m^3H_2O m^{-3} soil) plant plots. One-way Analysis of Variance (ANOVA) was used to investigate differences in soil VWC between treatment and control plots with large or small plants.

Control plots developed significantly greater mean VWC by July 20. Small plant control plots remained significantly wetter than did treatment plots throughout the summer. Plots with large plants had similar VWC except on August 5 and September 6, when the VWC of large plant control plots increased dramatically following major precipitation events.

There were no significant differences between control and drought treated plants of either size at the 0.6 m and 0.9 m depths. We found no consistent differences in VWC in mesquite treatment and control plots. However, on July 19 and again on August 19, soil in small mesquite control plots held significantly more moisture than did the treatment plots. These dates coincided with or were immediately after the two major precipitation complexes of summer 1993 at this site.

Plant Xylem Water Potential

Xylem water potential (Ψ_L) of small droughted creosotebush ranged from –2.5 to –5.4 MPa and was significantly (ANOVA, $p < 0.05$) lower than Ψ_L of small control plants (–1.7 to –4.8 MPa) through most of the summer. Large droughted creosotebush had Ψ_L ranging from –2.2 to –5.4 MPa and did not vary significantly from Ψ_L of large control plants, which ranged from –2.1 to –5.0 MPa. Xylem water potential of small droughted mesquite ranged from –1.2 to –2.5 MPa and was significantly lower than the Ψ_L of small control plants,

which ranged from –0.75 to –1.7 MPa. Statistically significant differences in Ψ_L were detected between large mesquite control plants (range –1.1 to –1.95 MP) and large droughted plants (range –1.3 to –2.4 MPa) on August 4, August 17, and September 4 only.

Photosynthesis

Overall, large and small creosotebush had similar seasonal patterns of daily net photosynthetic carbon assimilation rates (A_i), reaching maximal values around mid July and decreasing thereafter. Large control plants of creosotebush occasionally (on two out of seven measurement days) had A_i greater than that of large droughted plants (fig. 1A). On the same measurement days, control plants of small creosotebush showed clearly greater A_i than did droughted plants (fig. 1B).

Large droughted mesquite A_i reached a relatively stable maximum around mid-July and decreased substantially only at the end of the growing season, while at the same time A_i of large control plants fluctuated from treatment plant levels to significantly greater rates and back (fig. 2A). Small droughted mesquite A_i began to decrease and diverge from the A_i of control plants around early August, and this condition persisted throughout the summer (fig. 2B).

A simple regression model was used to investigate the relationship between VWC and Ψ_L, and between Ψ_L and A_i. For measurements taken during summer 1993, mesquite

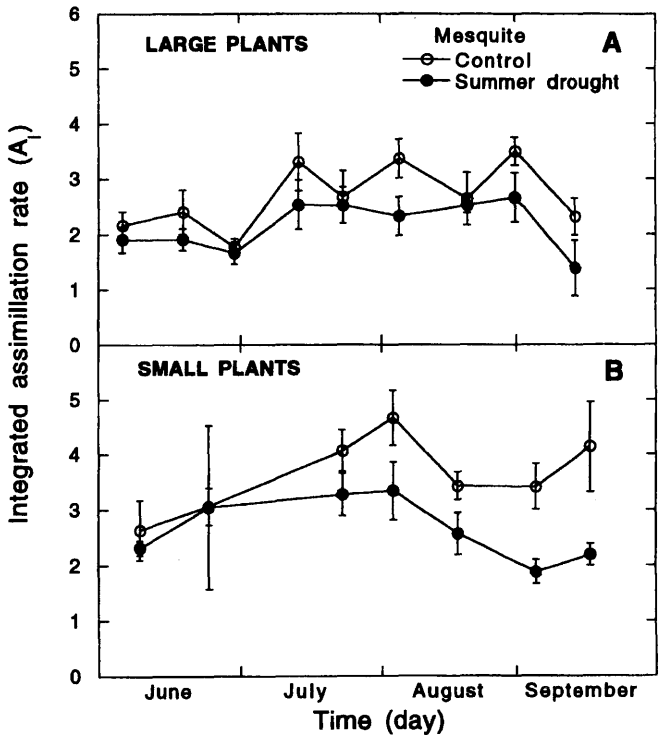

Figure 2—Net photosynthetic assimilation rate (A_i) of (A) large, and (B) small mesquite control plants and plants droughted during summer 1993, integrated between 7:00 and 17:00 Mountain Daylight Savings Time.

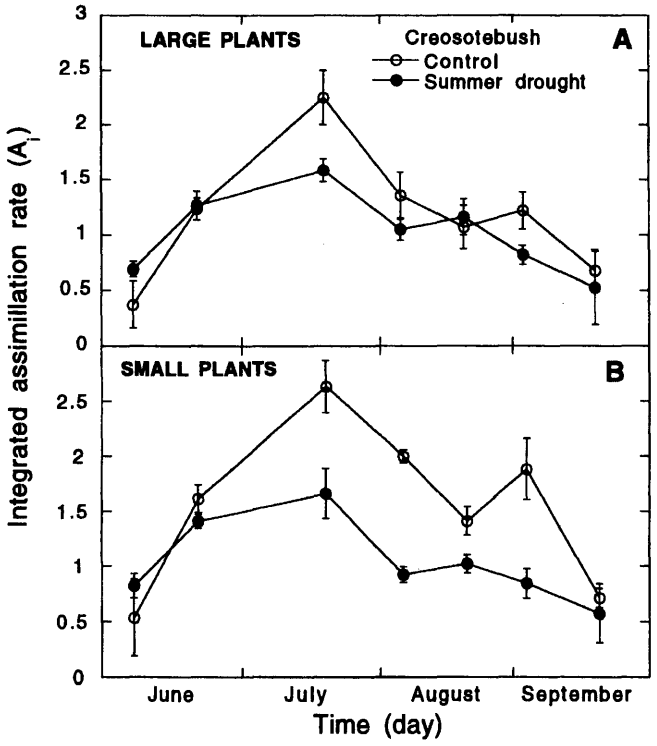

Figure 1—Net photosynthetic assimilation rate (A_i) of (A) large, and (B) small creosotebush control plants and plants droughted during summer 1993, integrated between 7:00 and 17:00 Mountain Daylight Savings Time.

VWC at 0.3 m was significantly and positively related to Ψ_L of large plants (n=28; $p < 0.05$), but Ψ_L was not significantly related to A_i in droughted or control plants (n=28; $p > 0.05$). In creosotebush VWP at 0.3 m was significantly and positively related Ψ_L of control plants of both size classes (n=23 to 27, $p < 0.05$), and Ψ_L was significantly and positively related to A_i of control and treatment plants of both size classes (n=23 to 27, $p < 0.05$). In both species there was no significant relationship between Ψ_L and VWC at 0.6 or 0.9 m.

Discussion and Conclusions

Although there were differences in physiological responses of the two species to induced drought, our data support the hypothesis that large and small plants may respond differently to environmental perturbation.

The rain-out shelters were effective in excluding meteoric water from experimental plots, as seen from the differences in soil VWC between control and treatment plots, particularly at the most shallow soil depth. In control plots soil VWC at the 0.3 m depth also appears to relate directly to plant xylem water potential in both species. The absence of a relationship between Ψ_L of droughted plants and VWC at any of the three soil depths suggests that under drought conditions plants of both species and size classes obtain some moisture from deep soil reserves.

Overall, if control plant A_i is representative of potential A_i, drought depressed the A_i of small plants more than the A_i of large plants. Interestingly, this was due to small control plants having an overall greater photosynthetic rate than large control plants—A_i of large and small droughted plants was very similar. Photosynthetic assimilation rate of large control creosotebush was only rarely different from that of large droughted plants. Days when control plant A_i was greater than treatment plant A_i coincided with recent precipitation events. This suggests that (1) large creosotebush A_i is not severely limited by depletion of soil water reserves, and (2) large creosotebush can respond to short-term environmental perturbation—for example, precipitation events—but the magnitude of the response is relatively small and short-lived. Drought caused small creosotebush to have significantly lower photosynthetic rates than did small control plants through most of the summer. However, while small control plants also responded to precipitation events, their A_i did not decline to droughted plant levels until the final measurement of the summer.

In mesquite also, if control plant A_i is representative of potential A_i under prevailing environmental conditions, the drought treatment caused significant declines in large and small plant A_i. While overall A_i levels were greater in small plants than in large plants, large droughted plant A_i remained approximately unchanged for much of the summer and small droughted plant A_i declined substantially from midsummer. In small plots, continued rapid loss of water with no replenishment may deplete water resources to levels that are limiting to photosynthetic gas exchange. The absence of a similar decline in large droughted plants suggests that these plants have access to other sources of moisture, probably from deeper soil layers.

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Tracking Environmental Change with the Desert Shrub Ocotillo (*Fouquieria splendens*): Prospects and Pitfalls

Keith T. Killingbeck

Abstract—Ocotillo is a drought-deciduous desert shrub capable of orchestrating rapid morphological and physiological adjustments to changes in environmental conditions. Lengths of over 2,500 stem segments from two populations of ocotillo growing in the Chihuahuan Desert were measured to explore the possibility that episodes of stem growth could be used to infer past environmental change. Stem growth was so intermittent and complex that historical projections of environmental conditions were not possible without first establishing benchmark stem segments. Once established though, benchmark stem segments and subsequent stem growth may be used as easily measurable integrators of ongoing environmental change in desert ecosystems.

Reconstructing past environmental changes with dendrochronological techniques has been highly successful in forest ecosystems (Fritts 1976; Fritts and Swetnam 1989), yet arid ecosystems typically lack an abundance of perennial species replete with measurable growth rings. Notable exceptions include *Artemisia tridentata* (Ferguson 1964), *Prosopis glandulosa* (Flinn and others 1994), and several species of chaparral shrubs (Keeley 1993), but few true desert endemics produce growth rings that are both measurable and interpretable. Anomalies such as "false rings" and "missing rings" (Fritts and Setnam 1989; Keeley 1993) that can obliterate attempts at correlating growth rings with climatic change are especially problematic for plant species growing in the highly variable climatic regimes common to most deserts.

Ocotillo (*Fouquieria splendens* Engelm.), a drought-deciduous shrub endemic to the Chihuahuan and Sonoran Deserts of North America, produces terminal segments on its stems that clearly demarcate pulses of growth (Hendrickson 1977). Segments are separated from one another on the same stem by obvious nodal "seams" that remain intact for the life of the stem. Thus, a separate chronosequence of growth episodes is available for measurement on every stem of an ocotillo plant.

Such a record of growth could be invaluable as a nondestructive phytometric means of tracking environmental change in the Chihuahuan and Sonoran Deserts. However, several prerequisites must be met before ocotillo stem growth can serve in this capacity.

First, ocotillo must be capable of making physiological and morphological adjustments to interyear changes in environmental conditions. The capacity for significant interyear change was demonstrated in 1989 when resorption of nitrogen from senescing ocotillo leaves was more than six times higher than that measured in the same plants three years before (72% versus 11% resorption, respectively; Killingbeck 1992, 1993). Additionally, interyear changes in stem growth have been documented in a population of ocotillo growing in the Sonoran Desert (Darrow 1943).

Second, the years in which stem segments are produced must be ascertainable. Evidence from the Sonoran Desert near Tucson, Arizona, suggests that the ages of extant segments may not be associated with a specific age because of "missing segments" (Darrow 1943) analogous to "missing growth rings." Further, because temperatures are relatively warm throughout the year and precipitation is distinctly bimodal in the eastern portion of the Sonoran Desert encompassing the Tucson area (Shreve 1951), ocotillo stems may even produce "false segments." On the contrary, the Chihuahuan Desert in New Mexico has but a single period of significant precipitation each year during the summer, thus increasing the possibility that ocotillo stems would produce only one segment each year. The consistent production of one segment per stem per year by ocotillos growing in New Mexico would enable the dating of stem segments, thus meeting the second prerequisite.

The primary goal of this contribution is to explore the efficacy of utilizing stem segment growth patterns in ocotillo to infer past environmental change, and to monitor ongoing environmental change in the Chihuahuan Desert. The specific questions I will attempt to answer include: (1) What are the relationships in length among the six uppermost segments of ocotillo stems between populations and within individual plants? (2) Is the presence or absence of new stem segments in a given year uniform among stems of the same plant, or among individuals in the same population? (3) Is it possible to determine the year in which unmarked, extant ocotillo stem segments were produced? (4) Do the number and length of newly produced stem segments in ocotillo differ between years or populations? (5) Are differences in stem segment production between years and between populations large enough to be useful in tracking environmental change?

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Methods

Site Identification and Field Measurements

Stem segment production was measured in 1993 and 1994 in two populations of ocotillo, one growing in the foothills of the Organ Mountains and another in the Jornada Long Term Ecological Research (LTER) Area. Both sites are located in the northern reaches of the Chihuahuan Desert in southern New Mexico and are less than 30 km apart. The Organ Mountains site (32°19′ N, 106°38′ W) lies approximately 11 km east of Las Cruces, New Mexico, and is characterized by rocky soils and moderate slopes. The Jornada LTER site (32°30′ N, 106°48′ W) lies within the New Mexico State University Jornada Experiment Range 20 km north of Las Cruces and is also characterized by rocky soils and moderate slopes.

In June 1993, the lengths of the terminal six growth segments (fig. 1) were measured on the stems of 12 plants in the Organ Mountains, and 23 plants in the Jornada LTER site. Stems less than 150 cm long were excluded from analysis as were stems that were branched in their terminal meter of length or that had obvious morphological defects. Each segment was measured separately and segregated according to its relative position within the sequence of six terminal segments. In the Organ Mountains, all stems fitting the above criteria were measured (193 stems, 1,158 segments) whereas in the Jornada LTER site, sampling was limited to ten stems per plant (228 stems, 1,368 segments; two plants had only nine stems each that met the above criteria). Because stem segments are not produced in these populations until July-August, measurement of the terminal segments in June reflected stem growth through 1992.

The most recently produced stem segment on each stem of 11 of the 12 study plants at the Organ Mountains site was marked with red nail polish in June 1993 so as to be able to identify future stem growth. In late May 1994, all new stem segments produced after June 1993 were located, tagged with color-coded pipe cleaners, and measured (length). The most recently produced stem segment on each stem of the previously unmarked plant was also tagged with a pipe cleaner. In early September 1994, all new stem segments produced on all 12 study plants after May 1994 were located, tagged with color-coded pipe cleaners, and measured (length).

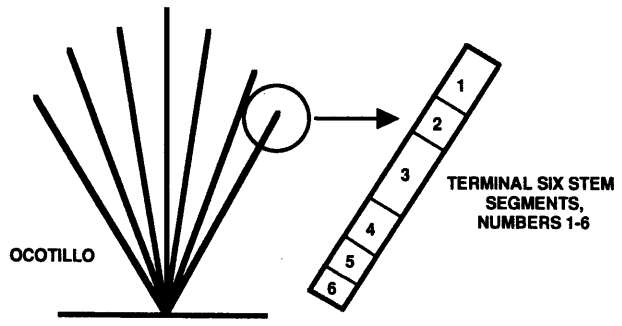

Figure 1—Diagram of terminal ocotillo stem segments (numbers 1-6) measured in this study.

All stem segments produced during 1994 on the 23 study plants at the Jornada LTER site were located, tagged with color-coded pipe cleaners, and measured (length) in early September 1994. None of the segments on these plants had been marked previously, yet new segments bore leaves that clearly identified the segments as newly produced. Because primary leaves only occur on newly produced stem segments and differ significantly in appearance from secondary leaves, segments holding primary leaves are easily identified as newly produced segments. However, because primary leaves can be dropped from a segment in the same growing season in which they were produced (petiole tissue is retained and develops into the stem spines characteristic of this species) and replaced by secondary leaves, the absence of primary leaves on a stem segment does not necessarily indicate that the segment was produced in years past (personal observation).

The number of stems on each plant of both populations was measured in April 1995.

Data Synthesis and Statistical Analyses

All 35 plants used in this study are also part of another study begun in 1989 to test the effects of trace metal fertilization on the resorption of nitrogen from senescing ocotillo leaves. Because fertilization treatment effects did not affect the outcome of the stem segment analyses, data for treatments and controls were not segregated in this paper.

To estimate the percentage of stems on each plant that produced new stem segments in a given year, I divided total number of stems per plant by total new segments produced in a specific year. Given the fact that a small number of stems produced terminal and lateral segments in a given year (i.e. more than one new segment per stem per year), the values presented (table 1) slightly overestimate the percentage of stems producing new segments in 1993 or 1994.

All statistical analyses were completed with SYSTAT software (Wilkinson 1992) on Macintosh computers. Normality of data distribution was determined with the Lilliefors test. When the assumption of normality was not met, the Kruskal-Wallis test was used to establish probabilities of difference among three or more means, and the Mann-Whitney U-test was used to determine whether pairs of means were statistically different. When the assumption of normality was met, Student's t-test was used to determine whether pairs of means were statistically different. Correlation analyses were all performed with the Pearson correlation statistic.

Results

Mean segment length in the terminal six ocotillo stem segments varied from 14.0-16.6 cm in the Organ Mountains and 12.0-17.0 cm at the Jornada site (table 1). Segments 3, 4, and 5 of both populations were the shortest segments, and segments 1 and 2 were the longest. Ranges of stem segment lengths were remarkably large. Lengths of stem segment 5 varied from 1-41 cm in the Organ Mountains and lengths of stem segment 1 varied from 1-44 cm at the Jornada site. Even for the segment with the smallest range in lengths (segment 4, Organ Mountains) there was more than a

Table 1—Length of the terminal six stem segments growing on 193 ocotillo stems in the foothills of the Organ Mountains, and 228 stems in the Jornada LTER site (mean and range, cm). Segment number '1' was the uppermost segment on each stem in spring 1993, and segments '2-6' followed in sequence down each stem. SE = standard error of the mean.

	Organ Mountains			Jornada LTER site		
Segment	Length	SE	Range	Length	SE	Range
1	16.6	0.5	1.3-35.6	16.3	0.5	1.3-44.5
2	15.8	0.5	1.3-38.1	17.0	0.6	1.3-41.9
3	14.0	0.4	1.3-38.1	12.0	0.4	1.3-35.6
4	14.6	0.4	2.5-35.6	13.3	0.5	1.3-43.2
5	15.4	0.5	1.3-40.6	12.7	0.4	1.3-30.5
6	15.7	0.5	2.5-40.6	14.0	0.4	1.3-35.6

14-fold difference between the shortest and longest individual segments.

Variability in segment lengths was also extremely high in different stems growing on the same plant. Data from plant #19 at the Jornada site are representative of this high variability (fig. 2). The uppermost segment on stem 5 (33.0 cm) was 8.7 times longer than the uppermost segment on stem 10 (3.8 cm). Lengths of segment 5 were the most uniform, but even the longest (on stem 4) and shortest (on stem 1) number 5 segments differed by a factor of 2.5. Patterns of segment growth were also dissimilar among stems. For example, segment rankings in descending order by length were 3 > 6 >1 > 4 = 5 > 2 for stem 7, and 6 > 2 > 1 = 5 > 4 > 3 for stem 9. Segment 3 was both the longest and shortest of the terminal six segments on different stems.

Differences in growth among stems were also appreciable when considered for periods of time greater than one growing season. Because the number of terminal stem segments produced by any stem of the 40 study plants in a given year was either one or none (i.e. never two or more, unpublished data), the combined lengths of the six terminal segments on each stem in figure 2 represent a minimum of six years of growth. Over this period of time, terminal growth of the fastest growing stem (stem 7, 95.3 cm) was twice that of the slowest growing stem (stem 10, 43.2 cm).

New stem segments produced in 1993 and 1994 suggest the presence of yet another tier of complexity inherent in ocotillo growth (fig. 3). Individuals in both populations of

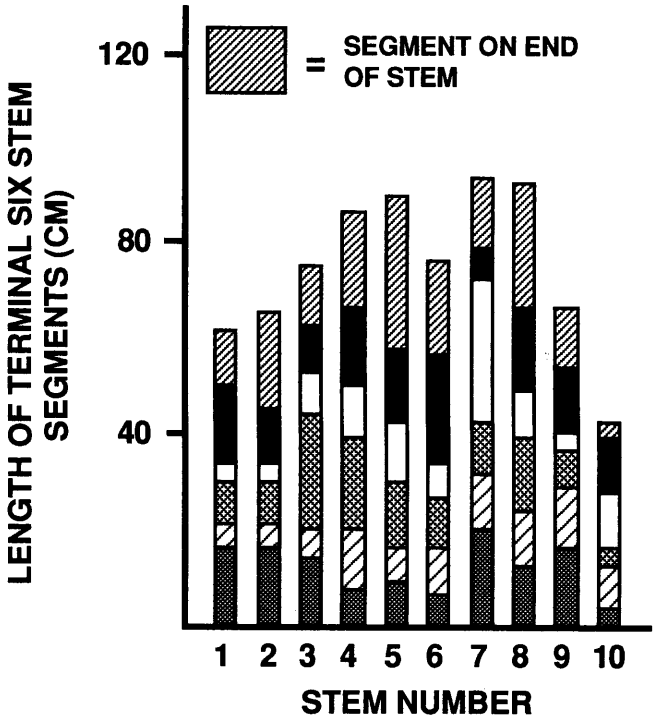

Figure 2—Lengths (cm) of the terminal six segments of 10 stems growing on one ocotillo (#19) at the Jornada LTER site. The uppermost, cross-hatched sector of each bar represents the most terminal segment on each stem, and the remaining sectors follow in sequence down the stems. Data for this plant were representative of the variability in stem segment growth displayed by all plants.

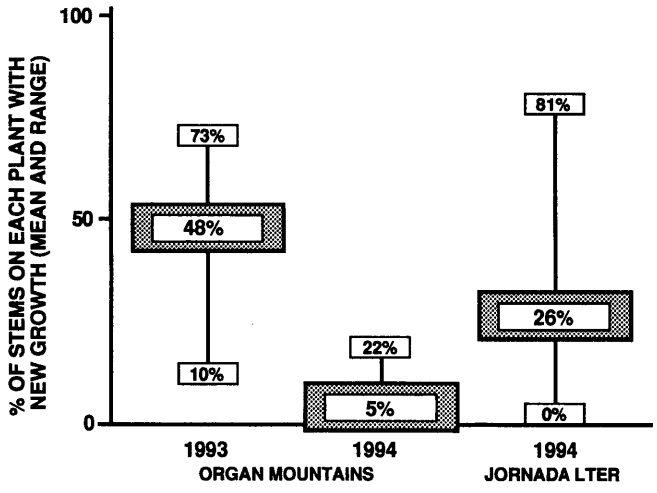

Figure 3—Percentage of stems on ocotillo plants that produced new stem segments at the Organ Mountains site (1993 and 1994) and the Jornada LTER site (1994). Values are means of individual plant percentages at each site in each year and are displayed within the shaded boxes. Ranges are indicated in the attached, unshaded boxes. The minimum percentage for the Organ Mountains population in 1994 was 0%. All means are statistically different from one another ($P < 0.01$; Mann-Whitney U-test).

ocotillo varied widely in the percentage of their stems that produced new segments. In 1993, 10-73% of the stems on individual plants growing in the Organ Mountains produced new growth. The range in percentages declined to 0-22% in 1994, but was 0-81% among individuals at the Jornada site in this same year. Therefore, in some years it is possible to find plants with no new terminal stem growth growing adjacent to plants with new terminal growth on the majority of their stems.

Mean percentages of stems with new growth differed significantly between years and sites (Organ Mountains 1994 < Jornada 1994 < Organ Mountains 1993, $P < 0.01$, Mann-Whitney U-test) in spite of the high variability among individual plants (fig. 3).

Both the number of new segments produced per plant and the total length of new segments produced per plant were lower in the Organ Mountains population in 1994 than in the same population one year earlier, or than in the Jornada population during the same year (table 2; $P < 0.001$, Mann-Whitney U-test). The total length of terminal stem growth per individual was seven times lower in the Organ Mountains population in 1994 than in the same population one year earlier, or than in the Jornada population during the same year.

To compensate for the fact that plants in the Organ Mountains had fewer stems (36 stems/plant, SE = 2.9) than plants at the Jornada site (50 stems/plant, SE = 4.6; $P < 0.05$, Student's t-test), lengths of new segments per plant were divided by the total number of stems per plant to produce a standardized measure of segment production (fig. 4). This analysis revealed that not only was new stem segment length lower in the Organ Mountains in 1994 than in 1993 or than at the Jornada site in 1994, but that plants in the Organ Mountains produced more new stem tissue in 1993 than did plants at the Jornada site in 1994 ($P < 0.05$, Mann-Whitney U-test).

Data expressing the number of new stem segments produced as a function of total number of stems per plant (fig. 3; for example, 48 new segments per 100 stems were produced in the Organ Mountains population in 1993) indicate that as with stem segment lengths, numbers of stem segments were lower in the Organ Mountains in 1994 than in 1993 or than at the Jornada site in 1994 on a per stem basis.

