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Disturbance and Climate Change in United States/Mexico Borderland Plant Communities:

A State-of-the-Knowledge Review

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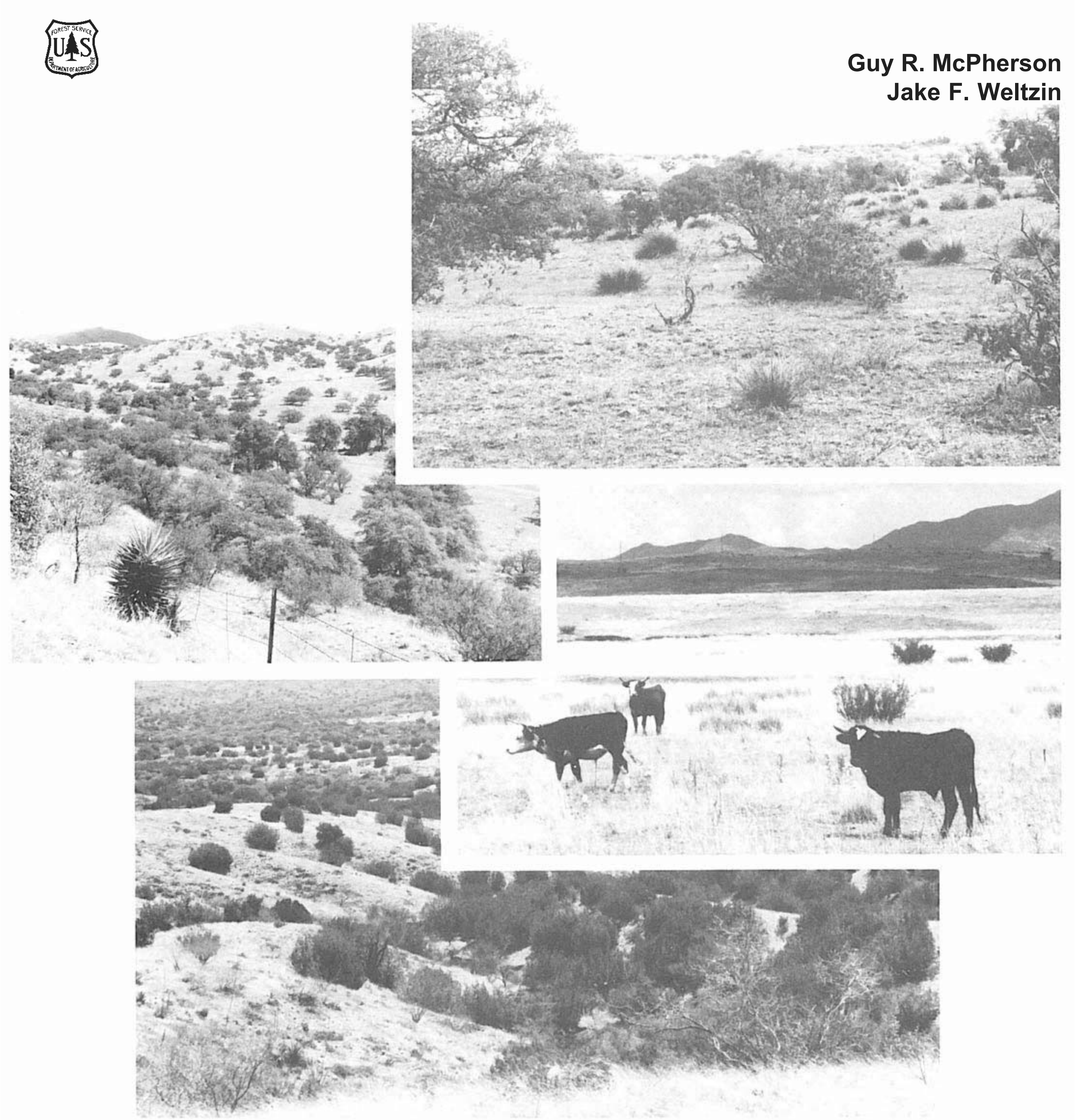

Abstract

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This review evaluates the effects and importance of disturbance and climate change on plant community dynamics in the United States/Mexico borderlands region. Our primary focus is on knowledge of physiognomic-level change in grasslands and woodlands of southeastern Arizona and southwestern New Mexico. Changes in vegetation physiognomy have broad implications for management and land use in the borderlands.

Historically, livestock grazing and fire were the dominant disturbances in borderland ecosystems. Livestock grazing accelerates the rate of establishment and growth of woody plants (notably mesquite) in the borderlands region. However, the current role of livestock grazing in this region may be considerably less important than the historic role. Excluding livestock from grasslands now would not prevent, and may not delay, a substantial increase in woody plant abundance. In general, frequent fires are detrimental to woody plants and beneficial to Lehmann lovegrass. Although fires favor herbaceous plants at the expense of woody plants, woody plant dominance on many sites precludes the deliberate application of fire without first using chemical or mechanical treatments.

Climate change is perhaps the most critical factor facing the current generation of land managers who are concerned about the future condition of borderlands ecosystems. Rising concentrations of CO_2 and other trace gases have the potential to replace grazing and fire suppression as important regulators of vegetation change. Increased atmospheric CO_2 concentrations may contribute to increased abundance of woody plants in borderlands grasslands, particularly if these increases are accompanied by shifts in seasonal precipitation or other climatic factors.

Much of the knowledge garnered about borderlands plant communities is derived from descriptive research such as comparative studies and “natural” experiments. This research has been valuable for documenting changes in vegetation and identifying candidate explanations for observed changes. However, because descriptive research is generally inappropriate for testing hypotheses, we outline and describe a strategy for hypothesis-testing and provide recommendations for future research in the borderlands. Implications for management are also outlined in this paper.

Keywords: Disturbance, climate change, experiments, fire, grazing

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Cover photos: Large areas of hilly terrain are co-dominated by woody plants and grasses in the borderlands region. The relative proportions of these life forms may be altered by changes in disturbance regime or climate *(see top and bottom photos)*; savannas, such as this southwestern oak savanna, may be particularly susceptible to on-going and impending changes in land use and climate *(see left photo)*; livestock grazing represents a large-scale land-use activity in the borderlands region *(see right photo)*. All photos by Weltzin.

Disturbance and Climate Change in United States/Mexico Borderland Plant Communities: A State-of-the-Knowledge Review

Guy R. McPherson and Jake F. Weltzin

Contents

Introduction

This review evaluates the effects and importance of disturbance and climate change on plant communities in the United States/Mexico borderlands region. Our primary focus is physiognomic-level change in grasslands and woodlands of southeastern Arizona and southwestern New Mexico. Disturbance is defined herein as any change in physical or biological factors that ultimately affects the structure and function of plant communities. Natural disturbances include fire, herbivory, and climatic extremes. Anthropogenically-mediated disturbances include effects of livestock grazing, mining, road building, and urbanization. Human activities interrupt some disturbances (such as fire and grazing by native herbivores), and increase the frequency or intensity of others (such as livestock grazing and recreational impacts). Because changes in climatic extremes are themselves disturbances, and because climatic factors interact with disturbances to produce vegetation changes, we also review the role of climate in structuring communities.

Mining, road building, urbanization, fuelwood cutting, and other high-intensity disturbances substantially disrupt ecosystem structure and function, and potentially result in complete loss of native flora and fauna. Impacts may extend well beyond the immediate area of disturbance and may be readily apparent for several decades or centuries. Recognition of the impacts associated with urbanization has contributed to the formation of local groups dedicated to the maintenance of open spaces. Although we acknowledge the dramatic and persistent impacts of high-intensity anthropogenic disturbances, they are not reviewed herein because of their limited spatial extent. Readers interested in human impacts are referred to Bahre (1991).

Regardless of cause, changes in vegetation physiognomy have broad implications for management and land use throughout the world. Life form changes in plant communities affect virtually all resources, including soil, water, wildlife, livestock, fuelwood, and recreation. In addition, changes from herbaceous- to woody plant-dominated communities constitute a potentially important global climate feedback affecting carbon sequestration, non-methane hydrocarbon emissions, and biophysical land surface-atmosphere interactions (albedo, evapotranspiration, surface roughness and boundary layer dynamics) (Archer 1994).

Changing management goals in the United States/Mexico borderlands region have contributed to changes in kinds and extent of disturbances. For example, pre-1900 goals of maximizing livestock production to feed a growing nation have yielded to goals based on multiple uses (many of them non-consumptive) and the maintenance of aesthetic, cultural and historic values. Management practices have changed to reflect these changing goals: livestock grazing is closely regulated and other uses, such as eco-tourism, have increased in importance. Altered management practices have contributed to changes in the type and extent of disturbances, which, in turn, have influenced the structure and function of ecosystems.

Documents mentioned throughout this review, and a recent book (Bahre 1991), provide ample evidence that human and natural disturbances have helped shape the plant communities of the southwestern United States and northwestern Mexico. Since Anglo settlement, vegetation has shifted from native grasses to non-native or woody plants across expansive regions, and other areas have been cleared for settlement (Bahre 1991). These changes have been attributed to altered disturbance regimes, but most of the published literature on the subject of vegetation change is in the form of untested hypotheses, and is therefore controversial. The descriptive nature of historical and paleoecological research, coupled with the complex interactions driving vegetation change, make it extremely unlikely that a consensus will be reached on this subject. Further, retrospective research is incapable of uncovering causal mechanisms of vegetation change (Campbell and others 1991; *sensu* Simberloff 1983).

