Potential Effects of Climate Change on Lower Treelines in the Southwestern United States

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Abstract.—Oak (*Quercus*) woodland and savanna biomes occupy several million hectares in the southwestern United States and northern Mexico. Despite their regional importance, our understanding of mechanisms that control their component vegetation populations is limited. Descriptive research to date has provided little predictive power to managers, and thus has had limited applicability to ecosystem management. Ongoing experimental investigations of constraints on seedling establishment suggest that vertebrate and invertebrate herbivory, interference from herbaceous plants, and climatic and edaphic conditions interact to produce low seedling establishment rates. These biotic and abiotic factors may be overwhelmed by predicted, directional changes in climate caused by anthropogenically-induced increases in atmospheric trace gas concentrations. For example, CO_2-induced increases in surface temperatures, and changes in amounts and seasonalities of precipitation may affect vegetation at the individual, population, or community level, with subsequent ramifications for ecosystem structure and function. As such, direct and indirect effects of increased CO_2 concentrations (e.g. CO_2 fertilization, changes in fire frequency and extent) may replace grazing and fire suppression as important regulators of plant community change in these biomes. We argue that knowledge gained from appropriately designed experimental research should enable managers to predict effects of management activities on oak woodlands and savannas, within the context of changing regional and global climatic conditions.

INTRODUCTION

Oak (*Quercus*) woodland and savanna biomes in the southwestern United States and northern Mexico occupy several million hectares of arid and semi-arid wildlands. Oak woodlands in Arizona have been utilized by settlers, miners, explorers and pastoralists for over a century. Oak trees provided mine timbers and smelter fuelwood between 1890-1910 (Bahre and Hutchinson 1985). Woodlands and savannas were heavily grazed by livestock in the 1880s, and grazing continues today, though at much lower stocking rates. Fire suppression and grazing-induced removal of fine fuels have altered historical fire frequencies.

Despite their areal extent, and economic, ecologic, and historic importance, we know little about the dynamics and processes of their component vegetation populations and communities. Although scientific knowledge about these areas is increasing, research to date has been largely descriptive (e.g. Brown 1982). One area of relatively recent scientific interest has focused on changes in plant community distributions.

Woody plant abundance has increased substantially during the last 50 to 300 years in many of the world's grasslands (e.g. Buffington and Herbel 1965, Archer et al. 1988, Walker et al. 1989). Although encroachment of woody plants into grasslands is widely recognized, the rates, patterns, and mechanisms of the process are not well quantified (Archer 1989), or are inconclusive. For example, increased woody plant abundance in

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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).

Changes in vegetation physiognomy (e.g. from grassland to woodland) have broad implications for management and land use throughout the world. Life form changes in plant communities affect virtually all resources, including wildlife, water, livestock, fuelwood, and recreation. Proper management of these and other systems depends on the accurate prediction of ecosystem response to perturbation and management.

The purpose of this paper is to review the current state of knowledge regarding changes in the distribution and boundaries of Madraen oak woodlands in the southwestern United States. We will focus on shifts in lower treeline, and the biotic and abiotic factors that constrain vegetation establishment and distribution. Further, since anthropogenically-induced changes in climate are an ongoing and increasingly important control over vegetation distribution, we will examine the effect of climate change on vegetation, and subsequent effects on vegetation distribution. Finally, we discuss possible directions for future research.

PRESENT STATE OF KNOWLEDGE

Shifts in Lower Treeline

Recent ecological research in the southwestern United States has focused on shifts in the oak woodland/semi-desert grassland boundary (e.g.

Hastings and Turner 1965, Bahre 1977, 1991, McPherson et al. 1993; figs. 1,2). Reports of historical changes in this 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 et al. 1990).

On a more contemporary temporal scale, Hastings and Turner (1965) examined matched, historical ground photographs from the southwestern United States, and concluded that the oak woodland/semi-desert grassland boundary moved upslope over the last century. They attributed oak mortality at this ecotone to an increasingly xeric climate. However, Hastings and Turner's interpretations were questioned by Cooke and Reeves (1976), whose analysis of precipitation patterns for the southwest indicated that precipitation had not varied significantly during the previous 100 years. Further, Hastings and Turner's latest photographs, taken soon after the severe regional drought of the 1950s, portrayed widespread top-kill among mature oak trees. This episodic event with relatively ephemeral effects may have colored their conclusions about ecotone shifts. Thus, their interpretation of treeline shifts was probably more suited to a scale of years rather than decades or centuries. In contrast with Hastings and Turner (1965), Bahre (1991) concluded that the distribution of oak woodlands has been stable since the 1860s, regardless of changes in livestock densities.