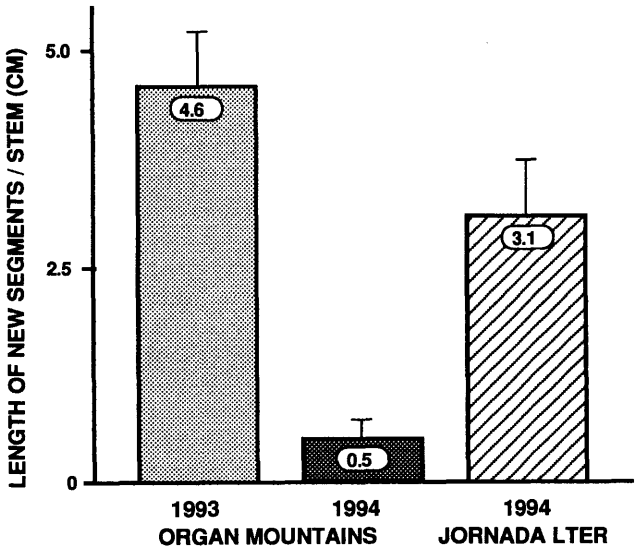

Figure 4—Means of the length (cm) of new stem segments produced per plant at the Organ Mountains site (1993 and 1994) and the Jornada LTER site (1994) divided by the total number of stems per plant. New growth was divided by total stems per plant to minimize differences in stem segment production that may have been a function of plant size and/or age as estimated by the total number of stems per plant. Error bars represent the standard error of the mean. All means are statistically different from one another ($P < 0.05$; Mann-Whitney U-test).

Discussion

Tier after tier of complexity characterized stem segment growth patterns in populations of ocotillo growing in the northern reaches of the Chihuahuan Desert. Stem segment production varied markedly between years (table 2, figs. 3, 4), between populations growing less than 30 km apart (table 2, figs. 3, 4), among individuals of the same population (fig. 3), and even among different stems growing on the same plant (fig. 2). While such complexity poses problems for using unmarked, extant stem segments to infer past environmental change, it also offers opportunities for using new growth to track environmental change.

The key to the effective use of ocotillo stem growth in tracking environmental change is the identification of an initial set of benchmark segments. Once a set of uppermost stem segments has been permanently marked, growth can be measured at any time interval deemed appropriate to the questions asked. Uppermost stem segments simply need to be marked at the end of each sampling interval to allow monitoring to continue into the future. Because maximum

Table 2—Mean total length (cm) and number of new stem segments produced per plant in 1993 and 1994 in the foothills of the Organ Mountains and in the Jornada LTER site. Parentheses contain standard error of the mean. Means with an asterisk are statistically different from all other means in the same row ($P < 0.001$; Mann-Whitney U-test).

	Organ Mountains		Jornada LTER
	1993	1994	1994
Length of new stem segments (cm)	142 (16)	20* (8)	147 (30)
Number of new stem segments	15.2 (1.8)	1.9* (0.7)	12.5 (1.8)

age in ocotillo is probably 150-200 years (Darrow 1943), a wide range of time increments are possible for analysis.

The opportunities for using stem segment production to monitor environmental change appear to be considerable given the large differences in growth measured between individuals, populations, and years (table 2, figs. 3, 4) in a period of time as short as two years. These differences in growth imply a sensitivity to environmental parameters that is essential if growth is to be used successfully as a phytometric measure of a changing environment. As in any organism, growth of any kind is also a function of internal, biotic regulation and allocation. However, distinct patterns of growth that emerge simultaneously over time in separate populations of ocotillo would signify environmental change. Changes including those spawned by such processes as desertification and global warming should all be susceptible to detection and measurement with ocotillo stem segment analysis.

Compared to other desert species and other methods of relating growth to environmental conditions, stem segment analysis in ocotillo has several distinct advantages.

First, analysis is nondestructive and therefore conducive to repeated application on known individuals. Growth ring measurement in the few desert shrubs that can support such analysis is, by necessity, destructive (for example, Flinn and others 1994; Keeley 1993).

Second, ocotillo stem segments are so clearly marked by obvious nodal seams that their lengths can be measured with high accuracy and precision. Nodes are particularly distinctive in the upper two-thirds of each stem, but even lower segments are usually visible and distinct.

Third, because the number of stems per ocotillo individual is small (usually 1-50; Humphrey 1935) and each stem is quite distinct, measurements can be made on every stem of a study plant thus integrating stem growth throughout the individual. While it is possible to measure all stem growth in a given year on common desert perennials such as creosotebush (*Larrea tridentata*) and mesquite (*Prosopis* spp.), the effort expended to do so compared to the analogous effort necessary in ocotillo would be considerable.

Fourth, measurements can continue year after year because ocotillo segments are produced terminally in sequence and are not subject to abscission during periods of drought.

Fifth, stem segment analysis in ocotillo can provide highly detailed data on short-term environmental events not accessible by techniques valuable in the analysis of long-term changes in climate and vegetation. For example, packrat middens have proved to be valuable repositories of plant materials from which long-term changes in vegetation and environment may be discerned (Betancourt and others 1990), yet highly detailed short-term changes can not be discerned from midden materials.

While the possibilities for using ocotillo to track future environmental changes are appealing, the apparent inability to use unmarked, extant stem segments to infer past changes is disappointing. The extreme variability in segment production among stems on the same plant (figs. 2, 3) would seem to completely obliterate any segment length patterns that might be useful in assigning dates of production to specific segments. Techniques analogous to crossdating in dendrochronology (matching variations in width of growth rings among trees to determine the year in which individual rings were produced; Fritts 1976) have not been rigorously applied yet to ocotillo stem segment length data, but the probability that such techniques will be successful in associating dates of production with segments appears to be low given the high degree of complexity inherent in ocotillo stem growth. Nevertheless, this approach should be tried.

One additional variation on the crossdating approach is to use the number of spines per unit length of segment rather than just segment length in correlation analysis. Because each spine on an ocotillo stem is formed from petiole tissue produced by each primary leaf (Hendrickson 1977; Scott 1932), there is a one-to-one relationship between ephemeral primary leaves and permanent stem spines. If the number of primary leaves produced per unit length of stem segment varies from year to year, it might be possible to at least identify all segments on a plant that were produced in a given year. These cohorts of associated segments might then form the basis for further cross-correlational analyses. For example, it might be possible to link mean lengths of segment cohorts to specific years in which precipitation was either abnormally high or low, thus allowing the assignment of dates to specific stem segments. The possibility of using stem spines as permanent markers of growth is tantalizing, but its potential is presently unknown.

Conclusions

In considering the efficacy of utilizing stem growth in ocotillo to track environmental change, there is a clear dichotomy between the utility of measuring the length of unmarked, extant stem segments, and the utility of measuring the length of stem segments produced after the establishment of benchmark segments. Unmarked, extant stem segments can not be assigned ages, or even be grouped into cohorts that were produced in the same year, and therefore can not be used to infer past environmental change. Conversely, segments produced after age-specific benchmarks have been established can be assigned dates of production and therefore, can be used to track ongoing environmental change.

Factors including the ease and accuracy with which the length of ocotillo stem segments can be measured, the nondestructive nature of stem segment analysis, and the potential sensitivity of ocotillo to environmental changes as evidenced by large differences in stem segment production between populations and years, collectively suggest that monitoring stem segment growth in ocotillo can be an effective method for tracking environmental change.

Acknowledgments

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Arroyo-Riparian Shrub Diversity Along a Transition Zone Between the Sacramento Mountains and Tularosa Basin, New Mexico

Joneen S. Cockman
Rex Pieper
Dennis Clason

Abstract—Four arroyos were examined in the Sacramento Mountains of New Mexico to determine type differences and describe vegetation diversity of the main channel relative to the surrounding watershed. Arroyos were selected to represent foothills and a submesa. Univariate analyses were conducted on shrub, half-shrub, grass, and forb functional groups. Each group responded to different effects depending on the response variable (cover, density, diversity). However, nonsignificant interactions were masked by the fact that response variables (especially diversity) were comprised of different species depending on the location of the arroyo in foothill or submesa types. Obligate and exclusive species were identified.

It has been suggested that arroyos in the southwestern United States are of recent origin, and are a feature of accelerated erosion on once-uniform grasslands and cienegas (Cooke and Reeves 1976; Bryan 1925). Antevs (1952) borrowed the term "wadis" from Israeli and Egyptian literature to describe ephemeral drainages that are not features of man-caused erosion. These drainages are limited to the headwaters of valleys, occur in moist areas, and are limited in size. The typical drainage described by Antevs is 3.6 meters deep, 15 meters wide, and .8 km long. The drainages of this study more closely resemble Antev's description of a "wadis."

Classification of riparian communities has been conducted by Pase and Layser 1977; Freeman and Dick-Peddie 1970; Anderson and Ohmart 1980). Apache plume (*Fallugia paradoxa*) has been described as the most commonly found riparian species in New Mexico, with more than 80% of the arroyos in a southern New Mexico study containing this shrub (Browning 1989). Littleleaf sumac (*Rhus microphylla*) and cutleaf bricklebush (*Brickellia laciniata*) were listed as close associates in areas of approximately 1,500 meters elevation. Burrobush (*Hymenoclea monogyra*) was listed as an associated species in washes at lower elevations (Browning 1989). The four arroyos described in this report resemble closely the Apache plume series described by Browning (1989) and also contain Burrobush at lower elevations.

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The importance of arroyo-riparian or ephemeral drainages for birds has been well documented (Carothers and others 1974; Carothers and Johnson 1975; Finch 1989; Reichenbacker 1984). Floral structure variables such as patchiness, volume, and foliage height diversity were found to be not independent of one another (Anderson and Ohmart 1980). Instead, variable complexes were identified as well as ties between bird use and time of year.

Research Purpose

At this time, environmental regulations do not protect arroyo habitat. Data are needed to support management decisions related to environmental quality.

Interest and concern for the protection of wetlands has increased since the inception of the National Environmental Policy Act (NEPA) of 1969. Four Federal agencies provide regulating authority for wetlands. These are the U.S. Army Corps of Engineers (USACE), the Environmental Protection Agency (EPA), the U.S. Fish and Wildlife Service (USFWS), and the Natural Resources Conservation Service (NRCS). Each agency provides a different definition of a wetland depending on the agency's function. However, all agencies include in their definition three basic elements: hydrology, vegetation, and soil characteristics (Mackenthun and Bregman 1992).

The USEPA and USACE have adopted the definition of wetland from the Clean Water Act Section 404 (Mackenthun and Bregman 1992):

> Those areas that are inundated or saturated by surface or groundwater at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions. Wetlands generally include swamps, marshes, bogs and similar areas.

It is important to note that this definition identifies saturated soil conditions and a prevalence of vegetation suited to saturated soils. The presence of indicator species such as cattails that grow only in saturated conditions has been used to identify wetlands.

Arroyos and wadis do not contain saturated soil conditions and do not qualify as a wetland by the USEPA definition. However, they do support plant species that will grow on no other site. They also support a variety of wildlife species and appear to be critical habitat.

However, little research has been done to quantify plant or animal species occurring in the arroyos. Studies are needed

to test if the arroyo does support unique species or a higher diversity compared to the adjacent watershed.

The purpose of this research is to describe and quantify vegetation along ephemeral drainages in the Sacramento Mountains of southern New Mexico. The study will provide baseline data to facilitate management decisions pertaining to NEPA compliance. The focus of the study is to test for vegetation differences between foothill and submesa arroyos. It also examines the main channel relative to adjacent vegetation types, and adds to our knowledge of these important habitats in the Southwest.

Study Area

The study area contains four arroyos particular to the research and one major drainage that connects the four (fig. 1). The area occupies approximately 13,000 hectares and is used jointly by the Bureau of Land Management as a grazing allotment and a wilderness study area. It is also designated military ground, identified as McGregor Range, a portion of the Fort Bliss military establishment.

Located at the southern tip of the Sacramento Mountains, the area is approximately 16 air km northeast from the village of Orogrande, NM, and 112 km northeast from El Paso, TX. Elevation ranges from 1,200 meters to 1,600 meters. Two of the arroyos (Indy and Carly) are located in a foothill area. The headwaters of these arroyos originate at approximately 1,800 meters, and the tailwaters drain into Culp Canyon at approximately 1,670 meters. The other two arroyos (Alien Temple and Four Bucks) are located on a submesa. Their headwater originates at the junction of Culp Canyon at approximately 1,500 meters, and they drain into the Tularosa Basin at approximately 1,370 meters.

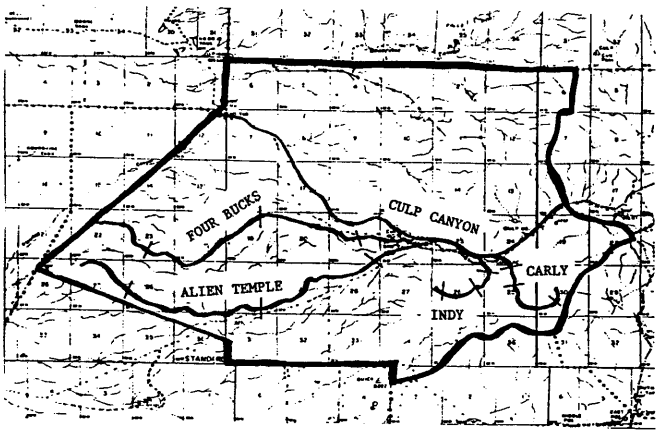

Figure 1—Location of arroyos in a 13,000 ha BLM grazing allotment. Indy and Carly arroyos are located in a foothill area. The headwater portions of these arroyos originate at approximately 1,800 meters and drain into Culp Canyon at about 1,670 meters. The headwaters of Four Bucks and Alien Temple arroyos originate in Culp Canyon at about 1,500 meters. They drain into the Tularosa Basin at about 1,370 meters. They are located on a submesa. Sample locations are marked on each arroyo at lower, middle, and upper elevations. Scale: grids represent 1 mile x 1 mile.

The annual average rainfall for the area is about 30 cm. However, there is a rain shadow between the submesa and foothill. No rain gauge data are available to quantify the difference between sites. However, a difference in vegetation between the sites suggests that the foothill area receives much greater rainfall. Also, many people who have worked in the area and have observed the weather pattern agree that thunderstorms build up over the Sacramento Mountains and flow south over the foothills. They have observed torrential rainfall in the foothills while the submesa area receives little or no rainfall. This pattern appears to be a frequent occurrence.

Soils of the area are dominated by rock outcrop and limestone hills. Gravelly alluvium is prevalent on the lower slopes. Narrow bands of alluvial soil line the arroyos. Of particular interest is a major separation in soil classification between the foothill and submesa areas. The submesa is mapped in southern desert soils while the foothill is mapped in soils from the neighboring mesic region. This is a transition zone between the true desert soils and cooler plains soils.

Methods

Site Selection

Field reconnaissance using soil maps and aerial photos was conducted prior to selecting study sites. Two similar arroyos (Indy and Carly) were selected in a foothill area (fig. 1). Two more (Alien Temple and Four Bucks) were selected within a submesa area. The submesa is positioned between an upper mesa with sharp vertical boundary and the Tularosa Basin. The land is hummocky and slopes gently between the mesa and basin. The foothill arroyos flow into a major drainage (Culp Canyon), and the submesa arroyos originate from Culp Canyon. The foothill arroyos are about 2.4 km in length. They range from 3-15 meters wide. The submesa arroyos are approximately 11 km long, and range from 2-30 meters wide. All arroyos range from 0.5-3 meters deep.

Sample locations were selected along each arroyo at headwater, midwater, and tailwater locations (upper, middle, and lower elevations) (fig. 2). An attempt was made to identify all vascular plant species in the study area. Plants too immature to identify were catalogued, and phenology was recorded. These plants were collected again when mature specimens were available. Vouchers were collected from as many species as possible to aid in accurate identification. This paper provides results pertaining to two shrubby functional groups, half-shrubs and shrubs. The half-shrub group contains cacti because cacti were infrequent and low in number in the study area. This was done to follow their presence rather than delete them from analyses. Similarly, the large shrub group includes trees because trees were infrequent in the study area.

Response Variables

Cover, density, and presence of all vascular plant species were measured for the greater study. This paper is limited to a discussion of diversity based on species richness which is derived from presence data. Belts with six replicate

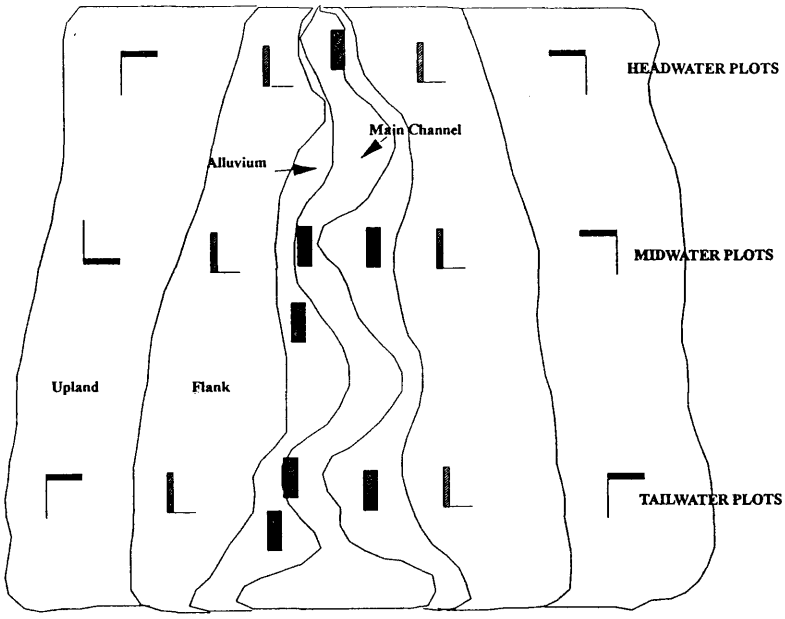

Figure 2—Sample locations were selected along each arroyo at headwater, midwater, and tailwater locations corresponding to upper, middle, and lower elevations. Alluvium, flank, and upland plots are paired by northwest and southeast exposure. The main channel plots are singular and contribute to an unbalanced treatment structure. Alluvium is missing at headwater locations, which also contributes to an unbalanced treatment structure.

subplots were used to facilitate data gathering. Obligate species are also discussed.

Analyzing an Unbalanced Treatment Structure

Two features of the experimental design are unbalanced and required that separate tests be conducted to facilitate one overall F-test in the analyses of variance. First, by nature of the arroyos, alluvium positions are absent from headwater zones (fig. 2). This required significance levels to be extracted from a series of three tests: a test with the whole arroyo, a test with no alluvium, and a test with no upper elevation. Second, the main channel belts are singular in an elevation zone where alluvium, flank, and upland belts are paired by northwest and southeast exposure. So, two separate tests were run to facilitate this imbalance (1) the main channel -v- northwest exposure and (2) the main channel -v- southeast exposure. A total of six F-tests were conducted to facilitate the unbalanced data.

Analyses of Species Richness

Univariate analyses were conducted using SAS General Linear Models (GLM) procedure. Data were averaged across species within a functional group. Appropriate error terms were selected for nested and crossed sampling structure. The analyses of variance for species richness is presented in table 1.

Half-Shrubs and Cacti

Univariate analyses for the species richness of half-shrubs and cacti was most sensitive to an elevation x position effect (northwest exposure Pr > F = 0.0425, southeast exposure Pr > F = 0.1813). The submesa and foothill types were averaged in figure 3. The least species richness was seen at the lowest

Table 1—Response of species richness to treatment effects.

Functional group	Effect	Pr > F
Shrubs and trees	Elevation x position	0.0343 NW exposure
	DF = 5, error = 16	0.0056 SE exposure
Half-shrub and cacti	Elevation x position	0.0425 NW exposure
	DF = 5, error = 16	0.1813 SE exposure

elevation with an increase in species richness moving away from the main channel. A similar response was seen for the middle elevation positions. That is, species richness was greater at the highest elevation in the main channel. It decreased in the main channel with a decrease in elevation

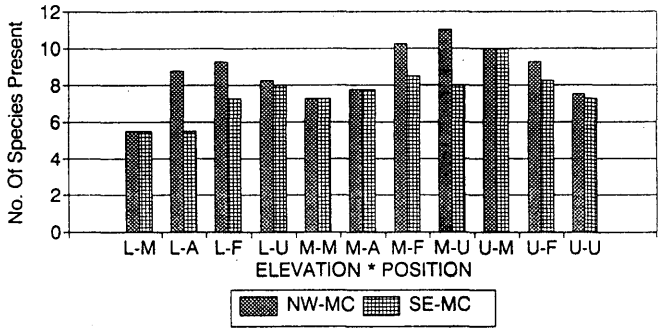

Figure 3—Half-shrubs and cacti were most sensitive to an elevation x position effect for species richness. Elevation = lower (L), middle (M), and upper (U). Position = main channel (M), alluvium (A), flank (F), and upland (U). NW-MC = main channel and positions with a northwest facing exposure. SE-MC = main channel and positions with a southeast facing exposure. Standard error for all treatments (NW-MC = 1.016, SE-MC = 0.973).

along the drainage channel. However, species richness increased while moving perpendicular away from the main channel and ascending along the position gradient from alluvium to flank to upland. This relationship was seen in the lower and middle elevation zones. However, the upper elevation zone showed a decrease in species richness moving away from the main channel. Species richness ranged from a low of 5.5 species per belt to a high of 11 species per belt. Significant comparisons are presented in tables 2a and 2b.

Shrubs and Trees

Analyses of species richness for shrubs and trees were most sensitive to an elevation x position effect (northwest exposure Pr > F = 0.0343, southeast exposure Pr > F = 0.0056). Differences between northwest and southeast exposure can be seen within elevation zones (fig. 4), suggesting an elevation x exposure interaction. However, exposure data are from separate tests, and comparisons between exposures are speculative. Significant changes in species richness across position can be seen within the lower and upper elevation zones. Species richness ranged from 4.25 species per belt to 10.5 species per belt. The main channel position produced the highest species richness of shrubs and trees with each elevation zone. This increase is probably due to the presence of true obligate riparian species as well as facultative species that also occur on other positions. Significant comparisons are presented in tables 3a and 3b.

Obligate Species

Obligate riparian and upper watershed species were identified in separate analyses for the foothill and submesa types (table 4). In the foothill, species were combined from both Indy and Carly arroyos. Data included all species recorded in cover, density, and presence records. Data were sorted by position across all elevation zones. Thus, the species list for a position represents the full length of an arroyo from headwater to tailwater. Submesa data were handled the same way by combining observations from Alien Temple and Four Bucks arroyos.

Riparian obligate species were identified by selecting species that were found in the main channel or alluvium positions but did not occur in other positions. The procedure

Table 2a—Significant comparisons for species richness of half-shrubs and cacti. Data are for the main channel and positions on the northwest exposure.

	L-MC	L-A	L-F	L-U	M-MC	M-A	M-F	M-U	U-MC	U-F	U-U
L-MC								*	*	*	
L-A	*						*				
L-F	*										
L-U											
M-MC								*			
M-A								*			
M-F					*						
M-U											*
U-MC											
U-F											
U-U											

H: LS mean (i) = LS mean (j).
Pr > T = 0.05.

Table 2b—Significant comparisons for species richness of half-shrubs and cacti. Data are for the main channel and positions on the southeast exposure.

	L-MC	L-A	L-F	L-U	M-MC	M-A	M-F	M-U	U-MC	U-F	U-U
L-MC							*		*	*	
L-A							*		*	*	
L-F									*		
L-U											
M-MC									*		
M-A											
M-F											
M-U											
U-MC											*
U-F											
U-U											

H: LS mean(i) = LS mean (j).
Pr > T = 0.05.

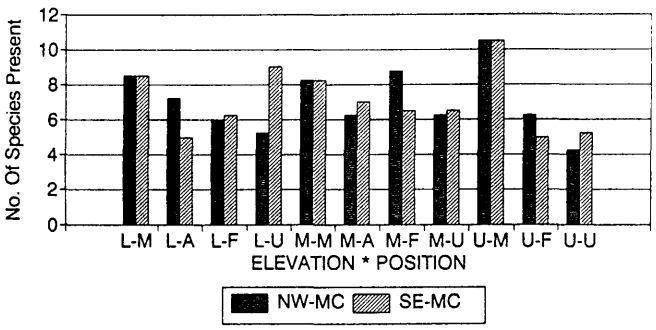

Figure 4—Shrubs and trees were most sensitive to an elevation x position effect for species richness. Elevation = lower (L), middle (M), and upper (U). Position = main channel (M), alluvium (A), flank (F), and upland (U). NW-MC = main channel and positions with a northwest facing exposure. SE-MC = main channel and positions with a southeast facing exposure. Standard error for all treatments (NW-MC = 0.764, SE-MC = 0.714).

recognizes the alluvium position as an integral part of the riparian channel. In the submesa type, it functions as a flood plain for the collection of soil and debris from the main channel during heavy rainfall events. In the foothill type, it functions as a flood plain for the collection of material from the main channel, and it collects runoff from lateral drainages.

