Ecological Implications of Livestock Herbivory in the West

Editors:

Martin Vavra
William A. Laycock
Rex D. Pieper

Woody Plant Encroachment into Southwestern Grasslands and Savannas: Rates, Patterns and Proximate Causes

Steven Archer

Abstract

Warm temperate grasslands and savannas which characterized many landscapes in southwestern North America at the time of European settlement have been replaced by shrublands and woodlands. These changes in plant life-form composition were coincident with the introduction of large numbers and high concentrations of livestock. While a cause-effect relationship is implied, it is difficult to demonstrate, since most evidence is based on anecdotal historical accounts or descriptions from localized long-term studies, many of which are conflicting. Case studies documenting the rate, pattern and extent of vegetation change are summarized and used to illustrate how historical inconsistencies might be resolved. Where vegetation history is reasonably known, causes for change are evaluated.

Explanations for the proliferation of woody plants and the associated decline of graminoids have typically centered around alterations in climatic, grazing and fire regimes. Each of these factors is addressed individually and in combination. It is argued that: (1) Atmospheric CO_2 enrichment and directional shifts in climate may have occurred, but have not been sufficient, to cause the vegetation changes observed to date; (2) Fire is not necessarily required to maintain grasslands or savannas; and (3) Although herbivory, lack of fire, atmospheric CO_2 enrichment and climate have interacted to produce recent vegetation change, selective grazing by large numbers and high concentrations of livestock has been the primary force in altering plant life-form interactions to favor unpalatable woody species over graminoids. Conceptual models illustrating the role of grazers in directing plant succession are presented in the context of ecosystem resilience, multiple steady states and positive feedbacks.

Introduction

In drylands around the world, including the North American southwest, desertification and/or the replacement of productive grasslands and savannas with shrublands and woodlands dominated by unpalatable species appears to have occurred since European settlement (Table 1). Explanations for these vegetation changes are the

Table 1. Documented instances of increased abundance of woody plants in arid and semi-arid ecosystems in recent history.

Geographic Location and Reference	Encroaching tree/shrub genera
North America	
Arizona	
Brown (1950)	*Prosopis*
Glendening (1952)	*Prosopis, Opuntia*
Humphrey and Mehrhoff (1958)	*Prosopis, Prosopis, Aplopappus, Opuntia*
Hastings and Turner (1965)	*Larrea, Prosopis, others*
Johnson (1962)	*Juniperus*
Martin and Turner (1977)	*Prosopis*
Smith and Schmutz (1975)	*Prosopis*
California	
McBride and Heady (1968)	*Baccharis*
Hobbs and Mooney (1986)	*Baccharis*
Williams et al. (1987)	*Baccharis*
Young and Evans (1981)	*Juniperus*
Kansas	
Bragg and Hulbert (1976)	*Rhus, Cornus, Symphoricarpos, Ulmus, Quercus, Juniperus*
Nebraska	
Steinauer and Bragg (1987)	*Pinus*
New Mexico	
Buffington and Herbel (1965)	*Prosopis, Larrea, Flourensia*
Hennessy et al. (1983)	*Prosopis*
York and Dick-Peddie (1969)	*Larrea, Prosopis, Juniperus*
Montana	
Arno and Gruell (1986)	*Pseudotsuga*
Nevada	
Blackburn and Tueller (1970)	*Pinus, Juniperus*
North Dakota	
Potter and Green (1964)	*Pinus*
Oklahoma	
Snook, E.C. (1985)	*Juniperus*
South Dakota	
Progulske (1974)	*Pinus*
Tieszen and Archer (1990)	*Quercus, Celtis, Fraxinus, Tilia*

Table 1 — continued

Geographic Location and Reference	Encroaching tree/shrub genera
North America (continued)	
Texas	
Archer (1990)	*Prosopis, Condalia, Zanthoxylum*
Bogusch (1952)	*Prosopis, others*
Ellis and Schuster (1968)	*Juniperus*
McPherson et al. (1988)	*Prosopis, Juniperus*
McPherson and Wright (1990)	*Juniperus*
Nelson and Beres (1987)	*Acacia, Larrea*
Smeins and Merrill (1988)	*Juniperus*
Scanlan and Archer (1991)	*Prosopis, others*
Wondzell (1984)	*Larrea*
Utah	
Madany and West (1983)	*Pinus, Juniperus, Quercus*
Sparks et al. (1990)	*Juniperus*
Other	
Humphrey (1958)	various species
Humphrey (1987)	various species
Robinson (1965)	*Tamarix*
Africa	
Acocks (1964)	*Acacia*
Trollope (1982)	various spp.
van Vegten (1983)	*Acacia, Dichrostachys, Grewia*
Skarpe (1990)	*Acacia, Grewia*
Australia	
Burrows et al. (1985)	*Eremophila, Dodonaea, Acacia, Cassia*
Harrington et al. (1979)	various shrub spp.
Booth and Barker (1981)	*Acacia, Cassia, Dodonaea*
Cunningham and Walker (1973)	*Acacia*
Lonsdale and Braithwaite (1988)	*Minosa*
India	
Singh and Joshi (1979)	various spp.
Scandinavia	
Rosen (1988)	*Juniperus*
South America	
Adamoli et al. (1990)	various spp.
Schofield and Bucher (1986)	various spp.

subject of some controversy, as retrogression and desertification can be natural (Haynes 1982), human-induced (Owen 1979, Gornitz and NASA 1985) or a combination of the two (Verstraete 1986). Anthropogenic activities may cause changes independent of climate, or they may reinforce, magnify, or accelerate changes instigated by natural processes. Retrogression associated with disturbance may be mitigated when climatic conditions for a given species are favorable or benign and magnified when conditions are unfavorable or stressful. In many cases, desertification and vegetation change has been coincident with the introduction of large numbers and high concentrations of livestock. However, while a cause-effect relationship is

implied, it is difficult to demonstrate, since most evidence is based on anecdotal historical accounts or descriptions from local, long-term studies, many of which are conflicting. Encroachment of woody plants into grasslands has been widely recognized, but the rates, patterns and dynamics have seldom been quantified.

Shifts in grass and woody plant abundance have broad implications for biodiversity, primary and secondary productivity, soil development and stability, livestock and wildlife composition and carrying capacity, recreational opportunities, water quality and water distribution. Changes from herbaceous to woody plant domination also constitute a potentially important global climate feedback by
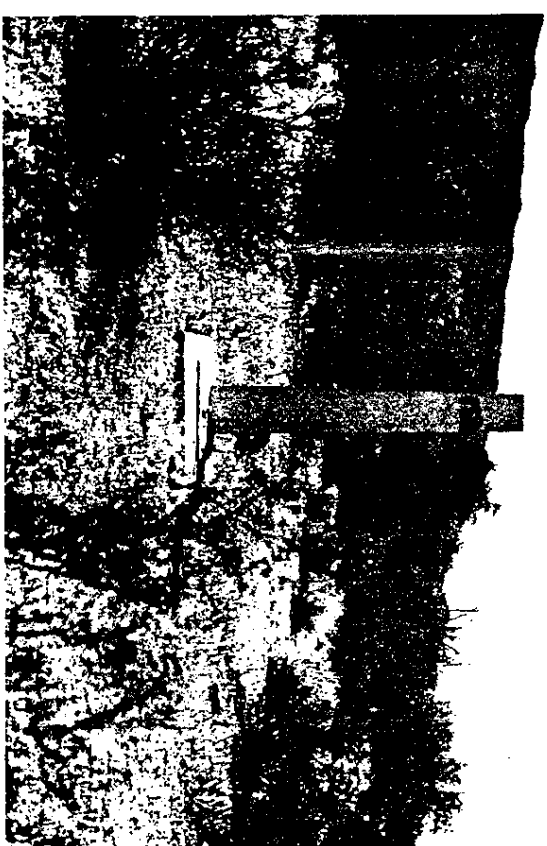
affecting carbon sequestering, non-methane hydrocarbon emissions and biophysical land surface-atmosphere interactions (albedo, evapotranspiration, surface roughness, boundary layer dynamics). As a result, an understanding of factors controlling the balance between grasses and woody plants is fundamental to developing natural resource management plans for sustained utilization of these globally extensive vegetation types.

This chapter will (1) provide a general overview of post-settlement vegetation change in the North American Southwest [see also Hastings and Turner 1965, Branson 1985, Grover and Musick 1990, Bahre 1991], emphasizing shifts from grassland or savanna to shrub- or woodland; (2) discuss why/how grass-woody plant ratios may have changed on some landscapes and not others by evaluating the role of atmospheric CO_2 enrichment, climate, soils, fire and grazing independently; and (3) evaluate proximate causes of shifts from grass-to-woody plant domination in the context of interacting factors.

Rate and Extent of Woody Plant Encroachment

Numerous historical accounts and photographic records indicate that shrublands, woodlands and forests of North America have expanded and replaced what were grasslands and savannas at the time of settlement (Fig. 1b, Table 1). Accounts of early settlers and travelers often describe expansive grasslands and savannas in what are now shrublands and woodlands (Table 2) (Inglis 1964, York and Dick-Peddie 1969, McCraw 1985). Although such historical accounts and historical-modern repeat photography are potentially limited in their information content (Forman and Russell 1983, Bahre 1991:14), they provide one of several types of information from which to gauge vegetation change. Despite some conflicting accounts of the extent of grasslands (Malin 1953) and the fact that woody vegetation may have characterized some landscapes at the time of settlement (Fig. 1a, c; Table 2), it seems unlikely that the livestock industry would have developed and flourished to the extent it did, were the acreages of grazable lands not substantial at the time of settlement. Subsequent studies of vegetation change, utilizing surveyor witness trees and notes, permanent plots, sequential ground and aerial photography, and stable carbon isotopes have documented shifts from grass-to-woody plant domination in recent history (Table 1). Such studies indicate that rates and patterns of this succession have been (1) rapid, with substantial changes occurring over 50- to 100-year time spans, (2) non-linear and accentuated by periodic drought, (3) influenced by topoedaphic factors, and (4) non-reversible over time frames relevant to management.

Factors Influencing Spatial/Temporal Patterns of Grass and Woody Plant Distribution and Abundance

Regional physiognomy and plant life-form distributions largely reflect the prevailing macroclimate (Box 1981). Yet substantial variation occurs across landscapes within a region, as soils, topography and elevation interact against a climate

(A)

Figure 1. Paired photographs illustrating temporal patterns of grass-woody plant abundance. (A) Upper: creosotebush was well-established on this landscape in the Lower Sonoran Desert in 1893; lower: physiognomy has changed little through 1984 (Monument #158 in Humphrey [1987]).
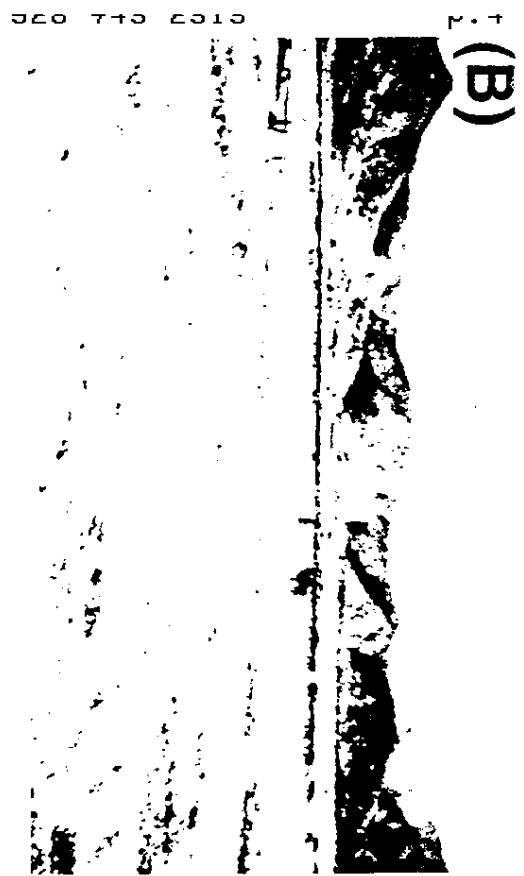
(B)

Figure 1. Paired photographs illustrating temporal patterns of grass-woody plant abundance. (B) Succession from desert grassland in 1903 (upper) to *Prosopis* shrubland by 1941 (lower) at the Santa Rita Experimental Range in southern Arizona (from Martin, 1975:8).
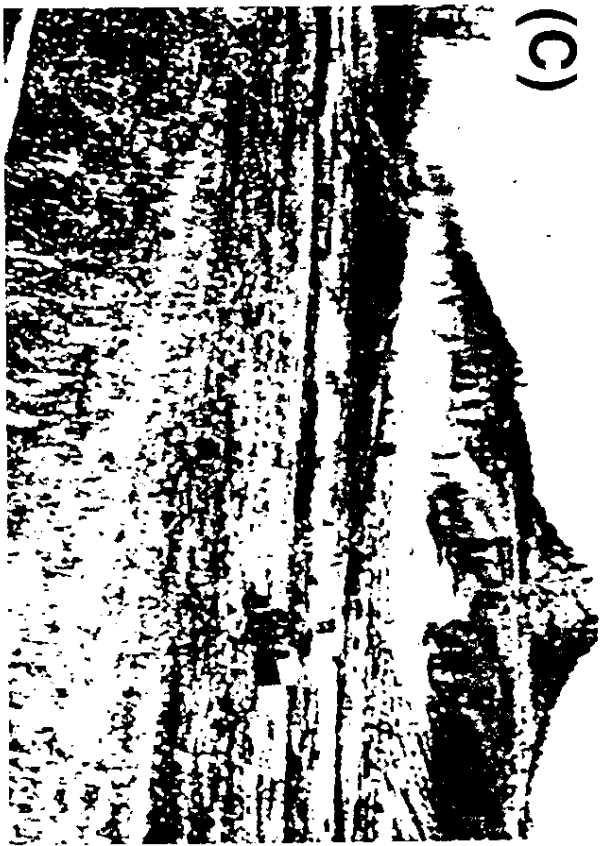

(C)

Figure 1. Paired photographs illustrating temporal patterns of grass-woody plant abundance. (C) Meadows and ponderosa pine (*Pinus ponderosa*) savannas in the Black Hills of South Dakota photographed in 1874 (upper) gave way to closed-canopy pine forest by 1975 (lower) (Progulske and Shidler 1983:104-105).

Table 2. Historical observations indicating differences in local and regional distribution and abundance of woody plant abundance on Texas landscapes. Most landscapes in both regions are presently dominated by woody vegetation.

NORTH-CENTRAL TEXAS (Marcy Expedition of 1854 as seen in Malin, 1953):

". . . nothing could be seen but one continuous mesquite flat, dotted here and there with small patches of open prairie. . . ."

"The country we are now passing is gently undulating and covered with mesquite trees."

"a broad level plain . . . covered with buffalo grass and mesquite trees, and extending as far as the eye could reach. . ."

"[Mesquite often grew] upon the most elevated arid prairies, far from water courses. . . ."