Traditional technologies for assessing changes in woody vegetation distribution include dendrochronology, historical accounts, and

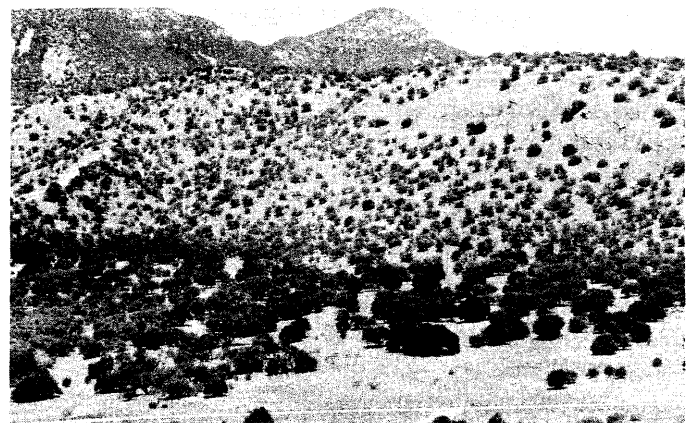Figure 1.—Oblique aerial photograph of Emory oak-dominated woodland/semi-desert grassland boundary.

Figure 2.—Emory-oak savanna at lower treeline.

repeat-photography. Dendrochronology is limited to woody species, usually trees, and is based on correlations between tree age and cross-sectional ring number. However, ages of trees that dominate woodlands and savannas at the tree/grass boundary in southeastern Arizona 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.

Historical accounts of vegetation change are usually anecdotal and imprecise, and thus do not allow accurate determination of historic (let alone prehistoric) vegetation physiognomy or plant community composition. Repeat ground photography has a limited and oblique field of view, and historic photographs usually portray anthropogenic manipulation of landscapes, all of which limits their usefulness for determining changes in plant distribution. Repeat aerial photography is limited in that even the earliest photographs (ca. 1930) were obtained after broadscale vegetation change had already occurred.

Recently, quantitative chemical analysis has provided yet another interpretation of vegetation boundary shifts in southeastern Arizona. McPherson et al. (1993) used stable carbon isotope analysis to investigate the direction and magnitude of vegetation change along oak-dominated woodland/semi-desert grassland boundaries. Their investigation focused on the two dominant woody species, velvet mesquite (*Prosopis juliflora* (Swartz) DC.) and Emory oak (*Quercus emoryi* Torr.) at lower treeline ecotones in the southwestern United States and northwestern Mexico. Emory oak and velvet mesquite, like almost all woody plants, have the C3 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 C4 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.

McPherson et al.'s (1993) analysis of $\delta^{13}C$ values of soil organic matter and roots from the woodland/grassland boundary indicated that both velvet mesquite and Emory oak were recent components of former grasslands. Their results were consistent with other reports of recent increases in woody plant abundance in grasslands and savannas throughout the world (e.g. Archer et al. 1988, Steuter et al. 1990, Tieszen and Archer 1990). Further, their interpretation of vegetation change was of similar temporal and spatial magnitudes relative to downslope shifts in lower limits of *Coleogyne ramosissima* (Cole and Webb 1985) and *Pinus longaeva* (LaMarche 1973) in eastern California.

Results of a subsequent investigation of within-savanna vegetation dynamics support the conclusions of McPherson et al. (1993), and indicate that grasslands immediately below existing woodland boundaries have been stable for at least 1700 years (McPherson and McClaran in review). In addition, this most recent data suggests that within-savanna dynamics are complex and not necessarily directional (e.g. grassland shifting to woodland). For example, $\delta^{13}C$ values of soil organic matter indicate that within the savanna proper, trees have established on sites not previously occupied by trees, but that some sites dominated by grasses previously supported trees. Results indicate that there is redistribution of trees over time within these savannas, and suggests that periodic disturbances (Whittaker 1975, Gillon 1983, Trollope 1984, Frost and Robertson 1987, Medina 1987) and soil resource partitioning by trees and grasses (Walter 1954, Walker and Noy-Meir 1982) contribute to long-term persistence of savannas.