Upper watershed obligate species were identified as those species recorded on flank or upland positions but not recorded elsewhere.

Shifting of Obligate Species Between Types

Some shifting of obligate species occurred between the foothill and submesa types. For example, David's mint (*Salvia davidsonii*) was a riparian obligate species in the foothill type, but occurred as an upper watershed species in the submesa type. Apache plume occurred as an obligate riparian species in the submesa type, but was not obligate in the foothill type because it occurred in the riparian zone as well as the flanks and uplands. The foothill type is mesic enough throughout the watershed to support it in many

Table 3a—Significant comparisons for species richness of shrubs and trees. Data are for the main channel and positions on the northwest exposure.

	L-MC	L-A	L-F	L-U	M-MC	M-A	M-F	M-U	U-MC	U-F	U-U
L-MC				*		*		*		*	*
L-A									*		*
L-F	*				*		*		*		
L-U					*		*		*		
M-MC									*		*
M-A							*		*		
M-F								*		*	*
M-U									*		
U-MC											*
U-F									*		
U-U											

H: LS mean(i) = LS mean(j).
Pr > T = 0.05.

Table 3b—Significant comparisons for species richness of shrubs and trees. Data are for the main channel and positions on the southeast exposure.

	L-MC	L-A	L-F	L-U	M-MC	M-A	M-F	M-U	U-MC	U-F	U-U
L-MC							*	*	*	*	*
L-A	*			*	*	*			*		
L-F	*			*	*				*		
L-U						*	*	*		*	*
M-MC									*	*	*
M-A									*	*	
M-F									*		
M-U									*		
U-MC											*
U-F									*		
UU											

H: LS mean(i) = LS mean(j).
Pr > T = 0.05.

Table 4—Species obligate to the riparian zone or upper watershed.

Shrubs and trees	Half-shrubs and cacti
Foothill riparian species	
Brickellia brachyphylla	None
*Brickellia laciniata***	
Cercocarpus montanus var. *glaber*	
Condalia ericoides *	
Garrya ovata subsp. *goldmanii*	
Rhus trilobata x *microphylla*	
Celtis laevigata var. *reticulata***	
Foothill upper watershed species	
Brickellia petrophila	*Choisya dumosa*
Fouquieria splendens *	
Isocoma wrightii	
Mimosa borealis	
Yucca torreyi *	
Coryphantha strobiliformis	
*Coryphantha vivipara***	
Echinocereus spp.	
Echinocereus Lloydii	
Submesa riparian species	
*Brickellia laciniata***	*Hymenoclea monogyra*
Chilopsis linearis	
Fallugia paradoxa *	
Celtis laevigata var. *reticulata***	
Submesa upper watershed species	
Baccharis pteronioides *	*Coryphantha macromeris*
Ceanothus greggii	*Coryphantha vivipara***
Chrysothamnus pulchellus *	*Mammillaria lasiacantha*
Condalia ericoides *	
Dasylirion spp. *	
Coldenia greggii	

*Lost as an obligate species when analyses combines foothill and submesa arroyo types.
**Also occurs in submesa/foothill arroyos.

locations. David's mint was well represented on the foothill main channel. However, its occurrence in the submesa type was infrequent, and it probably occupies a mesic microsite.

Shifting of obligate species probably occurs as elevation descends to other type locations. For example, neither little leaf sumac or large leaf sumac (*Rhus trilobata*) were identified as obligate riparian or obligate upper watershed species. (One exception occurred where a peculiar specimen thought to be a hybrid of the two shrubs occupied the main channel.) Both the foothill and submesa types are mesic enough throughout the watershed to support these shrubs in most positions. However, this might change if the arroyos positioned at lower elevations in the desert floor of the Tularosa Basin were examined. Both sumacs probably occur as obligate riparian species on the desert floor.

Species Obligate to all Four Arroyos

Obligate species were identified in a separate analyses that combined all four arroyos. The procedure follows that described above. A few species that were obligate in separate submesa and foothill analyses were no longer obligate when all four arroyos were combined (table 4).

The test with all 4 arroyos produced among riparian obligate species 47 forbs, 9 grasses, one half-shrub, 6 shrubs, and one tree species. The same test produced among upper watershed obligate species 6 cacti, 16 forbs, 3 grasses, 1 half-shrub, and 5 shrub species. These lists are larger than those produced for either the foothill or submesa types alone. This is a reflection in the shift in species composition between the two arroyo types.

It is interesting to note certain characteristics of individual obligate species relative to the overall vegetation story. The main channel position is filled with woody vegetation. Yet, the only obligate riparian half-shrub is burrobush. Similarly, the submesa type uplands are dominated by half-shrubs, but no obligate half-shrubs were recorded there.

No obligate cacti were recorded for the riparian corridor. Most cacti in the study area occupy rocky habitat in upland positions. Trees were scattered and infrequent in the study area. Most occurrences were in the foothill type. Sugar hackberry (*Celtis laevigata*) was the only obligate riparian tree. However alligator juniper (*Juniperus deppeana*), one-seed juniper (*J. monogyra*), pinyon pine (*Pinus edulis*), and oak (*Quercus* spp.) occurred infrequently in the foothill type.

Obligate riparian shrubs for the whole study area are limited to Guadalupe brickellia (*Brickellia brachyphylla*), cutleaf brickelbush, desert willow (*Chilopsis linearis*), smooth mountain mahogany (*Cercocarpus montanus* var. *glaber*), Mexican silktassel (*Garrya ovata* subsp. *goldmanii*), and hybrid sumac (*Rhus trilobata* x *microphylla*). The first three shrubs are completely senescent and easily recognizable as riparian species. The latter three species may not be obligate riparian species in all habitats. Three species of mountain mahogany are recognized in the Trans Pecos region (Powell 1988). Two of the three species occur in this study. Shaggy mountain mahogany (*C. m.* var. *paucidentatus*) occurs throughout the foothill type. Smooth mountain mahogany has a tree-like growth form in the main channel where it occurs infrequently. But, it has been reported to grow in upland positions in Brewster County Texas (Powell 1988). Mahogany are important browse plants. They are senescent but lose their leaves slowly. Mexican silktassel is evergreen. It is known to grow in upland positions where there is ample water concentrated by runoff such as in the Organ Mountains. Little leaf sumac and large leaf sumac both occurred throughout the study area. It appears that it could be capable of growing in other positions. Sumac are also important browse plants. Like mahogany, they are senescent but lose their leaves slowly. Because of the features of the latter three species, their identification as true obligate riparian species is questionable.

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Tarbush Leaf Surface Terpene Profile in Relation to Mammalian Herbivory

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Abstract—Cattle, sheep and goats were densely stocked in paddocks containing tarbush (*Flourensia cernua* DC) for six to nine days and defoliation of 160 plants was recorded daily during two years. Plants were separated into high, moderate or low defoliation categories. Leaves were collected from plants during the same stage of maturity during the third year. Leaf surface compounds were extracted with ethanol and mono- and sesquiterpenes were analyzed using gas chromatography/ion trap mass spectrometry. A set of 11 variables was identified that appeared most closely related to plant defoliation categories: dry matter, ash, limonene, camphor, borneol, α copaene, ß caryophyllene, α pinene, p-cymene, cis-jasmone and caryophyllene oxide concentrations. This group distinguished among all three defoliation categories ($P < 0.03$) when subjected to multivariate analysis. These data support the hypothesis that leaf surface chemistry is related to degree of defoliation of individual tarbush plants by livestock.

Land managers need environmentally safe and economically viable remediation technologies for shrub dominated areas. Managing large herbivores to deter shrub invasion while using shrubs as forage is a desirable option. An understanding of the role of secondary chemistry in mediating interactions of grazing ruminants and desert shrubs should yield useful information for manipulating diet selection. Antiherbivore compounds in desert shrubs are primarily terpenoids and phenolics (Meyer and Karasov 1991). Volatile plant substances are particularly effective herbivory defense mechanisms because herbivores are repelled before plant damage occurs (Levin 1976). Yabann and others (1985) reported that sheep selected individual sagebrush plants with a lower total monoterpenoid concentration. Morrison and others (1987) reported compounds present in the volatile fraction altered cattle preference for three *Panicum* spp. Other workers have reported relationships of individual terpenes, subgroups (for example, oxygenated monoterpenes) and/or total terpenoid concentration with herbivory by various mammals (Schwartz and others 1980; Reichardt and others 1985; Elliott and Loudon 1987; Bucyanayandi and others 1990; Goralka and Langenheim 1991; Zhang and States 1991).

Differential defoliation of tarbush (*Flourensia cernua* DC) when browsed simultaneously by cattle, sheep and goats in a previous study at this location was related to concentration of epicuticular wax and two unidentified terpenes (Estell and others 1994a). Tarbush contains several classes of secondary compounds (Kingston and others 1975; Dillon and others 1976; Bohlmann and Grenz 1977; Aregullin-Gallardo 1985). While relatively unpalatable, tarbush leaves can be consumed safely in moderate amounts for several weeks by sheep (Fredrickson and others 1994; King and others 1996). However, tarbush is acutely toxic to several mammalian herbivores during flowering (Mathews 1944; Hailey and others 1966; Dollahite and Allen 1975).

Our objective was to examine the relationship of tarbush leaf surface terpene profile with degree of defoliation by livestock. Our hypothesis was that tarbush plants defoliated to a lesser degree during the previous year would contain greater concentrations of one or more leaf surface terpenes than highly defoliated plants.

Materials and Methods

Study Site

The study site was located on the Jornada Experimental Range (JER) in southern New Mexico in an area heavily infested with tarbush. This area had been exposed to light to moderate stocking rates during the 75 years prior to the study. Annual precipitation for 1989, 1990 and 1991 was 239, 259 and 395 mm, respectively, for site 1 and 337, 275 and 390 mm, respectively, for site 2. The total growing season (July, August and September) precipitation for 1989, 1990 and 1991 was 164, 175 and 238 mm, respectively, for site 1 and 223, 172 and 223 mm, respectively, for site 2. Long term (1915 to 1993) mean annual and growing season precipitation for the area is 245 and 131 mm, respectively.

Sampling Protocol

This study was conducted in conjunction with a study of tarbush utilization by livestock (Anderson and others 1991). The study consisted of high density stocking (cattle, sheep

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and goats) of eight paddocks (0.6 ha) at two sites (four adjacent paddocks per site; sites approximately 1.6 km apart) for six to nine days (depending on forage availability) during two periods (approximately two weeks apart; four randomly selected paddocks browsed each period) in each of two years (1989 and 1990). Twenty plants in each paddock (10 in period 1 for 1989) on permanently marked transects were randomly selected and daily defoliation of each plant was recorded (ocular estimation to the nearest 5% defoliation class by an experienced observer) during the browsing period each year.

Individual plants were separated into high, moderate or low defoliation categories (HD, MD, or LD, respectively) based on daily defoliation patterns (HD: ≥50% defoliation at period midpoint; MD: <50% defoliation at midpoint and ≥50% defoliation at period end; LD: <50% defoliation at period end). For periods with an odd number of days, the midpoint was defined as midpoint plus one half day.

Livestock were excluded from paddocks during 1988 through 1991 except during the short browsing periods described previously. Tarbush leaf samples were collected from each plant (n = 154, six plants were not sampled) during the third week of August, 1991. Timing of collection was selected to coincide with the mature leaf stage when tarbush was browsed during 1989 and 1990. Approximately 50 g of leaves (entire current seasons growth removed and placed in plastic bags) were removed from each plant, immediately placed on dry ice and stored at –10 °C. A voucher specimen of tarbush was placed in the JER herbarium in Las Cruces, NM.

Chemical Analyses

Mature leaves (including petiole) of uniform size and appearance from the midpoint of the current seasons growth were subjected to chemical analyses. Dry matter was analyzed in duplicate using 10 whole leaves. Epicuticular wax (modification of the gravimetric procedure of Mayeaux and others 1981) was analyzed in duplicate by extracting 10 whole leaves with 20 ml of chloroform for 20 sec. Surface compounds from five whole thawed leaves were extracted and analyzed with modified procedures of Estell and others (1994b).

Leaves were extracted with 5 ml of 95% ethanol for 5 min and filtered through a glass fiber filter. An internal standard (2-carene, 10 ng/µl) was added and samples were refrigerated. Surface mono- and sesquiterpenes were analyzed using gas chromatography/ion trap mass spectrometry (electron impact ionization source, DB-5 column, 5% phenyl, 95% methyl silicone, 30 m, 0.32 mm i.d., 0.25 µm film thickness, helium as carrier gas at 1 ml/min, 300 sec filament multiplier delay time, 220 °C injector temperature, 260 °C transfer line temperature, initial column temperature of 50 °C, 1 °C/min ramp to 60 °C, 3 °C/min ramp to final column temperature of 240 °C, 5 min isothermal, 75 min total run time, 1 µl injection volume). Tentative and positive identification of leaf surface terpenes were described previously (Estell and others 1994b).

Statistical Analyses

Relationships of plant chemistry and herbivory were based on the 1990 tarbush defoliation categories. Univariate analysis of variance was conducted using the MANOVA procedure of SAS (1985) to examine relationships of plant defoliation categories with individual variables (dry matter, ash, epicuticular wax and 22 mono- and sesquiterpenes). Means were separated using Least Significant Difference when the overall model was significant ($P < 0.10$; SAS 1985).

A variable selection procedure (M. Mahrt, Experimental Statistics Department, New Mexico State University, personal communication) was used to examine each pair of categories prior to multivariate analysis. This procedure was used to reduce the number of variables subjected to multivariate analysis because of computational limitations. This selection process examined all possible combinations of variables for each number of variables and selected a set of variables based on the point at which removing a variable substantially reduced the ability to distinguish between two categories. This process was conducted separately for each category comparison (HD versus LD, HD versus MD and MD versus LD), resulting in a set of variables best separating each pair of categories. With few exceptions, variables important for separating MD plants from either HD or LD plants were also contained in the set separating HD and LD categories. Moreover, variables distinguishing between HD and LD were assumed most likely to have biological meaning. Thus, this group was subjected to multivariate analysis of variance using the MANOVA procedure of SAS (1985). The Wilks' Lambda test statistic was used to separate categories ($P < 0.05$).

Results and Discussion

Least square means for dry matter, ash, epicuticular wax and 22 mono- and sesquiterpenes by category appear in table 1. Four terpenes initially thought to be present in tarbush were not found: nerol, cis-nerolidol, cis-verbenol and o-cymene. Four terpenes were present but not quantified due to analytical difficulties: tricyclene, trans-jasmone, γ gurjunene and globulol.

A set of 11 variables from plant samples collected in 1991 which best distinguished between HD and LD categories in 1990 were subjected to multivariate analysis (dry matter, ash, limonene, camphor, borneol, α copaene, ß caryophyllene, α pinene, p-cymene, cis-jasmone, and caryophyllene oxide concentrations). While certain variables important for separating MD plants from HD and/or LD plants during pairwise comparisons were not included in this set, the separation of all categories was possible using only the above set of compounds ($P < 0.0001$, $P < 0.001$ and $P < 0.03$ for HD versus LD, MD versus LD and HD versus MD comparisons, respectively). This fact is not surprising given the number of variables common to all three pairwise separations.

Also, variables suggested to be important based on univariate analysis appeared in the subset selected for multivariate analysis. Separation of HD and LD categories

Table 1—Tarbush leaf surface chemistry and relationship to 1990 defoliation categories based on univariate analysis.[a]

Variable	RT[b]	HD[c]	MD[c]	LD[c]
Dry matter, %		65.9 (2.0)	66.6 (1.6)	71.6 2.6)
Ash[e], % of dry matter		11.5 (0.2)[f]	11.2 (0.1)[f,g]	10.8 (0.2)[g]
Epicuticular wax, % of dry matter		8.6 (0.4)	8.1 (0.3)	8.5 (0.6)
		μg/g of dry matter		
α Pinene[d]	621	136.2 (23.0)[f]	99.5 (18.1)[f]	214.3 (30.2)[g]
Camphene	669	70.2 (8.9)	60.0 (7.0)	71.9 (11.7)
Sabinene	748	12.6 (1.6)	9.5 (1.2)	13.3 (2.0)
ß Pinene	764	16.1 (2.7)	10.9 (2.1)	18.3 (3.5)
Myrcene	810	29.5 (3.3)	27.1 (2.6)	28.6 (4.3)
3-Carene	868	21.9 (3.7)	25.6 (2.9)	25.2 (4.8)
m-Cymene	907	0.57 (0.12)	0.49 (0.09)	0.65 (0.16)
p-Cymene	928	5.3 (0.7)	5.4 (0.6)	3.7 (0.9)
Limonene	937	84.4 (11.1)	94.3 (8.7)	97.3 (14.6)
1,8-Cineole	950	25.5 (6.6)	24.6 (5.2)	20.2 (8.6)
Camphor	1331	3.4 (0.6)	3.2 (0.5)	4.5 (0.8)
Borneol	1412	272.3 (41)	192.2 (32)	283.8 (54)
cis-Jasmone[d]	2063	53.5 (5.9)[h]	42.9 (4.6)[h]	26.0 (7.7)[i]
α Copaene	2016	5.3 (0.7)	3.8 (0.6)	4.9 (1.0)
α Gurjunene	2100	0.13 (0.06)	0.24 (0.04)	0.16 (0.07)
ß Caryophyllene	2133	93.9 (11.1)	81.8 (8.7)	76.9 (14.5)
Calarene	2162	1.7 (0.2)	1.3 (0.2)	1.3 (0.3)
α Humulene	2228	20.3 (2.1)	16.7 (1.6)	16.5 (2.7)
Ledene	2322	0.56 (0.11)	0.33 (0.09)	0.40 (0.15)
trans-Nerolidol[d]	2505	0.65 (0.09)[f]	0.39 (0.07)[g]	0.35 (0.12)[g]
Caryophyllene oxide	2549	36.8 (5.4)	47.2 (4.3)	37.3 (7.1)
Flourensadiol[e]	3196	2425.8 (285)[f]	2579.0 (224)[f]	3431.5 (373)[g]

[a]Least square means(standard error) of chemical concentrations in 1991; n = 48, 78 and 28 for HD, MD, and LD categories, respectively.
[b]RT = retention time (sec).
[c]HD, MD and LD refer to high, moderate and low defoliation categories, respectively.
[d]Overall model significant ($P < 0.05$).
[e]Overall model significant ($P < 0.10$).
[f,g]Defoliation categories differ ($P < 0.05$).
[h,i]Defoliation categories differ ($P < 0.10$).

is most critical in terms of practical application and design of future studies. While the procedure for selecting the group of variables to enter into multivariate analysis was somewhat subjective and based solely on compounds selected for separating HD and LD plants, this group distinguished among all three categories ($P < 0.03$).

When individual compounds were subjected to univariate analysis, several tarbush leaf surface components were related to defoliation category the previous year (table 1). Ash content was less ($P < 0.05$) for LD than HD plants, with MD plants not different than LD or HD plants. Flourensadiol and α pinene concentrations were greater for LD plants ($P < 0.05$), with no difference between HD and MD groups. Cis-jasmone concentration tended to be less ($P < 0.10$) for LD plants, with no difference between HD and MD plants. Trans-nerolidol concentration was greater ($P < 0.05$) for HD plants, with no difference between MD and LD plants.

Several variables not in the subset subjected to multivariate analysis may be related to herbivory. For example, sabinene, α humulene and flourensadiol were selected during the variable selection procedure as important for discriminating the MD category from both HD and LD categories. Trans-nerolidol was selected for separating HD and MD plants, and was a significant univariate variable (table 1). Camphene, 1,8-cineole and α gurjunene were selected for separating HD and MD plants, while ß pinene, 3-carene, calarene (ß gurjunene) and ledene (viridiflorene) were selected for separating MD and LD categories. Epicuticular wax, myrcene and m-cymene were not selected for discriminating among any categories.

Variables in the set subjected to multivariate analysis included dry matter and ash concentration, three hydrocarbon monoterpenes (limonene, α pinene and p-cymene), three oxygenated monoterpenes (camphor, borneol and cis-jasmone), two hydrocarbon sesquiterpenes (α copaene and ß caryophyllene) and one oxygenated sesquiterpene (caryophyllene oxide). Results of univariate analysis indicated ash content, one hydrocarbon monoterpene (α pinene), no hydrocarbon sesquiterpenes, one oxygenated monoterpene (cis-jasmone) and two oxygenated sesquiterpenes (trans-nerolidol and flourensadiol) were related to plant categories.

Specific terpenes (especially oxygenated monoterpenes), subclasses of terpenes and/or total terpene concentration in various plants have been associated with degree of herbivory

in several mammalian species. In deer, negative relationships have been reported for diet selection and crude terpenoid content (Longhurst and others 1968), volatile odor concentration (Elliott and Loudon 1987) and concentrations of oxygenated monoterpenes and total volatile oil or monoterpene concentration (Schwartz and others 1980; Goralka and Langenheim 1991). Zhang and States (1991) reported tree avoidance by Abert squirrels was related to total concentration and diversity of terpenes, as well as presence and concentration of specific terpenes.

Monoterpenes have also been associated with diet selection for voles (Bucyanayandi and others 1990) and hares (Reichardt and others 1985). While this relationship has rarely been evaluated in domestic ruminants, Yabann and others (1985) reported that sheep selected individual sagebrush plants with lower total monoterpene concentrations, and Morrison and others (1987) found compounds present in the volatile fraction of three *Panicum* spp. affected preference of cattle.

In a previous study at this location, concentrations of dry matter, ash, epicuticular wax and two unidentified terpenes were all related to the amount of defoliation by livestock (Estell and others 1994a). A positive relationship between water content and defoliation was observed in that study. Dry matter also was in the set of variables used to separate the three categories with multivariate analysis. A positive relationship between plant water content and grazing preference was described earlier by Archibald and others (1943). Components of ash such as sodium can have either a positive or negative influence on animal preferences depending on the post-ingestive consequences of previous dietary choices (Grovum and Chapman 1988). However, ash content was negatively related to level of herbivory in the previous study and positively related in this study (based on univariate analysis). Ash was also in the set of variables used during multivariate analysis for separating the three categories. Methodological differences (HD and LD plants were sampled in the previous study) or environmental factors may explain differences between studies.

The fact that epicuticular wax was related to defoliation in the previous study but not in this study with univariate analysis was surprising. However, the fact that epicuticular wax was not in the subset of variables subjected to multivariate analysis was expected, because the analysis takes into account the interrelationships of variables, and wax contains many of the compounds measured. Inherent differences in univariate and multivariate analyses can provide conflicting results because only one variable is considered at a time with univariate analysis while multivariate analysis considers all variables and their interrelationships simultaneously. The number of variables related to degree of defoliation with multivariate analysis illustrates the complexity of relationships among plant chemicals driving plant-animal interactions and the potential for synergistic and antagonistic relationships among phytochemicals involved in the diet selection process.

During the browsing study, degree of defoliation of individual plants was highly variable. Because ocular estimates of defoliation for individual plants were recorded daily during that study, we were unable to collect leaves from plants during 1989 and 1990. By exploring relationships of tarbush chemistry in 1991 with defoliation of the same plants in the previous year, we assumed that heavy browsing during 1989 and 1990 did not induce plant secondary chemistry changes which persisted in 1991.

Shrubs in a high-light, low-nutrient environment would be expected to exhibit slow growth and constitutive, carbon-based defense (Bryant and others 1985; Coley and others 1985). However, secondary compound production for chemical defense may be induced by herbivory in plant-herbivore systems (Gershenzon and Croteau 1991), and induction effects of biotic stresses such as herbivory on terpene synthesis may be very rapid (Carroll and Hoffman 1980; Gershenzon and Croteau 1991). Long-term induction and subsequent effects on herbivory may be less pronounced, because induction of secondary compounds is often short-lived (Faeth 1992; Furstenburg and van Hoven 1994).

For plants with defoliation data from both years, 65 plants were in the same category in 1989 and 1990, 31 plants were in a higher category in 1990 and 24 plants were in a lower category in 1990. Three plants in the LD category in 1989 were in the HD category in 1990 and no plants in the HD category in 1989 were in the LD category in 1990. The arbitrary nature of this classification system and the continuous nature of daily plant defoliation curves may account for some of the shifts among categories between years.

These shifts may also reflect slight differences in patterns of tarbush consumption resulting from year to year differences in availability of other plant species. However, the fact that only 24 plants were in a lower defoliation category in 1990 (after forced heavy browsing in 1989) than in 1989 (no previous browsing), and particularly that no plant in the HD category in 1989 was in the LD category in 1990, suggests that chemical induction was minimal and/or short term, or that differences in plant chemistry between HD and LD plants were great enough that differences existed in spite of induction.