SOUTHERN TEXAS (from Inglis, 1964):

Borders of creeks were well supplied with timber but there was "scarce a brush on uplands" — Lunday (1833), Jim Wells County

"The prairie was now dead level, the grass short...Not a bush or tree was to be seen . . . thousands of antelope. . . ." — Fremantle (1863), Nueces County

"high rolling prairie . . . covered with fine mesquite grass and interspersed with mesquite trees. . . ." — Richler (1849), Nueces County

"open country with mesquites" — Bollaert (1843), Frio County

---

matic background to influence vegetation patterns at smaller spatial scales. Disturbances and the utilization of plants by animals are superimposed on this background of topo-edaphic heterogeneity and climatic variability to further influence vegetation structure. As a result, plant species whose adaptations to prevailing climate and soil would make them the competitive dominants under one disturbance regime may assume subordinate roles or even face local extinction under other disturbance regimes. On grazed landscapes, it is often difficult to assess the extent to which herbivory influences ecosystem processes relative to abiotic factors (McNaughton 1983, Foran 1986). In some cases, comparisons of vegetation change between grazing systems have been shown to reflect differences in climatic conditions rather than differences in management (Herbel 1979, Chew 1982, Heitschmidt et al. 1982). In addition, frequent, small-scale perturbations (such as ant or termite mounds, rodent burrows, dung deposits, patch grazing) occur within larger-scale, less frequent disturbances (fire, floods) to produce a complex disturbance regime (Collins 1987, Coffin and Lauenroth 1990). To realistically understand cause-effect relationships in vegetation dynamics, environmental and disturbance variables must be dealt with simultaneously, in a spatially explicit manner and over a range of time scales. Given the lack of quantitative historical information and the short duration of most ecological investigations, few such studies exist.

The following sections review the independent role of atmospheric CO₂ enrichment, plant life history attributes, climate, soils, fire and grazing on grass and woody plant abundance in dryland ecosystems. The final section discusses interactions between these biotic and abiotic forces and attempts to evaluate conditions necessary and sufficient to elicit a change in vegetation from grassland or savanna to shrub- or woodland.

Atmospheric CO₂ Enrichment

Mayeux et al. (1991), Johnson et al. (1993), and Idso (1992) review an array of literature and data which support their hypothesis that increases in atmospheric CO₂ concentrations since the industrial revolution may have been a driving force for encroachment of woody plants into grasslands. Their arguments are based on observations which indicate: (1) woody plants typically possess the C₃ photosynthetic pathway, whereas the grasses they have replaced in the southwestern USA and tropical regions are primarily C₄; (2) increased atmospheric CO₂ may confer a significant advantage to C₃ species relative to C₄ species with respect to physiological activity, growth and competitive ability; (3) C₄ grasslands appear to have evolved at CO₂ concentrations below 200 ppm and thus at low CO₂/O₂ ratios; and (4) invasion of woody plants into C₄ grasslands has been accompanied by a 30% increase in atmospheric CO₂ over the past 200 years (from ca. 270 ppm to 350 ppm).

To what extent might historic increases in atmospheric CO₂ have contributed to the replacement of C₄ grasslands by C₃ shrublands or woodlands? A robust interpretation of the hypothesis suggests widespread replacement of C₄ grasses by C₃ grasses would also have occurred during this period, controlling for differences in land use and soils. Such does not appear to have been the case. This could reflect the fact that the predicted disparity in C₃ vs. C₄ plant response to increased CO₂ may be minimal. Indeed, recent modeling exercises (Hunt et al. 1991), controlled environment studies (Riechers and Strain 1988) and field investigations (Owensby et al. 1993) indicate C₄ grasses may be very responsive to CO₂ fertilization. The fact that C₃ woody plants have invaded some landscapes while C₄ grasses have persisted on others with similar soils and climate also argues against CO₂ enrichment as a proximate causal factor for community change. In addition, the differential effects of CO₂ enrichment on C₃ woody plants vs. C₄ grasses would not explain the invasion of woody plants into cold desert and temperate landscapes where dominant grasses were also C₃. The temporal correspondence between CO₂ enrichment and woody plant encroachment is also problematic. Although present-day atmospheric CO₂ levels are ca. 30% higher than those 200 YBP, enrichment has been exponential, with a prominent lag phase. In 1903-1925, CO₂ concentrations were ca. 300 ppm (Neftel et al. 1985), an 11% increase over that of the late 1700s. Yet, significant woody plant encroachment had occurred by this time on many sites (e.g., Fig. 1b). Would an 11% increase in atmospheric CO₂ have been sufficient to cause or contribute to woody plant encroachment into grassland? Finally, the extent to which benefits of increased CO₂ will be manifested in enhanced plant growth and competitive ability will be constrained by interactions of other environmental resources, stresses and higher-order ecological interactions (Bazzaz 1990, Mooney et al. 1991). Some data from tree rings indicate a significant CO₂ fertilizer effect on woody plants over the past century (LaMarche et al. 1984). However, others do not (Graumlich et al. 1989, Graumlich 1991), perhaps reflecting feedbacks to plant growth and alteration of biomass allocation patterns (Norby et al. 1992). In sum, these various exceptions limit the utility of the atmospheric CO₂ enrichment hypotheses as a robust explanation of the cause of woody plant encroachment into grasslands.

Life History Determinants

Different patterns of succession (or lack thereof) result from the interactions of species having various combinations of physiological and life history traits (Huston and Smith 1987). The rate, extent and dynamics of CO_2, climate- or disturbance-induced shifts between grassland and shrub- or woodland would be strongly influenced by the life history characteristics of the species involved (e.g., potential growth rate, seed production, rates of seedling establishment, plant size, longevity, shade tolerance). Differences in longevity between grasses and woody plants may be particularly important in accounting for observed patterns of post-settlement succession from grass-to-woody plant domination. Grasses are relatively short-lived in comparison to many woody plants. Maximum life-expectancy of established perennial grass species ranges from 4 to 43 years, with a mean of 3 to 10 years (Canfield 1957, West et al. 1979, Wright and Van Dyne 1976). Longevity in woody plants varies with growth form. Limited evidence suggests a positive correlation between "woodiness" and longevity (e.g., suffrutescent < suffruticose < fruticose < arborescent) and ranges from 22 to >>400 years (West et al. 1979, Vasek 1980, Goldberg and Turner 1986, McAuliffe 1988, Young and Evans 1981). Populations of suffrutescents and small shrubs such as burroweed (*Haplopappus tenuivertus*), bursage (*Ambrosia deltoidea*), cholla cacti (*Opuntia* spp.), four-winged saltbush (*Atriplex canescens*) and catclaw acacia (*Acacia greggii*), may fluctuate markedly in response to amount and seasonality of precipitation, whereas large shrubs and small trees [e.g., mesquite (*Prosopis* spp.), *Acacia constricta*, creosotebush (*Larrea tridentata*), ocotillo (*Fouquieria splendens*), little leaf palo verde (*Cercidium microphyllum*)] with longer life-spans persist for extended periods once established (Shreve and Hinckley 1937, Shreve 1942, Martin and Turner 1977, Goldberg and Turner 1986). For woody plants capable of sprouting, ramets (individual stems or shoots) that succumb to stress or disturbance may be replaced vegetatively, thus perpetuating the genet (individual plant), sometimes for thousands of years (Vasek 1980).

Differences in mean and maximum plant longevities would influence the frequency of gap formation and hence the propensity for community change. Skarpe (1990) cites studies in southern Africa where encroaching small trees and shrubs formed thickets stable for 30-50 years, then died suddenly, followed by the re-establishment of grasses. These short-term (10-50 year) cyclic changes in vegetation associated with disturbance, climatic fluctuation and differences in plant longevities may be missed in widely spaced (50-100 year) matched photographs or inventories of permanent plots (e.g., Gehlbach 1981). Other factors held equal, the availability of gaps for establishment of new plants would be highest for short-lived species with high rates of turnover. Given the generally short life-span of grasses, opportunities for woody plant establishment in gaps vacated by grasses may be relatively abundant, whereas the frequency of gap formation and hence opportunity for grass establishment in a shrubland may be relatively low. Differences in rates and frequencies of gap formation associated with grass and woody plant life-history traits may explain why successional transitions between grass- and woody plant-dominated states are highly asymmetrical (i.e., probabilities (P) of transition from grassland to woody plant domination [P(g→w)] may be high,

whereas P(w→g) is very low) (Scanlan and Archer 1991). The magnitude of gap formation discrepancies in grassland versus shrublands or woodlands would likely increase in response to stress and disturbance. For example, drought may increase mortality and hence gap formation in mesophytic grasses, but have relatively little impact on woody plants tolerant of moisture depravation. Preferential utilization by livestock may increase mortality rates and decrease seed production and seedling establishment of palatable grasses, while seed production, seedling establishment, growth rates and longevity of unpalatable woody plants remains constant or increases (see Livestock Grazing section).

Established individuals may tolerate the range of environmental stresses or disturbances likely to be encountered over a series of decades or even centuries. For example, in Texas the 1950s were characterized by the most severe, continuous droughts since 1698 AD (Stahle and Cleavland 1988). Even so, *Prosopis* spp. survival in southern Texas was observed to be >60% (Carter 1964). Although some subordinate shrubs died back to ground level, they were rarely killed and regenerated vegetatively. In the Edwards Plateau region of central Texas, *Quercus pungens* var. *vaseyana* (shin oak) mortality during the 1950s drought ranged from 7 to 47% depending on soils (Merrill and Young 1959). Shrubs such as *Diospyros*, *Acacia*, *Zanthoxylum*, *Eysenhardtia* and *Berberis* (*Mahonia*) were unaffected, despite *Quercus virginiana* (live oak) tree mortality of 38 to 68%. Older (=large= > 2 m height) *Juniperus* plants experienced about 90% mortality, but the drought induced no mortality in younger (=smaller= < 2 m height) plants. Chihuahuan desert populations of creosotebush experienced reductions in canopy area during the 1950s drought, but density was unaffected (Wondzell 1984). Rapid and large increases in shrub cover occurred in the post-drought period. Thus, severe as it was, the drought of the 1950s does not appear to have produced significant compositional changes or local extinctions of established woody plant populations. Disturbance or climate may therefore trigger episodes of establishment of woody plants, but not necessarily their subsequent extinction (Neilson and Wullstein 1985).

For woody plants with potentially long life-spans and low post-establishment mortality rates, the seedling recruitment phase would be the most critical in dictating the long-term dynamics of community structure. When conditions conducive to seedling establishment occur infrequently and sporadically, identification of determinants of community composition is problematic. Correlations between the distribution and abundance of adult plants and environmental factors may be misleading, since factors relevant and readily studied for mature plants may be quite different from those which determine the fate of seeds or seedlings (Harper 1977:112).

Species that endure chronically or periodically adverse conditions may persist long enough vegetatively to encounter rare or infrequent windows of opportunity for successful seed production, germination and seedling establishment. Recruitment of new individuals during these unpredictable windows may be sufficient to maintain the population and partially or fully compensate for mortality since the last recruitment episode and/or enable a species to increase in density by establishing in gaps left by other species. Jameson (1987) suggested for pinyon-juniper communities that "if during the life span of trees there are several weather events

...ceding to regeneration, a continuing tree stand should develop. On the other hand, if a stand of trees dies before the appropriate weather events leading to regeneration occur, the area of land will be occupied by trees intermittently."

Rates and patterns of woody plant establishment in grasslands would be influenced by physiological attributes of the woody species involved. *Prosopis* and *Juniperus* represent contrasting growth forms whose abilities to compete with grasses should vary markedly. *Prosopis* is a deciduous arborescent capable of N_2-fixation (Johnson and Mayeux 1990) whose seeds are widely and effectively dispersed by livestock (Brown and Archer 1987). *Prosopis* grows rapidly, has high rates of photosynthesis (Sharifi et al. 1982), and produces abundant seed. Seedlings exhibit rapid tap root development and effectively partition soil moisture with grasses soon after germination (Brown and Archer 1989, 1990, Bush and Van Auken 1991a). Within two weeks of germination, *Prosopis* seedlings can resprout following shoot disturbance (Weltzin 1990). A high proportion (>40%) of seedlings 2- to 3-years of age can tolerate temperatures associated with intense prairie fires (Wright et al. 1976). Not unexpectedly, *Prosopis* is an aggressive invader of grasslands not easily eliminated once established. In contrast, junipers are evergreens with slow growth rates, low rates of photosynthesis and possess many other features characteristic of stress tolerant plants. Many species of *Juniperus* cannot regenerate vegetatively and are highly susceptible to fire. However, despite these apparent limitations, it too has successfully invaded grasslands and savannas in recent history (Table 1). This suggests (1) woody plants possess common features that make them aggressive invaders of grass-dominated systems and/or (2) beyond certain thresholds of herbaceous retrogression or disturbance, establishment of contrasting woody growth forms is high and primarily regulated by abiotic factors.

Climatic Determinants

Ecosystem processes are ultimately constrained by climatic variables. Plant growth, microbial activity and soil development are directly influenced by radiation, temperature and precipitation. Climatic limits to the adequacy of particular combinations of leaf and plant size, architecture and longevity, as measured by positive water and energy balances, are among the most important mechanisms of environmental limitation to plant distribution and abundance (Box 1981). Climate also influences ecosystems indirectly, by causing or creating conditions conducive to natural disturbances such as fire (Clark 1988, Baisan and Swetnam 1990, Swetnam and Betancourt 1990), floods, wind-throw, and drought. On world maps, the boundaries of natural vegetation zones, soil types and climate roughly coincide (Fyre 1963, Trewartha 1968, Kuchler 1978, Walter 1979, Box 1981). Regional and global patterns of plant productivity (Rosenzweig 1968, Leith 1972, Sala et al. 1988) and soil organic matter content (Post et al. 1982) have also been related to climate. So strong are the correlations between vegetation and climate, that one is often used to infer the other.

In climate-vegetation models (e.g., Holdridge [1947, 1964] and Whittaker [1975]) grasslands (steppe) and savannas are precariously situated between shrublands, woodlands and forest with respect to mean annual temperature, rainfall and

evapotranspiration. Changes or fluctuations in one or more of these variables would shift the balance between grasses and woody plants and the areal extent of their respective domination. Regions where growth forms are near their climatic fringes would be particularly sensitive to climate change or fluctuation. However, in arid lands, episodic climatic events may mask, confound, override, reinforce or negate changes ostensibly attributed to changes in mean conditions (Beatley 1974, MacMahon 1980, Chew 1982, Griffin and Friedel 1985, Leonard and Judd 1985, Harrington 1991). Changes in the frequency and/or magnitude of extreme events (either favorable or unfavorable for plant establishment) may thus be more important than gradual shifts in mean values (Katz and Brown 1992).

Prehistoric Perspective.

Changes in grass and woody plant abundance since European settlement should be evaluated relative to changes which have occurred over longer time spans, if their significance is to be appropriately gauged and their potential causes understood. Evaluating causes of vegetation change in relation to anthropogenic activities since settlement requires an assessment of the extent to which vegetation was in equilibrium with climate. Were plant communities encountered by early settlers stable and in equilibrium with their environment? When one considers the paleoecological record, the answer would be "probably not." The fossil record, glacial ice cores and historical observations suggest appreciable climatic and vegetation instability on time scales of decades to centuries to millennia. Fossil pollen and pack rat midden data indicate that Late-Wisconsin landscapes of the North American Southwest were characterized by a cool, moist climate and sagebrush and chaparral shrublands, pygmy conifer and oak woodlands, extensive pine parklands and spruce, fir and pine forests (see Martin and Mehringer 1965, Van Devender and Spaulding 1979, Smeins 1984, Betancourt et al. 1990). The warmer, drier climates of the Holocene produced our modern landscapes whose potential natural vegetation was dominated by xerophytic, hot desert shrubs, warm-temperate grasslands and savannas, subtropical thorn scrub and, at higher elevations, oak and conifer woodlands and montane and subalpine forests (Kuchler 1964). However, this overall trend towards increasing aridity was apparently epicyclic rather than gradual and linear, with woodlands, desert grasslands and shrublands alternately expanding and contracting in response to numerous climatic shifts over the past several thousand years (Van Devender and Spaulding 1979, Van Devender 1980). Shifts between grassland and shrub- or woodland communities similar to those observed in historic times thus appear to have happened naturally, apparently in response to climatic fluctuations.