Consider, for example, relatively recent large-scale changes in the physiognomy of grasslands to woodlands or shrublands that have occurred throughout the world as well as in the borderlands (see Archer and others 1988; Buffington and Herbel 1965; Walker and others 1989). This dramatic change has captivated the scientific community, but mechanisms of vegetation change remain unknown after more than 3 decades of detailed investigation (Archer 1989). Increased woody plant abundance in North American grasslands has been attributed to climate change, reduced fire frequency, increased grazing by cattle, or combinations of these factors (as reviewed by Archer 1994). Hastings and Turner (1965, p. 289) concluded that "climate and cattle have united to produce" increases in the abundance of woody vegetation in former grasslands of southern Arizona. Conversely, Bahre (1991) stated that "probably more time has been spent on massaging the climatic change hypothesis than on any other factor of vegetation change, and yet it remains the least convincing" (p. 105), and "the increase of woody plants in rangelands ... is most likely the result of grazing and fire exclusion" (p. 187).

Regardless of scientific progress toward consensus on mechanisms of past vegetation change, such knowledge would provide little or no predictive power to current and future management of borderlands ecosystems. Even complete understanding of past vegetation changes may not improve our ability to predict future changes. Disturbances that caused past vegetation change (such as livestock grazing, decreased fire frequency, or specific timing of precipitation) may fail to produce similar responses today, because of profound changes in physical and biological environments over the last century. For example, plant communities in the borderlands region now experience:

- increased concentrations of atmospheric greenhouse gases, including CO_2 and methane (Archer and others 1995; Mayeaux and others 1991),
- increased abundance of native woody perennial (Archer 1994; Bahre 1991; Hastings and Turner 1965), and non-native plants (lovegrasses *(Eragrostis* spp.*)*, buffelgrass *(Pennisetum ciliare),* and several herbaceous dicots) (Bahre 1991; McClaran and Van Devender 1995), and
- decreased abundance of some plant and animal species (McClaran and Van Devender 1995).

Further, there are no historic analogs for conditions now widespread. For example, a return to fire regimes characteristic of historic and prehistoric semidesert grasslands, or open stands of ponderosa pine (*Pinus ponderosa*), is unlikely to occur without major cultural inputs.

It is unlikely that we will be able to accurately reconstruct the events and conditions contributing to dramatic vegetation changes since around 1860. Several authors (including Archer 1994; Bahre 1991; Hastings and Turner 1965) reviewed the role and importance of various factors responsible for vegetation changes, but did not reach consensus. Even if a consensus could be reached, pre-1860 events and conditions are unlikely to occur again. Therefore, this review:

- summarizes the literature on past vegetation change, and discusses the likely role and importance of various disturbances in regulating plant communities in the region; and
- specifies experiments necessary to determine causal mechanisms underlying current and future changes in vegetation.

Present State of Knowledge

Historical Research

A large body of literature addresses disturbance-induced vegetation change in the borderlands region. Recent reviews are provided by Archer and Smeins (1991), Bahre (1991), McClaran and Van Devender (1995), and McPherson (1995). Most of the available literature was derived from dendrochronological studies, historical accounts, repeat-photography, or comparative studies. These approaches are valuable for documenting vegetation change and generating hypotheses regarding mechanisms of change. In fact, these studies provided nearly all of the hypotheses regarding vegetation change now being used to direct further research. However, they cannot be used to *test* hypotheses and are characterized by methodological shortcomings, as described below.

Dendrochronology is limited to woody species, usually trees, and is based on correlations between tree age and cross-sectional ring number. Ages of several species of trees, including most oaks (*Quercus* spp.) and alligator juniper (*Juniperus deppeana*), that dominate woodlands and savannas in the borderlands region cannot be determined with current technology (McPherson 1992). First, since these species resprout after top removal, stem age does not necessarily represent individual plant age. Further, current dendrochronological techniques are not able to determine stem age. And finally, tree ages cannot be used to describe the vegetation history of sites currently unoccupied by trees. Similarly, if trees were once present but are currently absent, then reconstructions of stand age structure fail to elucidate this important change.

Historical accounts of vegetation change are usually anecdotal and imprecise, and thus do not allow accurate or precise determination of prehistoric or historic vegetation physiognomy or plant community composition. In addition, historical accounts are often contradictory and colored by fallacies (Bahre 1991). Even rigorous, long-term vegetation monitoring is incapable of revealing causes of vegetation change because of confounding among the many factors that potentially contribute to shifts in species composition (see Wondzell and Ludwig 1995).

Repeat ground photography has a limited and oblique field of view, and historic photographs usually portray anthropogenic manipulation of landscapes; this limits their usefulness for determining changes in plant distribution (Bahre 1991). Repeat aerial photography is limited in that even the earliest photographs (1930) were obtained after broad scale vegetation change had already occurred. Extensive analyses of matched photographs in the borderlands (see Bahre 1991; Gehlbach 1981; Hastings and Turner 1965; Humphrey 1987) have fueled, rather than simplified, the controversy over alternative mechanisms of vegetation change.

Recently, analyses of stable carbon isotopes have been used to assess physiognomic-level vegetation change in the borderlands (McPherson and others 1993). These analyses rely on differential fractionation of carbon isotopes during photosynthesis. Dominant woodland species all possess the C_3 metabolic pathway of photosynthesis. The grassland below the lower woodland boundary, as characterized and described by Brown (1982), is dominated by perennial bunchgrass species, all of which have the C_4 metabolic pathway (Gurevitch 1986). These two metabolic pathways ultimately affect the stable carbon isotope ($^{13}C/^{12}C$) ratio of living plant tissue, which is retained and incorporated into soil organic material after plant mortality and decomposition.

None of these techniques can be used to assess species-level changes in plant distribution, except at the limits of a species' range. Furthermore, their utility is limited to studying past vegetation changes, which may not be useful for predicting future changes. Finally, the use of different techniques may produce different interpretations of the same phenomena, as illustrated by the following example:

Reports of past changes in the oak woodland/semidesert grassland boundary ecotone are varied. Paleoecological data suggest that oak woodlands have shifted upslope in concert with warmer and drier conditions since the Pleistocene. This interpretation is consistent with upslope movement of most woody species in the last 40,000 years (Betancourt and others 1990). On a more contemporary temporal scale, Hastings and Turner (1965) used repeat ground photography to conclude that the oak woodland/semidesert grassland boundary moved upslope over the last century. In contrast, Bahre (1991) concluded that the distribution of oak woodlands has been stable since the 1870s. Finally, recent research based on stable carbon isotope technology and radiocarbon dating indicates that trees at the woodland/grassland boundary are recent inhabitants of former grasslands, which suggests that oak woodlands have shifted downslope into semidesert grasslands (McClaran and McPherson 1995; McPherson and others 1993). The latter finding matches Leopold's (1924) interpretation of downslope movement of oaks. Thus, boundaries between oak woodlands and adjacent semidesert grasslands have been variously reported as shifting upslope, remaining static, or shifting downslope.

Much of the knowledge garnered about borderlands plant communities is derived from descriptive research, such as comparative studies and "natural" experiments (*sensu* Diamond 1986). The commonly-cited mechanisms of past vegetation change in this region that implicate livestock grazing, altered fire frequency, and directional climatic change are based largely on descriptive research. Ironically, these studies allow only inference of mechanism, and as such are poorly suited for determining underlying mechanisms or causes of patterns (Keddy 1989). Thus, these studies are critically important first steps in the process of scientific research: they help identify hypotheses based on observations and pattern. A second step in the scientific process involves elucidation of driving variables, or underlying mechanisms, through experimentation. The following sections summarize the results of research conducted to date. The final sections outline experiments that can be used to test the hypotheses generated by these studies.

Herbivory

Livestock

Widespread increases in cover or density of woody plants coincident with the development of the livestock industry led many authors (reviewed by Archer 1994) to conclude that the activities of grazing livestock have been the ultimate cause of increased woody plant dominance in former grasslands throughout the world, including the borderlands region. Livestock grazing potentially increases the probability of woody plant recruitment in several ways (Archer 1994):

Livestock effectively disperse seeds of woody plants.

Removal of herbaceous biomass may increase light incident to the soil surface, and thus increase germination and establishment of woody seedlings.

Reductions in grass leaf area with resultant reductions in root activity and biomass can:

- increase surficial soil moisture and thus enhance establishment and growth of shallow-rooted woody species;
- increase the amount of water percolating to deeper soil layers, thereby benefiting established woody species with deep root systems;
- increase nutrient availability to woody plants; and
- release suppressed populations of woody plants.

Grazing decreases basal area, increases mortality rates, and decreases seed production and seedling establishment of palatable grasses. Grazing may also increase susceptibility of grasses to other stresses, such as drought. Together, these factors increase rates of above- and belowground gap formation and thus increase area available for woody plant seedling establishment, especially in post-drought periods.

Grazing-induced shifts in herbaceous species composition may result in herbaceous communities less effective at competitively excluding woody plants or limiting their growth and seed production.

Reductions in fine fuel biomass and continuity reduce fire frequency and intensity. Absence of fires accelerates shifts from grassland to woodland.

Woody species are often unpalatable relative to grasses and forbs and are thus not browsed with sufficient frequency or severity to limit their recruitment.

Reductions in soil fertility and alterations in physicochemical properties occur with loss of vegetative cover and erosion, thus favoring N_2-fixing woody plants such as mesquite (*Prosopis* spp.) and acacia (*Acacia* spp.), and shrubs tolerant of low nutrient conditions.

Systematic eradication of prairie dogs, with the purpose of increasing herbaceous biomass for livestock consumption, may have removed a significant barrier to woody plant recruitment on many southwestern landscapes.