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Growth Response of Wyoming Big Sagebrush to Heavy Browsing by Wild Ungulates

Trista L. Hoffman
Carl L. Wambolt

Abstract—An exclosure in a Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*)-bluebunch wheatgrass (*Agropyron spicatum*) habitat type on the northern winter range of Yellowstone National Park near Gardiner, Montana was used to compare browsed with unbrowsed plants. We tested the hypothesis that Wyoming big sagebrush plants that were not subjected to 35 years of winter browsing by elk, mule deer, and antelope would exhibit growth characters similar to browsed plants. Shrub production, seedhead number, and leaf morphology were significantly different ($P < 0.03$) between browsed and protected plants while leader characters were not. Although there were some intrinsic differences inside and outside the exclosure, browsing appears to be the most important factor influencing the morphological differences found.

Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beetle and Young) is recognized as an important winter food source for mule deer (*Odocoileus hemionus hemionus*), pronghorn antelope (*Antilocapra americanus*) and elk (*Cervis elaphus*), (Welch 1981; Wambolt and McNeal 1987). This species is not as well adapted to heavy browsing as many other shrubs (Wandera and others 1992; Bilbrough and Richards 1993). Browsing affects plant vigor and changes plant architecture, resource allocation, growth rate and reproductive capacity (Maschinski and Whitham 1989; Bilbrough and Richards 1993). Understanding the interaction between browsing, other environmental influences, and plant response is a complicated and often confusing process. The objective of this study was to compare morphological features of Wyoming big sagebrush that were either protected from ungulate browsing for 28 years or were subjected to heavy browsing during that period.

Study Area

The study site was located on the Northern Yellowstone Winter Range, 1 km northwest of Gardiner, Montana (45° N latitude, 112° W longitude). The elevation is 1,615 m, with a generally northeast aspect, and average annual precipitation is 305 mm, half of which is snow (Farnes 1975).

A one ha exclosure that was erected in 1957 in a Wyoming big sagebrush, bluebunch wheatgrass (*Agropyron spicatum*) habitat type allowed measurement of unbrowsed shrubs. This exclosure was constructed after biologists noticed severe impacts on the vegetation, including the sagebrush, by elk, mule deer and pronghorn antelope. These impacts continue today (fig. 1), especially from the wintering northern elk herd which is currently estimated at 25,000 to 30,000 animals.

Although the use of an exclosure and plants in close proximity was designed to minimize environmental influences on plants, some differences existed because of the exclosure. Wyoming big sagebrush was denser with greater canopy coverage inside the exclosure. Other vegetation included large amounts of bluebunch wheatgrass prairie junegrass (*Koeleria macrantha*), and clover (*Trifolium* sp.), with lesser amounts of greasewood (*Sarcobatus vermiculatus*), fringed sagewort (*Artemisia frigida*), and prickly

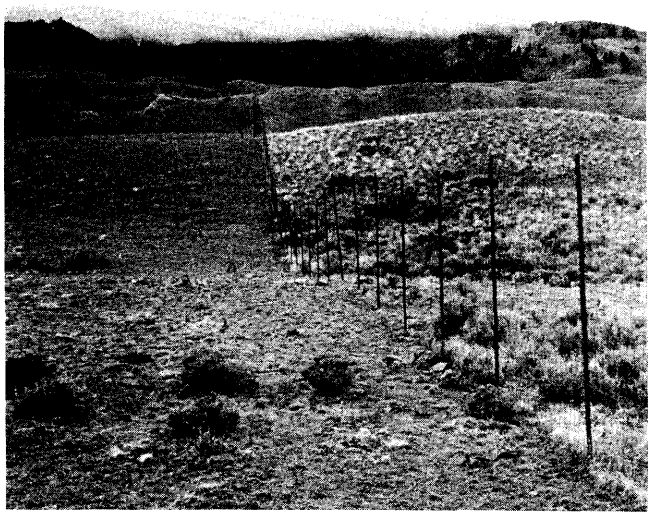

Figure 1—The ungulate proof exclosure near Gardiner, Montana in Yellowstone National Park used for this study. The exclosure was errected in 1957 after the Wyoming big sagebrush dominated plant community had been impacted by large numbers of ungulates. The shrubs on the outside (left) of the exclosure in this scene are spiny hopsage (*Grayia spinosa*). The shrubs inside the exclosure are Wyoming big sagebrush.

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pear cactus (*Opuntia polycantha*). The lichen *Xanthoparmelia chlorochroa* covered almost every soil interspace leaving little bare soil. Outside the exclosure, sagebrush cover was sparse with plants often 20 m apart. Other vegetation also was sparse and was dominated by prickly pear cactus, and weedy annuals, with small amounts of crested wheatgrass (*Agropyron cristatum*), prairie junegrass, needleandthread (*Stipa comata*), and fringed sagewort. The soil interspace was dry and bare.

Methods

Sampling

Ten plants were selected outside the exclosure, a few on each of the 4 sides of the perimeter. These plants were paired with 10 adjacent plants inside the exclosure to insure similar environmental conditions. Plants were measured for production according to Wambolt and others (1994). Seedheads were counted individually if there were less than 100 per plant and ocularly estimated if there were more than 100 per plant.

Ten current year leaders were clipped from each plant and refrigerated for transport. Because of heavy browsing, plants outside the exclosure had no terminal leaders. Therefore, axial long shoots were clipped. Inside the exclosure, plants were dominated by terminal growth, and axial long shoots were rare. Terminal long shoots were clipped from these plants. Harvesting took place in mid-September 1992 after all ephemeral leaves had fallen, but before heavy winter browsing by ungulates began.

Leaves were removed from leaders and separated into two categories: lobed and unlobed. Lobed leaves were fully developed in the typical tridentate shape associated with Wyoming big sagebrush. Unlobed leaves were small to fully extended, but had not developed the tridentate shape. Total leaf area for each leader was determined using a LI-3100 area meter (LI-Cor, Inc., Lincoln, NE). Leader length was measured from the top of the previous year's growth scar to the tip. Leaves and leaders were air dried at 40 °C and dry weight was measured with a Mettler H31AR balance.

Analysis

Normality testing indicated that most of the variables measured had non-normal distributions. Thus, non-parametric statistics were used (Sokal and Rohlf 1981). The Kolmogorov-Smirnov test, (SAS Institute 1988), was used to determine if the distributions between browsed and unbrowsed variables were similar, and the Wilcoxon test determined the significance of the distribution medians.

Results and Discussion

Growth and Forage Production

Unbrowsed plants had consistently higher production than browsed plants (table 1). Only 1 browsed plant produced more than 10.0 g of forage per plant, while 9 of 10 unbrowsed plants exceeded this amount. The maximum production measured on unbrowsed plants was 44.7 g/plant. These plants appeared vigorous, while plants outside the exclosure exhibited large amounts of dead crown and appeared to have little vigor.

Wyoming big sagebrush is susceptible to browsing for a number of reasons. It has an erect, linear architecture with many growing points on the ends of the stems (Bilbrough and Richards 1991). Also, it is heterophyllous, producing large ephemeral leaves in spring and small perennial leaves that live approximately one year (Beetle 1960; Miller and Shultz 1987). Plants with evergreen leaves depend more on these leaves for storage than plants with deciduous leaves (Bryant and others 1983). Sagebrush carries 50% of its nitrogen and total non-structural carbon (TNC) pool in its leaves (Bilbrough 1990), so each time a leaf is removed, this nitrogen and TNC is lost to the plant. With moderate browsing, sagebrush growth is reduced, vigor declines, and plants are unable to replace lost biomass (Bilbrough and Richards 1993).

Assimilate often moves from discrete portions of the sagebrush canopy to discrete portions of the roots (Watson and Casper 1984). Parts of a crown that are severely browsed thereby losing vigor may have a corresponding loss of vigor in a particular portion of the roots. Plants in this study were heavily browsed outside the exclosure and appeared to be losing vigor as portions of every crown were dead. It is likely that corresponding portions of roots were also dead.

Tiny insect galls were found in large numbers on the leaves of many unbrowsed plants. The removal of leaves by ungulates perhaps reduces the success of gall-forming insects outside the exclosure, because many insects overwinter in galls or use galls for several generations (Shorthouse and Rohfritsch 1992). The galls indicated that plants were not free of stress by growing in the exclosure. Competition evidenced by the density of sagebrush, grasses and forbs was another potential stress to these plants. However, the higher vigor and subsequent production of the protected sagebrush indicated that browsing most likely outweighs other stresses.

The high density of unbrowsed sagebrush and associated plants inside the exclosure increases competition for water and nutrients. Consequently, growth rates of plants inside the exclosure may be decreased by competition as well as insect herbivory. However, while high plant density increases competition, it also results in better developed canopy coverage. This additional coverage improves soil moisture content and heat storage, and reduces evaporation (Norman and Campbell 1991). Surface temperatures of soils are more variable between sagebrush plants than underneath them (Pierson and Wight 1991). Less interspace between plants inside the exclosure may reduce variability in soil temperatures. This has implications for germination and growth of

Table 1—Average differences between browsed and unbrowsed Wyoming big sagebrush plants.

	Browsed	Unbrowsed
Production (g/plant)	10.0[a]	44.7[b]
Seedheads per plant	0.08[a]	60.3[b]
Leader length (mm)	22.9[a]	22.3[a]
Leader dry weight (g)	0.02[a]	0.02[a]

Values followed by different letters are significantly different ($P < 0.05$).

sagebrush seedlings whose timing mechanisms depend on soil and air temperature (Meyer and others 1990; Meyer and Monsen 1992).

Canopy structure also slows soil evaporation by shading and by slowing wind. The presence of lichen on the soil interspace also reduces surface evaporation. Campbell and Harris (1977) found that soil evaporation was inversely related to site production. At our study site, soil evaporation was expected to be lower inside the exclosure and indeed, production was higher there.

Plants that are browsed replace lost carbon by increasing shoot production compared to root production (Chapin and others 1987). Browsed plants probably have difficulty acquiring nutrients due to lost tissue and lack of new root growth. Further, nutrients are quickly depleted near existing roots making the investment in new roots a necessity. The availability of nutrient resources is directly related to the ability of a plant to compensate for herbivory (Maschinski and Whitham 1989), and low resource availability reduces growth rate (Bryant and others 1983; Coley 1988). Therefore, browsed plants must balance vegetal production requirements with the need to produce new roots.

Seedhead Production

Perhaps the most striking difference between browsed and unbrowsed plants was in seedhead production (table 1). The maximum number of seedheads on browsed plants was 3, and over half of the browsed plants had none. One of the unbrowsed plants had no seedheads, but it was more common to find 60 to 100 seedheads per plant. Kay and Chaddie (1991) found similar results in heavily browsed willows (*Salix* spp.) growing in exclosures not far from those in this study. No aments were observed on stems that were within reach of ungulates.

Reproduction depletes plant resources as photosynthate is diverted from growth and maintenance to flower and seed production (Bazzaz and others 1987; Reekie and Reekie 1991). Studies indicate that stress such as herbivory may delay or prevent flowering for several years (Bazzaz and others 1987; Maschinski and Whitham 1989). In antelope bitterbrush (*Purshia tridentata*)and chamise (*Adenostoma fasciculatum*), grazing is inversely related to flower production (McConnell and Smith 1977). The lower overall production of browsed sagebrush plants may indicate that the allocation to replace vegetal biomass results in reduction to reproductive ability.

Miller and Schemske (1990) positively correlated flower number with biomass in common rape (*Brassica rapa*). While overall biomass was not measured in the present study, unbrowsed shrubs visually appeared to have far more biomass than browsed shrubs. Production, which may reflect biomass, was consistently higher in unbrowsed shrubs.

Bilbrough and Richards (1991) found that buds for flowering stems on mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) were located on short shoots at the distal end of the terminal leader. Because almost all terminal leaders were removed on browsed plants in this study, flowering stems on these plants would have to be initiated from elsewhere.

Leaders

Average leader length and dry weight were not found to be significantly different ($P < 0.05$) between browsed and unbrowsed plants (table 1). Browsed plants produced leaders averaging 22.9 mm in length, while unbrowsed leaders were 22.3 mm. Average dry weight was identical at 0.02 g. Although terminal leaders were compared with axial leaders, both leader types were long shoots as described by Bilbrough and Richards (1991). It is suggested that with the terminal leader removed, the axial shoot adopts the function of the former at least in length and weight. Most plants outside the exclosure were browsed so heavily that it was difficult to find leaders. These plants had leaders growing only where they were protected by masses of woody dead crown. Inside the exclosure, plants had hundreds of leaders growing on all parts of the crown.

No flowering stems were found on axial leaders, an observation similar to that of Bilbrough and Richards (1991). However it is not known if lack of seedheads was due to the axial position of the leader or to the prevention of flowering by browsing stress.

Leaves

Although browsed and unbrowsed plants had virtually the same total number of leaves (43 and 44 leaves/leader, respectively), unbrowsed plants had significantly ($P < 0.05$) more unlobed leaves, while browsed plants produced more that were lobed (table 2). Unbrowsed plants averaged 20 lobed and 24 unlobed leaves/leader while browsed plants produced 28 lobed and 15 unlobed.

The total leaf area was identical for plants in and outside of the exclosure (354 mm^2/leader, $P < 0.04$). However, plants that were browsed had significantly ($P < 0.0001$) larger lobed leaves and smaller unlobed leaves (table 2). Unlobed leaves on browsed plants averaged 273 mm^2/leader while there were 226 mm^2/leader on protected plants. Lobed leaves, in contrast averaged 81 mm^2/leader on browsed plants and 128 mm^2/leader on unbrowsed.

The mass of lobed leaves was not significantly different between treatments (table 2). However, browsed plants produced unlobed leaves averaging 0.01 g/leader, which was significantly less ($P < 0.05$) than the 0.03 g/leader average of unbrowsed plants. Total dry weight was also significantly ($P < 0.03$) less for browsed plants.

Table 2—Average differences among leaves per leader on browsed and unbrowsed Wyoming big sagebrush plants.

	Browsed			Unbrowsed		
	Lobed	Unlobed	Total	Lobed	Unlobed	Total
Leaf number	28^a	15^a	43^a	20^b	24^b	44^a
Leaf area (mm^2)	273^a	81^a	354^a	226^b	128^b	354^a
Leaf dry wt. (g)	$.05^a$	$.01^a$	$.06^a$	$.05^a$	$.03^b$	$.08^b$
SLA (mm^2/g)	5460^a	8100^a	5900^a	4520^b	4267^b	5027^b

Values followed by different letters in like columns (ie. lobed, unlobed, total) are significantly different ($P < 0.05$).

The area of a leaf divided by its dry weight is known as specific leaf area (SLA), and is often used as an indicator of photosynthetic efficiency or resource allocation by plants (Reekie and Reekie 1991). Browsed sagebrush had a significantly ($P < 0.0001$) higher SLA value than unbrowsed shrubs (table 2) which may indicate thinner leaves with a lower investment in leaf biomass (Porter and Remkes 1990). Increased SLA may help compensate for the decrease in leaf allocation due to herbivory (Reekie and Reekie 1991). SLA was especially high among the unlobed leaves of browsed plants at 8100 mm^2/g/leader, while the same type of leaves on unbrowsed plants had only half that value at 4,267 mm^2/g/leader. Browsed plants also had higher SLA values for lobed leaves and total leaves (5,460 and 5,900 mm^2/g/leader, respectively versus 4,520 and 5,027 mm^2/g/leader for unbrowsed plants).

Species may allocate assimilate toward increased photosynthesis or structural production, but not both (Reich and others 1991). Thin leaves are a means of maximizing leaf area with a minimal amount of resources. It appears that by producing leaves with high SLA, browsed plants used resources efficiently to compromise between photosynthesis and regrowth.

Conclusions

Shrubs that were protected from long-term browsing were larger and consistently produced significantly more forage than browsed shrubs. Seedhead production was also severely reduced by browsing. This may result in stands that have difficulty regenerating over the long term. Leaders on browsed shrubs have similar numbers of leaves and total leaf area as unbrowsed shrubs. However, browsed shrubs produce more lobed leaves as well as thinner leaves, probably to compensate for herbivory.

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Effects of Elevated Concentrations of Carbon Dioxide on Seedling Growth of Mesquite and Huisache

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Abstract—Plants such as mesquite (*Prosopis glandulosa*) and huisache (*Acacia smallii*) generally show positive growth responses to higher CO_2 concentrations. Growth of the two legumes was measured at five day intervals over 30 days from seedling emergence at 380, 700, and 1,000 ppm CO_2. Root elongation increased with CO_2 concentration in mesquite. Shoot mass of both species responded positively to elevated CO_2. Positive responses to CO_2 enrichment were evident within one week after emergence. Predicted increases in atmospheric CO_2 could increase seedling establishment and survival of these invasive shrubs, and ultimately contribute to a further change in the species composition of Southwestern rangelands.

Atmospheric concentrations of CO_2 are predicted to double (to about 700 ppm) by the middle of the next century. Plants possessing the C_3 photosynthetic pathway generally exhibit positive growth responses to superambient concentrations, while species with the C_4 photosynthetic pathway usually respond less to higher CO_2 (Mayeux and others 1991; Johnson and others 1993). This difference in response to CO_2 between C_3 and C_4 plant types may contribute to modify the species and growth form composition of rangelands across the Southwest (Polley and others 1994). Because most brush species are C_3 plants, while warm-season grasses are of the C_4 type, the predicted changes in CO_2 concentration should be selectively advantageous to invasive shrubs.

Once established, woody species may persist for a century or more unless controlled by humans. Gibbons and others (1992) found that only a small percentage of the mesquite (*Prosopis glandulosa*) that germinated survived into the second year. However, this small percentage of surviving seedlings was adequate to convert productive grassland into a mesquite-dominated ecosystem. Mesquite and huisache (*Acacia smallii*) have invaded vast areas of the Southwest in recent years, and in many cases completely dominate the landscape. Also, in cases where mechanical or chemical controls have reduced or eliminated stands of these plants, rapid recolonization of the site by seedlings quickly returns the area to its former vegetative composition (Gibbons and others 1992).

We determined effects of elevated CO_2 concentrations on shoot and root growth of mesquite and huisache seedlings, effects that may contribute to alter the competitiveness of these species on rangelands in the future.

Materials and Methods

Seedlings of both mesquite and huisache were grown in split PVC tubes 145 cm (5 ft) long in glasshouses maintained at atmospheric CO_2 concentrations of 380, 700, and 1,000 ppm. No supplemental lighting was provided. The split PVC tubes (held together with duct tape) facilitated easy removal of the entire tap root. The soil medium was amended with complete nutrient solution. Seedlings were harvested at 5 day intervals over 30 days following emergence. At harvest, shoot and root dry mass and length of taproots were determined.

Results

Plots of log total biomass vs. aboveground biomass indicated that CO_2 concentration did not modify allometric relationships between aboveground and total growth in young seedlings of either species (data not shown). However, the ratio of aboveground to total biomass decreased with age regardless of CO_2 concentration (fig. 1).

Rooting depth of huisache did not respond to CO_2, and was consistently lower than that of mesquite (fig. 2). Mesquite rooted more deeply at elevated CO_2 levels than at the current concentration. Rates of root depth extension for mesquite averaged 3.67 cm day^{-1} at the 380 ppm CO_2 level and 4.52 cm day^{-1} at elevated concentrations.

In mesquite, total biomass at the elevated CO_2 concentrations was greater throughout the experiment (fig. 3), with differences being statistically significant at day 30. For huisache, differences between atmospheres were not as pronounced (fig. 4), but trends were for greater biomass at elevated CO_2 concentrations.

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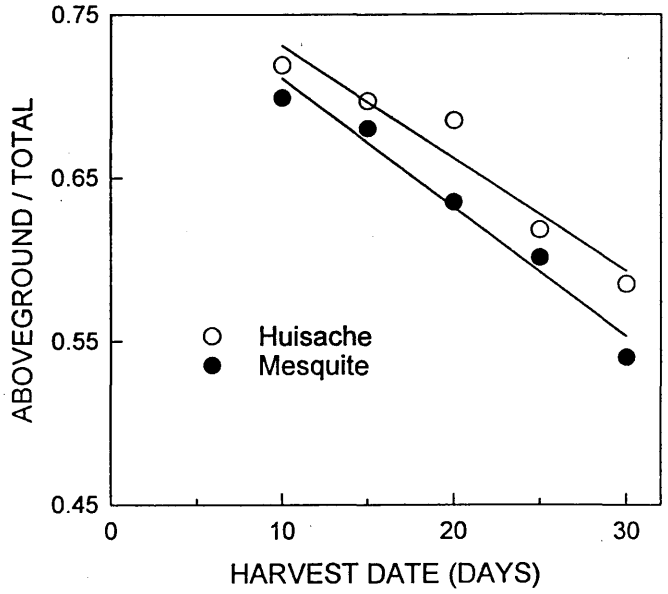

Figure 1—Means of the ratio of aboveground biomass to total biomass of mesquite and huisache seedlings after 10 to 30 days growth averaged across three CO_2 levels (Huisache: $r^2 = 0.63$, $P < 0.0001$, $n = 75$; Mesquite: $r^2 = 0.58$, $P < 0.0001$, $n = 75$).

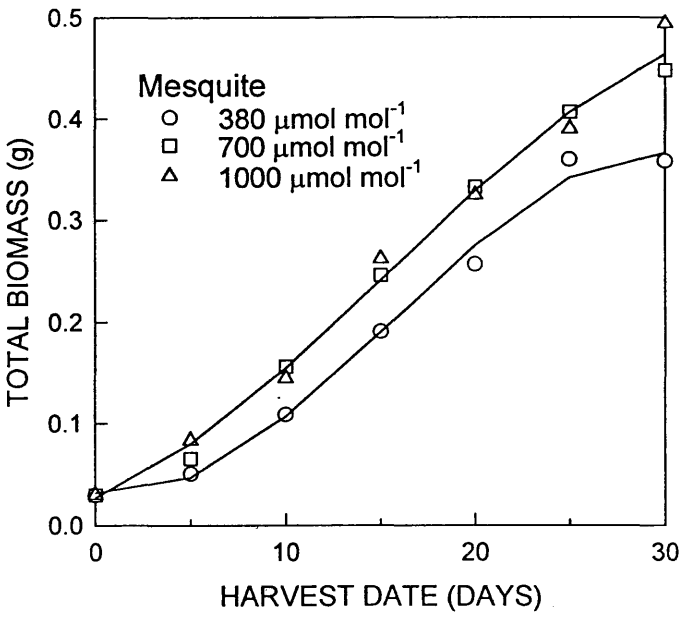

Figure 3—Means of total biomass of mesquite seedlings at zero to 30 days post-emergence grown at three CO_2 levels (at 380 ppm, $r^2 = 0.95$, $P < 0.0001$, $n = 35$; at 700 and 1,000 ppm, $r^2 = 0.95$, $P < 0.0001$, $n = 70$).

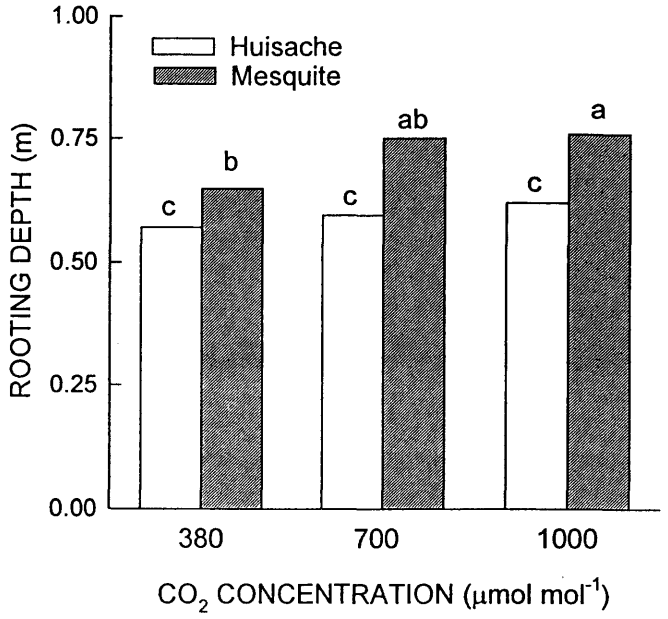

Figure 2—Rooting depth of mesquite and huisache seedlings (averaged over sampling days 5-30) at three CO_2 levels. Bars headed with the same letter are not significantly different ($P < 0.05$) by Student-Newman-Kuel's Test ($n = 35$).