Vegetation Inertia.

The extent to which shifts in vegetation structure lag behind climatic changes that drive them, and the extent to which vegetation can ever be said to be in equilibrium with climate are not easily determined (Davis 1982). Vegetation established from seed under one climatic regime may survive under a subsequent regime in a vegetative state. This phenomenon, whereby perennial plants persist for periods of tens to hundreds of years under conditions very different from those under

which they initially became established, represents biological inertia (Cole 1985, Lewin 1985). In these instances, correlations between recent changes in vegetation and short-term climatic variables or disturbance regimes may be spurious or low. If the present climatic conditions are such that the dominant plants cannot successfully reestablish from seed with sufficient frequency to maintain the population, community composition is destined to change. Neilson (1986) hypothesized that "the pristine vegetation of the Chihuahuan desert recorded 100 years ago, was a vegetation established under and adapted to 300 years of 'little ice age' and is only marginally supported under the present climate." If this hypothesis is correct, climate-driven succession from desert grassland to shrubland may have been in progress at the time of settlement, and augmented by anthropogenic alteration of grazing and fire regimes.

Evidence and Proposed Scenarios for Climate-Induced Vegetation Change.

Studies that utilize long-term records of plant cover and density provide perspectives into vegetation dynamics of long-lived plants not apparent from short-term experimental manipulations. Yet because such data are descriptive and typically lack a "control" it may be difficult to determine causal mechanisms behind change and to clearly sort effects of climate from those of disturbances such as fire and livestock grazing. However, in cases where livestock grazing or fire have been eliminated or experimentally accounted for, climatic influences over grass and woody plant abundance are apparent:

• Branson (1985:16) presents data from Weaver and Albertson that indicate changes in basal area of shortgrass steppe plants associated with light, moderate and heavy livestock grazing regimes were relatively minor in comparison to reductions in cover caused by the drought of the 1930s. Clarkson and Lee (1988) made similar observations in Australia. Rainfall (current and the previous year's) accounted for 69% to 93% of the variance in plant biomass in variously grazed ranges in western New South Wales, Australia (Robertson 1988).

• In the absence of fire, savannas in the Edwards Plateau of central Texas experienced a 2- to 4-fold increase in woody plant cover between 1949 and 1983, with the greatest increases occurring on pastures protected from livestock grazing (Table 3). The relative proportions of woody growth forms changed, with oak (*Quercus spp.*) decreasing and *Juniperus* increasing on all sites (Smeins and Merrill [1988]).

Table 3. Changes in relative cover (%) of *Quercus* and *Juniperus* spp. and changes in total absolute wood plant cover (%) under different grazing regimes on the Edwards Plateau, Texas (from Smeins and Merrill 1988).

Grazing Regime:	Continuous		Rotational		Exclosure	
Year:	1949	1983	1949	1983	1949	1983
Relative Cover:						
Quercus spp.	89	41	90	50	93	41
Juniperus spp.	7	40	4	39	3	32
Total Woody Cover	14	30	10	30	8	35

• Turner (1990) charted two *Prosopis* plants on permanent plots at a Sonoran Desert site inaccessible to domestic livestock and woodcutters in 1960. By 1982 the number of *Prosopis* plants had increased to 186. Most of the recruitment occurred in the early 1970s in conjunction with unusually large rainfall events. In other plots on the site, creosote bush populations declined 50-90% during the first half of this century with little or no recruitment since.

• In the absence of fire, woody plant encroachment occurred in grasslands and savannas characterized by a wide range of herbaceous standing crop, composition, density and/or a wide range of livestock grazing histories, suggesting that climate and soils are capable of supporting woody vegetation including *Juniperus*, *Artemisia* and *Prosopis* (Burkhardt and Tisdale 1969, Bragg and Hulbert 1976, Tisdale and Hironaka 1981, Young and Evans 1981, Johnson 1987, Smeins and Merrill 1988, Brown and Archer 1989 and references therein).

• Increased abundance of woody plants in grasslands and savannas has been geographically widespread (Table 1) and relatively synchronous, suggesting climate as a causal or contributing factor.
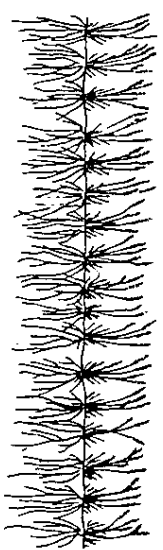
What climate-based scenarios might lead to the demise of grasses and the rise of shrubs such as *Larrea, Juniperus, Acacia* and *Prosopis*? Some combination of the following might elicit a shift from grassland to shrub- or woodland:

• *Increased rainfall.* Walter (1979:92) proposes a scenario for the role of annual precipitation in controlling the mixture of grasses vs. woody plants (Fig. 2). In addition, discrete pulses of high rainfall may trigger episodes of woody plant establishment. In years when surficial soil moisture is abundant, grasses may not competitively exclude woody plant seedlings and an opportunity for root development to exploit deeper and more abundant soil resources may be presented. Once established, woody plants may coexist with grasses in a dynamic equilibrium (tree or shrub savanna) by partitioning soil moisture (Knoop and Walker 1985, Stuart-Hill and Tainton 1989, Sala et al. 1989, Brown and Archer 1990). Alternatively, established woody plants may redirect successional processes and initiate a series of positive feedbacks (allelopathy, shade, soil resource depletion, decreased fire frequency) which eliminate grasses and enable development of shrublands or woodlands (Petranka and McPherson 1979, Archer et al. 1988, McPherson et al. 1988).
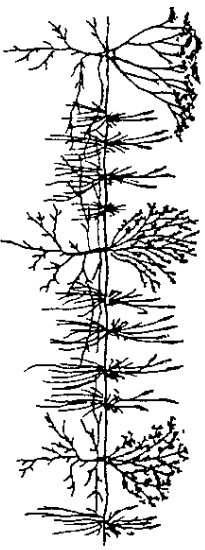
Increased rainfall may also induce shifts from woody plant to herbaceous domination. In the Great Basin of the western United States, extensive dieoffs of suffrutescent salt desert shrubs such as shadscale (*Atriplex confertifolia*) have occurred during and following successive years of above-average precipitation (Pyke and Dobrowolski 1989). Factors potentially contributing to shrub mortality included increased soil salinity and anaerobiosis in the root zone, iron deficiencies associated with increased soil bicarbonate concentrations, outbreaks of parasitic dodder (*Cuscuta spp.*) and soil-borne disease organisms (McArthur et al. 1990). Extended periods of inundation in lowlands of North American Coastal Prairie may periodically eliminate stands of Aca-
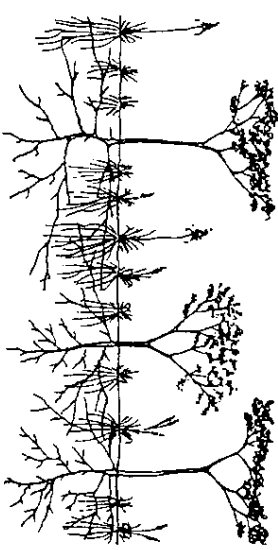
Figure 2. Schematic transformation from grassland to savanna to dry woodland with increasing annual rainfall (from Walter 1979).

SUMMER PPT.

100 mm — Short Grass
200 mm — Mid-Grass
300 mm — Shrub Savanna
400 mm — Tree Savanna

Percent Woody Cover

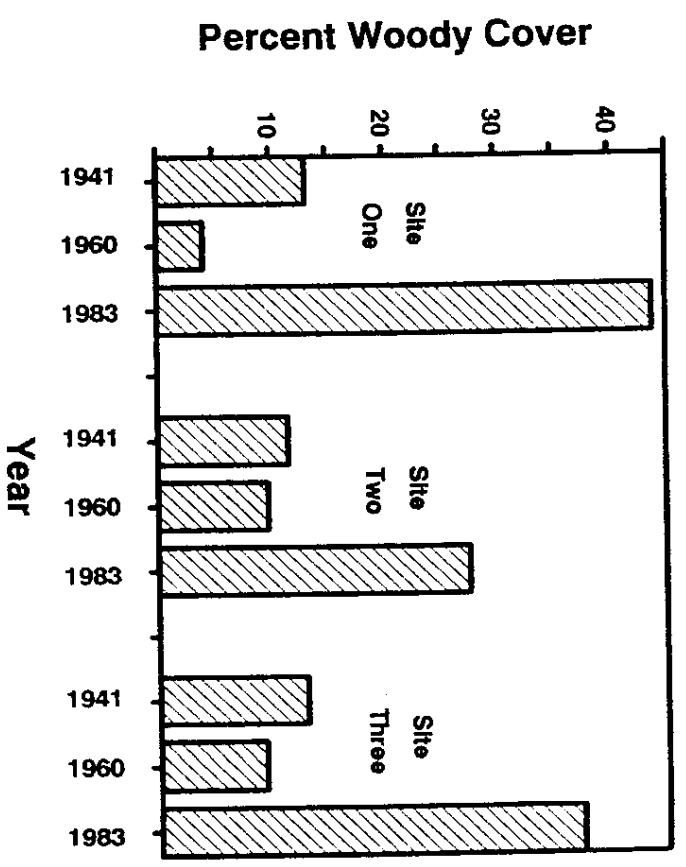Site One, Site Two, Site Three — Year (1941, 1960, 1983)

Figure 3. Changes in woody plant cover, 1941-1983 in southern Texas (from Archer et al. 1988). The 1941-1960 period was characterized by the severe drought of the 1950s; the 1960-1983 period received normal to above-normal annual rainfall.

cia, *Prosopis* and *Quercus* spp. (Scifres and Mutz 1975). In the Amboseli Basin of East Africa, Western and Van Praet (1973) attributed widespread mortality of *Acacia xanthophloea* to salinity associated with elevation of the water table over a series of high rainfall years.

• *Periodic drought.* During drought periods, grass cover, biomass and density decline, reducing the probability of fire and creating unoccupied gaps whose size and abundance would vary with soils and the duration and magnitude of drought (Nelson 1934, Paulsen and Ares 1962, Herbel et al. 1972). Woody plants may preferentially establish in some proportion of these gaps in subsequent pluvial periods (a function of seed bank and seed rain) and persist. Periodic drought may thus set the stage for subsequent episodes of woody plant establishment and canopy development (Fig. 3) (Herbel et al. 1972, Archer et al. 1988, Harrington 1991).

• *Decreased rainfall.* If conditions become chronically drier, grass mortality may increase while seed production and seedling establishment decrease and

the seed bank deteriorates. Resulting gaps may be colonized by woody plants that establish during moist periods and persist by tolerating or avoiding drought stress.

• *Shift in seasonality of rainfall.* Growth of woody plants in many arid and semi-arid systems is favored by cool season moisture, whereas growth and establishment of grasses (especially C_4's) is favored by warm season rainfall (Fritts 1976, Soriano and Sala 1983, Neilson 1986). Similarly, summer droughts may be more detrimental to grasses than woody plants, especially in years where there has been winter rain. When precipitation coincides with temperatures suitable for physiological activity, grasses may utilize soil moisture in upper horizons that might otherwise percolate to deeper depths for use by more deeply rooted woody plants; when precipitation occurs during the dormant or cool season, the soil wetting front may penetrate to deeper depths, and effectively uncouple woody plants with deep root systems from soil moisture conditions in upper horizons. Shifts in seasonality of rainfall and temperature over the past century may have contributed to the expansion of shrublands into southwestern grasslands (Hastings and Turner 1965, Neilson 1986). Shifts from summer to winter precipitation predicted to occur as a result of atmospheric CO_2 enrichment (Mitchell and Warrilow 1987) may increase susceptibility of existing grasslands to woody plant encroachment.

30

• *Shift in size class distribution of precipitation events.* When rainfall occurs as small, frequent events, grasses, with their opportunistic growth habit would be favored, particularly on fine-textured soils (Sala and Lauenroth 1982, Soriano and Sala 1983, Sala et al. 1989, Brown and Archer 1990). More deeply rooted woody plant growth forms would be favored by larger events, especially on coarse textured soils, where moisture may percolate to deeper depths and accumulate beyond the rooting zone of grasses. In addition, soils associated with woody plants typically have higher infiltration rates than soils associated with bunchgrasses and shortgrasses of interstitial zones (Pressland 1973, Thurow 1991) and deep percolation near shrubs may be facilitated via channels created by death of course roots. Larger rainfall events may therefore enhance moisture content of soils associated with woody plants, by influencing the lateral distribution of water between mosaic constituents (i.e., surface runoff and interflow from interstitial patches = runon to woody plant patches w/ greater infiltration and deep percolation) (Parsons et al. 1992).

• *Increased temperature.* Seasonal heat stress would be expected to increase, in conjunction with increased potential evapotranspiration and decreased plant water use efficiency. Stress tolerant shrubs would be more likely to persist under such conditions and potentially expand to occupy sites vacated by mesophytic grasses. Emanuel et al. (1985a, b) have compared contemporary maps of the distribution of Holdridge Life-Zones with maps resulting from changes in mean annual temperature increments predicted by models of climate under elevated CO_2. Their exercise provides an initial test of the sensitivity of the distribution of major vegetation associations to temperature change when other environmental factors were held constant. In tropical and subtropical grasslands, acreages of forest and woodland associations were predicted to increase 13 to 38%, while desert bush acreages in tropical, subtropical and cool temperate regions increased 30 to 67% (Table 4).

There is some evidence of a slight tendency toward increased winter precipitation, higher summer temperatures and an overall warming trend in the Northern Hemisphere from the late 1800s through the 1940s and extended regional droughts in the 1770s, 1860s, 1930s and 1950s (Hastings and Turner 1965, Bryson 1974, Stockton and Meko 1975, Norwine 1978, Mitchell 1980, Neilson 1986, Stahle and Cleaveland 1988). These climate-related factors may have contributed to changes in distribution and abundance of grasses and woody plants on some landscapes in the last 100-200 years.

Edaphic Determinants

Lowe and Brown (1982), in mapping the biotic communities of the Southwest, regarded desertland and grassland as the two "base" formations, encompassing more than 70% of the land area. They further noted that while montane and piedmont communities were subject to strong edaphic control, Great Basin and Chihuahuan desertscrub and semi-desert grassland communities were difficult to delineate as they often intergraded over broad areas. Slight changes in elevation, slope exposure, available soil moisture may therefore influence the local patterns

Table 4. Predicted changes in the areal extent of woody plant associations within tropical and subtropical grasslands and desert shrublands associated with changes in mean annual temperature anticipated to result from atmospheric CO_2 enrichment (from Emanuel et al., 1985a, b).

LIFE ZONE	AREAL EXTENT (X 10^6 KM^2) Base	Predicted	% CHANGE
Tropical Grasslands			
Very Dry Forest	4.7	6.3	+34
Thorn Woodland	2.4	3.3	+38
Subtropical Grassland			
Thorn Woodland	1.7	2.1	+24
Thorn Steppe	5.2	5.9	+13
Desert Bush			
Tropical	2.3	3.0	+30
Subtropical	1.5	2.5	+67
Warm Temperate	4.9	4.7	-4
Cool Temperate	3.6	5.0	+39
Boreal	1.3	2.5	+93
Total	27.6	35.3	+28

of grass versus woody plant distributions. Annual amounts of precipitation and seasonality of rainfall interact with soil texture and depth to influence the relative abundance of grasses vs. woody plants on a site (see Belsky 1991).