The net effect of livestock grazing is selection for long-lived, unpalatable plants at the expense of short-lived palatable plants. In the borderlands region, grazing favors recruitment and growth of woody plants and unpalatable or grazing-resistant herbs. Species likely to increase or decrease with livestock grazing are highly site specific. Range site guides and soil surveys provided by the Natural Resource Conservation Service (NRCS) (formerly Soil Conservation Service) are excellent sources of information regarding the response of individual species to livestock grazing. Unfortunately, these information sources implicitly assume that reducing or eliminating livestock grazing will precipitate vegetation changes similar to, but in the opposite direction of, grazing-induced changes in community structure. This "Clementsian" model of vegetation change is clearly inappropriate for semiarid plant communities, which rarely progress toward a stable state in a linear, predictable manner (Westoby and others 1989).

Livestock grazing accelerates the rate of establishment and growth of woody plants (notably mesquite) in the borderlands region (Archer and Smeins 1991). However, the current role of livestock grazing in this region may be considerably less important than the historic role. Excluding livestock from grasslands now is politically infeasible and it would not prevent, and may not delay, a substantial increase in woody plant abundance, as evidenced by numerous exclosure studies in the western United States (Brady and others 1989; Brown 1950; Gardner 1951; Glendening 1952; Hennessey and others 1983; Roundy and Jordan 1988; Smith and Schmutz 1975; Wright 1982). Many grasslands in the borderlands have apparently crossed an ecological threshold to stable domination by woody plants (Archer 1989). Furthermore, livestock grazing is not necessary for rapid spread of non-native grasses (Anable and others 1992; McClaran and Anable 1992). Thus, although livestock grazing (particularly in combination with other factors) played an important role in vegetation change shortly after Anglo settlement, excluding livestock from most sites now will have little or no impact on abundance of woody plants or non-native herbs during the next several decades.

Native Vertebrates

Native herbivores may affect plant communities to a greater extent than livestock. Relaxation of native herbivore pressure may contribute to enhanced recruitment of woody plants at local to regional scales. Browsing mammals can maintain grasslands or savannas or convert woodlands into more open systems (see Belsky 1984; Sinclair and Norton-Griffiths 1979; Yeaton 1988). In the southwestern United States, exclusion of kangaroo rats (*Dipodomys* spp.) contributes to increased cover of tall grasses (Brown and Heske 1990); prairie dogs (*Cynomys* spp.) may limit recruitment of woody plants (Weltzin 1990). Prairie dogs were eliminated from the borderlands around the turn of the century; this may have facilitated a transition from grassland to mesquite-dominated woodland (Weltzin and others 1991). Reintroduction of these native herbivores, which is being considered throughout western North America, may reduce density and cover of woody plants.

Native vertebrates kill Emory oak (*Q. emoryi*) seedlings primarily during autumn and winter months (Germaine and McPherson 1999). Temporal and spatial variability in herbivory (Germaine and McPherson 1999; McPherson 1993; Peck and McPherson 1994), a possible result of variable population dynamics of different animal species, doubtless contribute to the variability of native herbivore mortality vectors.

Invertebrates

Invertebrate herbivory is a potentially important source of seedling mortality that is commonly overlooked in field studies of semi-arid woody plant establishment (Allen-Diaz and Bartolome 1992; Borchert and others 1989; Brown and Archer 1989; Callaway 1992; Davis and others 1991; Hall and others 1992; Neilson and Wullstein 1983; Williams and others 1991; but see Adams and others 1992). For example, invertebrate herbivory is a common source of mortality in low-elevation oaks of southern Arizona (McPherson 1993; Peck and McPherson 1994), where invertebrates defoliate seedlings primarily during the summer (Germaine and McPherson 1999; Peck and McPherson 1994). Similarly, mesh exclosures over seedlings increased summer survival of blue oak (*Quercus douglasii*) and valley oak (*Q. lobata*) in California (Adams and others 1992). However, effects of exclosures on invertebrate herbivory and water stress are difficult to separate because exclosures create shade that may reduce water stress; shade is critical for establishment *of Q. douglasii* (Callaway 1992).

High rates of woody plant recruitment may occur in some systems even when invertebrates are not excluded and herb interference is presumably high. McPherson and others (1993) demonstrated that Emory oak trees have recently encroached into former grasslands in southern Arizona with herbs and herbivores present, and Turner (1990) documented a dramatic increase in mesquite density at a Sonoran Desert site inaccessible to livestock. These and other similar studies investigated the net outcome of various mortality factors interacting on a site and clearly demonstrated that Emory oak and mesquite, like many other woody plants throughout the world, have overcome numerous constraints on establishment. This suggests that abiotic constraints are more important than biotic constraints on woody plant establishment. Post-Pleistocene patterns of woody plant establishment in the Chihuahuan Desert support the hypothesis of strong abiotic control over vegetation physiognomy (Neilson 1986). At more local scales, biotic and edaphic factors and disturbance assume increased importance in determining vegetation patterns (Archer and others 1995; Prentice 1986).

Fire

Fire has long been a pervasive and powerful force structuring plant communities of the borderlands region. Kimmins (1987) suggested that fire was as important as precipitation in controlling ecosystem structure and function. The frequency, season, and behavior of fires shaped plant communities, and vice versa; as such, the long-term natural fire regime was probably more a consequence than a cause of vegetation patterns (Clark 1990). Fire was not external to, but rather a key component of, community organization and development.

Perhaps nowhere is the role of fire more widely acknowledged than in grasslands. It has been hypothesized that North American grasslands were a product of fires repeatedly set by aborigines (Sauer 1944; Stewart 1951). More contemporary views focus on the interactive role of fire and factors such as topography, soil, insects, rodents, lagomorphs, and herbaceous plants as constraints on woody plant establishment in grasslands (see Grover and Musick 1990; Wright and Bailey 1982). There is general agreement that fire is necessary, though usually not sufficient, to control the abundance of woody plants and maintain most grasslands. In the absence of periodic fires, many grasslands are replaced by woodlands. Exceptions to this general pattern appear to be associated with topo-edaphic constraints on woody plant establishment (Archer 1994; Loomis 1989; McAuliffe 1994; McPherson 1997).

Fire was historically prevalent in most grasslands and woodlands in the borderlands region. Humphrey (1958) reviewed historical accounts of frequent fires dating to 1528, and concluded that fire was critical to the maintenance of grasslands in this region. Bahre (1985) agreed with this assessment, but concluded that fire size and frequency have been greatly reduced in the last 130 years. Pre-1880 fires were extensive, sometimes covering hundreds of square miles (Bahre 1985; Humphrey 1949). Contemporary fires occur much less frequently and are limited in extent compared to pre-1880 fires. Considerable evidence suggests that widespread livestock grazing reduced fine fuel, and therefore fire frequency, in the southwestern United States after 1880. Historical accounts (Bahre 1985) and direct evidence of reduced fire frequency in pine forests (Savage and Swetnam 1990; Swetnam 1990) document reduced incidence of fires concomitant with the expansion of the livestock industry. In fact, forest administrators encouraged overgrazing to reduce fire hazard and promote tree growth (Leopold 1924).

Despite these accounts, prehistoric fire frequencies are difficult to determine for grasslands of the borderlands region because of the absence of fire-scarred trees (Wright and Bailey 1982). Therefore, historical accounts and indirect evidence are used to estimate pre-historic fire frequency. Although historical accounts indicate that fires were relatively common, they offer little precision for estimates of frequency or extent. For example, fires were noted by early settlers or newspaper reporters only if they were large or particularly destructive; no comprehensive records were maintained until well into the 20th century. However, several lines of indirect evidence suggest that fires occurred at least every 10 years.

Historical accounts agree that shrubs were inconspicuous in grasslands of the borderlands region before 1880, which suggests that fires, or other constraints, occurred frequently enough to prevent widespread shrub recruitment. Most shrubs in the region are susceptible to fire, at least as seedlings (Bock and Bock 1992; Cable 1967; Cox and others 1993; Glendening and Paulsen 1955; Humphrey 1949; Reynolds and Bohning 1956; Schmutz and others 1985; Wright and others 1976). For example, velvet mesquite (*Prosopis velutina*) plants usually do not resprout following fire until stems are larger than 1 cm in diameter (Glendening and Paulsen 1955) or over 3 years old (Wright and others 1976).

Many woody species do not produce seeds until they are at least 10 years old (Chew and Chew 1965; Humphrey 1958; Martin 1975).

Seeds on the soil surface are easily killed by fire (Cox and others 1993).

Extrapolation from ponderosa pine forests, where fires burned through grassy understories every 2 to 10 years, suggests that grasslands burned at similar frequencies (McPherson 1995; Wright and Bailey 1982).

Thus, a fire frequency of 7 years (Schmutz and others 1985) to 10 years (Griffiths 1910; Leopold 1924; Wright and Bailey 1982) could have maintained relatively shrub-free grasslands in the absence of livestock grazing; more frequent fires are necessary to maintain grasslands in the presence of livestock grazing. The plausibility of this explanation must be balanced with the realization that it relies heavily on indirect evidence. For example, alternate hypotheses not excluded by fire research include topo-edaphic constraints on shrub establishment (McAuliffe

1994), vertebrate and invertebrate herbivory (Germaine and McPherson 1999; McPherson 1993; Peck and McPherson 1994), and seasonality of precipitation (Neilson 1986). On-going research in gallery forests adjacent to grasslands will no doubt provide additional indirect evidence for relatively frequent prehistoric fires in grasslands.

It is virtually certain that fires occur less frequently today than they did before Anglo settlement (Bahre 1995). Given the magnitude of other changes that occurred during this settlement period, we may never know what changes in structure and function resulted directly from this change in fire frequency. Understanding factors that contribute to fire occurrence is central to interpreting ecosystem response to fire.