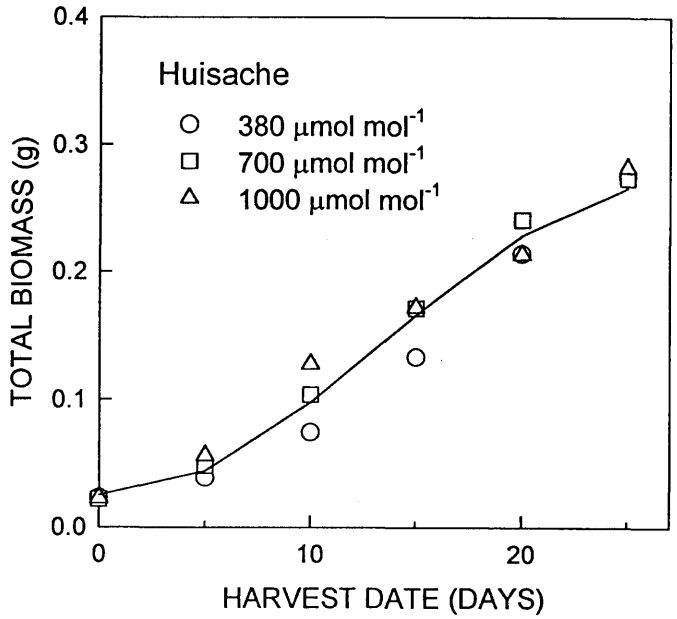

Figure 4—Means of total biomass of huisache seedlings at zero to 30 days post-emergence grown at three CO_2 levels (Single regression for all atmospheres, $r^2 = 0.84$, $P < 0.0001$,

Discussion

The response of mesquite seedlings to CO_2 enrichment was quite dramatic. Root and total biomass were increased as much as 38% at elevated CO_2. Positive responses to elevated CO_2 were evident in about a week. Positive responses were noted for huisache, but were not as impressive as those measured on older plants (H. B. Johnson, unpublished results). Differences in shoot mass present on days 15 and 20 between huisache plants grown at elevated CO_2 and the current level were not present at later harvests. We believe that this may reflect a temporary lag in growth at the elevated CO_2 levels, where the earlier abscission of cotyledons and lower leaflets precedes a burst of leaf initiation and growth. We have observed that leaf and cotyledon longevity may be shorter at elevated CO_2. Senescence of the cotyledons and lower leaves represents a significant shift in relative masses of seedling structures that further complicated growth analyses of these young plants.

Obviously, the root lengths we observed in the tube system represent maximum potential elongation, but are indicative of the significant amount of resources both species invest in deep rooting.

Further experimentation is required to determine responses of mesquite and huisache to elevated CO_2 where competition, water and heat stress, herbivory, and other complicating factors are also present.

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Energy Balance Dynamics Within a Shrub-Dominated Watershed

J. Ross Wight
Clayton L. Hanson
Gerald N. Flerchinger

Abstract—Components of the surface energy balance were measured within a shrub-dominated watershed in southwestern Idaho during the 1989, 1990, and 1991 growing seasons. On clear days, net radiation averaged between 40 and 50% of the incoming solar radiation with the highest values occurring during spring and early summer before the grasses and forbs began to senesce. The ratio of latent heat to net radiation varied from more than 0.75 in the spring to less than 0.05 in the fall at the low elevation site. Albedo averaged between 13 and 17% with little site, seasonal, or diurnal variation. Simulated energy fluxes using the SHAW model were in good agreement with field-measured values.

Components of the surface energy balance vary significantly in time and space within arid and semiarid ecosystems and have a direct impact on ecosystem processes. An understanding of these fluxes, their magnitude and dynamics, is important to the study of plant and animal dynamics and hydrological processes within these ecosystems. The latent heat flux (LE) or evapotranspiration (ET) is a major component of the hydrologic cycle and natural resource models. Technology to measure these fluxes, including LE, over arid and semiarid landscapes is now readily available (Wight and others 1993). The purpose of this study was to determine the energy balance dynamics of sagebrush-grass communities and to compare model-simulated values with field-measured values.

Methods and Procedures

Energy Balance

We measured the components of a surface energy budget over five sagebrush-grass plant communities (table 1) on the USDA, ARS Reynolds Creek Experimental Watershed during the 1989, 1990, and 1991 growing seasons. These components included: incoming solar radiation (Rs), net radiation (Rn), soil heat flux (G), and LE—all measured in (W/m^2). Sensible heat, also in W/m^2, was calculated from the surface energy balance equation. Albedo was also determined for Nancy, Lower Sheep, and Reynolds Mountain.

Bowen ratio-energy balance systems as described by Wight and others (1993) were used to measure the component fluxes. The positive-head, ceramic-wick, aspirated psychrometer (PCAP) system was used in 1989, 1990, and on the Nancy site in 1991. The cooled-mirror, dew-point hygrometer (CDH) system was used on the Lower Sheep and Reynolds Mountain sites during 1991. Energy fluxes were recorded at 12- and 20-minute intervals with the PCAP and CDH systems, respectively. Representative clear days are reported.

Table 1—Site characteristics.

Site	Elevation	Slope	Aspect	Growing season	LAI[1]	Average annual precipitation	Dominant vegetation
	m	*Percent*				*mm*	
Nancy	1,444	4	NE	3/20 -11/1	0.73	295	Wyoming big sagebrush *Artemisia tridentata wyomingensis*
Lower Sheep	1,649	10	NW	4/1-10/1	0.96	338	Low sagebrush *A. arbuscula*
Upper Sheep (A)	1,871	12	W	4/10-10/1	0.42	386	Low sagebrush *A. arbuscula*
Upper Sheep (B)	1,884	14	NE	4/20-10/1	1.2	491	Mountain big sagebrush *A. tridentata vaseyana*
Reynolds Mountain	2,073	4	S	5/10-10/1	1.38	748	Mountain big sagebrush *A. tridentata vaseyana*

[1]Leaf area index at peak standing crop.

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Model Simulation

The model simulation study used energy balance data collected during the 1990 growing season from the Upper Sheep A and B sites. Model simulations were compared with measured data on an hourly basis.

The energy balance was simulated using SHAW, a simultaneous heat and water model (Flerchinger and Pierson 1991). SHAW is a detailed, physical process model of a vertical, one-dimensional canopy-snow-residue-soil system which integrates the detailed physics of heat and water transfer through a plant canopy, snow, residue, and soil into one simultaneous solution. It provides daily and hourly predictions of the surface energy fluxes plus runoff, soil profiles of temperature and water, and snow and soil frost depths. SHAW can run using either hourly or daily inputs of solar radiation, air temperature, wind, and relative humidity. In this study hourly input data were used.

Results and Discussion

Energy Balance

Diurnal variations in the energy balance for three study sites for July 3, 1991, are illustrated in figure 1. Small differences among the three sites are reflected in the LE and Rn components which are associated with the amount of vegetation and available soil water present. The lowest values for these components were on the Nancy site which has less vegetation and dries earlier in the season than the other two sites. There was an increase in Rs going from the Nancy and Lower Sheep sites (elevations of 1,444 and 1,649 m, respectively) to the Reynolds mountain site (2,073 m elevation). Albedo remained relatively constant throughout the daylight hours.

Seasonal variation in the energy balance for three sites during a growing season is represented in figure 2. As expected, Rs increased from spring to mid summer and then decreased reflecting the change in the Earth's position relative to the sun.

On clear days, Rn averaged between 40 and 50% of the incoming solar radiation with the highest values occurring during spring and early summer before the grasses and forbs began to senesce. Net radiation was generally higher at Reynolds Mountain than at the other two sites reflecting slightly higher Rs and possibly small differences in site vegetation characteristics.

Albedo was relatively constant throughout the growing season and among sites averaging between 13 and 17%. The highest values were recorded on the Nancy site which was drier than the other sites. This site also contributed the most energy to downwind advection.

The LE component varied throughout the growing season, primarily a function of available soil water. The LE to Rn ratios varied from more than 0.75 in the spring to less than 0.05 in the fall at Nancy, the driest of the three sites. Maximum daily ET rates of about 5 mm occurred at the Reynolds Mountain site.

The G component increased slightly towards mid summer and then decreased thereafter.

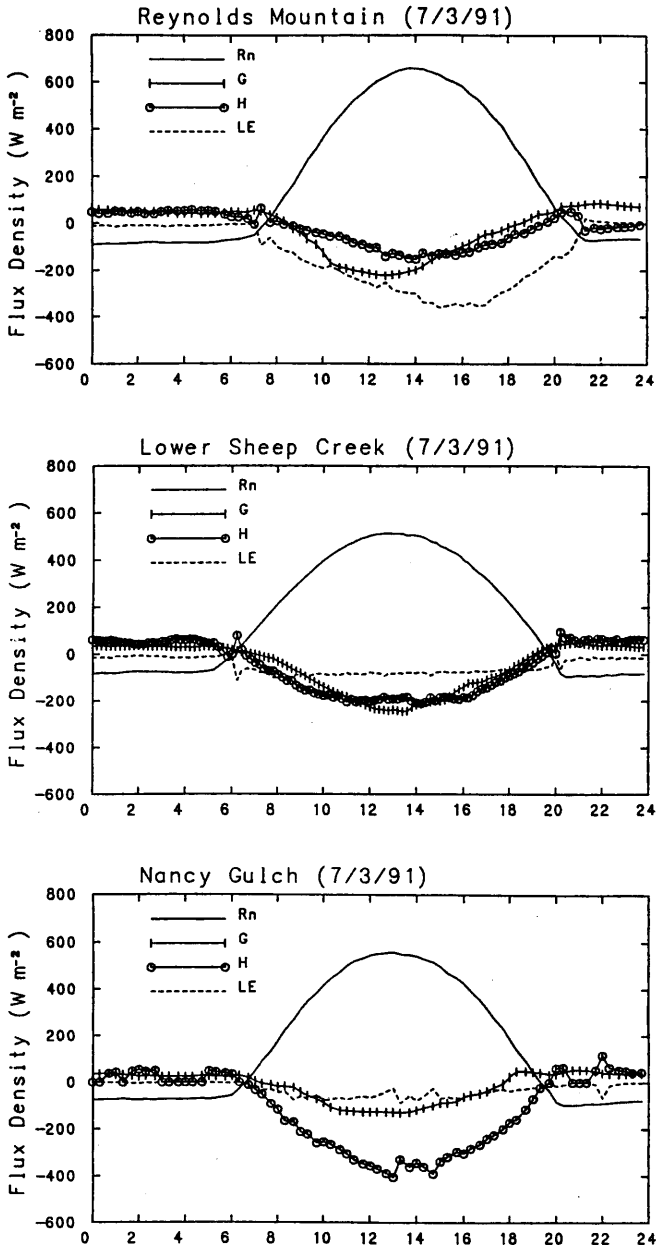

Figure 1—Diurnal dynamics of the energy balance fluxes within three sagebrush-grass communities.

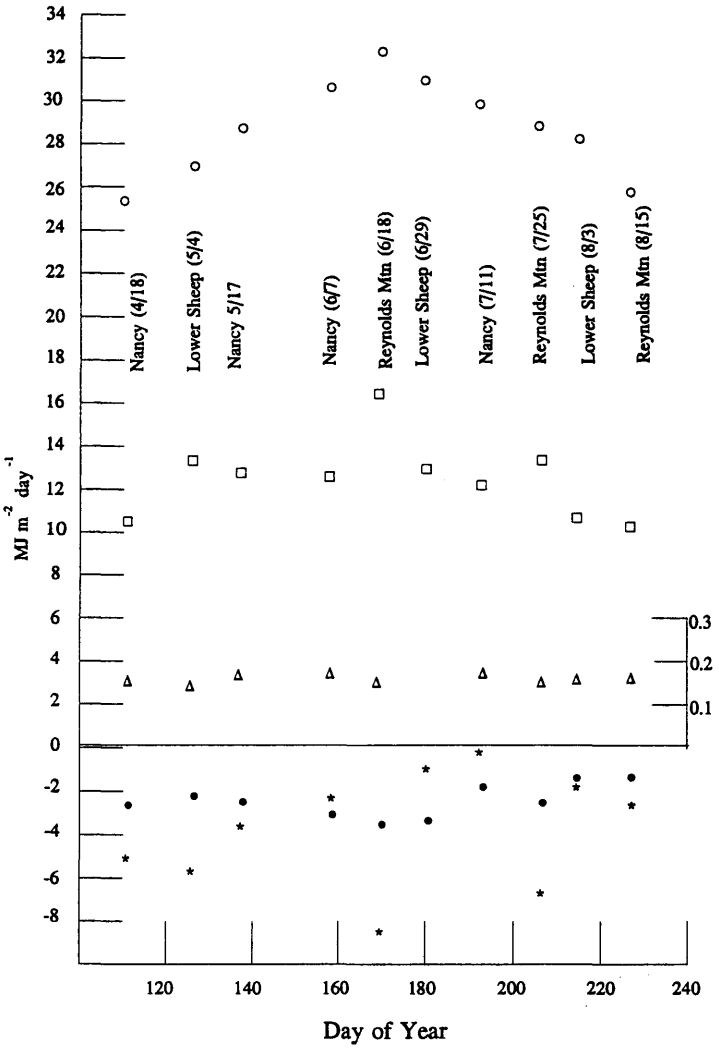

Figure 2—Seasonal dynamics of the energy balance components within three sagebrush grass communities. (O = Rs; □ = Rn; Δ = albedo; ● = G; * = LE)

Model Simulation

Simulated diurnal and daily energy fluxes compared quite well with measured data. Comparison of measured and simulated diurnal variation in each component of the surface energy balance is given in figures 3 and 4 for the Upper Sheep sites. The coefficient of efficiency (for example, the variation in measured values explained by the model and analogous to the coefficient of determination) for simulated Rn was over 0.95 for both sites. Coefficient of efficiency for hourly simulated latent heat ranged from 0.61 for the low sagebrush site (Upper Sheep A) to 0.72 for the mountain big sagebrush (Upper Sheep B). Measured and simulated ET accumulated over approximately 25 days of measurement were 41 and 44 mm, respectively, for the low sagebrush, and 74 and 69 mm for the mountain big sagebrush. Measured and simulated cumulative ET were within 7%.

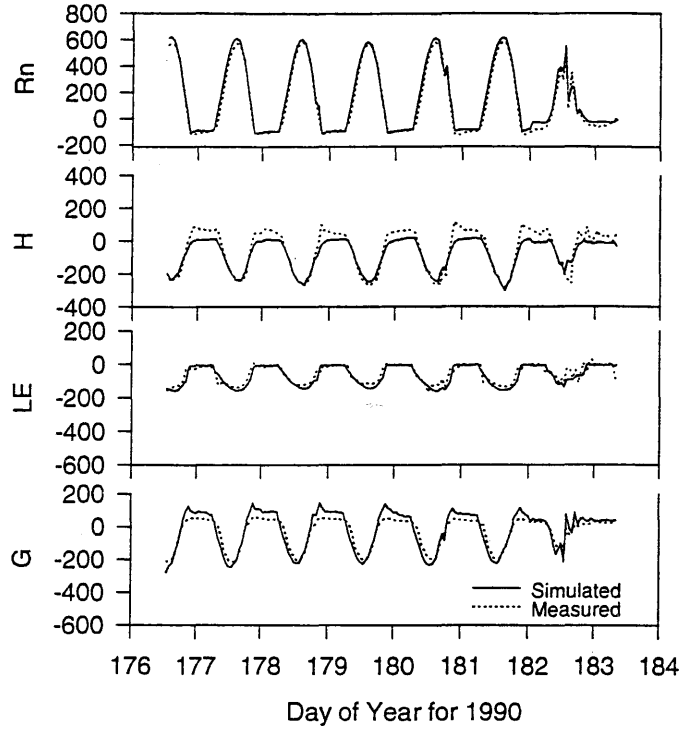

Figure 3—Comparison of field-measured and model-simulated surface energy fluxes on the Upper Sheep A low sagebrush site.

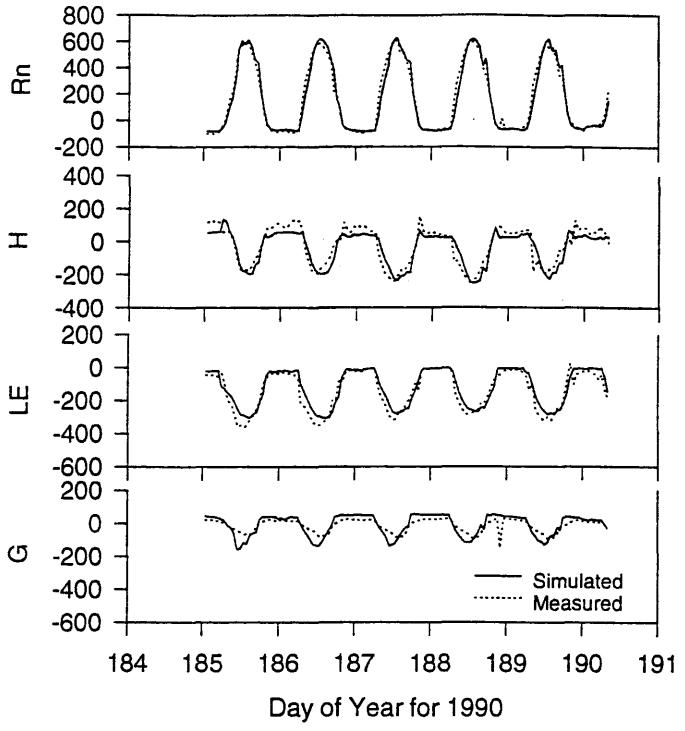

Figure 4—Comparison of field-measured and model-simulated surface energy fluxes on the Upper Sheep B mountain big sagebrush site.

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Role of Microbes in Resource Management in Arid Ecosystems

Jerry R. Barrow
Bobby D. McCaslin

Abstract—Three major classes of endophytic fungi were observed in the roots of native grasses and shrubs: (1) vesicular-arbuscular mycorrhizae (VAM), which are known to be important in water and nutrient uptake; (2) septate fungi that formed non-destructive interfaces within root cortex cells and exhibited mycorrhizal like characteristics; and (3) chytridiomycetes were the third major class of fungi observed and preliminary studies suggest they regulate colonization of VAM, septate fungi, and nutrient uptake. A hypothesis is proposed on how these fungi function in accessing and managing nutrients and water for survival in arid ecosystems.

In arid ecosystems many plant species live in harmony and are efficient and successful in accessing and managing limited nutrient and water resources. Generally, desert plants survive extended drought punctuated only briefly by cyclic and unpredictable precipitation events where moisture and nutrient mobility are sufficient for essential plant processes. We propose that this extraordinary task is accomplished by symbiotic associations. It is well documented that several classes of mycorrhizae increase production and survival of most vascular plants by enhancing water and nutrient uptake and in some cases they are essential for host plant survival (George and others 1991). Lichens are symbiotic associations between photosynthetic algae or bacteria with fungi. This association allows them to chemically weather rock surfaces through organic acid production to access highly immobile nutrients (Johnston and Vestal 1993). Similar microbe assisted mechanisms to access and manage nutrients and water in arid ecosystems may be essential for the survival and productivity of desert plants.

We surveyed dominant grasses and shrubs from the southwestern US and analyzed roots for endophytic fungal associations. Several experiments were conducted using native plants, alfalfa as a model plant, different fungi, nutrient levels and carbon sources. A brief summary of the results and the development of a hypothesis are presented here.

Incidence of Endophytic Fungi

Small (less than 1 mm in diameter) feeder roots of dominant grasses and shrubs were collected at different times from native populations from many sites varying dramatically in elevation, soil type, temperature, and precipitation. Roots were cleared by the method of Brundrett and others (1984) and stained with either acid fuschin, trypan blue, or chlorozol black E, all specific for fungal tissue. Stained roots were analyzed microscopically for fungal colonization. In summary, three major classes of endophytic fungi were observed in both grasses and shrubs.

Hyphae and vesicles of vesicular-arbuscular mycorrhizal fungi are considered to be important in most plant species for nutrient and water uptake. Arbuscules, an important VAM structure, responsible for carbon and nutrient transfer between the host and fungus (Gianinazzi and Gianinazzi-Pearson 1979; Cox and Tinker 1976) were rarely observed. Since these structures are short lived when observed under mesic conditions, their existence under arid conditions would be brief and rare.

Secondly, root cortex cells were also consistently colonized both inter- and intracellularly by septate fungi. These formed non-destructive interfaces within the cells, occasionally a sheath surrounded the root, varying from a very loose to a dense fungal mat. Most frequently, however, the extramatrical hyphal growth extended directly from the root surface into the adjacent soil and aggregating soil and sand particles adjacent to the root surface. A septate isolate from fourwing saltbush formed "ectendomycorrhizal like" associations with alfalfa root organ cultures with internal interfaces similar to those observed in the native population. This isolate was identified as *Fusarium solani* by Dr. Robert Linderman at Oregon State University. Several additional isolates from native plants species also formed "mycorrhizal like" associations with root-organ cultures. Presently, positive identification of the other isolates has not been made, but they appear to be common soil saprobes.

A seedborne septate fungus, *Alternaria alternata*, was found consistently on the seed capsule or utricle of fourwing saltbush (*Atriplex canescens*) and formed similar non-destructive interfaces with the cortex cells of the emerging radicle. We compared vigor of seedlings from seed excised from the utricle with intact seed germinated on carbon free and cellulose supplemented medium. Seedlings from excised seed were significantly more vigorous when germinated on cellulose supplemented medium compared to carbon free medium. This suggested that internal microbes (we suspect chytrids) and septate fungi utilized cellulose for seedling vigor. Seedlings from intact seeds were more vigorous than excised seeds, suggesting that the septate fungi decomposed the utricle and transferred nutrients to the seedling. Maximum seedling vigor was obtained by germinating intact seeds on cellulose supplemented medium and suggests that the septate fungi accesses nutrients not only from the utricle but from external organic matter. Orchid mycorrhizae have been shown to access carbon from organic resources and transfer it to the developing host plant. These fungi have been identified as species pathogenic to other plants or are decomposing fungi (Harley and Smith 1983).

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Similar septate fungi as well as VAM were observed in cultivated alfalfa populations. Alfalfa plants either inoculated with VAM + septate, septate fungi, or from surface sterilized seed were grown in phosphorus (P) deficient soil, or in P deficient soil supplemented with rates of elemental P ranging from 500 to 4,500 pounds per acre. These P rates are two to nine times greater than recommended fertilization rates in New Mexico and are considered excessive. Plants inoculated with VAM + septate fungi had the maximum growth response and plants inoculated with septate fungi were intermediate but significantly larger than the sterile controls in the non-P supplemented soil, suggesting a benefit from the septate fungi in P uptake. However, sterile plants were significantly larger than inoculated plants at all supplemental P treatments. This demonstrates that both VAM and septate fungi enhance P uptake at low concentrations and restrict or regulate uptake at high concentrations. In another experiment where toxic concentrations of mineral salts accumulated, plants inoculated with septate fungi were protected while non-inoculated plants died, further illustrating these organisms regulate mineral uptake.

No VAM or septate fungi were observed in plants from surface sterilized seed. However, from transmission electron microscope studies, seedlings from surface sterilized seed are colonized with internal microbes, which we suspect were either chytrids or bacteria that influence colonization of VAM and septate fungi, hydrolysis of cellulose, and nutrient uptake.

In summarizing several experiments we found that the morphological expression and colonization of VAM, septate fungi, and chytrids was greatly influenced by the level of P fertilization. Maximum expression of all three organisms were observed at low levels of P fertilization and fungal expression decreased as P concentrations increased.

Roots of broom snakeweed (*Gutierrezia sarothrae*) were also colonized with a septatate fungus that formed dense sand and soil aggregates at the root surface. This isolate also formed "mycorrhizal like" associations with root organ cultures similar to those reported above. Scanning electron and petrographic microscope studies of the attachment of the fungal hyphae with clay "skins" coating the sand particles and extensive hyphal networks within porous caliche suggested a nutrient harvesting role of these fungi.

Discussion

Benefits of VAM fungi are well known and documented (Harley and Smith 1983). Peyronel (1924) reported that nonpathogenic septate fungal colonization was common in plants and suggested that they may have potential importance. Odell and Trappe (1992) found widespread septate fungi on native legumes in Oregon and Washington and found no evidence of harm to the host. Bethlenfalvay (1992) reviewed potential roles of mycorrhizal fungi in the soil other than nutrient uptake such as serving as agents of nutrient transport between the host plant and microbe populations in the soil. In essence, they are the means by which other soil microflora receive carbon to function. Miller and Jastrow (1994) described the contribution of mycorrhizal fungi to soil aggregation. First, the hyphae form a skeletal structure that physically holds soil particles by physical entanglement. Second, roots and hyphae produce physical and chemical conditions, such as organic and amorphous materials for the binding particles. Third, the hyphae and roots, by forming these aggregates, create a means of water, carbon, and nutrient storage in the soil.