The spatial pattern and areal extent of life-form composition shifts from grass- to woody plant-domination (Table 1) is difficult to estimate without knowing something of the pre-settlement distributions. The major woody elements encroaching into grasslands in the North American southwest (e.g., *Prosopis, Larrea, Juniperus, Pinus, Opuntia*) have been present throughout the Holocene and historical accounts (see York and Dick-Peddie 1969, Gross and Dick-Peddie 1979, Malin 1953, Inglis 1964, photographic evidence (see Hastings and Turner 1965, Martin and Turner 1977, Humphrey 1987, Nelson and Beres 1987) and long-term records from permanent plots (Goldberg and Turner 1986, Turner 1990, Wondzell 1984) suggest that shrub and woodland communities may have characterized certain landscape units at the time of settlement (e.g., Fig. 1a, c; Table 2). It seems reasonable to expect that (1) patchy, discontinuous mosaics of grass vs. shrub- or tree-dominated vegetation existed at the time of European settlement, their distributions dictated primarily by topography, soils and fire; and (2) these patches served as sources of population expansion subsequent to changes in climate and/or disturbance regimes. For example, Johnston (1963) argues that the geographic range of honey mesquite (*Prosopis glandulosa*) has changed little over the past 300-500 years and that this plant has merely increased in stature and abundance within its historic range. Some landscapes of southern Texas presently dominated by *Prosopis*-thorn woodlands were described in the early 1800s as open prairies with woody plants confined to areas adjacent to watercourses, suggesting the spread of woody vegetation has been lateral from lowlands and drainages to uplands; in other

31

regions of Texas, *Prosopis* may have been a natural, historical component of upland landscapes (Table 2)(Bogusch 1952, Inglis 1964, Tharp 1926), its density within those landscapes increasing in recent decades. Woody xerophytes such as *Larrea* and *Juniperus* may have historically inhabited shallow, rocky, calcareous erosional sites such as hilltops and ridges prone to runoff, while transport and depositional sites with deeper soils receiving runoff may have supported mesophytic grassland vegetation (Gardner 1951, Hallmark and Allen 1975, Stein and Ludwig 1979, McCraw 1985).

Topography, Texture and Geomorphology

Topography and soil texture, depth, fertility and chemistry can influence patterns of grass and woody plant distribution. Moisture may accumulate and depth to water table may be reduced on intermittent drainages, arroyos and other landscape "run-on" sites, thus favoring woody vegetation. Coarse-textured soils that permit greater infiltration and deeper percolation may enable water to accumulate beyond depths effectively exploited by grasses. These deeper stores of moisture would enable woody plants, with their generally deeper and more extensive root systems, to co-exist with grasses or dominate such sites. Finer-textured soils that retain moisture and nutrients in the upper soil layers generally favor grasses with high root densities in upper horizons by limiting water penetration to lower horizons (see Streng and Harcombe 1982, Johnson and Tothill 1985, Davis and Mooney 1985, Knoop and Walker 1985, Liang et al. 1989, Brown and Archer 1990).

Rates and patterns of woody plant encroachment into grasslands is influenced by topography and texture (e.g., Bragg and Hulbert 1976, McPherson and Wright 1988). Soil texture can also influence patterns of grass and woody plant survival. During the extended and severe drought of the 1950s, Carter (1964) observed highest rates of *Prosopis* mortality on fine-textured soils and lowest mortality on gravelly sites in southern Texas. During this same period, Herbel et al. (1972) observed reductions in grass cover to be greatest on deep, sandy soils and least on soils where cemented caliche layers were relatively shallow. Where topoedaphic conditions are not conducive to development of herbaceous vegetation (extremely shallow and/or rocky, gravelly soils), fine fuels required to initiate or carry a fire would also be lacking. Woody plants inhabit such sites by exploiting fissures and crevasses, thereby accessing resources accumulating beneath such barriers.

Depth to structural barriers such as ironstone or caliche layers can also influence the distribution and abundance of woody vs. graminoid life-forms. Grasses may monopolize resources when soils are present but relatively shallow, with woody plants dominating sites where geomorphic barriers are relatively deeper or where their roots exploit fissures, crevasses or subterranean catchments were water and nutrients might accumulate (Morison et al. 1948, Walter 1979, San Jose and Farinas 1983). Many upland landscapes in central and southern Texas support discrete clusters (mottes) of woody vegetation embedded within a matrix of grasses (Whittaker et al. 1979, Amos and Gehlbach 1988). It appears that these striking contrasts in life-form distributions over small spatial scales are related to subterranean characteristics. For example, field investigations on cluster-soil relationships in southern Texas have revealed that laterally extensive argillic horizons con-

tain inclusions of coarse-textured, non-argillic soils. Where the argillic horizon was present, the vegetation was dominated by grasses interspersed with small woody plant clusters, typically with a single *Prosopis* plant and several subordinate shrubs. Vegetation of non-argillic inclusions consisted of large groves with numerous *Prosopis* trees and subordinate shrubs (Fig. 4c). The favorability of these non-argillic inclusions for woody plants is demonstrated by the fact that *Prosopis* plants in groves were larger and had mean radial growth rates more than twice that of *Prosopis* plants growing on argillic soils (Table 5). In addition, the size and shape of groves coincided with that of the non-argillic inclusions suggesting edaphic constraints to shrub cluster expansion and coalescence (Loomis 1989).

Soil Nutrients

Grasses generally have high densities of fine roots concentrated in upper soil horizons, whereas many dryland trees and shrubs have lower root densities and coarser, deeper root systems. These contrasting rooting patterns suggest grasses may have a competitive advantage for acquisition of surficial soil resources. However, even
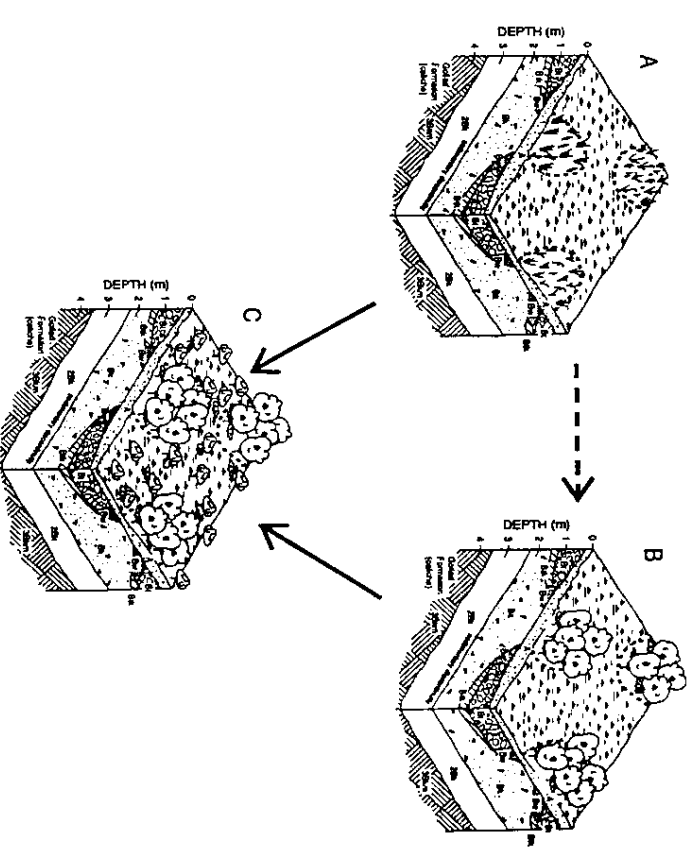

Figure 4. Hypothesized role of subsurface soil texture and grazing in regulating tree (*Prosopis*)-grass distribution in a savanna parkland Texas (Archer, unpublished). The argillic (B_t) horizon on uplands is laterally extensive except where groves occur (Loomis 1989). The savanna parkland physiognomy described at the time of settlement (A or B, Table 2) may have been edaphically regulated. With advent of livestock grazing transpirational grass leaf area and root biomass would have decreased enabling shrubs to establish. In addition, *Prosopis* seed dispersal would have increased and fire frequency would have decreased. Available data suggest mottes and groves began forming about the same time, with plants on the non-argillic inclusions developing faster (Table 5).

34

Table 5. Mean (+SD) size of *Prosopis glandulosa* stems on upland landscapes in southern Texas. *Prosopis* plants in discrete clusters occurred on soils underlain with a distinct argillic (clay) horizon. This horizon was absent within groves (Fig. 4) (Archer and Flinn, unpublished data).

	Discrete Clusters	Groves
Canopy Diameter (m)	6.5 (1.1)	7.2 (2.2)
Basal Diameter (cm)	15.7 (2.4)	24.1 (6.2)
Height (m)	3.7 (0.6)	5.8 (0.7)
Radial Trunk Growth[a] (mm/month)	0.04 (.03)	0.10 (.07)
Trunk Age[b] (yr) Mean	49.3 (11.9)	74.6 (5.5)
Max	64	81

[a] From dendrometer bands over a 2 year period

[b] From annual ring counts (Archer and Flinn 1991, Flinn et al. 1991). Ages *not* adjusted for time required for stems to produce rings at height of cutting; ages are thus underestimated by ca. 5-10 years.

grasses that share similar characteristics in terms of canopy architecture, shoot phenology and root distribution may differ substantially in their ability to compete with woody plants for water and nutrients (Fig. 5) (Eissenstat and Caldwell 1988). Higher cation exchange capacities of shrub roots (mean = 33.5 meq/100g based on survey of 11 species from 9 genera) in comparison to grass roots (mean = 14.7 meq/100g based on survey of 9 species from 7 genera) (Woodward et al. 1984) may also reduce differences in nutrient absorption that might otherwise be expected from differences in growth form root densities. N_2-fixation may also enable Leguminous or Rhamnaceous trees and shrubs to exploit low fertility sites more successfully than grasses (Klemmedson 1979, de Faria et al. 1989, Hogberg 1989, Johnson and Mayeux 1990). Adaptations for nutrient conservation and integrated nutrient use efficiency by evergreen woody plants (slow growth rates, low nutrient demands, low maintenance costs, sclerophylly, low leachability of foliage, low rates of leaf turnover, effective resorption of nutrients from senescing leaves) (Gray 1983, Gray and Schlesinger 1983, Merino et al. 1984, Aerts 1989) may give these growth forms an advantage over deciduous growth forms (Chapin and Shaver 1989, Schlesinger et al. 1990) on nutrient poor sites. Relative to grasses, woody growth forms may thus be better suited to shallow or low fertility sites, or to sites where erosion associated with grazing or other disturbances has reduced fertility. However, other factors held equal, these adaptations to nutrient and water stress tolerance may limit the ability of evergreen trees and shrubs to effectively compete with grasses and other deciduous growth forms on more mesic and fertile sites (Fig. 6) (Grime 1977, 1979; Chapin 1980, Leps et al. 1982, McGraw and Chapin 1989).

Some studies suggest growthform responses to nutrient availability are inversely related to rooting depth and plant longevity (Gray and Schlesinger 1983, Witowski 1989). In tundra communities, the growth response to nutrient additions is generally in the following order: graminoids > deciduous shrubs > evergreen shrubs (Lechowicz and Shaver 1982, Henry et al. 1986). Herbaceous growth forms, with their intercalary and basal meristems, are more plastic in their morphological

35

Relative P Uptake Rate by Shrub 0 ... 1.0
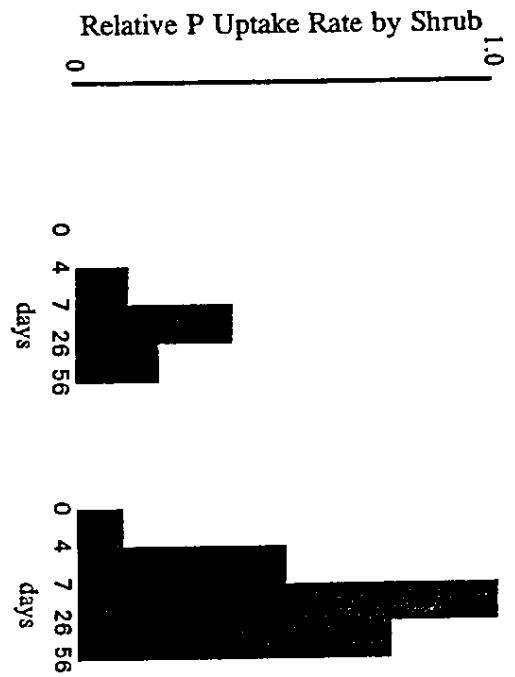
Grass Root Density (cm/cm³) 1.0

Crested Wheatgrass   Big Sagebrush   Bluebunch Wheatgrass
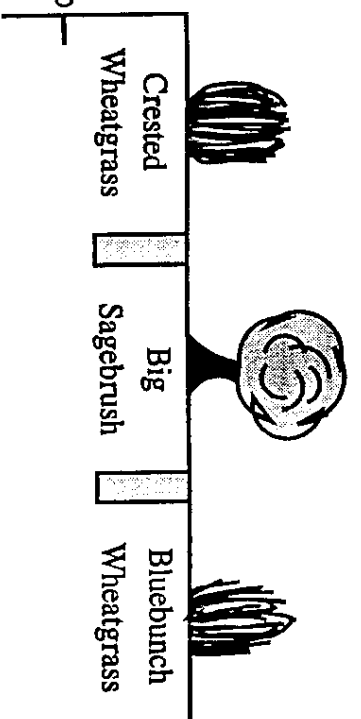
days   0 4 7 26 56

Figure 5. Phosphorus uptake by big sagebrush growing in association with crested wheatgrass vs. bluebunch wheatgrass (from Caldwell et al. 1985). Sagebrush plants acquired significantly more P from bluebunch wheatgrass neighborhoods than from crested wheatgrass neighborhoods, even though these grass species were strikingly similar with respect to root density, shoot phenology and canopy architecture.

growth responses to nutrient and moisture additions than are shrubs and arborescents (Sala and Lauenroth 1982, Soriano and Sala 1983, Knoop and Walker 1985, Aerts 1989, Witowski 1989). Differential life-form growth responses to nutrient availability would ultimately be expressed in community composition. Nutrient additions to Australian heathlands over a period of 20 years produced a shift in species and growth form composition from predominantly sclerophyllous evergreen shrubs to herbaceous species (Heddle and Specht 1975, Specht et al. 1977). Application of N and N+P to Californian chaparral resulted in increased proportions of annuals and graminoids (McMaster et al. 1982).