Three conditions must be met for fires to spread: an ignition source must be present, there must be adequate fine fuel (fuel smaller than 0.5 cm in diameter), and the fuel must be dry enough to burn. In grasslands and low-elevation woodlands of the borderlands region, ample ignition sources are provided by dry lightning storms that signal the beginning of the southwestern monsoon in late June or early July. Additional ignitions probably were provided by Native American Indians as an aid to their hunting activities (Bahre 1985; Dobyns 1981). With adequate rainfall and no livestock grazing, there is sufficient biomass and continuity of fine fuel to support fire spread in most borderlands grasslands. After fire, grasses generally recover to pre-burn levels of abundance within 3 years (Cable 1967; Wright and Bailey 1982). An extended hot, dry period occurs virtually every year in the borderlands region, in late spring. Very dry fine fuels result from this weather pattern. Thus, conditions conducive to fire ignition and spread occurred frequently in grasslands and woodlands of the borderlands region before the advent of widespread livestock grazing. Currently, inadequate fine fuel is the most common constraint on fire spread in semidesert grasslands of the borderlands region (McPherson 1995).

Although fire is a potentially important force shaping plant communities, no two fires produce identical responses. Response to fire varies widely between and within species, and is affected by fire behavior and post-fire physical and biological conditions. Fire behavior (size, intensity, and rate of spread) is influenced by:

- physical factors such as fuel conditions (moisture, total combustible material, and continuity), weather conditions (wind, temperature, and relative humidity), and topography (slope and aspect), and
- biological factors such as plant morphology and physiology and community composition.

A comprehensive review of the effects of fire on physical environments and individual plants is beyond the scope of this paper, and is provided by Krammes (1990), McPherson (1995), and Steuter and McPherson (1995). We focus on the response of life forms to fire in the region's grasslands and woodlands.

In general, response of the semidesert grassland to fire is much more dependent on the frequency and season of fire than fire area and intensity. For example, post-fire production is not correlated with fire intensity (Roberts and others 1988). Despite the widely-recognized importance of fire frequency on community structure and function, this aspect of fire ecology has been largely ignored in the borderlands region (but see Robinett 1994).

The impact of a single fire on plant communities has been documented with comparative studies. Wright and Bailey (1982) and McPherson (1995) provided comprehensive reviews of this literature, which is summarized here. Plants are most susceptible to damage from fires when they are actively growing, but are relatively tolerant of fire when dormant. Most perennial plants are susceptible to high mortality from early-summer fires, when growth rates are increasing rates (Cable 1965, 1967, 1973). In contrast, spring, fall, and winter fires produce significant mortality only in the few herbaceous plants, such as plains lovegrass (*Eragrostis intermedia*), and forbs that initiate growth during the cool season. Thus, effects of early-summer fires are more obvious and longer lasting than effects during other seasons (Glendening and Paulsen 1955; Martin 1983; Pase 1971; Tschirley and Martin 1961). For example, November fires produce virtually no reduction in cover and density of velvet mesquite, but June fires can have substantial impact. Shrubs associated with many borderlands grasslands generally resprout following fire, and some readily establish from seed. Resprouting species are well adapted to maintaining their presence when the interval between fires is less than 20 years (Cable 1965, 1973).

The response of grass to fire is variable and generally less conspicuous than the response of shrubs. However, production of big sacaton (*Sporobolus wrightii*) and buffelgrass (*Pennisetum ciliare*) are slightly higher following fires in summer than in fall or winter (Cox and others 1990). It has recently been suggested that long-term abundance of plains lovegrass is fire dependent (Bock and others 1995). Many herbs are easily killed by fires, but may establish at high densities from seed within 1 to 2 years after fire (Bock and Bock 1990; Bock and others 1976). Winter fires typically kill herbs that germinate in autumn, such as annual broomweed (*Xanthocephalum dracunculoides*), but do not harm, and may even favor, herbs that germinate in early spring, such as annual sunflower (*Helianthus annuus*).

Within the last 130 years, cattle grazing has reduced biomass enough to limit fire spread during most years. However, the number of cattle grazing southwestern ranges has declined in the last few decades (Allen 1992), and this trend is expected to continue for the foreseeable future (McClaran and others 1992). Exotic species such as Boer lovegrass (*Eragrostis chloromelas*), buffelgrass (*Pennisetum ciliare*), and Lehmann lovegrass (*Eragrostis lehmanniana*) produce more fine fuel than native species (Cable 1971; Cox and others 1984). This suggests that the recent, and continuing spread of these species may contribute to increased fire frequency and spread (see Anable and others 1992; Cox and others 1988; Cox and Ruyle 1986; Rogers and Vint 1987). At least one of these species (Lehmann lovegrass, the most common introduced species) increases after fire (Ruyle and others 1988; Sumrall and others 1991), suggesting that a positive feedback pattern may develop (Anable and others 1992). Therefore, decreased cattle stocking rates coupled with the introduction of exotic grasses could result in more frequent, widespread fires than occurred over the last century. Alternatively, the fragmented nature of semidesert grasslands and more efficient and effective fire suppression activities may constrain the frequency and extent of contemporary and future fires.

Further evidence of land-use impacts on fire frequency is found in cross-border comparisons of land use, fire frequency, and vegetation structure (Bahre 1991; Bahre and Bradbury 1978; Chou and others 1993; Minnich 1983; Minnich and Bahre 1995; Villanueva-Diaz and McPherson 1995). Increased fire frequency in northern Mexico compared to the southwestern United States has contributed to the maintenance of grasslands and even-aged forests. However, structure of chaparral vegetation appears little changed by differences in fire frequency.

The long-term absence of fire may produce dramatic changes in community structure and function, particularly if soils do not limit shrub establishment (Burgess 1995; McAuliffe 1994). In the absence of fire, grasslands of the borderlands region may develop dense woody canopies that significantly reduce herbaceous production. This lack of fine fuel reduces fire intensity and frequency, and the community changes from grassland to shrubland (Archer 1989; Brown 1982). Crossing this threshold from grassland to shrubland has serious implications for land management (Archer 1989; Westoby and others 1989). Once a site is dominated by woody plants, fine fuel is too scarce and discontinuous to produce fires of sufficient intensity to kill woody plants. Thus, fire alone cannot return the site to its earlier composition, and barring significant cultural inputs, such as herbicides or mechanical shrub control, woody plants become permanent occupants of the site.

In summary, fire intervals in semi-desert grasslands averaged about 10 years prior to Anglo settlement. Over the last 130 years, fire regimes have changed considerably. Due to changes in biological, political, and managerial factors and activities, most sites have not burned since settlement, and virtually none have burned at historic frequencies. Currently, use of fire as a management tool is restricted to areas that have sufficient fine fuel to support fire spread. Conversion of woodland to grassland can not be accomplished with fire alone; chemical or mechanical manipulation generally must precede prescribed fires.

Climatic Factors

Climate is naturally variable, particularly in arid and semiarid regions. This variability exerts considerable control over structure and function of ecosystems in the borderlands region, with impacts that may be similar to those caused by disturbances such as herbivory or fire. For example, drought may contribute to reductions in cover and productivity of grasses in a manner similar to livestock grazing. Mortality or top kill of woody plants caused by drought or frost may have the same effects as fire. Climate change has the potential to replace grazing and fire as an important regulator of vegetation change (Weltzin and McPherson 1995). Therefore, climatic factors are discussed within the context of their impacts on borderlands ecosystems.

Research on climate effects on vegetation in the borderlands region has been scarce. Some authors attribute this to the absence of convincing evidence for directional regional climate change within the last 150 years (Bahre 1991; Bahre and Shelton 1993; Cooke and Reeves 1976). Most research on climate and vegetation has been correlative, and as such has limited predictive or explanatory power. In addition, research has focused on shifts in the distribution of communities that have resulted from climate change (Neilson 1986). Yet all available evidence indicates that species respond individualistically, not as communities, to changes in climate (see Davis 1985; Peters and Darling 1985; Van Devender and Spaulding 1979). Finally, climate-vegetation correlations have only been demonstrated at a resolution scale of thousands of years, too coarse to be useful to ecosystem managers.

Drought is one of the principal factors limiting seedling establishment (Osmond and others 1987) and forest productivity on a world-wide basis (Schulze and others 1987). Moisture-controlled differences in recruitment and establishment form an important control on vegetation physiognomy and pattern (see Bowman and Panton 1993; Cornelius and others 1991; Neilson and Wullstein 1983). For example, the distribution and extent of some oak-dominated woodlands and savannas are thought to be controlled primarily by gradients in soil available moisture (Griffin 1977; Pigott and Pigott 1993; Weltzin and McPherson 1999).

A few studies of climate change are exceptional in their fine taxonomic resolution and spatial scale (Neilson 1986; Neilson and Wullstein 1983; Wondzell and Ludwig 1995). However, these efforts are correlative and therefore cannot distinguish between the many confounding factors associated with vegetation change. Wondzell and Ludwig (1995) suggest that experiments should be used to differentiate between the many climate-related hypotheses forwarded to explain changes in vegetation.

Precipitation, and its attendant effects on plant-available moisture (Solbrig 1991), is often considered the climatic factor that most constrains woody plant establishment in grasslands and savannas (Skarpe 1992). There is no evidence of a single, directional trend in precipitation amount or seasonal distribution in the borderlands region since 1870 (Bahre and Shelton 1993). However, extreme events may be more important than shifts in means (Archer 1994; Katz and Brown 1992). Thus, episodic climatic events in the borderlands may mask, confound, reinforce, or negate changes in vegetation distribution ostensibly attributed to changes in mean climatic condition. For example, periodic droughts can be critically limiting to woody plant establishment in grasslands (Archer 1994; Wright and Bailey 1982). Marshall (1957) observed considerable top kill of low-elevation oak trees at the end of a severe drought in the 1950s; this event was recorded in the photographic collection of Hastings and Turner (1965). On the other hand, extended periods of above-average precipitation may facilitate woody plant recruitment (McPherson and Wright 1990; Turner 1990; Weltzin and McPherson in press); once established, these woody plants may persist for several decades regardless of climatic conditions.