We propose that these three endophytic classes of fungi function in harmony or as a suite of organisms. They form non-destructive interfaces with the host cortex cells that allow bidirectional movement of water, carbon, and nutrients between the host, microbes, and soil. Nutrients and water would be accessed by the saprophobic endophytic fungi and associated microbes from immobile organic and organic resources. These resources would be accumulated and immobilized in soil aggregates, or in fungal tissue, under its metabolic control. This would enhance survival of the host during extended stress periods such as drought. Ling-Lee and others (1975) suggested that phosphorus absorbed by uninfected roots is readily translocated throughout the plant. In ectomycorrhizal infected roots, phosphate is taken up into the sheath and is distributed between two phosphate pools: a small pool that supplies an immediate source of metabolic phosphate to the host and a larger immobile storage pool. When external phosphorus uptake ceases, phosphorus is slowly remobilized from the large pool and transferred to the metabolic pool, where it becomes available to the host. A similar mechanism operating between these endophytic fungi and the host would be a survival mechanism during periods of stress.

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Time Series Satellite Data to Identify Vegetation Response to Stress as an Indicator of Ecosystem Health

Judith Lancaster
David Mouat
Robert Kuehl
Walter Whitford
David Rapport

Abstract—One measure of health in an ecosystem is the response of that ecosystem to an environmental perturbation (such as rain) over time. Healthy and unhealthy systems may have different phenological response patterns. Grassland and shrubland sites were selected, and metrics derived from temporal profiles of vegetation index values from Advanced Very High Resolution Radiometer satellite data from 1987 through 1993. The temporal profiles show that the vegetation types may be statistically discriminated, and metric values demonstrate different responses to rainfall.

The term "ecosystem health" is widely used by scientists, land owners and managers, and policymakers at all levels to indicate a condition that is both aesthetically and economically acceptable. However, the expression has varying meaning for different interest groups, and the criteria by which it is assessed often vary from one ecosystem to another. Before health can be judged, for any ecosystem, it is necessary to identify indicators such as keystone species, and acceptable ranges for measured values of these indicators (Haskell and others 1992). Haskell and others (1992) argue that each ecosystem has a specific suite of indicators, however, we propose that certain ecosystem structural and functional characteristics may be used as measurements of health.

Net primary production has been identified as the most important carbon cycle variable for quantifying and comparing biological activity across regions and biomes (Running 1990), and is an indicator of ecosystem function. Changes in ecosystem structure, such as biomass or leaf area index, may be identified and monitored using spectral radiance data acquired by sensors on-board satellites or aircraft to determine species composition and vegetation patterns (Mouat 1995). The repeated measurement of an ecosystem variable from the synoptic perspective of an aircraft or satellite sensor permits ecosystem analyses at varying spatial and temporal scales, facilitating the analysis of ecosystem dynamics which are reflected in temporal changes in vegetation. Studies of shrub and forest communities (Law and Waring 1995; Yoder and Waring 1994) demonstrate that vegetation operating under severe environmental constraints caused, for example, by prolonged drought, will show lowered photosynthetic rate and therefore decreased productivity throughout the year. This might be an indicator of ecosystem health.

Based upon assumptions that numerous stressors affect arid ecosystems, including climate, grazing, herbicide use and recreation, and that vegetation composition and cover is a response to ecosystem stress, it is hypothesized that satellite data may be used to evaluate ecosystem response through the use of a vegetation index such as the Normalized Difference Vegetation Index (NDVI). Ecosystems respond in different ways to stressors, such as drought, depending on their structural and functional integrity. Vegetation composition and cover may be seen as a response to stress, either natural as in the case of climate, or anthropogenic, in origin. Vegetation responds to water stress caused by severe or prolonged drought by closing leaf stomata, which decreases conductance of carbon dioxide from the atmosphere into leaf tissues and limits the plant's ability to absorb carbon through photosynthesis (Schulze and Hall 1982).

The research objective specific to the study reported here was to statistically evaluate the suitability of a suite of metrics derived from NDVI temporal profiles for discriminating variation in response to climate between mesquite and grassland systems.

Methods

An experimental design was developed which involved the selection of sites in both grassland and mesquite dominated areas, and verification of their vegetation and soils homogeneity using spectral response of vegetation during periods of maximum photosynthetic activity. Values for NDVI for each site at approximately biweekly periods during the growing season were extracted from satellite imagery, and plotted as annual temporal profiles for a seven year period from 1987 through 1993. The profiles were smoothed using a locally weighted regression, and metrics characteristic of phenological response calculated for each site for each year of the study. Values for the metrics were correlated with seasonal and annual rainfall totals, and the differences in photosynthetic response between vegetation types statistically validated.

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Satellite Data

The Advanced Very High Resolution Radiometer (AVHRR) is carried on-board the NOAA series of satellites, orbiting the earth twice daily on a sun synchronous schedule (NOAA 1986). Ground based radiance is collected in five spectral bands: red (Channel 1, 0.58-0.68 um), near infrared (Channel 2, 0.72-1.10 um), mid infrared (Channel 3, 3.55-3.93 um) and two thermal infrared bands (Channel 4, 10.3-11.3 um and Channel 5, 11.5-12.5 um) from pixels measuring 1.1 x 1.1 km in size when the satellite is at a nadir viewing angle. With heterogeneous land cover types, the 1.1 km pixel size results in the integration of varying spectral responses, which makes it suitable for regional scale studies. At these scales, the AVHRR has been used to monitor herbaceous cover in Botswana (Prince and Tucker 1986), correlate vegetation biomass with rainfall patterns in the Sahara (Malo and Nicholson 1990) and assess biological diversity for California (Walker and others 1992). Mouat (1995) hypothesizes that the spatial scale of AVHRR is directly applicable to the examination of ecosystem health, based on the premise that it is appropriate for the ecosystem processes involved (Malingreau and Belward 1992).

These studies typically use the Normalized Difference Vegetation Index (NDVI):

$$NDVI = (NIR - RED) / (NIR + RED)$$

where NIR is reflectance in near infrared wavelengths and RED is red waveband reflectance. The NDVI minimizes the effects of topography and atmosphere (Holben and Justice 1981), requires no prior knowledge of ground conditions, and is sensitive to the amount of photosynthetically active vegetation present (Myneni and others 1992; Tucker 1979).

With synchronous data collected on a daily basis, the AVHRR offers the most appropriate data set for temporal studies, and cloud-free images are usually available at 10 to 15 day intervals for the western U.S. Temporal profiles of NDVI or other indices capture and quantify differences in the extent and intensity of physiological activity throughout the growing season. Vegetation temporal response has been used to detect the effects of short-term drought in New Mexico, based on the differences between wet (1988) and dry (1989) years (Peters and others 1993), and to observe phenological differences between natural and cultivated vegetation throughout North America (Goward and others 1985). Seasonal range conditions in Senegal were monitored using NDVI time-series data (Tappan and others 1992), and Malo and Nicholson (1990) found that spatial and temporal patterns of NDVI closely followed rainfall in west Africa.

Site Selection Criteria

A prerequisite for the selection of a study area was current vegetation with variation in composition and cover which had originated as a uniform vegetation type. The Jornada Experimental Range (JER), near Las Cruces, New Mexico, comprises a mixture of vegetation types, having experienced an increase in shrub species and decrease in area occupied by perennial grasslands since the first vegetation survey in 1858 (Buffington and Herbel 1965). In addition, the JER has maintained climatic and land-use records since 1915, which is critical for a historical perspective on climatic variability. Covering an area of over 40,000 hectares, the JER is within the Chihuahuan Desert, ranges in elevation from 1,260 to 2,833 m, and has a mean annual precipitation of 247 mm (Agricultural Research Service 1994). Soils contain little organic matter, and root and water penetration are limited by a thick caliche layer often over 2 m in thickness (Agricultural Research Service 1994).

According to the work of Buffington and Herbel (1965), the western portion of the JER originated as perennial grassland, although it is now a spatially diverse mixture of mesquite dominated shrubland, grassland, and combinations of both vegetation types. This area met the site selection criteria for the project, and four sites were located in mesquite dominated areas, and another four in grassland areas in the western portion of the JER (fig. 1), thus providing a replication of study sites for purposes of statistical analysis.

Evaluation of Site Homogeneity

In order to compensate for satellite drift of up to one pixel in any direction, it was necessary for study sites to be spectrally homogeneous over a 3 x 3 km area. This homogeneity was established from spatial variance of reflectance in red and near infrared wavebands using imagery from the Landsat Multispectral Scanner (MSS) with a pixel size of 80 x 80 m. MSS images for April and August were chosen to capture the periods of maximum photosynthetic activity for mesquite and grassland communities respectively. The area of the eight study sites and four less homogeneous sites (as controls) was clipped from each image, and red and near infrared waveband reflectance index values were calculated for aggregates of 81 MSS pixels in 9 x 9 pixel matrices to approximate 1.1 km AVHRR pixels. The among pixel variance for the vegetation index values for the 16 aggregated pixels provided a measure of site homogeneity. An *a priori* coefficient of variation of 10% was chosen as the minimum value for site homogeneity, and study sites met this criteria.

The Department of Geography at New Mexico State University was able to provide AVHRR High Resolution Picture Transmission (HRPT) images for the JER, covering the period 1987 through 1993. Preprocessing of the AVHRR data was carried out by New Mexico State University, and extraction of the NDVI values for the study sites was done at the Desert Research Institute. Values for AVHRR red and near infrared reflectance were calculated from cloud-free imagery acquired at 10 to 15 day intervals throughout the annual active photosynthetic cycle and used to calculate NDVI. An area slightly larger than each 3 x 3 km study site was clipped from each AVHRR image, the NDVI value for the center pixel of the matrix was extracted, and the resulting values were plotted against time to give a temporal profile of NDVI response. Some early spring and late summer values for NDVI were higher than expected (the "terminator effect", Goward and Peters, personal communication, 1994). As a result these data were excluded from the study, resulting in nine to 12 data points between April 29 and September 19 for each study year.

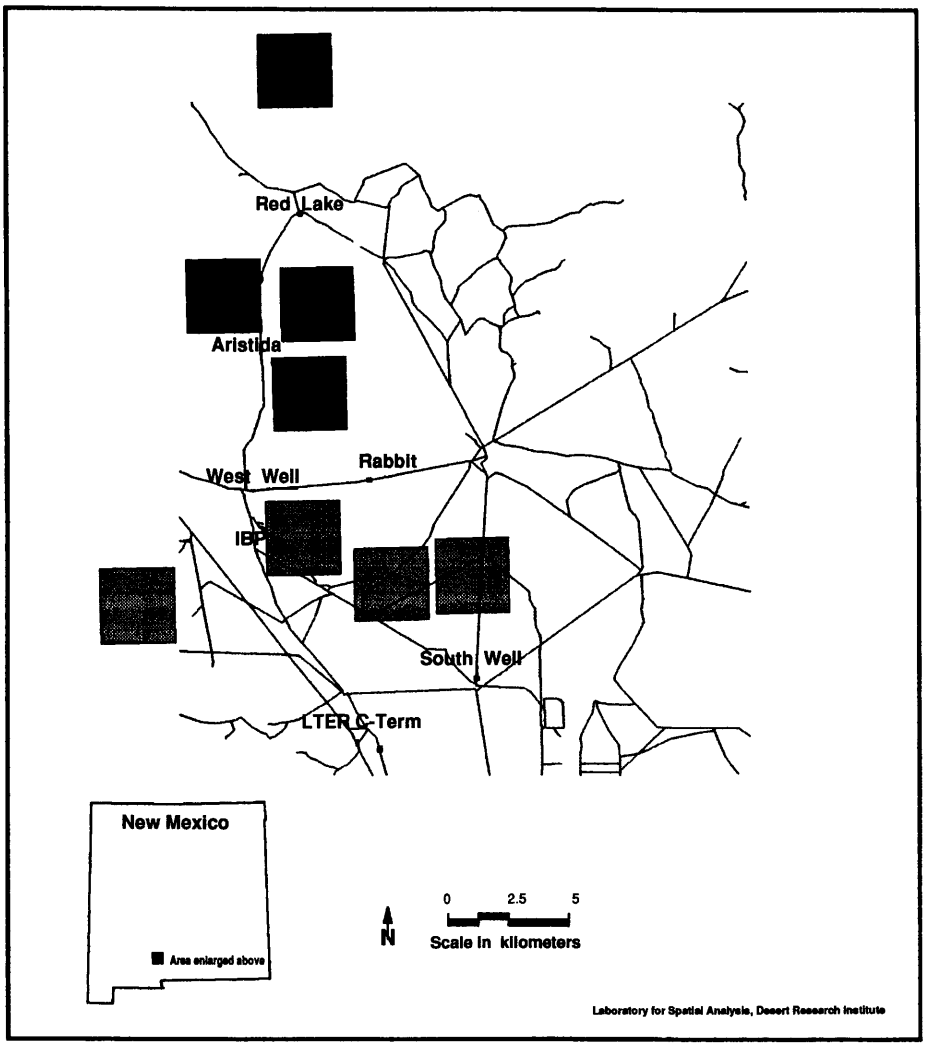

Figure 1—Location of study sites (squares) and rain gauges (named locales) at Jornada Experimental Range. Dark gray sites are mesquite dominated, pale gray sites are grassland areas.

NDVI Analysis

A daily profile of NDVI response or trend over time at a given site was felt to characterize the distinct pattern or shape of the NDVI response on the site. Various metrics could then be derived from the NDVI time profile with the potential to distinguish the patterns or shapes of the profiles between the two vegetation types. Since NDVI data were available for only 9-12 dates at each site, a daily profile of NDVI response for each site had to be estimated from these 9-12 NDVI observations.

An implementation of robust locally weighted regression or LOESS (Cleveland 1979; Cleveland and Devlin 1988) was used to estimate the NDVI profile for each of the sites in each of the years. LOESS is a nonparametric function to describe the relationship between two variables.

In the case of the NDVI profiles the NDVI response was assumed to be some unknown function ("g") of time:

$$g(T_i) \text{ or } NDVI_i = g(T_i) + e_i$$

where i = 1,2, t and e(i) is random error, and T is time. The NDVI responses were smoothed as a function of time in a moving fashion analogous to how a moving average is computed for time series, however, a locally weighted linear or quadratic regression is used for the smoothing rather than a simple average.

The LOESS smoothed fit illustrated for one of the grassland sites in 1989 (fig. 2) includes the twice standard error band around the smooth fit which corresponds roughly to 95% confidence limits for the nonparametric smoothing (Hastie and Tibshirani 1990). NDVI values for each observation over the 1989 growing season were aggregated for the four grassland and four mesquite sites respectively, showing significant variations in phenological response between the two vegetation types (figs. 3 and 4).

A number of metrics derived from NDVI temporal profiles have been proposed as indicators of ecosystem identification, behavior and response to perturbation, (Samson 1993; Reed and others 1994). These derived metrics include total NDVI response measured as an integration of the NDVI profile, seasonally integrated NDVI, duration of NDVI response, maximum NDVI, date of maximum NDVI, rate of NDVI increase during the greenup periods, and rate of NDVI decrease during the brown-off periods.

Six primary metrics calculated from the yearly profiles at each of the eight sites are illustrated in figure 5. They are total NDVI response, or integrated area under the profile

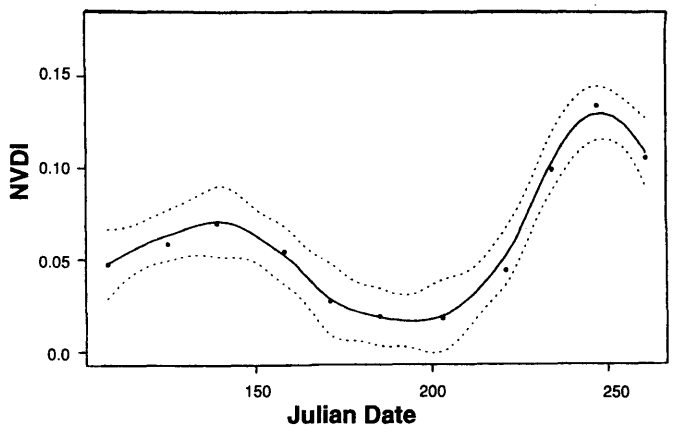

Figure 2—NDVI temporal profile LOESS fit for a grassland site with NDVI values plotted as points, and twice standard error limits shown as a dotted line.

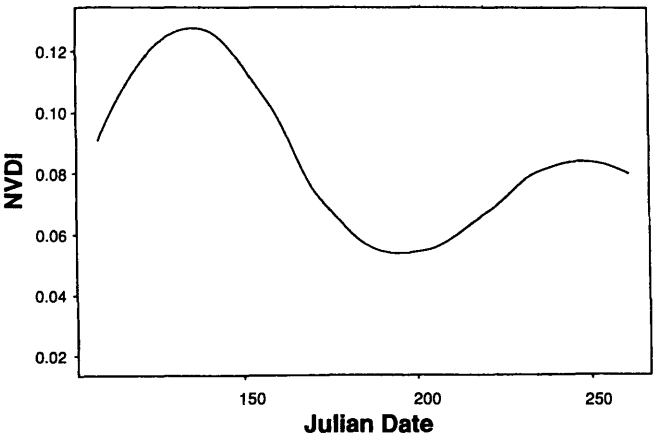

Figure 4—LOESS smoothed fit for aggregated site NDVI data for mesquite in 1989.

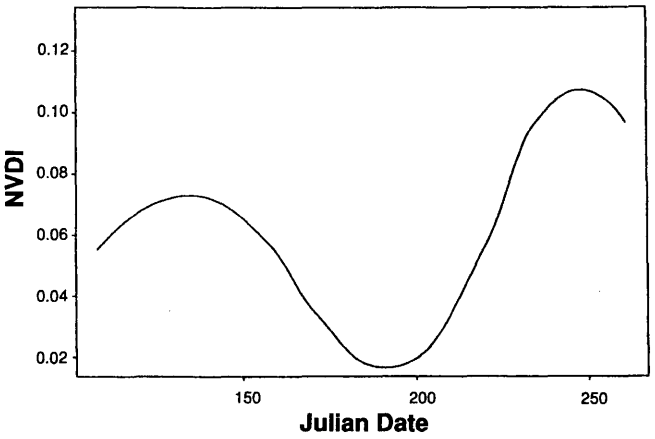

Figure 3—LOESS smoothed fit for aggregated site NDVI data for grasslands in 1989.

with NDVI above 0.03; duration of NDVI response, or number of days with NDVI above 0.03 between April 29 and September 19; NDVI response between April 29 and June 15; NDVI response between August 1 and September 19, maximum NDVI; and date of maximum NDVI. Examples of NDVI metrics, also given for 1989, are shown in table 1.

The climate data used for the analysis comprised previous year total rainfall, previous winter rainfall (October-January), current year spring rainfall (February-April), current year (May and June) rainfall, current year summer rainfall (July-September), current year total rainfall, and degree days above 5 °C between January 1 and May 15 for the current year. The rainfall data were collected at separate rain gauges for the mesquite sites and the grassland sites resulting in distinct rainfall values for the two types of sites. The degree days were common for the two vegetation types.

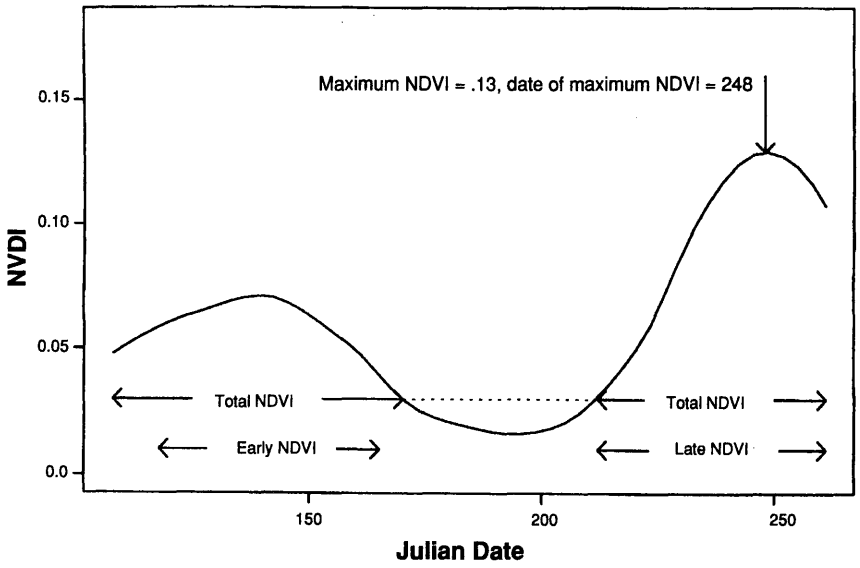

Figure 5—LOESS smoothed NDVI profile showing criteria for deriving the metrics.

Table 1—Values for NDVI metrics for 1989.

Site[1]	Early[2]	Late[3]	Maximum NDVI[4]	Maximum date[5]	Duration[6]
1	3.459	7.358	0.081	132	121
6	2.893	9.682	0.130	248	110
7	3.263	10.328	0.137	247	117
8	2.954	10.459	0.149	245	121
2	5.072	8.341	0.128	140	153
3	6.038	9.485	0.150	139	153
4	5.934	9.066	0.141	135	153
5	5.037	8.848	0.118	138	153

[1]Sites 1, 6, 7, and 8 are grassland and sites 2, 3, 4, and 5 are mesquite dominated.
[2]The "early" variable is the integrated NDVI profiles from April 29 to June 15.
[3]The "late" variable is the integrated NDVI profiles from August 1 to September 19.
[4]Value of maximum NDVI.
[5]Julian date of maximum NDVI.
[6]Number of days in which NDVI ≥ 0.03.

Table 2—Rainfall covariates for which the NDVI metrics had a statistically significant positive (increased) response to increased rainfall (indicated with "+").

	Rainfall				
	Previous year	Previous winter	Feb-April	May-June	July-Sept
Grassland					
Total NDVI	+				+
NDVI duration		+	+		+
Spring NDVI	+				
Summer NDVI	+			+	+
Maximum NDVI	+		+		
Date of max NDVI					+
Mesquite					
Total NDVI	+		+		
NDVI duration			+		
Spring NDVI	+		+		
Summer NDVI	+		+		
Maximum NDVI	+		+		
Date of max NDVI		+			+

The generalized linear model (McCullagh and Nelder 1989) was used to estimate the relationships between the NDVI metrics and the climate covariates in order to determine whether the NDVI metrics for mesquite and grassland systems had differential responses to climate. The generalized linear models allow for a broad range of statistical error model families in the parameter estimation routine, and as such are not limited to the normal distribution error model.

The response variables for the generalized linear model were the NDVI metrics. The independent variables or covariates included the study design variables of vegetation type (grassland or mesquite) and replicate sites within each vegetation type as well as the climate covariates. The rainfall covariates were included in the model with separate regressions for each of the vegetation types since there were separate rainfall measures for each vegetation type. Degree days was entered as a common regression for both vegetation types since the degree days covariate was common to both types. The analysis for regression of the NDVI metric on rainfall covariates was conducted to determine whether the regression coefficients were significantly different for the two vegetation types or of similar value for the two vegetation types.

Results

The results of the best fitting models for each of the vegetation types are shown in table 2, indicating those covariates to which the NDVI metrics had a statistically significant positive response (for example, increased). In no instance was the "degree days" variable significantly related to any of the NDVI metrics.

In general the patterns of positive responses of the two vegetation types to rainfall have some similarities and some differences. This study was in part designed to identify those NDVI metrics, if any, which show differential responses for grassland and mesquite sites to climatic variables as an indicator of relative health. The primary difference between the two vegetation types was manifested by NDVI metrics for the mesquite sites which were predominantly responsive to spring rainfall, and the same NDVI metrics for grassland sites which were predominantly responsive to summer rainfall. The NDVI metrics for the two vegetation types responded similarly to total rainfall in the previous year. Total, early, and late NDVI response as well as the maximum NDVI metrics all increased with previous year rainfall.

Total NDVI response for grassland sites increased with summer rainfall, whereas the total NDVI response for mesquite sites increased with spring rainfall.

The duration of NDVI response increased with spring rain for both grassland and mesquite sites. This was probably a function of prolonging the growing season. However, the duration of NDVI for grassland sites also increased with previous winter and summer rain, while the duration of NDVI response for mesquite sites was significantly related only to spring rainfall.

Early NDVI response (April 29 to June 15) for mesquite sites increased with previous year and spring rainfall, while the early NDVI response for grassland sites was significantly related only to previous year rain. This may have been a result of the response of a minor C_3 shrub, grass and forb component.

Late NDVI response (August 1 to September 19) for grassland sites increased with May-June and summer rainfall, whereas the late NDVI response for mesquite increased only with spring rainfall.

The maximum NDVI for sites of both vegetation types increased significantly with spring and previous year rainfall. As might be expected, the date of maximum NDVI was significantly later with increased summer rainfall for the grassland sites, but for mesquite sites the date was significantly later with increased previous winter rainfall as well as increased summer rain.