Given the differences in plant growth form response to nutrient availability, the kinds of woody plants (e.g. evergreen vs. deciduous) that replace grasses may
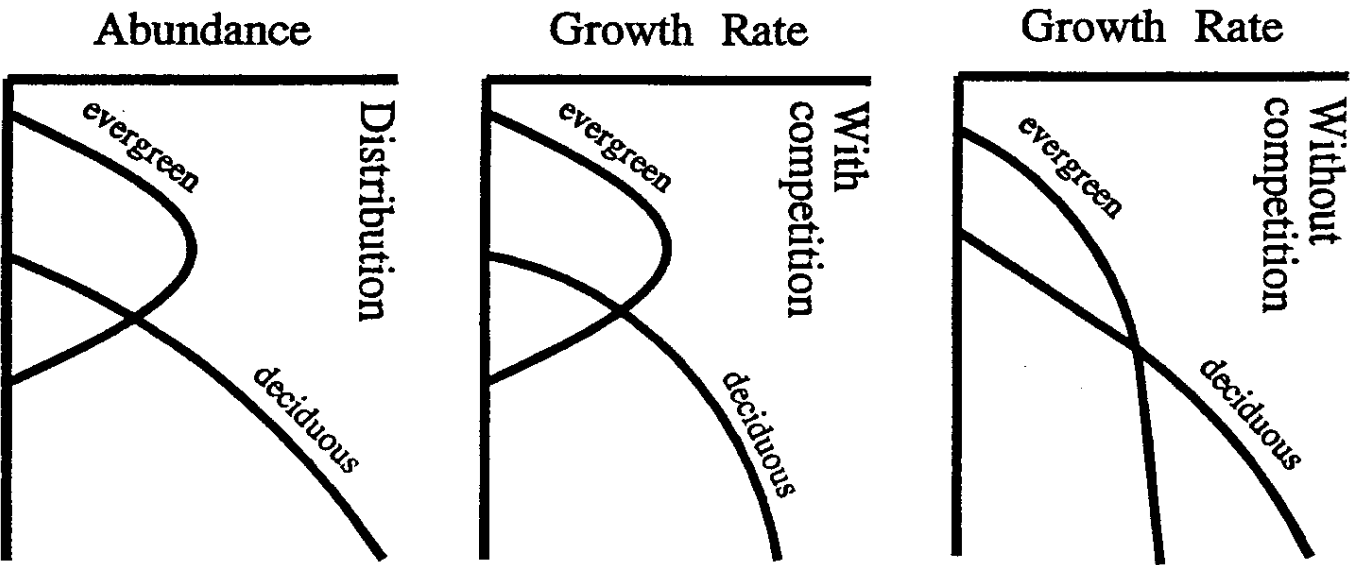
Figure 6. Conceptual model of response of evergreen vs. deciduous plants to nutrient availability (from Goldberg 1982).

depend upon site fertility characteristics (Fig. 6). In addition, the likelihood of succession from grassland to shrub- or woodland, or the reverse, may depend upon the extent to which site fertility and chemistry has been affected by grazing or by other disturbances.

Pyric Determinants

It is commonly assumed that fire is a primary determinant in the creation and/or maintenance of grasslands and savannas. Fires caused by lightning are a potentially frequent occurrence and the active and accidental uses of fire by aboriginals is well-known. However, for such fires to occur, continuity of fine fuels (grasses) must exist, i.e., in order to have a prairie fire, you must first have a prairie (Gleason 1913). This argues for climatic and/or edaphic controls over physiognomy in some systems, with fire playing a secondary role in shaping community structure (Walter 1979:76, 91; Wright and Bailey 1982:82). The extent to which fire occurred in southwestern grasslands is geographically variable and related to seasonal and annual rainfall, elevation, slope aspect and inclination. Fire may have been rare in desert grasslands and limited in areal extent, owing to erratic topography and low biomass and continuity of fine fuels (York and Dick-Peddie 1969, Hastings and Turner 1965). In more mesic grassland and savanna systems where fire was a prevalent and recurring force, pre-historic frequency and intensity appear to have been regionally synchronized by climatic conditions (Swetnam and Betancourt 1990). However, fire frequencies have decreased since settlement, a result of fine-fuel removal by livestock grazing, cessation of ignition by Native Americans and active fire suppression (Young and Evans 1981, Madany and West 1983, Arno and Gruell 1986, Baisson and Swetnam 1990, Savage and Swetnam 1990). Reductions in fire frequency may have enabled fire-sensitive woody species to invade and establish in grasslands and savannas and/or may have enabled fire-tolerant, but suppressed woody species to assume greater dominance and subsequently redirect successional processes by altering soils and microclimate. In cases where woody plants suppress herbaceous production and/or create discontinuities in fine fuel distribution, a positive feedback may develop, whereby the propensity for fire is reduced as additional woody plants establish and assert dominance. On many shrub- and woodlands, the potential for ignition and spread of fire is low, owing to woody plant-induced discontinuity in fine fuel (e.g., McLaughlin and Bowers 1982).

Temporal patterns of fire and soil moisture are the primary factors influencing woody plant-grass biomass ratios in the semi-arid woodlands of Australia (Harrington and Hodgkinson 1986). Under the influence of above-average rainfall in critical seasons, shrub seedling establishment is high (Harrington 1991). However, because such rainfall events also produce an unusually large grass biomass, fire becomes a possibility which, if realized, kills most juvenile shrubs. Grazing may increase the frequency of woody plant seedling establishment by reducing the soil moisture utilized by grasses and by reducing fire frequency. These two factors combine to favor vegetation dominated by woody plants.

With a sufficient fire-free interval, woody plants can eventually overtop grasses and persist despite subsequent fires (e.g., Bragg and Hulbert 1976). The length of the fire free period required for a tree or shrub to reach sufficient size or age to tol-

37

38

crate fire varies among species. Western juniper (*Juniperus occidentalis*) plants less than 50 years old are quite susceptible to wildfires (Burkhardt and Tisdale 1969). In contrast, survival of 2- and 3-year old honey mesquite seedlings exposed to flame temperatures approximating that of hot grass fires exceeded 60 and 90%, respectively (Wright et al. 1976). Only short fire-free intervals would thus be required for its establishment. Recurring fire may have kept *Prosopis* plants low in stature in pre-settlement grasslands, but would not necessarily have eliminated them from a site. Plants thus suppressed might persist for long periods, then enter a rapid phase of aboveground growth (Fig. 7) and overtop the herbaceous vegetation and achieve heights less sensitive to subsequent fire. Trunks and crowns of taller plants may incur minimal damage from surface fires, or, if crowns and trunks are killed, rapid vegetative regeneration from crowns, burls or roots occurs for many species. Following fire, recovery of shrubs may equal or exceed that of perennial grasses (Cornelius 1988). Prehistoric wildfires, which might typically occur at the end of the growing season when dry litter has accumulated and air temperatures are high, may have been more effective in causing woody plant mortality than prescribed fires implemented during cooler periods. However, reductions in grass production, basal area and survival following late-summer fires (Ewing and Engle 1988) may also generate windows of opportunity for invasive species.

PROSOPIS GROWTH (1984-1991)
Overall Survival 31-35%

PLANT HEIGHT (cm)

Grazed Site — n = 247
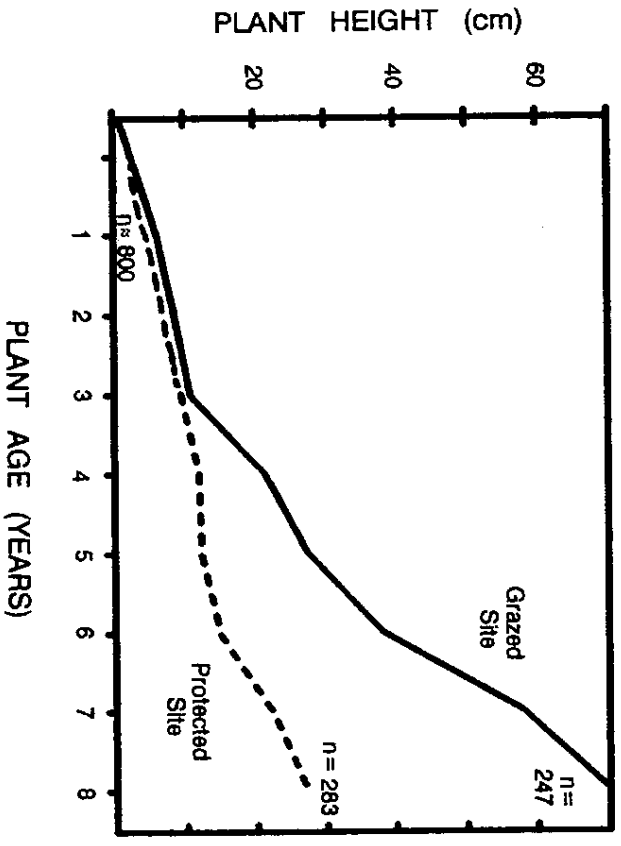
Protected Site — n = 283

n ≈ 800

PLANT AGE (YEARS)

Figure 7. Recruitment and growth of *Prosopis glandulosa* seedlings on sites with contrasting long-term grazing histories and differing in herbaceous biomass production and composition (Archer, unpublished). See Brown and Archer (1989) for details on site characteristics and emergence and survival over first two years. About 800 seedlings emerged on each site; after 8 years, survival was highest on the site protected from grazing (283 vs. 247 plants) but growth rates were greatest on the grazed site. Note lack of shoot development for first 3-4 years on both sites.

Herbivore Determinants

Changes or fluctuation in broad-scale climatic regimes or atmospheric CO_2 enrichment in recent history cannot account for small-scale vegetation patterns and cannot explain why grasslands and savannas have persisted on some landscapes within a region, but not others. As spatial and temporal frames of observation are diminished and resolution increased, edaphic heterogeneity and disturbance assume greater importance in determining vegetation structure (Prentice 1986). The utilization of plants by animals is superimposed on a backdrop of topoedaphic heterogeneity and climatic variability to influence ecosystem processes. As a result, plant species whose adaptations to the prevailing climate and soils would make them competitive dominants of the community when herbivore populations are low may assume subordinate roles or even face local extinction as levels of herbivory increase.

Native Herbivores

Numerous examples exist to illustrate the role of vertebrate and invertebrate herbivores in regulating vegetation structure, composition and productivity (see special issue of BioScience 38 (11) [1988] on "How Animals Shape Their Ecosystems"). Specific examples illustrate how browsing mammals can maintain grasslands, meadows and savannas and/or change closed woodland, thickets or heathland into open, grass-dominated systems (see Crisp and Lange 1976, Sinclair and Norton-Griffiths 1979, Hunter et al. 1980, Belsky 1984, Berdowski 1987, Yeaton 1988, Cantor and Whitham 1989). Patterns of Holocene vegetation development subsequent to extinction of megafauna (Martin 1975, Lundelius 1976) were potentially much different from those which would have occurred had these herbivores persisted. The conversion of open, park-like woodlands and mosaic grasslands of the Pleistocene to the more uniform forests, shrublands and grasslands of today may, to some extent, reflect faunal extinctions and alteration of browsing and seed dispersal influences (Janzen 1986, Owen-Smith 1987).

Differential levels of grazing, browsing, and granivory on grasses and woody plants by various classes of herbivores can be a locally important control over vegetation composition. However, the influence of various classes of herbivores (e.g., root-feeding nematodes, grasshoppers, termites, rodents, lagomorphs, jackrabbits) on vegetation relative to that of more conspicuous ungulate herbivores is difficult to assess. When taken into account, the influence of native herbivores on vegetation can be pronounced. For example, in the 12 years following removal of kangaroo rats (*Dipodomys* spp.) from a Chihuahuan Desert site in southeastern Arizona, the cover of tall grasses increased (Fig. 8), bare ground decreased, litter accumulated and snow cover persisted longer relative to plots where kangaroo rats remained (Brown and Heske 1990). Exclusion of livestock only produced no significant or detectable change in vegetation during the same period. The herbaceous vegetation maintained by kangaroo rats (shortgrasses, annuals) may be less effective at competitively excluding woody vegetation. In addition, kangaroo rats may be an important agent of woody plant seed dispersal (Reynolds and Glendening 1949, Reynolds 1954). Changes in vegetation ostensibly attributed to livestock may thus be similarly effected by activities of less conspicuous rodent herbivores.

39

40

Cover %

Perennial tallgrasses

Annual grasses

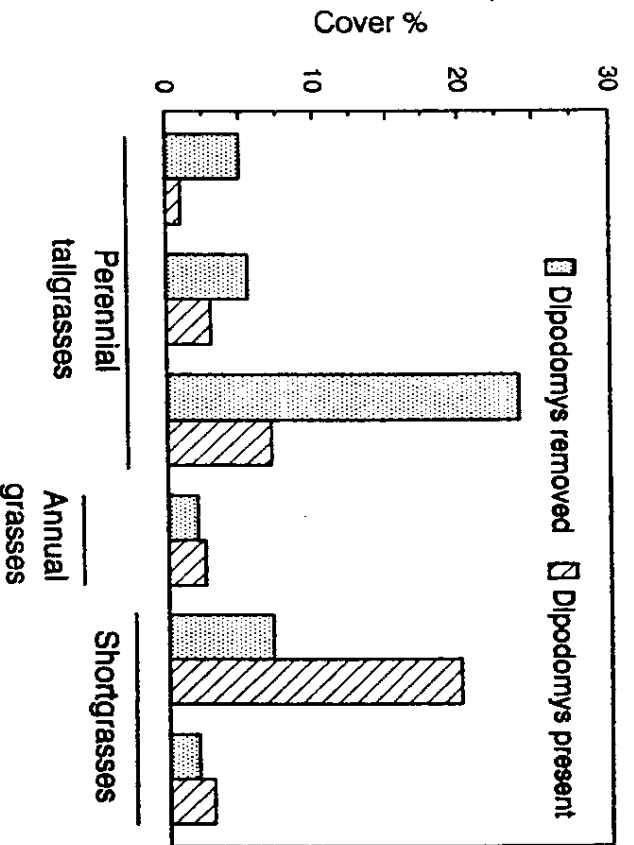Shortgrasses

☐ Dipodomys removed   ☒ Dipodomys present

Figure 8. Differences in perennial tall and shortgrass cover on Chihuahuan Desert sites with kangaroo rats (*Dipodomys* spp.) and after 12 years of *Dipodomys* exclusion (from Brown and Heske 1990).

Prairie dogs (*Cynomys spp.*) represent another example of a once wide-spread native herbivore whose activities are known to influence grassland patch structure, nutrient cycling and feeding-site selection by other herbivores (Whicker and Detling 1988 a, b). However, their role in regulating the distribution and abundance of trees and shrubs in grasslands has not been widely considered. Available data (Weltzin 1990) suggests that on landscapes otherwise suited for woody plants, recruitment of trees and shrubs would be minimal when prairie dogs were present (Fig. 9). Spatial/temporal variation in prairie dog distribution may help explain inconsistencies in historical accounts of woody plant distribution and abundance. Elimination of prairie dogs from landscapes by natural (drought, famine, disease) or anthropogenic (poisoning) causes would remove a primary and locally pervasive mortality factor and either release suppressed populations of woody plants or make new habitats available for their colonization.

Livestock

Utilization of grassland vegetation by domesticated and feral livestock in southwestern North America dates back to the 1500s (Lehman 1969, Wagoner 1949, Hastings and Turner 1965, Jordan 1981, Hanselka and Kilgore 1987, Wagner 1989, Robinett 1990). By the early 1900s, uncontrolled grazing by horses, sheep, cattle and burros had so degraded vegetation and soils that federal legislation (the Taylor Grazing Act of 1934) was enacted in an attempt to curtail further deterioration (Stoddart et al. 1975). Scenarios paralleling those of the North American Southwest occurred in Australia (Harrington et al. 1979) and South America (Schofield
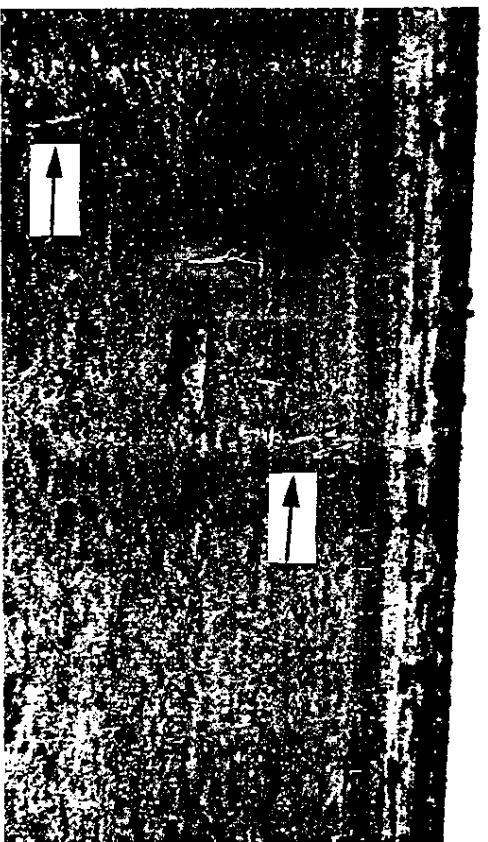
41

(A)

Figure 9. (A) Landscape in the Rolling Plains of northern Texas illustrating a grassland maintained by prairie dogs (*Cynomys ludovicianus*) and a *Prosopis* shrubland off-colony. Seedlings and transplanted *Prosopis* saplings were eliminated on-colony, unless protected by exclosures (arrows denote transplanted saplings). Seedlings and saplings planted off-colony had high rates of survival both in and out of exclosures. (B) A prairie dog colony on this landscape was poisoned out in 1950. Aerial photographs from the late 1940s showed this site to be grassland with scattered *Prosopis* trees. By the time of this photograph (1989) a *Prosopis* woodland had developed. See Weltzin 1990 for additional details. (Photo by S. Archer).

and Bucher 1986, Bucher 1987). The widespread invasion of woody plants into grasslands, "thicketization" and increases in their stature and density in savannas (Table 1) typically coincide with the development of the livestock industry and intensification of grazing.