Community boundaries in the borderlands region occur across wide ranges of elevational limits. For example, the oak woodland/semidesert grassland boundary occurs between 1,200 and 1,800 m (Brown 1982). This fact, coupled with the ability of woody plants to establish at locations beyond current boundaries during some years for example, *Quercus emoryi* below lower tree line (McPherson 1993; McPherson and others 1993; Peck and McPherson 1994; Weltzin and McPherson 1999; Weltzin and McPherson in press), suggests that temperature alone does not constrain woody plant seedling establishment. However, interactive effects of temperature and soil water balance are probably critical to seedling establishment. Further, meso-climatic, edaphic, and geomorphic factors doubtless interact to constrain woody plant establishment to a greater extent than any single factor.

Potential Effects of Future Climate Change

Recent scientific consensus is that the activities of humans, especially since the beginning of the industrial revolution, have contributed to increased greenhouse gas concentrations (Keeling and others 1989; Neftel and others 1985; Trabalka and others 1985) and increased global temperatures (Jones 1993; Karl and others 1993; Nasrallah and Balling 1993a, 1993b). Further, there is considerable evidence predicting rapid increases in greenhouse gas concentrations, mean global temperatures, and climatic variability within the next 50 years (Houghton and others 1990, 1992).

Changes in climate are important to resource managers because:

- directional change has occurred, and is virtually certain to continue,
- previous and potential impacts on vegetation will be profound,
- effects will occur over larger areas, and have potentially greater impacts than changes in management practices, and
- the influence of management practices on vegetation will be difficult to predict or interpret without explicit consideration of relatively rapid climate change.

Accurate prediction of ecosystem response to climatic change will allow proactive resource management. Conversely, if managers are unaware of potential and ongoing changes in climatic conditions and their associated effects on ecosystems, efforts to effectively manage those ecosystems could be severely handicapped. See Management Implications section below.

Directional climatic change is often cited as an important factor affecting recent and future redistribution of vegetation types (Hastings and Turner 1965; Mayeux and others 1991; Neilson 1986). Climate change will likely affect competitive interactions between species coexisting under current equilibrium conditions (Ehleringer and others 1991). Changes in interactions between plant species may be manifested at the community level of ecosystem organization, and vegetation distribution may be affected on regional scales (Emanuel and others 1985; Melillo and others 1993; Neilson 1993; Neilson and others 1989; Schlesinger and others 1990). For example, on-going and predicted changes in global climates may increase the susceptibility of the world's grasslands to increases in woody plant abundance (Emanuel and others 1985). Conversely, vegetation communities may shift upslope, with grasslands expanding into woodlands (Bolin and others 1986).

Because of the spatial and temporal scales involved, scientific understanding of climate change effects on ecosystems is limited. Neilson and Wullstein (1983) pointed out that an actual cause-effect relationship between climatic change and biogeographic dynamics has rarely been demonstrated. Further, results of empirical studies that indicate North American savannas and grasslands have recently converted to woodland (Archer and others 1988; McPherson and others 1993; Steuter and others 1990) are contrary to those expected from changes in global climate alone. Global warming and drying since the Pleistocene has generally caused woody plant species to shift upslope (Betancourt and others 1990). However, changes in climate, with attendant effects on vegetation, are almost certain to occur on local, regional, or global scales (Houghton and others 1990, 1992, 1995).

As might be expected, climate change has great potential to change the physiognomy of many borderlands landscapes over a few decades. Unfortunately, the potential for future vegetation change in this region has been largely ignored, with the exception of general circulation models too coarse-scaled to be useful for management applications. Rather, research to date has focused on historic and geologic shifts in vegetation distribution (see Betancourt and others 1990; Schlesinger and others 1990; Van Devender and Spaulding 1979). Although these studies provide a context for understanding current ecosystem structure, they have limited utility for current and near-future vegetation management because of:

- incompatible temporal scales (millennial vs. annual and decadal information needed by managers),
- non-analogous conditions (changes in fire frequency, grazing intensity, and atmospheric conditions), and
- their inability to define or clarify mechanisms responsible for observed patterns.

Therefore, the following sections describe predicted climate changes, and possible subsequent effects on vegetation and vegetation distribution. Since there have been no investigations of potential impacts of extreme climatic events on vegetation in this region, our discussion will necessarily focus on directional change rather than extreme events.

Global and Regional Climate Change

Since the beginning of the 19th century, fossil fuel consumption and agricultural conversion have increased atmospheric carbon dioxide concentrations (CO_2) about 27 percent (Keeling and others 1989; Neftel and others 1985) and are expected to cause CO_2 to double by the mid- to late-21st century (Trabalka and others 1985). Atmospheric mixing is sufficient to ensure that global measurements of atmospheric CO_2 reflect local increases. Increases in atmospheric CO_2 will continue to cause global- and regional-scale changes in environmental conditions and climate (Jones 1993; Karl and others 1993; Nasrallah and Balling 1993a, 1993b).

Increases in atmospheric CO_2 are expected to produce an increase in mean global surface temperatures of between 1.5 °C and 4.5 °C, with a best guess of 2.5 °C in the light of current knowledge (Houghton and others 1992, 1995; Mitchell and others 1990). CO_2-induced changes in the amount and distribution (or seasonality) of precipitation have also been predicted (Houghton and others 1990, 1992, 1995). General circulation models for central North America predict precipitation increases of 0 to 15 percent in winter and decreases of 5-10% in summer. Perhaps more importantly, summer soil moisture may decrease by 15 to 20 percent (Mitchell and others 1990).

Regional shifts in precipitation seasonality have been linked to global warming and cooling trends (Neilson and Wullstein 1983). However, there is considerable uncertainty about the direction and magnitude of future shifts in precipitation distribution, especially on a regional basis. For example, although Manabe and Wetherald (1986) predicted a decrease in summer soil moisture, Schlesinger and Mitchell (1987) suggested that summer precipitation in desert regions may increase. Finally, increased atmospheric CO_2 concentrations are expected to increase the severity and frequency of droughts in North America (Balling and others 1992; Idso and Balling 1992; Manabe and Wetherald 1986).

The potential temporal and spatial magnitude of anthropogenically-induced changes in climate is debated (see Lindzen 1993). These changes may not be directional. Changes in climate may result in increased frequency of extreme climatic events (Katz and Brown 1992; Wigley 1985). Also, climate may become more serially correlated, which will result in sequences of warm or cold and wet and dry years and greater overall climate variability (Cohen and Pastor 1991). These cycles may contribute to pulsed recruitment when wet or mortality when dry, of woody plants (Archer 1989; Neilson 1986). Almost any change in climate is likely to affect vegetation at the individual, population, or community level, with subsequent ramifications for ecosystem structure and function.

Climate Change and Vegetation

Physiological effects of increasing CO_2 on vegetation include increased net photosynthesis, reduced photorespiration, changes in dark respiration, and reduced stomatal conductance, which decreases transpiration and increases water use efficiency (as reviewed by Patterson and Flint 1990; Rozema and others 1993). Ambient temperature affects plants directly and indirectly at each stage in their life cycle (as reviewed in Long and Woodward 1988). Soil moisture is usually the abiotic factor most limiting to vegetation, especially in arid and semi-arid regions. CO_2, temperature, and soil moisture effects on plant physiology are exhibited at the whole-plant level in terms of growth and resource acquisition. For example, elevated atmospheric CO_2 enhances growth of tree seedlings, even under conditions of water and nutrient stress (Mooney and others 1991), but heat stress may increase seedling mortality rates (Nobel 1984).

Responses to CO_2, temperature, and soil moisture vary among species, particularly between plants with C_3 and C_4 photosynthetic metabolisms (Bazzaz and Carlson 1984; Johnson and others 1993; Patterson and Flint 1990). C_3 plants exposed to elevated CO_2 exhibit greater increases in growth and photosynthesis than do C_4 plants grown under the same conditions (as reviewed by Bazzaz 1990 and Patterson and Flint 1990). Growth and photosynthesis of plant species with the C_4 metabolic pathway are limited by cool temperatures (Long 1983; Potvin and Strain 1985). When grown with elevated CO_2, water use efficiency (WUE) of C_3 plants generally is affected more than WUE of C_4 plants (Polley and others 1992; Polley and others 1993; Sionit and others 1981). When temperatures are consistent, physiological changes favor C_3 plants over their C_4 counterparts in multi-species competition experiments in controlled environments with elevated CO_2 (Bazzaz 1990; Patterson and Flint 1990; Wray and Strain 1987).

Perhaps more important than individual effects of increasing atmospheric CO_2 and increasing temperatures, however, is their interactive effect on photosynthetic productivity and ecosystem-level process (Long 1991). Unfortunately, the relatively few studies of interactive effects of temperature and CO_2 on vegetation (Bazzaz 1990; Farrar and Williams 1991) have conflicting, poorly understood results (Long and Hutchin 1991). For example, photosynthesis and growth of plants in elevated atmospheric CO_2 may be stimulated by increases in temperature (Allen and others 1989; Grulke and others 1990; Idso and others 1987; Idso and others 1993 Sionit and others 1987). Alternatively, temperature may have little or no effect on CO_2-enriched plant growth (Jones and others 1985; Tissue and Oechel 1987). Nonetheless, analysis of vegetation response to CO_2 as mediated by atmospheric temperatures suggests that relative effects of CO_2 increase with temperature (Drake and Leadley 1991; Idso and others 1993), perhaps because of upward shifts in photosynthesis temperature optima with increasing CO_2 (Pearcy and Bjorkman 1983). For example, Mooney and others (1991) predicted that elevated CO_2 will amplify the effect of CO_2 enrichment on ecosystem productivity when daytime temperatures are above 30 °C, as in the middle-latitude grasslands. Conversely, low temperatures may attenuate CO_2-induced growth enhancement (Hofstra and Hesketh 1975; Idso and others 1993; Sage and Sharkey 1987).