Summarizing the differences in the response of NDVI metrics to rainfall variables it was found that total NDVI response for grasslands increased with summer rain, whereas the total NDVI response for mesquite increased with spring

rain. The duration of NDVI response was prolonged in grasslands by increased previous winter, spring, and summer rainfall, whereas it was prolonged only by spring rainfall in the mesquite. The early NDVI response of grasslands increased only with previous year rainfall, but the early response of mesquite also increased with spring rainfall. The late NDVI response of grasslands increased with May-June and summer rainfall whereas the late response of mesquite increased only with spring rainfall. The date of maximum NDVI for grasslands occurred later only with increased summer rainfall, but the maximum NDVI for mesquite also occurred later with increased previous winter rainfall. Maximum NDVI relationships to rainfall were similar for the two vegetation types since both increased with previous year and spring rainfall.

Conclusions

Of primary significance in the results is the demonstrated statistical discrimination, in a site replicated study, between the two vegetation types with metrics derived from their NDVI response. Equally important, the results are consistent with differences in biological responses of the two vegetation types to rainfall patterns found in other studies (Donovan and Ehleringer 1994; Neilson 1986; Van Devender in press).

The effective statistical discrimination of two distinct vegetation types with satellite derived metrics provides the potential framework for a technique useful to discriminating these ecosystem characteristics in other settings.

NDVI metrics derived from temporal profiles are a measure of phenological response, and may indicate primary productivity. Changes in values for individual metrics, or the suite of metrics, occurring over a period of several years, might indicate changes in ecosystem structure, and may be used to monitor the condition, or health, of the system.

We have hypothesized that one measure of health in an ecosystem is the response of that ecosystem to an environmental perturbation (such as rainfall) over time. A healthier system may have a different phenological response pattern than the less healthy system and will maintain this pattern over time. The less healthy system will have a phenological response pattern which will diverge from the healthier one. The research reported illustrates a landscape which was predominantly grassland in the early 19th century. Following human disturbance, much of the grassland was replaced by shrubs (dominantly mesquite). We feel that the shrub-dominated areas took advantage of winter rains and "green up" earlier in the year. The AVHRR NDVI temporal response profiles support this observation. Continuing analysis will help to elucidate these relationships and either support or reject the hypotheses.

Acknowledgments

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Evaluation of Root Growth of Selected *Medicago* and *Hedysarum* Species

Mohamed Jabbes
Douglas Johnson
Paul Doescher

Abstract—Rapid rates of root elongation benefit plant establishment in semiarid environments. We tested five annual and two biennial leguminous species that show potential for revegetating central Tunisia rangelands under temperature regimes of 5, 10, and 15 °C. High temperature accelerated rates of root elongation, and low temperature retarded the rates. The degree of retardation varied with the species and the temperature range. Maximum root elongation occurred at 15 °C, and minimum root elongation occurred at 5 °C. *Medicago laciniata* had the fastest root elongation rate at 5 °C and 15 °C. *Medicago truncatula* was equal to *Medicago laciniata* at 5 °C. *Hedysarum carnosum* had fastest root elongation at 10 °C and 15 °C. A Tunisian accession, *Medicago polymorpha*, had the slowest root elongation at all temperatures.

Tunisia is a North African country characterized by a Mediterranean climate. Winters are cool to cold and relatively wet; summers are hot and dry. Most of the central and southern portion of the country is classified as rangeland. The people that live there and the livestock they raise are heavily dependent upon these rangelands.

Traditionally, these rangelands have supplied the forage upon which livestock depend. In recent times, livestock numbers have increased dramatically. Overgrazing has resulted in reduced yield of beneficial plants and a shift in plant species composition to unpalatable plants. In addition, soil erosion has been accelerated which contributes to ecological retrogression. Precipitation that should be held by vegetation so that it can percolate into the soil runs off very quickly carrying with it topsoil and causing gullies and washouts. Gintzberger (1983) reported rangeland improvement and regeneration is a matter of great concern in North Africa and the Middle East.

Commercially available annual legumes, especially medics, have been suggested as a method of improving the forage resource of central Tunisian rangelands. However, low yield and lack of competitiveness against weeds have been observed in central Tunisia.

In: Barrow, Jerry R.; McArthur, E. Durant; Sosebee, Ronald E.; Tausch, Robin J., comps. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Mohamed Jabbes, Douglas Johnson, and Paul Doescher are with the Department of Rangeland Resources, Oregon State University, Corvallis, OR 97331. Mohamed Jabbes' current address is Forest Resources Department, University of Idaho, Moscow, ID 83843. This paper was originally given at the Wildland Shrub and Arid Land Restoration Symposium, October 19-21, 1993, in Las Vegas, NV. This paper is included in the current proceedings because of its relevance to shrubland ecosystem dynamics.

In this study we hypothesized that successful medics would exhibit higher rates of root growth at cool temperatures than weedy species common on these sites. Specifically, the ability to elongate roots at low temperatures may be a primary factor aiding the establishment of plants under conditions of central Tunisia.

Our primary objective was to quantify the rates of root elongation of these species and accessions under controlled temperatures. This information can suggest the effect of such rates on competition for moisture later in the season and plant survival. Faster growing roots should be able to preempt resources from slower growing species.

Materials and Methods

Five collections of *Medicago* and two collections of *Hedysarum* species that were used to determine root dynamics:

1. *Medicago truncatula*, (W. Graves) Tunisian accessions
2. *Medicago truncatula* var. Jemalong
3. *Medicago polymorpha*, (W. Graves) Tunisian accession
4. *Medicago polymorpha* Circle Valley
5. *Medicago laciniata*, (W. Graves) Tunisian accession
6. *Hedysarum carnosum*, (INAT) Kairouan, Tunisia
7. *Hedysarum carnosum*, (INAT) Tunisian

The imported *Medicago truncatula* var. Jemalong and *Medicago polymorpha* var. Circle Valley were selected because they have been widely used in Tunisia in the ley farming system and have failed in some areas.

The experiment was conducted during the spring of 1990 in controlled environment growth chambers. Plants were grown at three constant temperatures: 5 °C, 10 °C, and 15 °C. A period of 16 hours per day with constant daily irradiance of 1,000 ft-c illumination at plant level was followed by 8 hours darkness (night). Plants were grown in glass tubes (51 mm outer diameter and 60 cm long for the 5 °C treatment, and 51 mm outer diameter and 90 cm long for the 10 °C and 15 °C treatments). The tubes were sealed at the bottom with a rubber stopper that contained a small opening to allow excess water drainage yet prevent leakage of soil. Tubes were filled with washed river sand.

To prevent the exposure of the roots to light, the glass tube was slipped into an ABS black pipe of 5 cm diameter. Tubes were placed in wooden racks at an angle of 17° from vertical to ensure that roots grew against the glass. Each rack had 36 squares of 7.5 cm on each side and 45 cm long legs. Tubes were watered to field capacity with nutrient solution which was mixed according to a soil analysis completed two days prior to the beginning of the experiment. Five seeds of each species were sown per glass tube at a

depth of 1 cm. Plants were allowed to grow in the glass house for seven days at 18 °C, thinned to one plant per tube then moved to growth chambers for temperature treatments. Total root length was measured and recorded every week for six weeks.

Data Analysis

The study was conducted as a completely randomized design. Root elongation was evaluated by Analysis of Variance performed with the Statistical Analysis Systems (SAS Institute Inc. 1989).

The plot of root length versus time for each species at each temperature was tested for linearity. A regression line was generated for each experimental unit (individual plant) at each temperature. Each temperature was analyzed separately using thirty-five regression lines (7 species * 5 observations). Analysis of variance was performed on the slopes (Δ length in cm per week) of these regressions which were considered as treatment responses. Planned contrasts were performed to identify differences in root elongation rates.

Results

Analysis of variance revealed significant differences among the species tested (figs. 1-4). Root elongation rate was slowest at 5 °C (fig. 1), intermediate at 10 °C (fig. 2), and highest for all species at 15 °C (fig. 3). Elongation varied with species and temperature. The average root elongation rates of species tested at 5 °C, 10 °C, and 15 °C is shown in figure 4.

A sharp decrease in rate of root elongation occurred as temperature declined for *Hedysarum carnosum* Kairouan accession and *Hedysarum carnosum* Tunisian accession. The rate of elongation declined from 11.7 and 9.8 cm/week at 15 °C to 3.6 and 3.5 cm/week respectively at 5 °C.

Roots of *Medicago laciniata* and *Medicago truncatula* penetrated faster than other species at 5 °C (p = .0001), however at higher temperatures (15 °C), *Hedysarum carnosum* KA and *Medicago polymorpha* var. Circle Valley had similar growth rates (fig. 4).

Contrasts were used to test whether there was a difference in root growth among groups of these species. There was no significant difference in response between local and imported species tested at all temperatures (table 1). *Medicago laciniata* had the highest growth rate at 5 °C, 15 °C and slightly lower at 10 °C (P = .0001 at 5 °C, p = .18 at 10 °C, and P = .0001 at 15 °C). This species had slower elongation at 10 °C because one of the plants was stunted which reduced mean root growth for the entire treatment. *Medicago truncatula* TA elongation was not different than other species at 10 °C (P = .18) and 15 °C (p = .62).

Medicago species had greater rates of root elongation than the *Hedysarum carnosum* accessions at 5 °C but this difference disappeared as temperature increased (table 1). *Hedysarum carnosum* accessions showed greater response

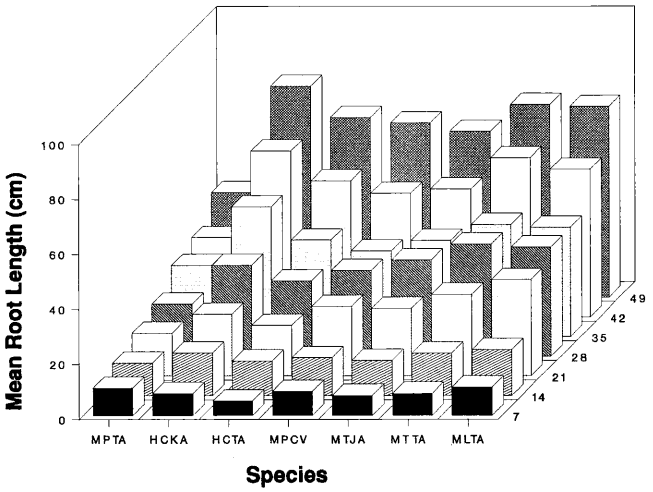

Figure 2—Mean root length of *Medicago* and *Hedysarum* species grown at 10 °C.

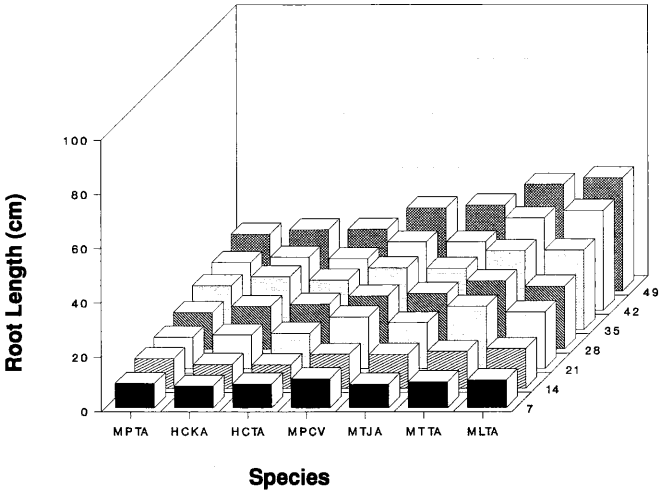

Figure 1—Mean root length of *Medicago* and *Hedysarum* species grown at 5 °C.

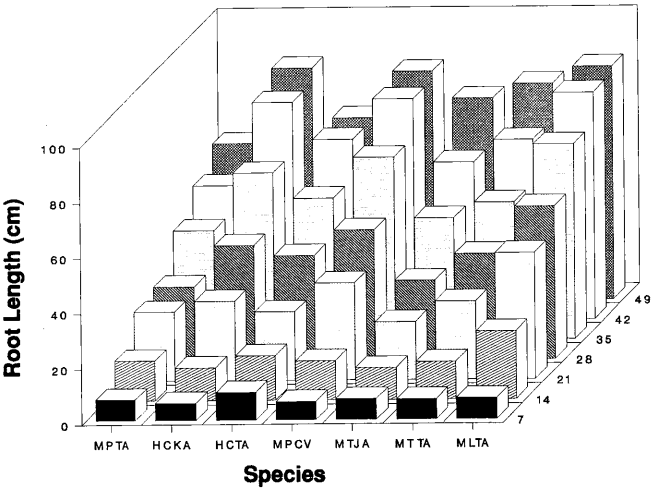

Figure 3—Mean root length of *Medicago* and *Hedysarum* species grown at 15 °C.

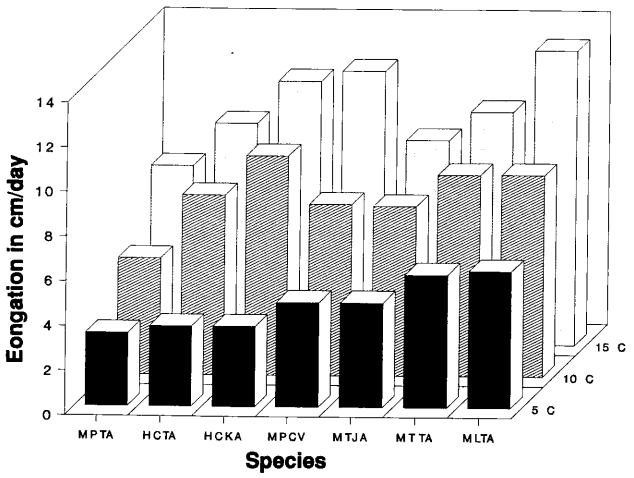

Figure 4—Rate of root elongation of *Medicago* and *Hedysarum* species grown at 5, 10, and 15 °C.

to increased temperature than *Medicago* accessions, especially between 5 °C and 10 °C. *Hedysarum* species had an increase of 55% in rate of root elongation between 5 °C and 10 °C compared to about 33% increase of the medic species (fig. 4). At higher temperature 15 °C there was no difference in speed of elongation between medics and *Hedysarum* accessions (table 2). Both *Hedysarum* accessions have similar rate of root elongation at 5 °C, however, when temperature was increased *Hedysarum carnosum* KA had higher rates (P = .01).

Table 1—P-values for source of variation of contrasts of root length at 5, 10, and 15 °C.

Source	Root length
Temperature 5 °C	
Local species vs imported species[a]	.4598
Local Medics vs imported Medics	.1023
Medics vs *Hedysarums*	.0001
Medicago truncatula TA vs others	.0001
Medicago laciniata vs others	.0001
Hedysarum carnosum TA vs *Hedysarum carnosum* KA	.9698
Temperature 10 °C	
Local species vs imported species	.2678
Local Medics vs imported Medics	.6994
Medics vs *Hedysarums*	.063
Medicago truncatula TA vs others	.1825
Medicago laciniata vs others	.1779
Hedysarum carnosum TA vs *Hedysarum carnosum* KA	.0905
Temperature 15 °C	
Local species vs imported species	.8933
Local Medics vs imported Medics	.7022
Medics vs *Hedysarums*	.5894
Medicago truncatula TA vs others	.6158
Medicago laciniata vs others	.0001
Hedysarum carnosum TA vs *Hedysarum carnosum* KA	.011

[a]Local species = *Hedysarum carnosum* TA & KA, *Medicago laciniata*, *Medicago polymorpha* TA, and *Medicago truncatula* TA. Imported species = *Medicago polymorpha* Circle Valley, and *Medicago truncatula* Jemalong.

Discussion and Conclusions

Species used in restoration of depleted rangelands in central Tunisia must be able to germinate and establish under adverse conditions of temperature and water stress. Rates of root elongation have been found to be an important aspect of seedling survival on dry sites. Several investigations on root development of several plant species have demonstrated the importance of root development and that marked differences between species occur. Plummer (1943) found marked differences in root elongation between several range species. He found correlations between rate of root development and subsequent establishment. Kasper (1984) found that a soybean genotype with a dominant, rapidly elongating taproot may have a deeper root system and better water availability than a genotype with a weak, slow growing taproot. Total root development prior to the season of drought appears to be directly associated with initial success or failure (Plummer 1943). In addition, development of roots during cold winter months would promote an ecological advantage during the growing season as root systems are already established. Such a mechanism has been shown to be an important variable in competition between a successful annual grass, *Bromus tectorum* L., and a less successful perennial grass *Agropyron spicatum* (Pursh.) Scribn. & Smith (Harris 1967).

The results of this experiment showed a difference among collections in their ability to grow roots under a range of temperatures. The species tested can be classified into three groups. Group A, the local *Medicago truncatula*, and *Medicago laciniata* were collected in areas where the winter temperature is low and showed good growth under the cold temperature treatment. Group B, *Hedysarum carnosum* Tunisian accession and *Hedysarum carnosum* Kairouan accession collected in warmer sites had slow root growth at low temperature, but when temperature was increased their rate of root elongation increased. Group C, the imported commercial strains, *Medicago polymorpha* cv Circle Valley and *Medicago truncatula* var. jemalong showed low root elongation rates. The result correlated with field observations (Ben Ali 1986, Cocks and Ehram 1987) that Australian varieties are adapted to milder areas near the Mediterranean Sea, and when used in cooler sites result, in slow growth and high winter kill. From these results it is very important to focus on sites of origin and screen for species that show potential for revegetation in central Tunisia.

Our results are consistent with the findings of others. The distinct relationship between cold tolerance, low temperature growth, and survival and climate of origin has been shown for white clover (Ollrenshaw and Baker 1981, 1982, and 1983) for perennial grass (Lorenzetti and others 1971), and for *Medicago* species (Cocks and Ehram 1987). Ollrenshaw (1984) found that ecotypes of *Trifolium repens* collected from cold environment are more tolerant to cold temperature and grow better root and shoot materials than species of more temperate regions, and that populations from high altitude are more tolerant than those of low altitude. Lorenzetti and others (1971) have found the same relationship between low temperature growth and the winter temperature at the place of origin from *Lolium perenne*.

In conclusion, the high degree of phenotypic plasticity of *Medicago laciniata* root system could be an adaptive mechanism which permits the species to survive harsh climatic conditions. Its high rate of root elongation and wide adaptations to a range of temperatures constitute an ecological advantage.

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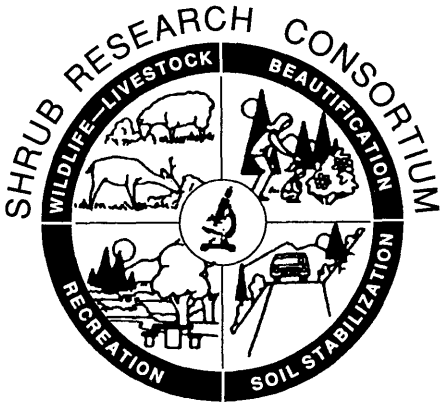
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Field Trip

Research in the Jornada Basin of Southern New Mexico: A Field Tour

Kris Havstad
Reldon Beck

Abstract—During the Ninth Wildland Shrub Symposium in Las Cruces, New Mexico, May 22-24, 1995, a field trip took participants to the southern end of the Jornada del Muerto Basin, an area of intensive research in desert ecology and rangeland management throughout the 20th century. The tour highlighted some of the historical studies in grazing management as well as current interdisciplinary research projects involving dozens of scientists from many institutions. Cooperating institutions and agencies include the USDA Agricultural Research Service, New Mexico State University, the National Science Foundation and the Environmental Protection Agency.

History

The Jornada Basin in southcentral New Mexico is often called the Jornada del Muerto (journey of the dead). It lies to the east of the Rio Grande on a plain 100 m above the river. The San Andres Mountains border it on the east. The plain varies in width from 8 - 50 km and is about 150 km long. The basin is primarily closed with limited external drainage on the west edge.

One can still see remnants of the Camino Real which resulted from Spanish traders, soldiers, and others traveling in the 1500's between Chihuahua City, Mexico, and Santa Fe. The trail was used into the early 1900's. The plain received its "del Muerto" label because of the many hazards along this segment of the trail. The rough terrain along the Rio Grande forced the development of this route across the sandy basin. The 140 km stretch in the Jornada Basin was typically dry and generally required four to five days for a caravan to traverse.

Livestock were introduced into the region during the early part of the 17th century, but grazing was generally limited to the Rio Grande valley and adjacent slopes because of lack of surface water in the surrounding basin. Some water could be found in springs and seeps in the mountains, but supplies were ephemeral. In the late 1800's the first permanent well was dug in the basin which allowed a continuous source of water for livestock. With development of surface water large livestock operations were established. One of the largest was the Detroit and Rio Grande Livestock Company. Around the turn of the century, Mr. Charles T. Turney acquired many of the water rights from the Detroit Company and other ranchers in the area. It was from the land holdings associated with these water rights and the surrounding public domain that eventually the USDA Jornada Experimental Range and the New Mexico State University's Chihuahuan Desert Rangeland Research Center were established.

The USDA's Jornada Experimental Range (JER) was established in 1912 by Presidential Executive Order from Turney's lands (and water rights) and public domain withdrawal. The current holdings are only slightly less than the original 78,297 ha withdrawn at establishment. Elevations range from 1,275 m on the plains to 3,790 m in the San Andres Mountains.

The University's Center was established in 1927 by the U.S. Congress giving public lands to the State of New Mexico for research, educational and demonstrative purposes. Today, the total area within the Center is over 25,500 ha. It is bordered on the west by the Rio Grande at an elevation of 1,220 m and includes Summerford Mountain on the eastern side with an elevation of 1,780 m. The eastern border is shared with the Jornada Experimental Range. On the experimental ranges, annual rainfall is near 24 cm with 53% falling in July through September. Soils vary from unconsolidated alluvium in the mountains, to sandy loams in the plains, to clay in the playas and along the river. Seven different vegetation types are present.

General Features

Vegetation

The Jornada plain is usually classified as semidesert grassland, an ecosystem which covers about 10.5 million ha in southeastern Arizona, southern New Mexico, western Texas, and northern Mexico. The area is within the northern portion of the Chihuahuan Desert (fig. 1). Although called "grassland," the region contains a complex of vegetation types ranging from nearly pure stands of grass, through savanna types with grass interspersed by shrubs or trees, to nearly pure stands of shrubs. The mountains, plains, and drainageways provide a great variety of habitats for plants, and the flora is rich in species. Some 545 species of higher plants have been collected in the area.

The major grass species on sandy soils are black grama (*Bouteloua eriopoda*), mesa dropseed (*Sporobolus flexuosus*), and red threeawn (*Aristida purpurea* var. *longiseta*). Shrubs or shrub-like plants on sandy soils include honey mesquite

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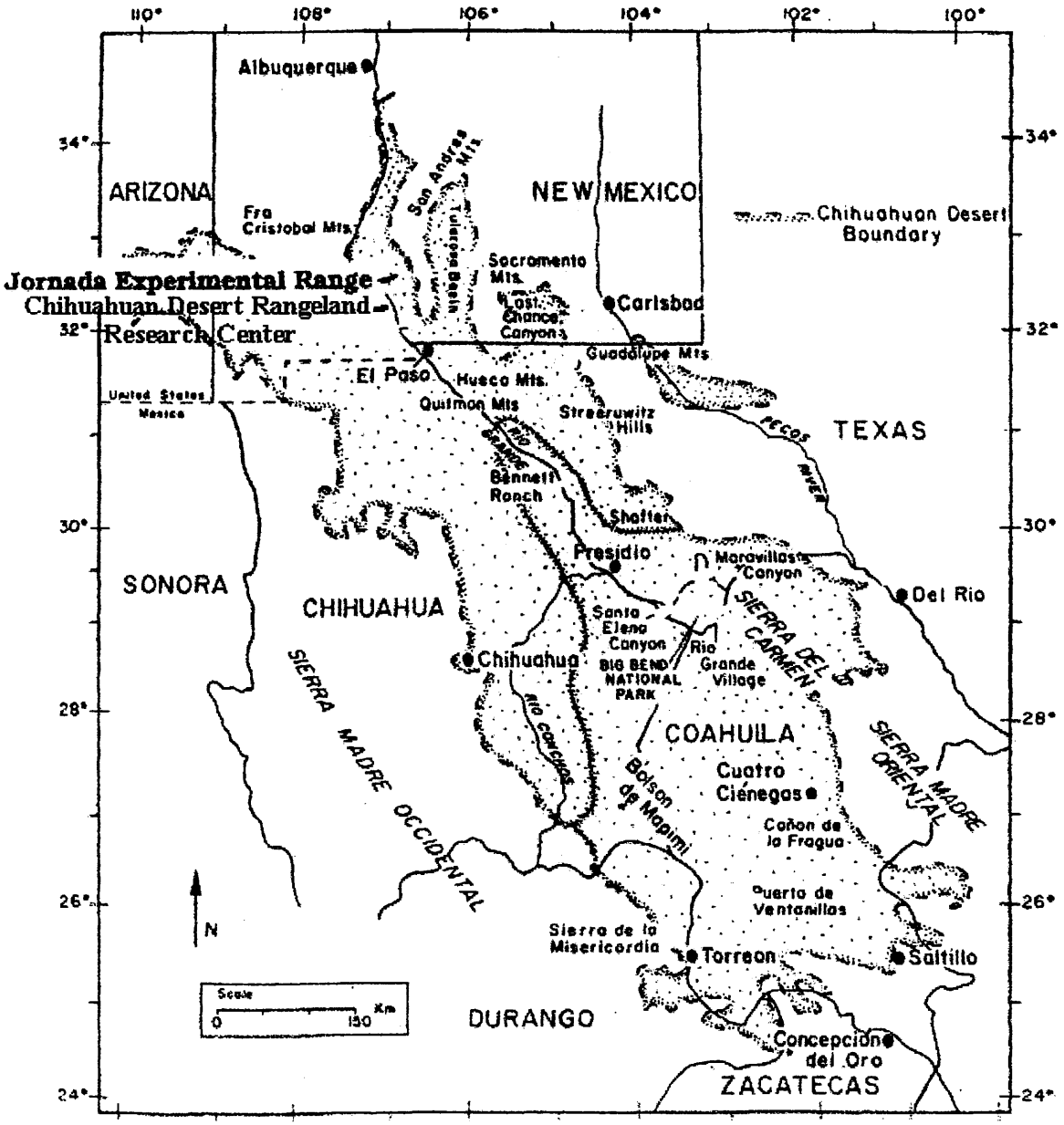

Figure 1—Boundary of the Chihuahuan Desert of North America.