Constraints on Seedling Establishment

Ultimately, shifts in lower treeline reflect temporal integration of tree seedling establishment and persistence at the woodland/grassland boundary. Thus, assessments of treeline shifts are dependent upon an understanding of the mechanisms that limit or constrain seedling establishment at lower treeline.

In southern Arizona, oak seedling establishment occurs infrequently in grasslands below current lower treeline and in the grassland phase of low-elevation savannas (Weltzin and McPherson 1994; fig. 3). Factors that may be responsible for low recruitment include herbivory, interference from herbaceous plants, and climatic and edaphic constraints. These factors, and possibly others, probably interact to produce low seedling establishment rates. For clarity, their effects on

oak seedling establishment will be discussed individually.

Invertebrate herbivory is a potentially important source of seedling mortality that is commonly overlooked in field studies. Although it is rarely mentioned in studies of semi-arid woody plant establishment (e.g., Neilson and Wullstein 1983, Borchert et al. 1989, Brown & Archer 1989, Davis et al. 1991, Williams et al. 1991, Allen-Diaz & Bartolome 1992, Callaway 1992, Hall et al. 1992; but see Adams et al. 1992), invertebrate herbivory is the most common source of mortality in the low-elevation oaks of southern Arizona (McPherson 1993, Peck and McPherson 1994). In Arizona, invertebrates defoliate seedlings primarily during the summer (Peck and McPherson 1994, Eggleston and McPherson unpubl. data). Similarly, mesh exclosures over seedlings during the summer increased survival of *Quercus douglasii* and *Q. lobata* in California (Adams et al. 1992), but effects of exclosures on invertebrate herbivory and water stress could not be separated; evidence from another experiment indicates that shade is critical for establishment of at least the former species (Callaway 1992). Vertebrates kill *Q. emoryi* seedlings primarily during autumn and winter months (Eggleston and McPherson unpubl. data). Temporal and spatial variability in herbivory (McPherson 1993, Peck and McPherson 1994, Eggleston and McPherson unpubl. data), combined with differential population dynamics of different animal species, doubtless contribute to the variability of invertebrates and vertebrates as sources of mortality.

Interference from herbaceous plants also constrains oak establishment. Aboveground interference from herbs slightly reduced seedling survival, but had no effect on growth (McPherson 1993). More importantly, removal of all interference (above- and belowground) substantially increased survival and growth of Emory oak seedlings. Belowground interference impedes survival and growth of oak seedlings in southern Arizona, underscoring the importance of accessing soil resources. Emory oak, like many semi-arid woody species, allocates significant resources belowground in the seedling stage. Rapid early root growth (exceeding 90 cm/year for some individuals; unpubl. data) allows oak seedlings to access soil moisture largely unavailable to herbs (Richards 1986) within a year after germination.

The combination of herbivory and interference from herbs constrains oak seedling survival in the field, and may account for infrequent recruitment beyond the seedling stage in these (e.g., Ffolliott et al. 1992, Borelli et al. 1994) and other (e.g., Griffin 1971, McClaran & Bartolome 1989, Davis et al. 1991) oak woodlands. Other factors (especially climatic and edaphic) have been the subject of considerable speculation, but no experimentation. Thus, interpretation of the relative importance of the latter factors should be conducted with considerable caution.

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

Precipitation and temperature are often considered the climatic factors that most constrain woody plant establishment in grasslands and savannas. McPherson (1993) concluded that during most years in southern Arizona, oak germination and early survival are not constrained by low soil moisture. Subsequent research suggests that variability between sites contributes substantially to differential emergence and early survival (Eggleston and McPherson unpubl. data, Weltzin and
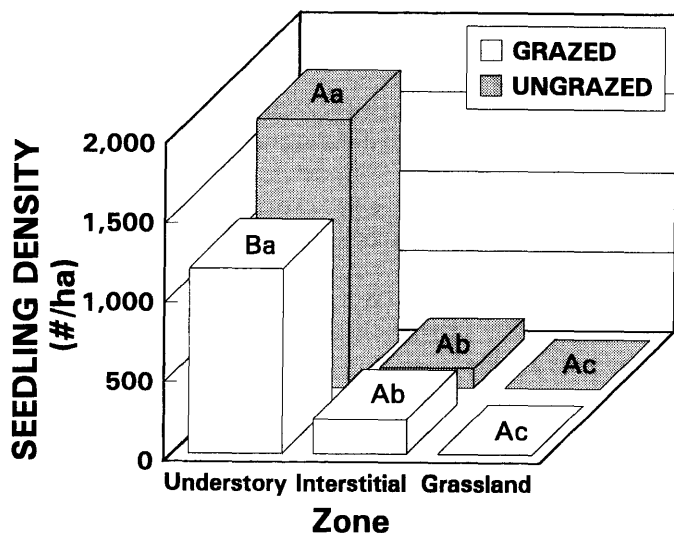