Grasslands of the Great Plains and southwest evolved with grazing animals. Yet, in contrast to native herbivores whose numbers or patterns of grazing may vary widely, concentrations of domestic livestock can be artificially maintained at consistently high levels by supplemental feeding and watering and by protection from natural predation and disease. Fences prevent migration to new areas when the abundance of preferred forages decreases, resulting in higher frequencies and intensities of defoliation and maintenance of grazing pressure over a greater portion of the year and over a higher frequency of years than might otherwise occur. The end results can be radical changes in species composition and significant soil erosion that are not reversible over time-frames relevant to management. The impacts of domestic herbivory on plants (see Archer and Smeins 1991, Thurow 1991, Skarpe 1991, Pieper, this volume) have been recently reviewed. In this section, factors contributing to the replacement of grasses with woody plants are considered.

Preferential utilization of grasses variously tolerant of defoliation alters plant competitive interactions in a community and changes patterns of resource distribution and availability. Grazing by livestock can potentially increase the probability of woody plant recruitment in numerous, self-reinforcing ways:

• Livestock may effectively disperse woody plant seeds, particularly those of some leguminous shrubs and arborescents (see Brown and Archer 1987).

• Increased light levels at the soil surface could increase chances for germination and early establishment of woody seedlings.

• Concomitant reductions in transpirational leaf area, root biomass and root activity associated with grazing of grasses can

• increase surficial soil moisture (Archer and Detling 1986) to enhance woody seedling establishment and growth of shallow-rooted woody species

• increase the amount of water percolating to deeper depths and benefit established woody species with deep root systems

• increase nutrient availability to woody plants (Fig. 10)

• "release" suppressed populations of established tree or shrub seedlings (e.g., Merz and Boyce 1956, Harper 1977:634, Grubb 1977, Hara 1987) (Fig. 7)

• Grazing decreases plant basal area, increases mortality rates and decreases seed production and seedling establishment of palatable grasses (e.g., O'Connor 1991, O'Connor and Pickett 1992). Grazing may also increase susceptibility of grasses to other stresses such as drought (Nelson 1934, Paulsen and Ares 1962, Herbel et al. 1972, Clarkson and Lee 1988). These factors would combine to increase the rate of gap formation and available area for woody plant seedling establishment, especially in post-drought periods.

Artemisia tridentata

P-isotope from side with clipped grass (%)

[Graph showing P-isotope (%) axis from 30 to 100 vs. Time (days) 0, 7, 14, 21, 28, with curves labeled A. spicatum and A. desertorum]
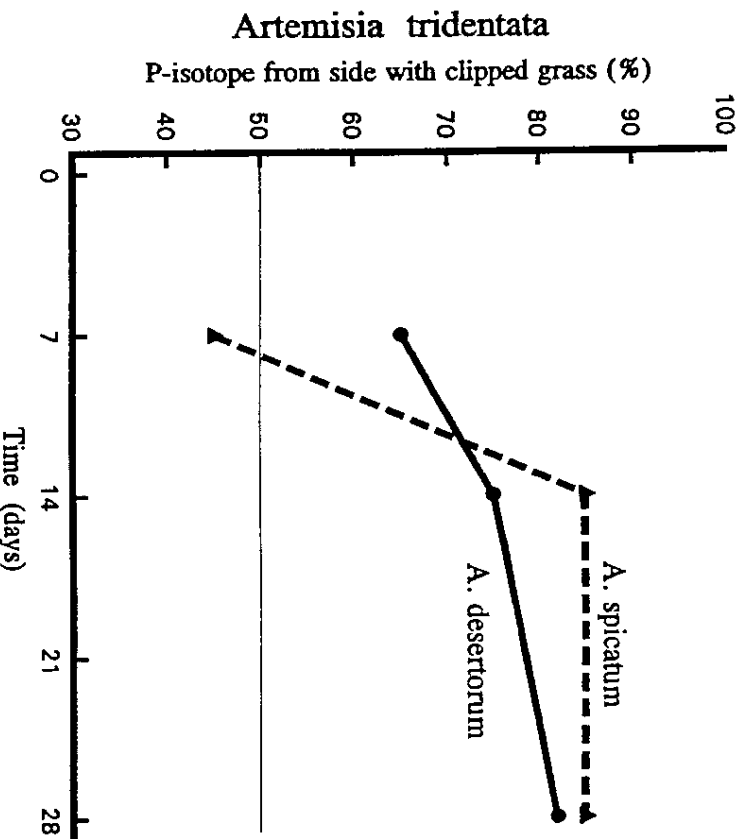
Figure 10. Phosphorus uptake by *Artemisia tridentata* plants with defoliated vs. non-defoliated *Agropyron spicatum* and *A. desertorum* neighbors (from Caldwell et al. 1987). P-uptake by *Artemisia* increased significantly from the side with defoliated grass plants within one week.

• Shifts in herbaceous composition accompanying grazing may be to assemblages less effective at sequestering resources and competitively excluding woody plants or limiting their growth and seed production.

• Reductions in fine fuel biomass and continuity would reduce fire frequency and intensity (Savage and Swetnam 1990).

• Invading woody species are often unpalatable relative to grasses and forbs and are thus not browsed with sufficient regularity or severity to limit establishment or growth.

• Reductions in soil fertility and alterations in physicochemical properties occur with loss of vegetative cover and erosion (Harrington et al. 1979, Denevan 1967, Thurow 1991). This would favor N_2-fixing woody plants (e.g., *Prosopis*, *Acacia*) and growth forms tolerant of low nutrient conditions (Cohn et al. 1989, Bush and Van Auken 1989, Van Auken and Bush 1989)(Fig. 6).

• Widespread eradication of prairie dogs, viewed as competitors with livestock for forage and whose burrows pose injury hazards, would have removed a significant barrier to woody plant recruitment on many landscapes (Weltzin 1990).

44

Modification of microclimate, plant competitive interactions, soil fertility and fire frequency associated with the defoliation and preferential utilization of grasses can thus result in increased likelihood of successful woody plant invasion, establishment and growth (Fig. 7)(Blackburn and Tueller 1970, Bush and Van Auken 1990, Van Auken and Bush 1987,1988, 1990, McPherson et al. 1988, Brown and Archer 1989, Owens and Norton 1989, McPherson and Wright 1990, Skarpe 1990), decreased time to reproductive maturity (McPherson and Wright 1987), increased frequency and magnitude of seed production, and extended woody plant longevity (West et al. 1979).

The rate, pattern and extent of livestock-induced change in community structure would be expected to vary with the type of animal and degree of grazing pressure (stocking rate, frequency, duration, season and intensity of plant utilization). Within a landscape or watershed, livestock grazing pressure is effectively controlled by distance from water and by topography (Andrew 1988, Stuth 1991). Vegetation change on grazed landscapes may be accentuated or mitigated, depending on climatic influences (see **Climatic Determinants** section) and may be non-linear and abrupt once critical disturbance thresholds are exceeded (Figs. 3 and 11). Once established on a site, woody plants may re-direct successional processes and persist, despite subsequent relaxation of grazing (Archer and Smeins 1991, Laycock, this volume).

The effects of livestock grazing may be most important in influencing establishment of woody plant seedlings. Most research on woody plant germination and establishment has focused on abiotic factors. Studies of woody plant seedling establishment in competition with grasses are often short-term or involve potted plants with restricted rooting volumes experiencing relatively low light intensities and (likely) artificially high CO_2 concentrations. Field investigations pertaining to biotic limitations, are scarce. Based on controlled-environment experiments and non-experimental field observations, it has been generally assumed that established, climax-dominant grassland species would exclude woody seedlings and that grazed areas are more prone to woody plant invasion, other factors held equal. There are few guidelines for relating changes in woody plant seedling establishment probabilities to grazing intensity. It is also well-known that herbaceous retrogression accompanies intensive grazing, yet there are few reliable guidelines for determining how grazing at different stages of retrogression alters susceptibility of sites to invasion by woody plants. In the case of honey mesquite, field experiments and diverse field observations indicate that level of grazing and grazing history may have little influence on *Prosopis* seedling emergence or survival in present-day systems (Brown and Archer 1989 and references therein; but see Bush and Van Auken 1991b). Thresholds of herbaceous biomass production or composition required to limit establishment of some woody seedlings may thus be exceeded even at low levels of grazing. However, site grazing history and herbaceous composition markedly influence *Prosopis* growth rate and time to reproductive maturity (Fig. 7).

Given the potential ability of *Prosopis* to successfully establish in stands of highly productive, late seral grasses, why has its abundance within its historic range increased since settlement? One hypothesis is that prior to settlement and the intro-
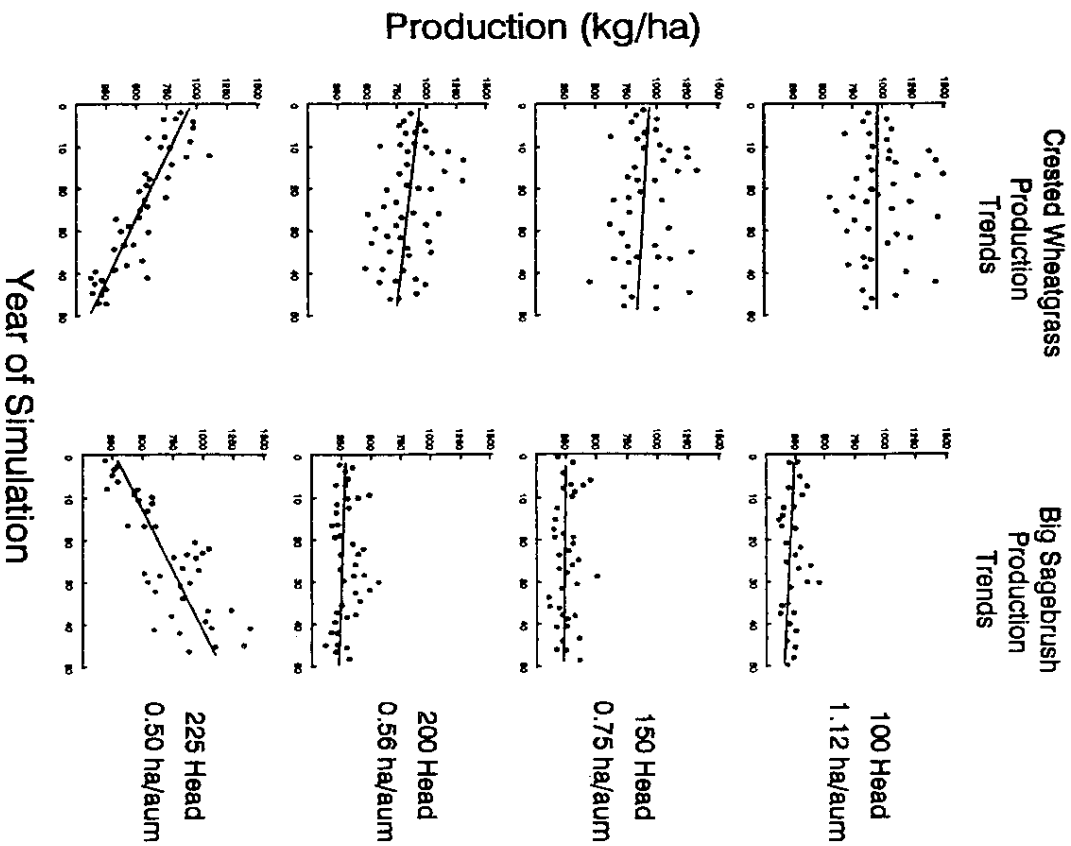
duction of livestock, *Prosopis* was absent from grass-dominated portions of the landscapes because of dispersal limitations (Brown and Archer 1987). Alternatively, *Prosopis* may have been present, but suppressed (not eliminated) by herbaceous competition and periodic fire (see Pyric Determinants section). With the advent of livestock grazing, seed dispersal would have been greatly increased, competition from grasses would have been relaxed and set-backs associated with periodic fire eliminated. *Prosopis* plants would then have rapidly increased their stature and dominance.

Production (kg/ha)

Year of Simulation

Crested Wheatgrass Production Trends

Big Sagebrush Production Trends

100 Head
1.12 ha/aum

150 Head
0.75 ha/aum

200 Head
0.56 ha/aum

225 Head
0.50 ha/aum

Figure 11. Predicted changes in crested wheatgrass and big sagebrush production under different stocking rates (from Torell 1984). Doubling the number of animals from 100 to 200 had little impact on production. However, increasing stocking from 200 to 225 head (12.5% increase) had a marked impact.

45

Evaluation of Proximate Causes of Woody Plant Invasion

The preceding sections highlight the potential independent role of climate, atmospheric CO_2, soils, fire and herbivory in regulating the balance between grasses and woody vegetation. Three important concepts in evaluating the relative contribution of these factors are: (1) interactions; (2) necessary and sufficient conditions; and (3) feedbacks. Case studies indicate that direct and indirect effects of livestock grazing (including reductions in fire frequency), augmented by climatic fluctuation, are reasonable explanations for replacement of grasslands and savannas by shrub and woodlands.

Interactions

In experimental manipulations, the significance of main effects and interactions are tested. In an ecosystem context, we are interested in identifying the primary factors governing ecosystem processes (i.e. the main effects) and the extent to which the influence of those primary factors might be mediated (lessened or magnified) when other factors are operational (i.e., interactions). Main effects, in the context of identifying factors controlling grass vs. woody plant composition, would include climate, soils, fire and grazing. Unfortunately, because of logistical constraints, most experimental research has focused on but one of these main effects.

Results from such studies are thus out of context, since other potentially important factors and interaction terms are not taken into account. Simulation models are one tool for circumventing this problem. However, the degree to which such models can successfully represent a system will be directly related to our level of understanding and the quality and availability of information used in their construction. Conceptual models of woody plant encroachment into desert grassland (Fig. 12), sagebrush steppe (Fig. 13), *Prosopis* savanna (Fig. 14), and pinyon-juniper savanna (Fig. 15) illustrate the variety of factors that have interacted since settlement to produce the current vegetation. The driving force for the changes depicted in each of these models centers around livestock grazing.