(*Prosopis glandulosa* var. *glandulosa*), fourwing saltbush (*Atriplex canescens*), soaptree yucca (*Yucca elata*), and broom snakeweed (*Gutierrezia sarothrae*). Extensive dunes have developed where mesquite has invaded sandy soils. Low-lying areas with heavier soils, and which receive water from surface runoff, are dominated by tobosa (*Pleuraphis mutica*) and burrograss (*Scleropogon brevifolius*). Tarbush (*Flourensia cernua*) is a frequent dominant of these heavy soils. Slopes with gravelly soils near the mountains are typically dominated by creosotebush (*Larrea tridentata*). In years with favorable winter and spring moisture, many annual grasses and forbs are also abundant across soil types.

Within the mountains, shrub types are mixed. Major dominants include honey mesquite, creosotebush, sotol (*Fouquieria splendens*), ocotillo (*Dasylirion wheeleri*), and whitethorn (*Acacia constricta*). Some areas of scrub woodland are dominated by red-berry juniper (*Juniperus erythrocarpa*) and Mexican pinyon pine (*Pinus cembroides*).

The increase in brush on the Jornada Plain is well documented. A land survey made in 1858 included notes on soils and vegetation. From these notes, the relative abundance of brush types in 1858 was reconstructed. Extent of brush types was also determined from vegetative surveys made on the Jornada Plain in 1915, 1928, and 1963.

In 1858, good grass cover was present on more than 90 percent of the 58,492 ha studied. By 1963, less than 25 percent of the area had good grass cover. Table 1 shows the percentage of area occupied by dense (55 to 100 percent of perennial plant composition) brush cover of the major shrubs at various dates.

Table 1—Shrub increase in areas of the Jornada Basin during a 105 year period.

Vegetation cover[1]	1858	1915	1928	1963
			Percent	
Brush-free	58	25	23	0
Honey mesquite	5	24	22	50
Creosotebush	0	3	5	14
Tarbush	0	2	5	9

[1]Dense cover ≥ 55% of perennial plant composition.

Mesquite is the primary invader on sandy soils. Tarbush has increased on the heavier soils, and creosotebush occupies shallow and gravelly soils. Collectively, the spread of brush has been ubiquitous and rapid. As a result, range carrying capacities have been drastically lowered. Periodic droughts, unmanaged livestock grazing in the 19th century, and brush seed dispersal by humans, livestock, and many different wild species have all contributed to the spread of the shrubs. Brush has increased in permanent livestock exclosures erected during the 1930's demonstrating that brush invades grasslands even in the absence of livestock grazing. Once established, brush effectively monopolizes soil moisture and nutrients, and grass reestablishment is generally very limited without selective control of brush species. However, traditional brush control practices are expensive and frequently only of short-term effectiveness. New technologies are needed, but at present there are few economical management options for controlling continued brush encroachment.

Geology

The ages of geologic material in the Jornada vicinity range from Precambrian granites to Historical eolian and arroyo sediments. The Precambrian rocks are exposed on the east side of the San Andres and Organ Mountains where they have been uplifted thousands of meters by folding and faulting. Covering the Precambrian rocks are Paleozoic marine rocks, predominately limestones, that record shallow seas having spread across the once level Precambrian landscape. The San Andres and Franklin Mountains are mainly composed of these Paleozoic marine rocks.

Mesozoic rocks are less common, indicating uplift in the Las Cruces area until the Cretaceous when seas again spread across the area to deposit sandstones. Many Cretaceous rocks in southern New Mexico, however, are nonmarine and contain paleosols and dinosaur fossils. The Mesozoic ended and the Tertiary was ushered in by a period of mountain building—the Laramide orogeny—documented by bouldery alluvial fan deposits. Much of the Jornada Basin is filled with sediments derived from erosion of adjacent Laramide uplifts.

By middle Tertiary (ca. 30 million years ago), the Jornada region was a place of immense volcanic activity, as volcanism associated with the Organ Mountains produced sequences of igneous rocks over 3 km thick. Since the Dona Ana mountains are chemically and chronologically similar to the Organ Mountains, they are probably part of the same volcanic cauldron.

Following the middle Tertiary volcanism was the beginning of the last chapter of geologic evolution in the Jornada region: tectonic extension. The pulling apart of the crust formed the fault-block mountains in the region, such as the Franklin, San Andres, and Robledo mountains, as well as the intermontane basins between them. Movement continues and the mountains are still rising as testified by displacement of late Holocene alluvial fans along faults on the eastern side of the Organ and San Andres mountains. Many of the playas in the Jornada region have been produced by normal faults.

As the Tertiary ended and the Quaternary began, the ancestral Rio Grande was rapidly filling the Jornada, Mesilla, and Hueco basins with river sediment. At that time, the ancestral river emptied into a large lake, Lake Cabeza de Vaca, in northern Chihuahua. Carried along with the river sediment was datable pumice clasts from the Jemez volcanic center in northern New Mexico. One of these pumice layers has been uncovered west of the JER Headquarters. Around 750,000 years ago, Lake Cabeza de Vaca, like an overly full bathtub, spilled over its rim at El Paso, and northern Mexico was instantly robbed of a huge freshwater lake. Subsequently, the ancestral Rio Grande downcut through its sediments to eventually make the confined river valley present today. When the ancestral Rio Grande entrenched, like a giant drainage ditch, it lowered the regional ground water with it.

Tour

The trip across the Jornada plain included six stops (fig. 2). Stops were chosen to reflect a cross section of ecological and management-oriented research conducted on the approximately 100,000 ha devoted to field experimentation under the stewardship of NMSU and the ARS.

Stop 1. Creosotebush—Effects of Water and Nutrients

Experimental and descriptive studies have shown that in the Chihuahuan Desert, creosotebush growth is regulated as much by nitrogen availability as by water. Field experiments using two patterns of irrigation and one level of nitrogen fertilization were conducted to discern water and nitrogen interactions that control primary production of creosotebush. Irrigation provided as small, frequent events (6 mm/week) caused larger increases in vegetative production and fruit production than large, infrequent events (25 mm/month). Nitrogen fertilization plus small, frequent events resulted in the highest vegetative production and fruit production. These data provide the basis for understanding variation in creosotebush productivity measured over successive years.

Creosotebush production was significantly lower in the second wet year than in the first year of high rainfall. High biomass of annual plants produced during the first wet year provided the carbon inputs (as dead plant roots) that was the energy source for the soil microbiota that immobilized soil N during the second year. In the Chihuahuan Desert creosotebush production is limited by both soil moisture and

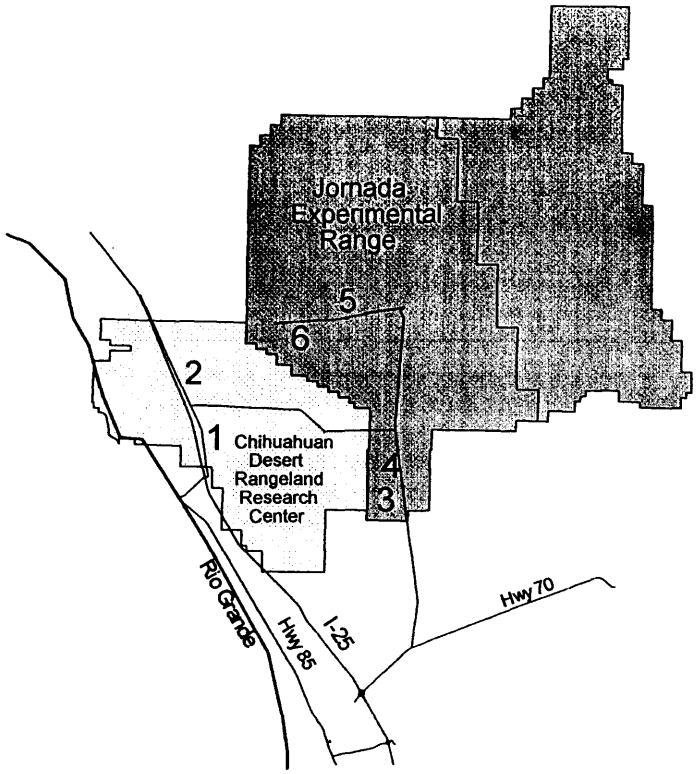

Figure 2—Jornada Basin tour route.

nitrogen availability, and patterns of rainfall appear to be more important than amount as a variable affecting productivity.

Several studies have demonstrated that much of the interplant variability in arthropod populations on creosotebush were related to foliar growth and foliar nitrogen content. Phytophagous sap-sucking insects accounted for most of the arthropods on creosotebush. When shrubs were selected that were judged to have higher foliar nitrogen (based on morphology and extent of below canopy litter layer), those shrubs supported higher insect populations than creosotebushes selected at random. Variations in rainfall patterns as produced by irrigation had little effect on creosotebush insect populations.

Stop 2. Pasture 15 on Chihuahuan Desert Rangeland Research Center

Grazing Study—A grazing study using cattle was initiated in 1967. The purpose of this study was to determine the type of plant response on pastures grazed only in a specific season each year as compared to a pasture grazed continuously yearlong. Annual rainfall is near 235 mm, with 53% falling from July through September. Amount of precipitation varies widely among years and, therefore, herbage production has varied from less than 5 kg/ha in 1994 to over 550 kg/ha in 1986. Because herbage production varies so much among years, there is considerable variation in animal performance, with calf crop averaging 83% and calf production averaging 3.2 kg/ha/yr. Because of the wide variation in rainfall patterns and herbage production, few differences in plant response exist between the two grazing strategies.

Mesquite—Mesquite populations have increased and expanded into neighboring grassland for the last 100 years. Considerable effort has been expended in research and management in learning how to control mesquite populations. Starting in the 1950's and continuing into the 1970's there were many herbicide treatments applied in the Jornada Basin for controlling mesquite. At this site individual plants were sprayed with 2,4,5-T. At that time the mesquite population was less than 125 plants/ha. Cost of the treatment was $2.82/ha. Rootkill of the treatment was 95%. Mesquite populations today in the sprayed area are still less than when it was controlled in 1958 (table 2).

Stop 3. Tarbush Community on the JER

The Jornada Experimental Range is one of 19 sites in the Long-Term Ecological Research (LTER) network, a set of locations for research into long-term and large-scale ecological processes, supported by the National Science Foundation. Ecosystems represented range from Alaskan tundra to Puerto Rican tropical forest, with two sites in Antarctica. The Jornada site represents the most xeric extreme in the network and is a valuable point of comparison for ecological studies done in other grassland and shrubland systems. The extensive history of research on this site (from early USDA work through the years of the International Biological Programme) make this one of the most truly long-term of the LTER sites.

LTER research is planned and carried out by a cooperative group of researchers from various institutions including Duke, Dartmouth, New Mexico State University, and the USDA's Agricultural Research Service. Initiated in 1981, LTER research at this site focused first on the role of soil water and nitrogen in determining patterns of production and dynamics in major plant and consumer species on a topographic gradient from the Dona Ana Mountains to a playa 3 km downslope.

In 1989, research was expanded to the general question of heterogeneity of soil resources (especially water and nitrogen) in a wider range of communities in the Jornada area. Scientists hypothesized that the conversion of semi-desert grassland to shrub-dominated ecosystems has resulted in a more patchy distribution of soil resources, and that the shrubs themselves reinforce this patchiness by positive feedback on resource redistribution (for example, infiltration, erosion, litter deposition). This alteration of resource distribution is suspected to be responsible for the difficulty in reversing the vegetation change.

This stop provided a look at one of the 15 sites currently being monitored—three sites from each of 5 major vegetation

Table 2—Changes in mesquite density, Pasture 15, CDRRC.

Treatment	Number mesquite/ha		
	1982	1993	Percent increase
Sprayed in 1958	44	61	39
Not sprayed	256	323	26

types (black grama grassland, creosotebush stands, mesquite-dominated areas, tarbush flats, and grassy playas). Data from these ecosystems are being used to answer questions about differences in productivity between grassland and shrubland systems, and about the relationship between plant diversity and ecosystem function in these arid lands.

The Jornada is one of a few LTER sites managed explicitly as a collaboration between academic scientists and Federal agency researchers (others include the Central Plains Experimental Range in Colorado, the Coweeta Hydrologic Laboratory in Georgia, and the Andrews Experimental Forest in Oregon). The synergy of this collaboration propels our research effort on the implications of vegetation change in the arid southwest and the ecological basis for sustainable management of dryland systems.

Stop 4. Plant/Animal Interactions

In this arid environment, encroaching shrubs are often chemically-defended. Grazing use of these shrubs is generally influenced by preingestive sensory cues and post ingestive consequences. Our studies of grazing preferences are based on the model outlined in figure 3. We utilize tarbush as the shrub for experimentation based upon this model.

To date, we have learned that tarbush's nutrient composition is similar to alfalfa, although nitrogen availability is less. Digestion studies showed that tarbush added to the diet improved utilization of low quality forages, a response largely due to the high nitrogen concentration of tarbush. Added nitrogen from tarbush also partially alleviated nutritional stress due to dietary intake of poor quality forages, a condition common during drought years. Results of toxicological studies have been variable. Tarbush leaves fed to ewe lambs up to 30% of the diet for 28 days did not appear to cause toxicosis; however, sheep fed 15% tarbush for 120 days (60 days pre- and post-weaning) developed muscular and liver lesions. Lesions observed included apoptosis, or individual cell death, in liver hepatocytes. However, in a subsequent study, 15% tarbush fed to ewes for 120 days did not elicit toxicosis. Work is currently being initiated to develop appropriate assays for isolation of potential toxicant(s).

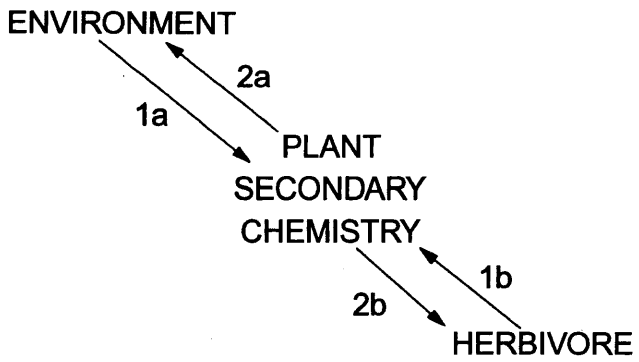

Figure 3—Central role of secondary chemistry of Chihuahuan Desert shrubs in plant-animal-environment interactions. Although plant secondary chemistry is genetically determined and a constitutive component of the plant, it is also plastic. Plant secondary chemistry profile and concentration can be altered by the environment and consumers. Environmental biotic and abiotic factors (phenology, light, water, nutrients, insects, small mammals, microbes, etc.) can modify plant chemistry (1a) and herbivores can modify secondary plant chemistry via induction (1b). Plant secondary chemistry has consequences to the environment and to consumers. Plant secondary chemistry affects the environment by allelopathy, soil/litter accumulation, soil microbe activity, nutrient sequestering, etc. (2a), and plant secondary chemistry affects diet selection, behavior and physiology (learning, postingestive consequences, metabolic effects, toxicities, etc.) of herbivores (2b).

Despite the nutritional value of tarbush, domestic herbivores generally eat tarbush only in limited amounts. Experiments comparing the diets of beef cattle, sheep, goats, camels, guanacos and llamas revealed limited use of tarbush. Sheep and goats exhibit greater use of tarbush, with it constituting between zero and 15% of their diet. Studies using sheep found considerable variation in animal preference for tarbush. Some tarbush plants were readily eaten while others were avoided, and differences in plant palatability were related to leaf surface chemistry. Specific mono- and sesquiterpenes have been identified that allow prediction of whether a tarbush plant will be browsed. Studies directed toward selecting animals exhibiting greater preference for tarbush and identifying factors influencing their diet selection are ongoing.

Several biologically potent compounds in tarbush leaves, including compounds known to have analgesic, herbicidal, insecticidal, nematocidal, neuroactive and neoplastic activity have been identified. Some of these compounds may explain the use of tarbush as a curative for digestive disorders by people in Mexico and more recently in the United States. Additionally, compounds causing apoptosis are of interest to researchers studying the role of individual cell death in embryology, autoimmune diseases and fertility. Researchers from the Jornada Experimental Range are working with researchers at the University of New Mexico Medical School studying apoptosis. We now have an organic chemist exploring the natural products chemistry of tarbush and several other desert plant species.

Stop 5. Natural Revegetation Exclosure

In 1934, Jornada scientists established a one section (256 ha) exclosure along an ecotone between black grama dominated rangeland and mesquite dominated rangeland. Their assumption was that the black grama grassland would become reestablished with livestock exclusion. The entire exclosure today is now dominated by mesquite. Much of the remaining black grama failed to survive the extended drought during the 1950's.

In the early 1930's, scientists at the Jornada Experimental Range were concerned with the spread of mesquite and concomitant wind erosion. As part of their research program, transects were established in mesquite dunelands and on ecotones between grassland and mesquite dunelands. Soil levels were marked on a large number of grid and transect stakes. This farsighted action provided a unique opportunity to quantify soil movement. Soil levels at the

Table 3—Deposition and deflation of soil in 1935 and 1980 at 105 grid stakes on the 259-ha natural revegetation exclosure where soil levels were marked in 1933, and 1980 soil levels at 113 transect stakes on the exclosure on which soil levels were marked in 1935.

Database	Year of measurement	Soil movement category	Number of points	Maximum	Minimum	Mean	Net Loss (–) or Gain (+) (cm)
				---------- cm ----------			
Grid stakes	1935	No change	9				
		Deposition	36	6.0	0	1.1	
		Deflation	60	4.9	0	1.4	–0.4
	1980	Deposition	33	78.3	1.8	23.8	
		Deflation	72	61.9*	0.9	17.4	–4.6*
Transect stakes	1980	Deposition	43	78.6	0.6	2.5	
		Deflation	70	45.1*	0.9	2.1	–3.5*

*Represent minimum values because one stake was completely excavated by wind erosion.
(Adapted from Gibbens and others 1983).

original stakes were remeasured in 1980. Soil movement during the 45 year period shows that mesquite dunelands, while having an appearance of stability, are actually a dynamic, constantly shifting system (table 3).

The magnitude of soil movement within the mesquite dunelands indicates that considerable degradation of the soils as a plant growth medium has occurred. Other studies have identified the soil components lost in suspension as being predominately from the silt and clay fractions as the dunelands are "churned" by wind erosion. Loss of silts and clays would reduce the soil binding properties imparted by these two size fractions, and the remaining fraction would be even more susceptible to wind erosion. In this arid environment, appreciable changes in water holding capacity alone could be a factor causing shifts in vegetation associated with the mesquite dunes and in potential site productivity. Identification of the redistribution and depletion of soil biota within the mesquite dunelands is the object of continuing studies.

Similar to many semiarid lands and deserts, soils in the Jornada region accumulate calcium carbonate (caliche). The older the soil, the more calcium carbonate it accumulates. Leland Gile (retired scientist formerly with the then Soil Conservation Service) and others defined a sequence of carbonate stages related to soil age. Young soils pass from being non-calcareous to having stage I filaments, then stage II nodules, then a stage III plugged horizon, and finally a stage IV horizon composed of a laminar zone formed atop the carbonate plugged horizon. A stage IV carbonate horizon takes about 500,000 years to form in non-gravelly soils, but much less time, about 50,000 years, in gravelly soils. The gravelly soils become cemented faster by carbonate because they have less pore space and less surface area than finer textured soils.

Although caliche horizons are often a barrier to root growth, caliche is permeable to water in most cases. Therefore, caliche horizons have the ability to absorb and store water, and possibly nutrients, and thus play an important role in rangeland vegetation dynamics.

Hundreds of papers have been written about caliche formation, which in the southwestern US is predominately the result of atmospheric additions of calcareous dust and Ca^{2+} dissolved in rain water mediated, in part, by soil microorganisms. Caliche has recently taken on additional importance because of its carbon storage capacity and its isotopic signatures that provide information about vegetation changes in the past.

Although caliche formation is a prominent pedogenic process in semiarid and arid soils, other processes such as chemical weathering, clay mineralogy, water holding capacities, bioturbation, mineral-microbe-root relations, and erosion-sedimentation have major impacts on rangeland vegetation. Many questions involving below-ground mechanisms and their link to the amazing drought tolerance of many wildland shrubs remain to be answered.

Stop 6. Multiple Stressor Experiment

In 1993, an experiment to address empirical tests of the sensitivity of a variety of indicators of ecosystem health as measures of exposure to single and multiple environmental stressors was initiated. The Environmental Protection Agency co-funds this research with the Jornada Experimental Range and the LTER program. The experiment was initiated in August 1993 with the establishment of plots and the collection of baseline data. The experiment was designed to address hypotheses concerning the effects of environmental stressors on ecosystem properties and processes: (1) exposure to more than a single stressor results in simple additive responses and (2) removal of invasive shrubs, such as mesquite, reduces the impact of other stressors on a desert grassland ecosystem. There are a number of sub-hypotheses concerning the effects of stressors on selected populations and ecosystem properties and processes.

To date, the data show some interesting patterns. Small mammals have been affected by shrub removal with some species disappearing on plots where shrubs were removed (wood rats most affected). There has been no change in the ant community as a result of shrub removal. Soil depth varies dramatically at a scale of meters, not 10's of meters, as we originally hypothesized; and there were no obvious patterns of soil depth and distribution of perennial plants.

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Additional information on the research programs in the Jornada Basin can be accessed at three locations on the Internet at:

http://www.nmsu.edu/~jornada
http://atlantic.evsc.virginia.edu/regionalization/jrn.html
http://shamu.psl.nmsu.edu/Jornada.html

These home pages outline current research objectives and bibliographies of prior published research.

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This proceedings contains 50 papers including an overview of shrubland ecosystem dynamics in a changing environment and several papers each on vegetation dynamics, management concerns and options, and plant ecophysiology as well as an account of a Jornada Basin field trip. Contributions emphasize the impact of changing environmental conditions on vegetative composition especially in the Jornada Basin and Chihuahuan Desert but also in other parts of western North America and the world.

Keywords: climate change, environmental change, deserts, desert plants, land management, plant ecology, plant ecophysiology

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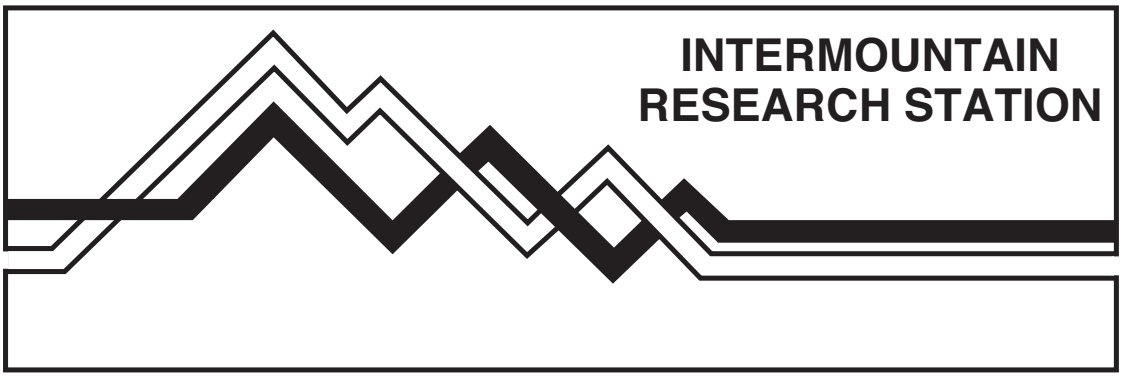

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