Figure 3.—Mean Emory oak (*Quercus emoryi*) seedling densities (#/ha) under mature Emory oak trees, in grass-dominated interstitial zones between trees, and in semi-desert grassland below lower treeline, for three grazed and three ungrazed sites in the Huachuca mountains of southeastern Arizona (from Weltzin and McPherson 1994). Means within grazing treatment with the same lower-case letter and means within zone with the same upper-case letter were not different (P 0.05).

McPherson unpubl. data). These data hint at the importance of meso-climatic, edaphic and geomorphic factors (and their interactions) in the constraint of woody plant establishment.

The fact that the oak woodland/semi-desert grassland boundary occurs at a wide variety of elevational limits within Arizona (1,200-1,800 m; Brown 1982), coupled with the ability of oak seedlings to establish at locations below the current treeline during some years (McPherson et al. 1993, McPherson 1993, Peck and McPherson 1994, Weltzin and McPherson unpubl. data) suggests that temperature alone does not constrain seedling establishment. However, the influence of temperature on soil water balance is probably critical to seedling establishment. Again, interactions between various factors are doubtless more important than single effects.

It has been suggested that soil argillic horizons constrain establishment of woody plants. McAuliffe (1994) hypothesized that water-impermeable argillic horizons (1) reduce water availability to woody plants in summer below thresholds necessary for survival, or (2) 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.

It should be noted that high rates of woody plant recruitment occur in some systems even when invertebrates are not excluded and herb interference is high. McPherson et al. (1993) demonstrated that Emory oak trees have recently encroached into former grasslands in southern Arizona. Their study investigated the net outcome of various mortality factors interacting on a site (i.e., it was not designed to partition out the relative contributions of various factors), and clearly demonstrated that Emory oak, like many other woody plants throughout the world, has overcome the many constraints on establishment at some time during the past. In fact, preliminary results of a large-scale manipulative experiment in southern Arizona indicate that Emory oak is capable of establishing in the presence of herbaceous vegetation and invertebrates under existing climatic conditions (Eggleston and McPherson unpubl. data).

EFFECTS OF CLIMATE CHANGE

Directional climatic change is often cited as an important factor affecting recent and future redistribution of vegetation types (e.g. Hastings and Turner 1965, Neilson 1986, Mayeux et al. 1991). For example, the world's grasslands may become increasingly susceptible to succession toward woodland as a consequence of anticipated global climate change (Emanuel et al. 1985). Conversely, vegetation communities may shift upslope, with grasslands expanding into woodlands (e.g. Bolin et al. 1986). Results of empirical studies that indicate North American savannas and grasslands have recently converted to woodland (e.g. Archer et al. 1988, Steuter et al. 1990, McPherson et al. 1993) 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 et al. 1990). Further, Neilson and Wullstein (1983) argue that an actual cause-effect relationship between climatic change and biogeographic dynamics has rarely been demonstrated. However, changes in climate, whether similar to or different than those predicted by general circulation models, are almost certain to occur on either local, regional, or global scales (Houghton et al. 1990, 1992).

Climate change will likely affect competitive interactions between species coexisting under current equilibrium conditions (Ehleringer et al. 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 (e.g. Emanuel et al. 1985, Neilson et al. 1989, Melillo et al. 1993, Neilson 1993).

Although climate change has great potential to change the physiognomy of many southwestern landscapes over relatively short time scales (e.g. decades), research to date has focused on historic and geologic shifts in vegetation distribution (e.g. Betancourt et al. 1990, Van Devender and Spaulding 1979). The potential for future vegetation change in the southwestern United States has been largely ignored (with the exception of general circulation models that are too coarse-scaled to be useful for management decisions). Therefore, the following sections describe predicted climate changes, and possible subsequent effects on vegetation and vegetation distribution.