Necessary and Sufficient Conditions

It is necessary for some conditions to change if ecosystems are to change. However, because of thresholds, inertia and negative feedbacks, a change in some conditions does not necessarily mean that a change in ecosystem status will occur. Thus, certain kinds of changes may be necessary, but by themselves are not sufficient to elicit a change in ecological systems. The influence of changing a certain variable(s) on ecosystem structure will be determined by the magnitude, direction and duration of the change and the extent to which the change is either augmented or negated by other variables.

Figure 3 shows changes in woody plant cover at a savanna parkland site in southern Texas. The site had experienced continuous, high levels of cattle grazing since the late 1800s, extending through the early 1980s. During the severe drought of the 1950s, woody cover decreased on all three sites. In the subsequent period characterized by normal to above-normal annual rainfall, woody cover increased 3- to 4-fold. Would an increase of this magnitude have been observed at pre-settlement
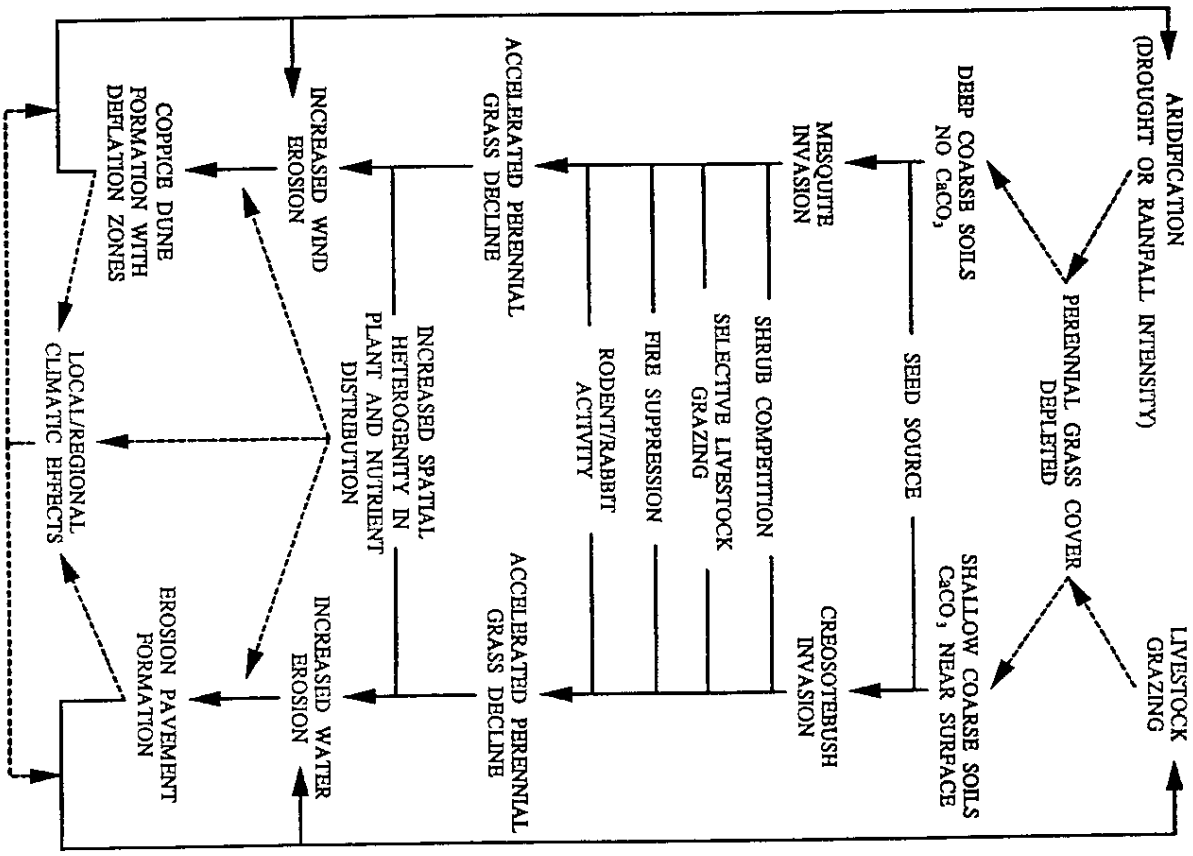

Figure 12. Conceptual model of *Prosopis* and *Larrea* invasion of desert grassland (from Grover and Musick 1990).

levels of atmospheric CO_2? Drought, with its adverse affect on grasses, may have been necessary to set the stage for woodland expansion, but would drought acting alone have been sufficient to produce the pattern and magnitude of change observed? Grazing by livestock during the drought period likely increased grass plant susceptibility to drought-related stresses. In addition, *Prosopis* pod production during the drought period was likely maintained or even stimulated (El Yousfi 1991). Utilization of pods and subsequent dispersal of seed by livestock dur-
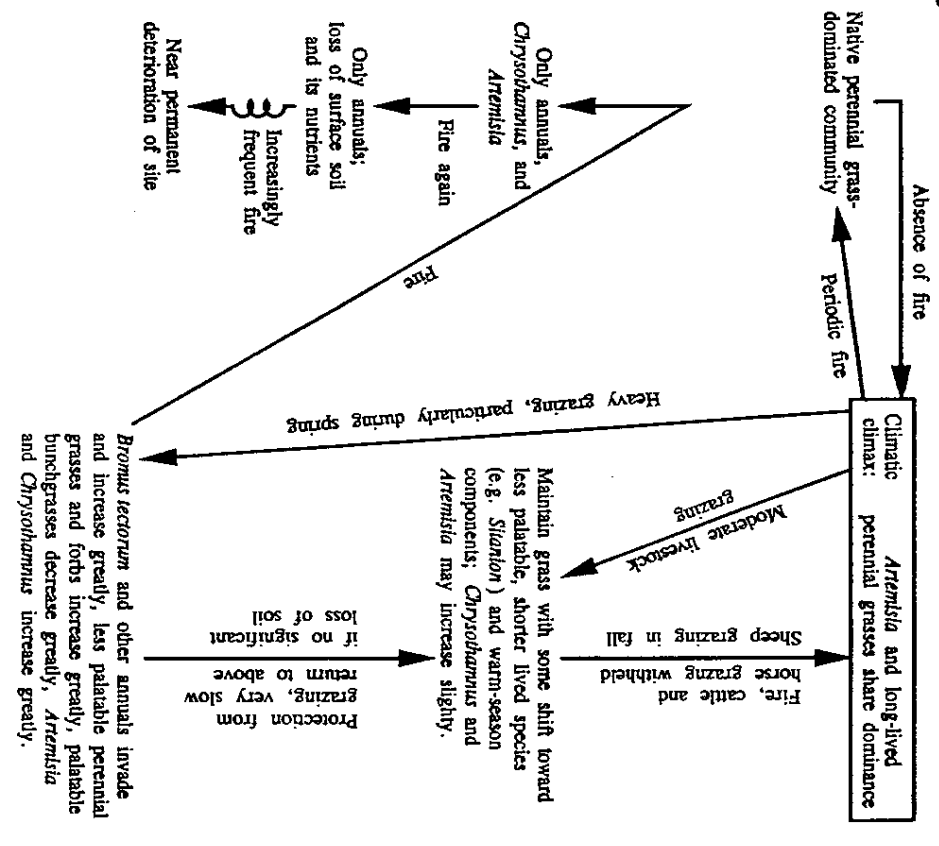
Figure 13. The role of grazing, fire and introduced annual weeds in changing grass-shrub balance in the Great Basin over the past 150 years (from West 1988).

Feedbacks

Interactions among ecosystem components are often regulated by positive or negative feedbacks which confer a degree of homeostasis. Positive feedbacks are those which reinforce deviations from a set point, whereas negative feedbacks are those which halt or reverse movement away from a steady-state condition. Positive feedbacks can thus accelerate change, whereas negative feedbacks may enable systems to resist change. Schlesinger et al. (1990) hypothesize that positive feed-

ing the drought period would translate to increased opportunities for *Prosopis* recruitment in the post-drought period, especially where the density and productivity of grasses had been reduced. Grazing in the post-drought period would have slowed grass recovery and minimized the likelihood of fire. The interaction between drought, atmospheric CO_2 levels, and livestock grazing may therefore have generated a change in vegetation that could not have been produced by these factors operating independently.

Time or Cultural Energy Increments Required to Drive System to New Configuration

A = Tall/Mid-Grasses
B = Mid-/Short Grasses
C = Short Grass/Annuals
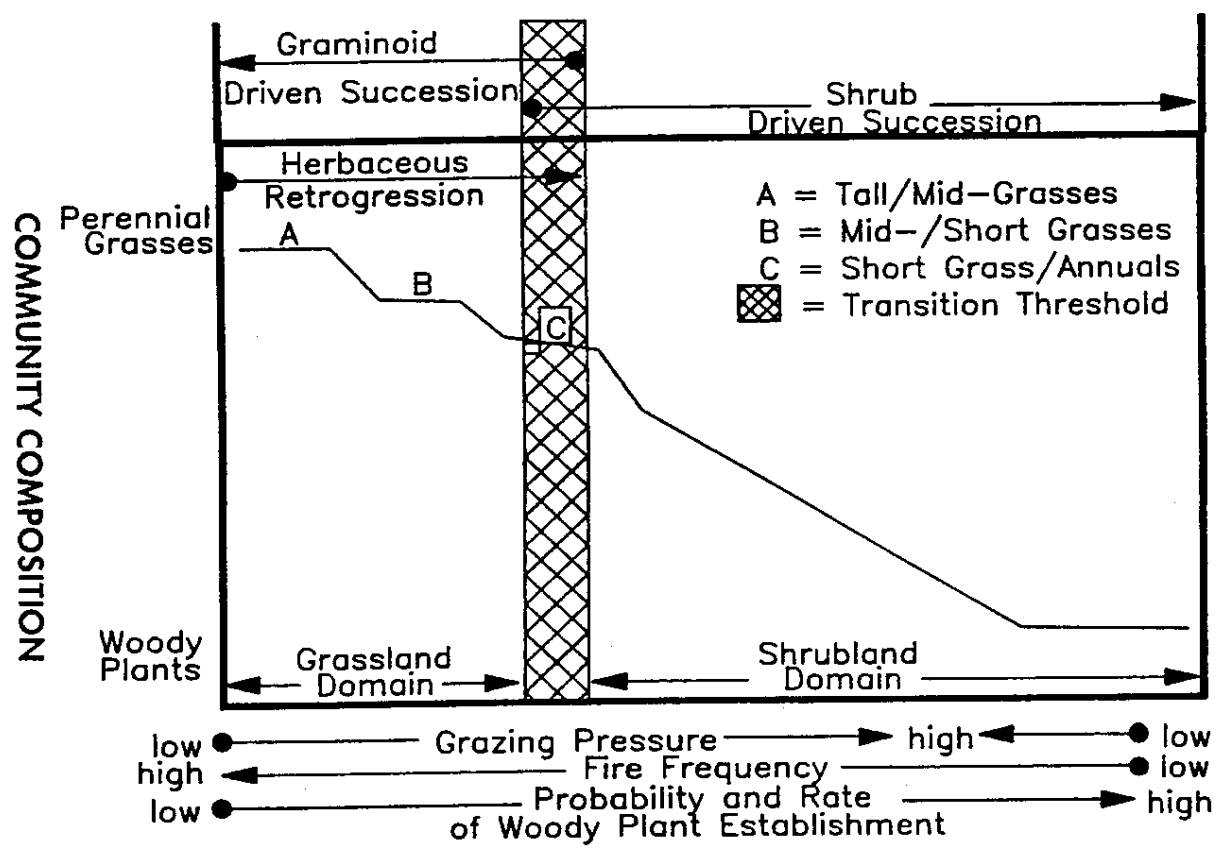☒ = Transition Threshold

Figure 14. Conceptual model of the conversion of grassland or savanna to shrub- or woodland, postulating the existence of a threshold of grazing disturbance (e.g., Fig. 1) in triggering a successional transition between alternate steady states (from Archer 1989).
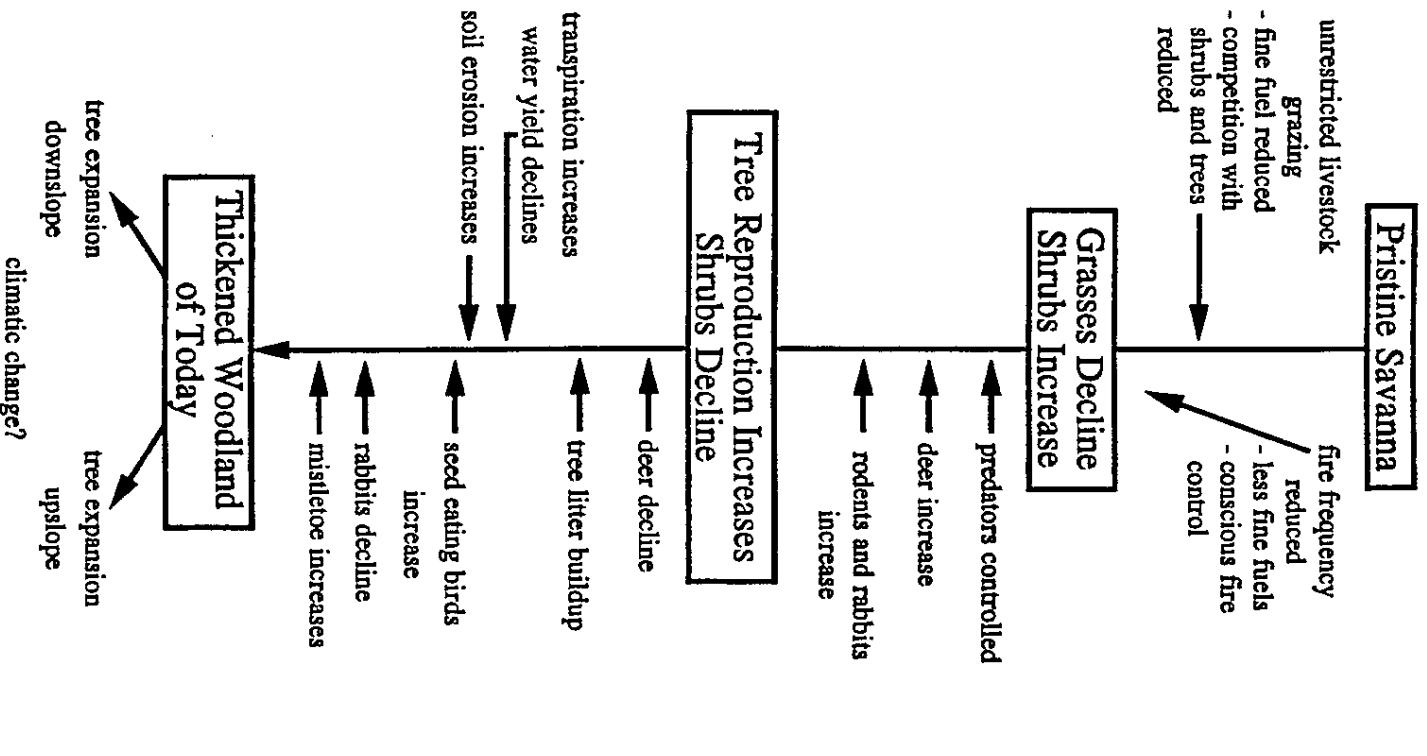
Pristine Savanna

unrestricted livestock grazing
- fine fuel reduced
- competition with shrubs and trees reduced

fire frequency reduced
- less fine fuels
- conscious fire control

→ **Grasses Decline Shrubs Increase**

→ predators controlled

→ deer increase

→ rodents and rabbits increase

→ **Tree Reproduction Increases Shrubs Decline**

→ deer decline

→ tree litter buildup

transpiration increases
water yield declines
soil erosion increases

→ seed eating birds increase

→ rabbits decline

→ mistletoe increases

→ **Thickened Woodland of Today**

tree expansion downslope

climatic change?

tree expansion upslope

Figure 15. Tree expansion and conversion of Great Basin savanna to pinyon-juniper woodland (from West and Van Pelt 1987).