Two primary conclusions can be drawn from previous research on climate change and vegetation:

- interactive effects of changing abiotic conditions may be more important than main effects in terms of changes in plant response and subsequent changes in vegetation distribution, and
- impacts of CO_2 enrichment may be mediated by other environmental constraints such as temperature or nutrient limitations.

Thus, a caveat is in order: because of environmental constraints, ecosystems likely will have muted responses compared to studies conducted in small pots or chambers. However, research designed to evaluate the relevance of mesocosm experiments to real world conditions is limited (Bazzaz 1990; Rozema and others 1993) (see Experiments for the Borderlands section).

Climate Change and Vegetation Distribution

Shifts in the relative competitive ability of plants that experience changes in CO_2, surface temperatures, or soil moisture may result in changes in their spatial distribution (Bazzaz 1990; Curtis and others 1989; Davis 1989; Long and Hutchin 1991; Neilson 1993; Neilson and Marks 1994). It has been hypothesized that increases in CO_2 may enhance growth and establishment of C_3 shrubs in C_4-dominated grasslands of the southwestern United States (Idso 1992; Johnson and others 1993; Mayeux and others 1991; Polley and others 1994). Further, CO_2-induced increases in WUE or fine root biomass (see Idso and Kimball 1992; Norby and others 1986; Polley and others 1997) of C_3 shrubs suggest they may be able to expand their distribution into ecosystems where water is otherwise a limiting factor (Long and Hutchin 1991; *sensu* Mellilo and others 1993). This is supported by correlative evidence that higher WUE is positively correlated with growth and survival of plants in dry habitats (Ehleringer and Cooper 1988). A simple WUE model developed by Idso and Quinn (1983) suggested that a doubling of CO_2 would cause oak woodlands in the southwestern United States to shift downslope and displace extensive regions of semidesert grassland. However, their hypothesis has not been tested in this, or any other, system.

Conversely, global increases in temperature may enhance the competitive ability of C_4 plants, such as grasses, relative to C_3 shrubs and trees, especially where soil moisture (Neilson 1993) or temperatures (Esser 1992) are currently limiting. This could result in regional, upslope shifts of semidesert grasslands at the expense of woodlands (*sensu* Long and Hutchin 1991).

It is hypothesized that the present distribution of vegetation in the southwestern United States is highly dependent on precipitation (Van Devender and Spaulding 1979). Bimodal patterns of precipitation distribution are thought to allow stable coexistence of woody plants and grasses: shallow-rooted grasses use growing-season precipitation; deep-rooted woody plants use moisture that percolates through surface soil layers when grasses are dormant (Archer 1989; Lauenroth and others 1993; Walker and others 1981; Walker and Noy-Meir 1982). In addition, woody plants with the C_3 photosynthesis pathway are reportedly favored by cool-season precipitation; perennial grasses with the C_4 pathway are favored by warm-season precipitation (Neilson 1986). Thus, changes in quantity and seasonality of precipitation should affect competitive interactions between species coexisting under current equilibrium conditions (Ehleringer and others 1991). Increased summer precipitation is hypothesized to favor shallow-rooted grasses over more deeply rooted woody perennials (Ehleringer and others 1991; Eissenstat and Caldwell 1988). In contrast to this prediction, experimental increases in summer precipitation favored woody plant recruitment (Weltzin and McPherson in press). Predicted increases in winter soil moisture (Manabe and Wetherald 1986; Mitchell and Warrilow 1987) may contribute to the expansion of C_3-dominated shrublands into C_4-dominated grasslands in the borderlands region (Melillo and others 1993; *sensu* Neilson 1986), although experimental research to date does not support this contention (Weltzin and McPherson in press). Thus, minor changes in precipitation pattern in this region, especially at ecotones (Neilson 1987, 1993; Neilson and others 1989), may cause major shifts in plant distribution (*sensu* Stephenson 1990). Although these hypotheses are intuitively palatable, they have not been tested adequately. Intensive, long-term monitoring in the borderlands region has failed to adequately test these hypotheses (Wondzell and Ludwig 1995). In fact, further experimental manipulation of plant communities will be necessary to distinguish between competing hypotheses for plant community change (Wondzell and Ludwig 1995, p. 377).

Implications for the management of plant communities under different scenarios of seasonal precipitation change are profound. If partitioning of soil moisture does occur, then shifts in precipitation seasonality may affect interactions between trees and grasses where they currently coexist, or allow one or the other life form to establish where it is currently excluded by environmental constraints. Thus, if the seasonality of precipitation changes within the next few decades, as expected, rapid and dramatic changes in tree/grass ratios may occur.

Anthropogenically-induced changes in climate are also likely to affect fire frequency and extent. Changes in community structure caused by changes in atmospheric composition or climate may have substantial effects on fire regimes (*sensu* Clark 1990). A shift from grassland to woodland will reduce herbaceous biomass and subsequently reduce fire frequency because of decreased accumulation of fine fuel (McPherson 1995). Conversely, increased surface temperatures may either increase fire frequency because hotter, drier conditions cure fuel more quickly, or decrease fire frequency because of decreased fine fuel production. Increases in summer or winter precipitation may increase fine fuel loading and thus increase fire frequency (Rogers and Vint 1987; Swetnam and Betancourt 1990). Obviously, the effects of climate change on fire frequency are difficult to predict, in part because of the scarcity of knowledge about future climate change, and also because of interactive effects of climate change, biological factors, and activities related to management and politics.

Already-observed increases in post-industrial atmospheric CO_2 may have greatly increased production of some plants (Allen and others 1991; Baker and others 1990; Polley and others 1992), although this is debated (Archer 1994; Archer and others 1995). One explanation for recent increased C_3 woody plant abundance in C_4 grasslands is based on increased atmospheric $[CO_2]$ over the last century (see Idso 1992; Idso and Kimball 1992; Johnson and others 1993; Mayeux and others 1991). Encroachment of woody plants (with the C_3 photosynthetic pathway) into C_4 grasslands has been accompanied by a 27 percent increase in atmospheric CO_2 over the past 200 years. Increases in atmospheric CO_2 are said to have conferred a significant advantage to C_3 woody plants relative to C_4 grasses in terms of physiological activity, growth rates, and competitive ability.

In contrast, Archer and others (1995) argued that changes in CO_2 alone are not the proximate cause for observed shifts in woody plant distribution, because (among other arguments):

- substantial increases in woody plant abundance in grasslands occurred before CO_2 rose more than 11 percent over levels of the 1700s;
- widespread replacement of C_3 grasses by C_3 shrubs has occurred in temperate zones and cold deserts; and
- C_4 species have quantum yields, photosynthetic rates, and water use efficiencies that are greater than C_3 species, even under current atmospheric CO_2.

Thus, there is no ecophysiological basis for a historic change in competitive interactions that favored C_3 over C_4 plants.

In agreement with these arguments, we suggest that increased atmospheric CO_2 has not contributed significantly to historic shifts in lower tree lines in the borderlands region, especially relative to the effects of livestock grazing and fire suppression (Archer and others 1995; Bahre and Shelton 1993; Weltzin and McPherson 1995). However, it is unlikely that presettlement fire or livestock grazing regimes will be restored in the foreseeable future. Even if changes in fire regimes and livestock grazing were instituted, former grasslands now dominated by woody plants are relatively stable in the absence of major cultural inputs, which are not feasible (Archer 1989; Archer and Smeins 1991; Westoby and others 1989). Although past increases in CO_2 may have had little or no impact on vegetation interactions, continued increases in CO_2 may contribute to increased abundance of woody plants in grasslands of the borderlands region, particularly if these increases are accompanied by shifts in seasonal precipitation or other climatic factors. Thus, the direct and indirect effects of rising concentrations of CO_2 and other trace gases have the potential to replace grazing and fire suppression as important regulators of plant community change.

In summary, changes in climate that may occur in the borderlands region include increased atmospheric concentrations of CO_2, increased surface temperatures, changes in the amount, seasonality, and distribution of precipitation, more frequent climatic extremes, and greater climatic variability. However, determination of impacts of CO_2 enrichment on native and non-native vegetation is complicated and controversial. First, effects may be mediated by other environmental constraints such as temperature and soil moisture. Second, interactive effects of changing abiotic conditions may be of greater importance than main effects in terms of changes in plant response and subsequent changes in vegetation distribution. Nonetheless, it is widely hypothesized that increases in atmospheric CO_2 and winter precipitation should favor woody plant establishment and growth at the expense of grasses, and may cause woodland boundaries to shift downslope. Alternatively, increases in temperature and summer precipitation would favor C_4 grasslands at the expense of C_3 woodlands. However, increases in monsoonal (July through September) precipitation may favor germination and establishment of plant species, such as Emory oak, that reproduce coincident with the monsoon. These critical hypotheses should be investigated using experimental research techniques as urged by Gurevitch and Collins (1994), Keddy (1989), McPherson (1997), and Wondzell and Ludwig (1995).

Identifying Critical Experiments

As described above, considerable research has investigated vegetation change in the borderlands region. This research has been instrumental in the determination of biogeographical, biogeochemical, environmental, and physiological patterns that characterize plant communities of the borderlands. In addition, previous research has illustrated some of the underlying mechanisms that control patterns of species distribution and abundance. Most importantly, however, borderlands research to date has successfully identified many hypotheses for observed and predicted ecological phenomena. Few of these hypotheses have been explicitly tested. For example, characteristics of soils associated with different geomorphic surfaces are thought to form important constraints on vegetation distribution in the borderlands region (e.g., Burgess 1995; McAuliffe 1994), but this hypothesis remains untested. Geomorphic constraints on woody plant recruitment have not been investigated, and the importance of geomorphic properties on vegetation distribution has not been considered in Madrean and higher elevation vegetation communities. The scarcity of hypothesis testing has limited the ability of ecology as a discipline to foresee or help solve managerial problems (Underwood 1995).