Global and Regional Climate Change

Since the beginning of the 19th century, fossil fuel consumption and agricultural conversion have increased atmospheric carbon dioxide concentrations ($[CO_2]$) ca. 27% (Neftel et al. 1985,

Keeling et al. 1989) and are expected to cause [CO_2] to double by the mid- to late-21st century (Trabalka et al. 1985). Such increases in atmospheric [CO_2] will cause global- and regional-scale changes in environmental conditions (e.g. climate).

Increases in atmospheric [CO_2] are expected to produce an increase in mean global surface temperatures of between 1.5δC and 4.5δC, with a "best guess" of 2.5δC "in the light of current knowledge" (Mitchell et al. 1990, Houghton et al. 1992). CO_2-induced changes in the amount and distribution (or seasonality) of precipitation have also been predicted (Houghton et al. 1990, 1992). General circulation models for central North America predict precipitation increases of 0-15% in winter and decreases of 5-10% in summer. Perhaps more importantly, summer soil moistures may decrease by 15-20% (Mitchell et al. 1990). Although there is broad consensus that seasonal precipitation patterns will change, there is considerable uncertainty about the direction and magnitude of these changes, especially on a regional basis. For example, although Manabe and Wetherald (1986) predict a decrease in summer soil moisture, Schlesinger and Mitchell (1987) suggest that summer precipitation in desert regions may increase.

The potential temporal and spatial magnitude of anthropogenically-induced changes in climate is debated (e.g. Lindzen 1993). For example, there is considerable uncertainty in predictions at local or regional scales (Mitchell et al. 1990). Further, anthropogenically-induced changes in climate may not be directional. For example, changes in climate may result in increased frequency of extreme events (Wigley 1985, Katz and Brown 1992). Also, climate may become more serially correlated which will result in sequences of warm or cold (wet and dry) years and greater overall climate variability (Cohen and Pastor 1991). Almost any change in climate, however, is likely to affect vegetation at the plant, 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 et al. 1993). Ambient temperature affects plants directly and indirectly at each stage in their life cycle (as reviewed in Long and Woodward 1988). Water (i.e. 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 et al. 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, Patterson and Flint 1990, Johnson et al. 1993). 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 (Sionit et al. 1981, Polley et al. 1992, Polley et al. 1993). 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] (Wray and Strain 1987, Bazzaz 1990, Patterson and Flint 1990).

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 (Gifford 1990). For example, photosynthesis and growth of plants in elevated atmospheric [CO_2] may be stimulated by increases in temperature (Sionit et al. 1987, Allen et al. 1989, Grulke et al. 1990, Idso et al. 1987, Idso et al. 1993). Alternatively, temperature may have little or no effect on CO_2-enriched plant growth (Jones et al. 1985, Tissue and Oechel 1987). Nonetheless, a posteriori analysis of vegetation response to CO_2 as mediated by atmospheric temperatures suggests that relative effects of CO_2

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increase with temperature (Drake and Leadly 1991, Idso et al. 1993), perhaps because of upward shifts in photosynthesis temperature optima with increasing CO_2 (Pearcy and Bjorkman 1983). For example, Mooney et al. (1991) predict that elevated CO_2 will amplify the effect of CO_2 enrichment on ecosystem productivity when daytime temperatures are above 30δC, as in the middle-latitude grasslands. Conversely, low temperatures may attenuate CO_2-induced growth enhancement (Hofstra and Hesketh 1975, Sage and Sharkey 1987, Idso et al. 1993). Thus, 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.

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 (Curtis et al. 1989, Davis 1989, Bazzaz 1990, Long and Hutchin 1991, Neilson 1993, Neilson and Marks 1994). For example, it has been hypothesized that increases in $[CO_2]$ may enhance growth and establishment of C3 shrubs in C4-dominated grasslands of the southwestern United States. (Mayeux et al. 1991, Idso 1992, Johnson et al. 1993, Polley et al. 1994). CO_2-induced increases in WUE or fine root biomass (e.g. Norby et al. 1986, Idso and Kimball 1992, Polley et al. 1994) of C3 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 et al. 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 dominated by Emory oak 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 C4 plants (such as grasses) relative to C3 plants (e.g. 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).

Changes in quantity and seasonality of precipitation will also affect competitive interactions between species coexisting under current equilibrium conditions (Ehleringer et al. 1991). For example, increased summer precipitation is hypothesized to favor shallow-rooted grasses over more deeply rooted woody perennials (Eissenstat and Caldwell 1988, Ehleringer et al. 1991). Conversely, predicted increases in winter soil moisture (Manabe and Wetherald 1986, Mitchell and Warrilow 1987) may contribute to the expansion of C3-dominated shrublands into C4-dominated grasslands in the southwestern United States (*sensu* Neilson 1986, Melillo et al. 1993). It is hypothesized that the present distribution of vegetation in the southwest is highly dependent on precipitation (Van Devender and Spaulding 1979). Thus, minor changes in precipitation pattern in this region, especially at ecotones (Neilson 1993), may cause major shifts in plant distribution (*sensu* Stephenson 1990).

Already-observed increases in post-industrial atmospheric $[CO_2]$ have greatly increased production of some plants (Baker et al. 1990, Allen et al. 1991, Polley et al. 1992), although this is debated (Archer 1994, Archer et al. 1994). Further, one explanation for recent increased C3 woody plant abundance in C4 grasslands is based on changes in atmospheric $[CO_2]$ over the last century (e.g. Mayeux et al. 1991, Idso 1992, Idso and Kimball 1992, Johnson et al. 1993). Invasion of woody plants (with the C3 photosynthetic pathway) into C4 grasslands has been accompanied by a 30% increase in atmospheric $[CO_2]$ over the past 200 years. Increases in atmospheric $[CO_2]$ are said to have conferred a significant advantage to C3 species relative to C4 species in terms of physiological activity, growth rates, and competitive ability.

In contrast, Archer et al. (1994) argue that changes in $[CO_2]$ alone are not the proximate cause for observed shifts in woody plant distribution, because (among other arguments) 1) substantial increases in woody plant abundance in grasslands occurred before $[CO_2]$ rose more than ca. 11% over levels of the 1700s; 2) widespread replacement of C3 grasses by C3 shrubs has occurred in temperate zones and cold deserts; and 3) C4 species have quantum yields, photosynthetic rates, and water use efficiencies that are still greater than C3 species, even under current atmospheric $[CO_2]$--thus, there is no historic

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ecophysiological basis for a change in competitive interactions that favored C3 over C4 plants.

Elsewhere, Archer (1994) has argued that direct and indirect effects of grazing by domestic livestock are the proximate cause of woody plant encroachment into arid and semi-arid ecosystems throughout the world. However, Archer et al. (1994) do suggest that interactive effects of post-industrial atmospheric CO_2 enrichment and domestic livestock grazing may have facilitated observed increases in woody vegetation abundance.

In concord with these arguments, we suggest that increased atmospheric [CO_2] has not contributed significantly to historic shifts in lower treelines in the southwestern United States, especially relative to the effects of livestock grazing and fire suppression (Bahre and Shelton 1993, Archer et al. 1994). However, it is unlikely that pre-settlement 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, Westoby et al. 1989, Archer and Smeins 1991). Thus, whereas 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 southwestern grasslands, particularly if these increases are accompanied by shifts in seasonal precipitation or other climatic factors. Thus, we argue that rising atmospheric [CO_2] has the potential to replace grazing and fire suppression as an important regulator of plant community change.

In summary, predicted changes in climate that may occur in the southwestern United States include increased atmospheric concentrations of CO_2, increased surface temperatures, changes in the amount, seasonality, and distribution of precipitation, more frequent climatic extremes, and a greater variability in climate patterns. Increases in atmospheric [CO_2] and possible increases in 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 possible increases in summer precipitation would favor C4 grasslands at the expense of C3 woodlands. However, increases in monsoonal (July through September) precipitation may favor germination and establishment of plant species that reproduce coincident with the monsoon (e.g. Emory oak).

Climate-Induced Changes in Fire Frequency and Extent

Prior to settlement, fire frequencies in semi-desert grasslands were on the order of 10-20 years (Wright and Bailey 1982). Over the last 130 years, however, fire regimes have changed considerably, due to changes in biological, political, and managerial factors and activities. Inadequate fine fuel is the most common constraint on fire spread in semi-desert grasslands--ignition sources are plentiful, and an extended drying period occurs virtually every year (McPherson in press).