The Role of Experiments in Ecological Research

Land managers need reliable scientific information to effectively manage plant communities and ecological processes. Thus, land managers must distill a large body of information, some of which is contradictory or inconsistent, into management decisions. The disciplines of science should be able to offer explanatory and predictive power to ecosystem managers. The scientific process, which includes stating and testing hypotheses, is among the most valid and efficient of techniques available to scientists for the purpose of acquiring information. The willingness of many scientists to answer questions about disturbance or climate change based on simple descriptive studies has trapped them into being asked to make predictions about things they know they cannot predict (Peters 1991; Underwood 1995).

From a modern scientific perspective, a hypothesis is a candidate explanation for a pattern observed in nature (Matter and Mannan 1989; Medawar 1984). A hypothesis is not merely a statement likely to be factual, which is then tested by observation. Further, use of sophisticated technology or statistics does not imply that hypothesis-testing is involved, if these tools are used merely to detect a pattern. Unfortunately, most ecological research is terminated after discovery of a pattern, but before the cause of the pattern is determined (Romesburg 1981; Willson 1981).

Experimentation is the most efficient technique available for determining the relative importance of competing hypotheses (Campbell and others 1991; Simberloff 1983). The use of field experiments in ecology is increasing, and Gurevitch and Collins (1994) made a compelling case for continuing and strengthening this approach. They pointed out that manipulative field-based experimental research will help disentangle important driving variables because of strong correlations that often occur between factors under investigation (Gurevitch and Collins 1994). Identification of underlying mechanisms of vegetation change will enable prediction of vegetation response to changes in climate or land use with a level of certainty and on temporal scales useful to management.

Observation of shifts in lower tree line, as outlined in the Historical Research section, demonstrates the limitations of descriptive research. A documented pattern, for example, a shift in lower tree line, does not explain why the pattern exists. In fact, without experimental research, interpretations of underlying mechanisms may actually conflict. In this case, as yet untested candidate explanations for observed tree line shifts include climate change, increased livestock grazing, and decreased fire frequency. Descriptive studies (including "natural" experiments, *sensu* Diamond 1986) are forced to infer a mechanism based on a pattern, and are therefore poorly suited for determining underlying mechanisms or causes of patterns because there is no test involved (Keddy 1989; Popper 1981). Experimentation, the artificial application of treatment conditions coupled with monitoring of target vegetation, is an efficient and appropriate means for testing hypotheses about ecological phenomena.

Experiments for the Borderlands

Examples of "natural" experiments abound in the ecological literature, but results of these studies should be interpreted with caution. For example, in the borderlands region scientists have compared recently-burned areas to adjacent unburned areas and concluded that observed differences in species composition were the direct result of fire. Before reaching this conclusion, it is appropriate to ask why one area burned while the other did not. Pre-burn differences in productivity, fuel continuity, fuel moisture content, plant phenology, topography, or edaphic factors may have caused the observed fire pattern. Since these factors influence, and are influenced by, species composition, they can not be ruled out as candidate explanations for post-fire differences in species composition.

We join a large number of ecologists in suggesting that field-based manipulative experiments represent a logical approach for future research. Although the results of ecological research are likely to be highly site specific (Keddy 1989; Tilman 1990) it is not feasible to conduct experiments in each type of soil and vegetation. Therefore, experiments should be designed to have maximum possible transferability to other systems (Keddy 1989). The pattern under investigation should be widespread, selected species should be representative of the area's life forms, the factors manipulated in experiments should have broad generality, experiments should be arranged along naturally-occurring gradients, and experiments should be conducted at spatial and temporal scales appropriate to management of plant communities.

Experimental research should be spatially and temporally relevant to management of borderlands ecosystems (Allen and others 1984). Obviously, experiments should focus on realistic environmental conditions and likely management strategies. Physiognomic-level vegetation change is fundamentally important to vegetation managers in the borderlands region. In particular, understanding the factors that constrain establishment of woody plants in this region is fundamental to predicting responses of plant communities to management, disturbance, and environmental change. The research outlined herein should enable managers to better predict patterns of woody plant establishment and persistence in grasslands.

Management Manipulations—Herbivory, Fire, and Woody Plant Control

Continued research on livestock grazing systems and woody plant control is not generally recommended. An extensive literature on grazing management (reviewed by Heitschmidt and Stuth 1991; Hodgson 1990; Vallentine 1990) provides a basis for rate and timing of livestock grazing. On most sites in the southwestern United States, many years of practical experience are especially useful in generating site-specific guidelines for appropriate stocking rates and seasons of use. Research on woody plant control was popular throughout the 1950's and 1960's, and this research produced abundant literature (reviewed by Vallentine 1989). This expansive literature continues to serve as a basis for site-specific recommendations for prescribed fire frequency and both chemical and mechanical woody plant control measures.

Effects of native herbivores are poorly known and little studied, but of great potential importance. In particular, research on native herbivores should focus on potential effects of different animal species on establishment and persistence of woody plants. Prairie dogs, once common in the region, may have played an important role in regulating mesquite abundance (Weltzin 1990). Limited research (Germaine and McPherson 1999; McPherson 1993) suggests that vertebrates and invertebrates form seasonally-important constraints on oak seedling survival. However, the spatial extent and importance of these mortality vectors have not been determined, nor has the particular species responsible for observed mortality. Invertebrate herbivory may change dramatically in a CO_2-enriched world as a result of altered forage quality (Korner and Miglietta 1994; Lincoln and others 1993; Owensby 1993; Poorter and others 1992).

Determining the effects of different frequencies and seasons of fires is critical to our understanding of fire ecology. Research on fire effects should focus on the influence of different fire frequencies on physiognomy, species composition, and nutrient cycling. This research should apply experimental fire regimes to semidesert grassland, shrub-grassland, and grassland/woodland ecotones. Fire frequencies and seasonalities necessary to prevent establishment of woody plants should be investigated with appropriate experimental designs. Such experiments have been initiated on the Sevilleta National Wildlife Refuge. On-going comparative research may facilitate the determination of appropriate fire frequencies for future experimental research.

Climatic Factors

The greatest gap in our knowledge about plant communities in the borderlands region is the potential effects that global and regional climate change may have on vegetation interactions and community- and ecosystem-level processes. Currently, prediction of future changes in distribution and composition of borderlands plant communities is difficult, given the background of recurrent disturbances and the possible complexity and general paucity of knowledge about regionally-specific climate change (Mitchell and others 1990). However, the determination of most-likely scenarios of climate change is relatively straightforward, and these may be tested experimentally. Experiments that focus on interactions between various concentrations of greenhouse gases and temperature and precipitation will likely provide the greatest simultaneous contribution to ecological theory and management.

Experiments on climate change should be designed to maximize their contribution to the scientific community. For example, resource partitioning is widely-invoked to explain apparent long-term stability of savannas and woodlands (Brown and Archer 1990; Bush and Van Auken 1991; Knoop and Walker 1985; Sala and others 1989; Walter 1954, 1979). Bimodal patterns of precipitation distribution are thought to allow stable coexistence of woody plants and grasses. Shallow-rooted grasses use growing-season precipitation; deep-rooted woody plants use moisture that percolates through surface soil layers when grasses are dormant (Archer 1989; Lauenroth and others 1993; Neilson 1986). Although this hypothesis is intuitively palatable, it has yet to be explicitly tested. Implications for the management of plant communities are profound. If resource partitioning does occur, then shifts in precipitation seasonality, predicted to occur as a result of atmospheric CO_2 enrichment, may affect soil moisture pools. In turn, changes in soil moisture may affect interactions between woody plants and grasses where they currently coexist, or allow one or the other life form to establish where it is currently excluded by environmental constraints. If the seasonality of precipitation changes within the next few decades, rapid and dramatic changes in woody plant/grass ratios may occur. This structural change would have important implications for ecosystem functions such as nitrogen cycling, productivity, and carbon flux. Experimentation will enable managers to predict not only:

- the relative importance of current precipitation regimes on woody plant/grass ratios and distribution, but also
- the potential effect that changes in seasonality of precipitation may have on the relative distribution of woody plants and grasses.

Stable isotope analysis represents a quantitative technique to assess differential utilization of soil moisture by trees and grasses. This technique is based on comparisons between isotopic composition of source waters and plant waters. Different source waters have characteristic oxygen and deuterium isotopic ratios (expressed as d^{18}O and dD, respectively) because of differential evaporation of meteoric waters. In regions with bimodal precipitation patterns such as the southwestern United States, these isotopically-labeled waters occupy different portions of the soil profile. Uptake of water by plants does not affect its isotopic composition. Therefore, comparisons of isotopic ratios of potential water sources and plant xylem sap water can indicate sources of plant water. Comparisons of dD and d^{18}O between seasonal precipitation, soil water at different depths in the soil profile, and plant sap water should clarify differential utilization of source waters by oak trees, oak seedlings, and grasses (*sensu* Weltzin and McPherson 1997). An understanding of differential utilization will allow prediction of changes in tree/grass ratios and woody plant distribution as effected by management or global climate change.

Effects of soil moisture and temperature on competitive interactions, particularly those involving different life forms, are largely unknown. These topics are related to precipitation seasonality and edaphic features, and can be investigated with controlled-environment chambers, greenhouses, and field experiments. Relationships between woody and herbaceous plants should be studied at life-history stages ranging from seed germination to mature plants. In existing vegetation, quantifying overstory/understory relationships and determining the effects of canopy removal on vegetation are among the applied questions that can be addressed with basic research.

The role and importance of short-term climatic events on community structure represent a critical gap in our knowledge of borderlands ecosystems. Do periodic cold or hot temperatures constrain woody plant establishment in grasslands? How do they affect different grass species, annual vs. perennial and native vs. non-native? What role do extreme temperatures play in the mortality of established woody plants and grasses? What is the role of drought in shaping observed patterns of woody plant establishment? Recent research in other systems (Bassow and others 1994) illustrated the kind of experiments that can significantly improve our understanding of short-term climatic controls on borderlands plant communities.

The importance of the southwestern monsoon on plant communities has not been fully determined. How do initiation and cessation of the monsoon control woody plant and grass germination, emergence and early survival? What are the effects of intra-monsoon precipitation events on germination and emergence? For example, are woody plant or grass seeds dependent on evenly-spaced precipitation events, or will one large event provide enough soil moisture for germination and establishment? Are there important species-specific responses to precipitation events?

Edaphic Factors

Soils and vegetation are inextricably linked, and soil properties are strongly correlated with overlying vegetation. Natural Resource Conservation Service range site guides provide numerous detailed examples of the high correlation between soils and vegetation; these guides are widely available and offer a level of resolution appropriate to management. In some cases, these relationships may need to be refined. This is primarily a mapping exercise, which may be enhanced by geographical information systems technology.

Additional research in this area should focus on determination of edaphic and geomorphic constraints on woody plant establishment in grasslands. It has been suggested that soil argillic horizons constrain establishment of woody plants in many borderlands grasslands (Archer 1994; Loomis 1989; McAuliffe 1994). McAuliffe (1994) hypothesized that water-impermeable argillic horizons

- reduce water availability to woody plants in summer below thresholds necessary for survival, or
- result in perched water tables in the winter, which may contribute to woody plant mortality.

Although these hypotheses are intuitively palatable, and are often cited, they have not been tested.

Different types of soil may constrain overlying vegetation recruitment. What is the importance of soil depth, particle size distribution, substrate, and nutrient content on vegetation distribution? Since soil properties are often highly correlated, controlled experiments will be required to determine the relative importance of driving variables. Finally, fundamental information about soil nutrient availability and spatial and temporal distribution, and processes affecting these phenomena, are generally lacking in the borderlands region.

Reciprocal transfer of soils and common garden experiments are two techniques for experimentally studying the role of soil in controlling plant distributions. For example, transferring grassland and woodland soils to the opposite communities is a straightforward test of the relative importance of soil and microenvironment in plant establishment and persistence (Weltzin and McPherson 1999). Reciprocal-soil-transfer experiments coupled with nutrient and water supplementation allow identification of factors limiting plant recruitment. Finally, incorporation of more than one species into experimental designs permits determination of effects of different soil types and microenvironments on competitive interactions. Use of controlled-environment chambers or greenhouses enhances experimental control, but may sacrifice realism compared to field experiments. Controlled-environment trials should thus be used in conjunction with experimental field trials.

In summary, an understanding of the mechanisms underlying changes in the distribution of vegetation in the borderlands is critical to predicting the response of plant communities to management, disturbance, and environmental change. Descriptive studies, including historical analyses, repeat-photography, correlation, and “natural” experiments, although important for assessment of pattern, are not well suited for clarifying driving variables. Rather, experimentation is the most appropriate technique for determining effects of environmental factors on vegetation. Experiments should be field based and focused on representative species, and should be conducted on spatial and temporal scales most appropriate to management. Well-designed manipulative experiments should enable managers to predict effects of management, disturbance, and changing climatic conditions on specific plant communities.

Management Implications

This document does not provide explicit recommendations for resource managers for two important reasons. First, we believe that management decisions must be temporally, spatially, and objective-specific. Since this review is focused on broad-scale spatial and temporal disturbances, it should not be used for site-specific management decisions. Rather, management decisions made by managers most familiar with individual systems should be couched within this temporally and spatially broad discussion. Second, specific management activities, though based on scientific knowledge, are conducted within the context of relevant social, economic, and political issues. These specific issues and concerns are beyond the scope of this article.

Although ecologists have generally failed to conduct experiments relevant to managers (Underwood 1995), managerial agencies have frequently resisted criticisms of performance or suggestions for improvement (Longood and Simmel 1972; Underwood 1995; Ward and Kassebaum 1972). These factors contribute to poorly developed and sometimes adversarial relationships between managers and scientists. Managers should be familiar with scientific principles, and ecologists should be proactive, rather than reactive, with respect to land management issues.

Managers in need of scientific information are encouraged to:

- use existing data,
- work closely with the scientific community, and
- communicate the need for specific information.

However, it is critical that resource managers understand how scientific knowledge is obtained. Not all scientific information will enable managers to accurately predict the response of a plant community to a specific disturbance or manipulation. Some research findings may actually present untested hypotheses rather than observed responses to well-controlled experimental manipulations. Other research may not be applicable to temporal or spatial scales relevant to management. The results of such research should be judiciously interpreted.

At regional and larger scales of resolution, managers must recognize and appreciate the importance of on-going and impending climate changes on current and future vegetation. This is perhaps the most critical factor facing the current generation of land managers who are concerned about the future condition of borderlands ecosystems. Proactive managers will want to know the probability of various climate scenarios and subsequent vegetation response. This information can be determined with a combination of models and experiments. By contrast, retrospective studies of climate and vegetation changes are inadequate for predicting future climate-vegetation interactions.

Rising concentrations of CO_2 and other trace gases have the potential to replace grazing and fire suppression as important regulators of vegetation change. It is unlikely that pre-settlement fire or livestock grazing regimes will be restored in the foreseeable future, and even if they were, sites dominated by woody plants would not revert to grasslands without major cultural inputs. Although past increases in CO_2 may have had little or no impact on vegetation, continued increases in CO_2 may contribute to increased abundance of woody plants in borderlands grasslands, particularly if these increases are accompanied by shifts in seasonal precipitation or other climatic factors. Implications for management are clear: if increased atmospheric CO_2 concentrations and/or associated changes in precipitation patterns enhance recruitment of undesirable woody plants, then management efforts must consider such climatic changes when developing long-range management goals and objectives. Alternatively, if changes in CO_2 and precipitation do not affect woody plant recruitment, or if changes that occur are desirable, then management plans need not necessarily consider direct effects of these changes on vegetation dynamics and ecosystem processes.

Interactions between fire and the physical and biological environment indicate that vegetation response to fire is site-specific. This fact, coupled with objectives that vary between sites, precludes the development of simple recommendations concerning prescribed fire frequencies. In general, frequent fires are detrimental to woody plants and beneficial to Lehmann lovegrass. Fire frequencies of 10 to 20 years do not appear to diminish resource values or productivity (Robinett 1994). Deep-soiled, highly-productive sites can be burned more frequently than erosion-prone or shallow-soiled sites.

If woody plant control is a primary objective of management, then periodic fires should be implemented on most grassland or shrubland sites. All available evidence suggests that fire is an inexpensive, appropriate tool for retaining or restoring the physiognomy of grasslands. Fires that occur during the pre-monsoon spring appear to be most detrimental to woody plants. Although fire is necessary, it is usually not sufficient to control the abundance of woody plants and maintain grasslands. Rather, appropriate grazing management, and in many cases major cultural inputs, are required to create and maintain grasslands.

Chemical or mechanical manipulation may be essential to convert communities dominated by woody plants into grasslands. Many former grasslands have not burned since Anglo settlement. On most such sites, woody plants have replaced grasses as the dominant life form. Once a site is dominated by woody plants, fine fuel may be too scarce and discontinuous to produce fires of sufficient intensity to kill a significant number of woody plants. If woody plants preclude the spread of wildfires or the deliberate application of prescribed fires, other technologies such as herbicide application or mechanical brush control must precede the re-introduction of fire.

The current role of livestock in structuring vegetation is considerably less important than its historic role. In addition, excluding livestock from grasslands will not prevent, and may not delay, a substantial increase in woody plant abundance. Livestock exclusion in areas smaller than thousands of hectares will not produce islands of grass in a sea of shrubs.

Trial and error has been the dominant means of determining stocking rates and grazing systems. This is not surprising, considering the site-specificity of edaphic factors, species composition, and cultural features. Similarly, future livestock activities in borderlands ecosystems will be dictated by site-specific edaphic, ecological, and cultural factors. In addition, social, economic, and political factors will become increasingly important determinants of the role and importance of livestock grazing, particularly on public lands. Livestock operators who anticipate and respond to:

- affected ecosystems, altered by changing climates and fire regimes, and
- changing social and political and attitudes, should fare well compared to inflexible operators.

Long-term meteorological records indicate that periodic droughts often occur in the borderlands region. In fact, annual precipitation is below the long-term average during at least 60 percent of years for most meteorological stations. Management actions should account for episodic and unpredictable precipitation patterns. For example, stocking rates of livestock should reflect herbaceous production associated with years of below-average precipitation. Management should be flexible enough to respond to above-average precipitation by implementing prescribed fires, using stocker animals, or altering grazing patterns across elevational gradients during wet years.

Finally, re-introduction of prairie dogs may be a cost-effective strategy for maintaining the physiognomy of semidesert grasslands susceptible to woody plant encroachment. It should be noted that the role of this once common native herbivore in reducing the abundance of woody plants such as *Larrea*, *Quercus*, or *Mimosa* has yet to be determined. Further, prairie dogs may have an undesirable effect on herbaceous species composition or aboveground net primary production. However, well-controlled experimental reintroduction of these easily exterminated herbivores should clarify their potential role in the control of woody plants within the borderlands region.

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Authors' Note

This manuscript was prepared in 1995 and accepted for publication in 1996. A lengthy delay in the publication process precluded incorporation of considerable recent literature.

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