Within the last 150 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 et al. 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 et al. 1984), which suggests that the recent (and continuing) spread of these species (e.g. Cox and Ruyle 1986, Cox et al. 1988, Anable et al. 1992) may contribute to increased fire frequency and spread. At least one of these species (Lehmann lovegrass, the most common introduced species) increases after fire (Ruyle et al. 1988, Sumrall et al. 1991), suggesting that a positive feedback pattern may develop (Anable et al. 1992). Therefore, decreased cattle stocking rates coupled with the introduction of exotic grasses could result in more frequent, widespread fires than those that occurred over the last century. Alternatively, the fragmented nature of semi-desert grasslands and more efficient and effective fire suppression activities may constrain the frequency and extent of contemporary and future fires relative to those that occurred a century ago.

Anthropogenically-induced changes in climate are also likely to affect fire frequency and extent. Previously reviewed 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 (Haworth and McPherson 1994), and subsequently reduce fire frequency because of decreased accumulation of fine fuel. Conversely, increased surface temperatures may either increase fire frequency (because hotter, drier conditions cure fuel more quickly), or de-

crease fire frequency (because of decreased fine fuel production caused by hotter, drier conditions). Increases in summer precipitation may increase fine fuel loading and thus increase fire frequency. Obviously, the effects of climate change on fire frequency are difficult to predict, in part because of the paucity of knowledge about future climate change, and also because of interactive effects of climate change, biological factors, and activities related to management and politics.

FUTURE RESEARCH POSSIBILITIES

Considerable research has investigated vegetation change in the southwestern United States. This research has generated many hypotheses (i.e. candidate explanations) regarding shifts in woodland/grassland boundaries, but few of these hypotheses have actually been tested. For example, soil types and characteristics associated with different geomorphic surfaces probably form an important constraint on vegetation distribution in the semi-arid southwest (e.g. McAuliffe 1994), but have yet to be investigated within the Madraen and higher elevation vegetation communities. Fundamental information about soil nutrient availability and spatial and temporal distribution, and processes affecting these phenomena, are generally lacking.

Resource partitioning is another hypothesis widely-invoked to explain apparent long-term stability of savannas and woodlands (e.g. Walter 1954, 1979, Knoop and Walker 1985, Sala et al. 1989, Brown and Archer 1990, Bush and Van Auken 1991). Seasonal patterns in precipitation distribution are thought to allow stable coexistence of woody plants and grasses: woody plants use moisture that percolates through surface layers when grasses are dormant, and grasses take advantage of growing-season precipitation (Neilson 1986, Archer 1989, Lauenroth et al. 1993). Although this hypothesis is intuitively palatable, it has yet to be explicitly tested. If resource partitioning does occur, then shifts in precipitation seasonality caused by atmospheric CO_2 enrichment may affect resource pools (i.e. soil moisture). Changes in soil moisture may in turn affect interactions between trees and grasses where they currently coexist, or may allow one or the other to establish where currently excluded by environmental constraints.

In addition, although research to date (Eggleston, unpubl. data) suggests that vertebrates and invertebrates are both seasonally important

constraints on oak seedling survival, the spatial extent and importance of these mortality vectors has not been determined, let alone the particular species responsible for observed mortality.

The greatest gap in our knowledge about the Madraen oak woodland biome 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 oak woodlands is difficult, given the background of recurrent disturbances and the possible complexity and general paucity of knowledge about regionally-specific climate change (Mitchell et al. 1990). However, the determination of most-likely scenarios of climate change is relatively straightforward, and these may be tested using experimental research designs.

The use of field experiments in ecology is increasing, and Gurevitch and Collins (1994) make a compelling case for continuing this experimental approach. First, manipulative field-based experimental research will help disentangle important driving variables because of strong correlations between factors under investigation (Gurevitch and Collins 1994). Second, identification of underlying mechanisms of vegetation change will enable us to predict vegetation response to changes in driving variables (e.g. climate or land use) with a level of certainty useful to management. Most research conducted in southwestern ecosystems to date has lacked a rigorous experimental approach, which has limited its utility to managers. We join Gurevitch and Collins (1994) in calling for the implementation of appropriately designed experiments that contribute to the proper management of these ecosystems.

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