---

backs are operational in desertification. In their proposed scenario, long-term grazing of semi-arid grasslands by livestock produces spatial and temporal heterogeneity of soil resources such as nitrogen and water. Heterogeneity of soil resources subsequently promotes invasion by desert shrubs which leads to a further localization of soil resources under shrub canopies. In the grazed areas between shrubs, soil fertility is lost by erosion and gaseous emissions, further increasing susceptibility to shrub encroachment. As grassland is replaced by shrubland a greater percentage of the soil surface is exposed. Soil surface and air temperatures thus increase and produce a warmer, drier micro- and mesoclimate which favors drought-tolerant shrubs over grasses. This positive feedback process continues until a new steady-state is achieved (see Archer 1990, Grover and Musick 1990 and Laycock, this volume for other examples).

Lessons From Case Studies

As discussed in the Climatic Determinants section, the fact that succession from grassland and savanna to shrub- and woodland has occurred over similar time frames and over such broad geographic areas constitutes one line of evidence that broad-scale factors like climate change and atmospheric CO_2 enrichment may be operating. Local and regional studies also offer some evidence that seasonal patterns of rainfall and temperature may have changed in recent history to favor woody plants over grasses in portions of North America. In addition, grasslands and savannas which established under previous climatic regimes may be only marginally suited to the recent climate and were perhaps prone to woody plant invasion. However, changes or fluctuations in broad-scale climatic regimes cannot explain how grasslands and savannas have persisted on some sites within a climatic zone but not others. Most lines of evidence point to grazing effects as the proximate cause for recent vegetation shifts:

Case 1. In their analysis of primary production and carbon balance of the central Great Plains, Burke et al. (1991) concluded that land management decisions may be more important than climate change in affecting carbon balance. In many arid land ecosystems, these land management decisions center around livestock grazing.

Case 2. "Although the grasslands of southern New Mexico were extensive and dominated the area, they were on the xeric edge of the continental Grassland Formation. A single factor such as grazing was evidently enough to set in motion a series of relatively rapid events which culminated in a desert shrub vegetation" (York and Dick-Peddie 1969:165).

Case 3. The stability of grass-shrub mosaics in relation to climate, soils, fire and grazing is being investigated in an ongoing field project in southern Texas (Archer 1990). While all have interacted to influence rates and patterns of woody plant encroachment, grazing appears to have been the driving force. The potential natural vegetation of this region has been classified by plant geographers as tial natural vegetation of this region has been classified by plant geographers as *Prosopis-Acacia* savannas (Kuchler 1964), and historical accounts suggest the upland vegetation was grassland or savanna (Table 2). Field investigations indi-

cate that upland soils are characterized by a laterally extensive argillic or clay pan horizon (fine-textured clays) which contain non-argillic inclusions (soil texture coarse throughout profile) (Loomis 1989). The historic grasslands or savannas may thus have been edaphically controlled, with mid- and shortgrasses dominating the upland, but interspersed with patches of tall grass species on the non-argillic inclusions (Fig. 4a). Alternatively, Prosopis and other shrubs may have dominated the non-argillic inclusions (Fig. 4b). In either case, woody vegetation would have been competitively excluded under the historic rainfall regimes where the argillic horizon was present. Such a system would have been prone to fire, which may have served as a secondary deterrent to woody plant establishment.

Present day landscapes in southern Texas contain high densities of discrete shrub clusters where the argillic horizon is present; groves of larger Prosopis trees occur where the argillic horizon is absent (Fig. 4c). Clusters dominated by C_3 shrubs occur on soils whose organic carbon reflects prior domination by C_4 grasses (Tieszen and Archer 1990). Models based on shrub growth rates (Archer 1989) and transition probabilities (Scanlan and Archer 1991) indicate this vegetation transformation occurred over the past 100-150 years. Three pathways of succession are hypothesized in Figure 4: (1) A→C (2) B→C or (3) A→B→C. Even though Prosopis trees growing on the non-argillic soils are much larger than the largest Prosopis plants now growing on argillic soils in terms of height, canopy area and trunk diameter, they are comparable in age (Table 5). The differences in size therefore reflect the fact that the growth rate of Prosopis plants on the non-argillic soils is greater than that of plants on the argillic soils. This suggests that the prior state of the vegetation would have been as shown in Figure 4a, with Prosopis invasion occurring across the landscape, but growing and developing faster on the non-argillic microsites.

A climatic explanation for the observed shift in vegetation structure would have to center around increased rainfall or a shift to increased winter rainfall (see Climatic and Edaphic Determinants Sections; Scanlan and Archer 1991). However, there is little evidence to suggest this has occurred (Norwine 1978). An alternative explanation centered around livestock grazing seems plausible. Reductions in transpiring leaf area, concomitant with reductions in initiation, extension, and biomass of grass roots, would increase soil moisture in the fine-textured upper horizons for establishing shrub seedlings. Shifts in herbaceous species composition to assemblages potentially less effective at sequestering soil resources would also occur. At the same time, livestock would have greatly increased Prosopis seed dispersal from populations restricted to intermittent drainages into surrounding grassland (Brown and Archer 1987) while fire frequency decreased. Periodic drought may have magnified grazing-induced stresses on the herbaceous vegetation and set the stage for subsequent pulses of woody plant recruitment (Fig. 3). The result has been a rapid, non-linear shift from grassland to woodland over a short (150-200 y) period, coincident with the intensification of livestock grazing.

Case 4. On a local scale, fire, grazing and soil properties interact within a variable climate to determine the balance between grasses and woody plants. How might the relative contributions of these interacting factors be determined? In a unique field study in Utah, Madany and West (1983) have documented a case in which a savanna protected from cattle grazing was maintained, whereas nearby edaphically-similar sites subjected to cattle grazing changed from savanna to dense woodland soon after the introduction of livestock in the late 1800s. Low frequencies of fire were documented on the savanna site protected from grazing, indicating that frequent fire was not required to maintain the grass/tree balance in this system. Both sites experienced the same climate and atmospheric conditions (e.g., CO_2 concentrations), yet one changed dramatically over the past 100 years, whereas the other did not. Such data indicate that livestock grazing has been the proximate cause of vegetation change on this site, not changes in fire or climatic regimes. Although climate change or fluctuation in recent history may have been necessary to have caused the change on the grazed site, it was not sufficient to cause change on the ungrazed site.

Case 5. The photograph in Figure 16 depicts a fenceline contrast in the Mitchell grass plains of central Australia. The properties on both sides of the fence have similar soils, have experienced the same climate and have the same general history of livestock grazing. However, prickly acacia (Acacia nilotica) plants from Africa were introduced along water courses on the property to the left of the fence in the 1940s (J.O. Carter, pers. comm.). At the time of this photograph (1988), prickly acacia had spread throughout the pasture and formed dense
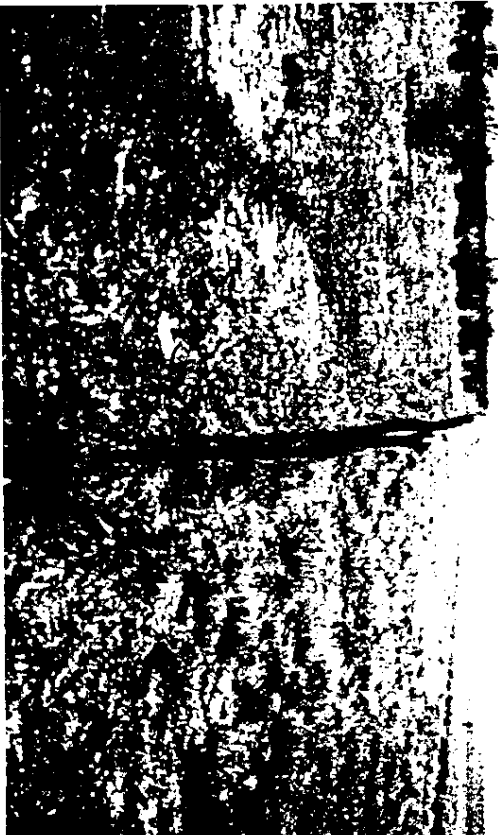
Figure 16. Fenceline contrast in the Mitchell Grasslands, Queensland, Australia showing stand of Acacia nilotica which has developed since the 1940s on one property, but not the other. Local contrasts in physiognomy suggest differences in land management practices as the cause for vegetation change and not broad-scale factors such as changes in climatic or atmospheric conditions. (Photo by S. Archer).

54

stands. The plant was not introduced to the property on the right. The fact that the spread of the plant has been limited by the fence suggests that livestock rather than native fauna were the principal agents of seed dispersal. Field observations indicate that seed production and seedling establishment of prickly acacia away from watercourses is episodic, occurring only during periods of sufficient rainfall which are infrequent and widely spaced (Burrows et al. 1986, 1990). Thus, while climatic variables are a key component in dictating the dynamics of prickly acacia seedling establishment and stand development, they cannot account for the differences in vegetation structure on these adjacent properties.

Case 6. Woody plant densities in an arid Botswana savanna fluctuated over a 5-year period in areas with no and moderate grazing by cattle (Skarpe 1990). Over the same period, the density and growth of shrubs increased on areas receiving heavy grazing.

Case 7. Redberry juniper (*Juniperus pinchotii*) densities on sites inaccessible to livestock in western Texas were an order of magnitude lower than those observed on edaphically similar sites with a history of livestock grazing (288 vs. 2123 plants/ha)(McPherson et al. 1988).

Case 8. With the implementation of the Taylor Grazing Act of 1934, land management practices in the southwestern United States were modified. Such was not the case in Mexico. Differences in grazing management practices since that time have produced sharp discontinuities in vegetative composition and cover along the international border in the Sonoran Desert (Bahre and Bradbury 1978). There are manifested in remotely sensed surface temperatures, greenness, soil moisture and convective cloud formation (Bryant et al. 1990). Border-line and fence-line contrasts (e.g., Case 7) reflect the importance of grazing and overall land use practices in shaping ecosystem structure relative to that of climate (see also Knight 1991).

Case 9. "About cause, then, the best answer seems to be that the new vegetation . . . has not arisen from climatic variation alone, but in response to the unique combination of climatic and cultural stress imposed by the events of the past eighty years; that climate and cattle have united to produce it" (Hastings and Turner 1965:289).

Case 10. Gehlbach (1981) examined vegetation in repeat photography along the international boundary between the Rio Grande and the Colorado River and concluded "man's landscape tinkering has been more influential than climate in creating unidirectional trends . . ." and that ". . . short-term climatic cycles not climatic change, have exacerbated man-made vegetative changes" (pp. 239-241).

Case 11. Bahre (1991) used repeat photography to demonstrate changes in woody plant distribution and abundance in southeastern Arizona since the 1870s. After a detailed review of existing literature and historic land-use practices, he concluded: (1) "probably more time has been spent on massaging the climatic change hypothesis than on any other factor of vegetation change, and yet it

55

remains the least convincing" (p. 105); and (2) "the increase of woody plants in rangelands . . . is most likely the result of grazing and fire exclusion" (p. 187).

Summary

Replacement of grasslands and savannas with shrub- and woodlands dominated by unpalatable species appears to have been widespread since European settlement. Available data suggest these changes have been (1) rapid, with substantial changes occurring over 50- to 100-year time spans, (2) non-linear, (3) accentuated by climatic fluctuation, (4) locally influenced by topoedaphic factors, and (5) non-reversible over time frames relevant to management.

Post-industrial atmospheric CO_2 enrichment and climate change may have facilitated shifts from grass to woody plant domination. However, case studies documenting differences in the rate and pattern of woody plant encroachment on nearby landscapes with similar topoedaphic properties suggest these were not the proximate factors driving vegetation change. In contrast, numerous case studies have established a strong link between livestock grazing and the encroachment of unpalatable woody plants. Direct and indirect effects of livestock grazing (preferential utilization of grasses, alteration of soil structure and chemistry, seed dispersal, reduction of fire) generally favor woody plant establishment and stand development. In addition, differences in livestock species and levels of grazing pressure across landscapes over time would explain why rates and patterns of vegetation change have varied substantially for similar habitats within climatic zones.

Grasslands and savannas are globally significant for their production of forage, food and fiber. An understanding of factors controlling the balance between grasses and woody plants is fundamental to developing natural resource management plans for sustained utilization in these ecosystems. Shifts in grass and woody plant abundance have broad implications for biodiversity, primary and secondary productivity, soil development and stability, livestock and wildlife composition and carrying capacity, recreational opportunities, water quality and water distribution. Changes from herbaceous- to wood plant-domination also constitute a potentially important global climate feedback affecting carbon sequestering, non-methane hydrocarbon emissions and biophysical land surface-atmosphere interactions (albedo, evapotranspiration, surface roughness, boundary layer dynamics). Additional information is required if we are to understand mechanisms and predict the rate, pattern and extent of change in grass and woody plant distribution in the face of expanding human populations and human-induced climate change.

Literature Cited

Acocks, J.P.H. 1964. Karroo vegetation in relation to the development of deserts, pp. 100-112. *In:* D.H.S. Davis (ed), Ecological studies of southern Africa. Dr. Junk Publishers, The Hague.

Adamoli, J., E. Sennhauser, J.M. Acero, and A. Rescia. 1990. Stress and disturbance: vegetation dynamics in the dry Chaco region of Argentina. J. Biogeography 17:491-500.

Aerts, R. 1989. Above ground biomass and nutrient dynamics of *Calluna vulgaris* and *Molina caerulea* in dry heathland. Oikos 56:31-38.

Anos, B.B. and F.R. Gehlbach. (eds). 1988. Edwards plateau vegetation. Baylor Univ. Press, Waco, TX. USA.

Andrew, M.H. 1988. Grazing impact in relation to livestock watering points. Trends Ecol. Evol. 3:336-339.

Archer, S. 1989. Have Southern Texas savannas been converted to woodlands in recent history? Am. Nat. 134:545-561.

Archer, S. 1990. Development and stability of grass/woody mosaics in a subtropical savanna parkland, Texas, U.S.A. J. Biogeography 17:453-462.

Archer, S. J.K. and Detling. 1986. The potential role of herbivores in mediating plant water status. Oikos 47:287-291.

Archer, S. and R.C. Flinn. 1991. Longevity of *Prosopis glandulosa var. glandulosa* ramets and genets in a subtropical thorn woodland. Bul. Ecological Soc. America 72:57.

Archer, S., C.J. Scifres, C.R. Bassham, and R. Maggio. 1988. Autogenic succession in a subtropical savannaз: conversion of grassland to thorn woodland. Ecol. Monogr. 58:111-127.

Archer, S. and F.E. Smeins. 1991. Ecosystem-level processes, pp. 109-139. *In:* R.K. Heitschmidt and J.W. Stuth (eds), Grazing management: an ecological perspective. Timberline Press, Portland, OR.

Arno, S.F. and G.E. Gruell. 1986. Douglas fir encroachment into mountain grasslands in southwestern Montana. J. Range Manage. 39:272-276.

Bahre, C.J. and D.E. Bradbury. 1978. Vegetation change along the Arizona-Sonora boundary. Ann. Assoc. Amer. Geog. 68:145-165.

Bahre, C.J. 1991. A legacy of change: historic human impact on vegetation in the Arizona borderlands. Univ. Arizona Press, Tucson. 231 p.

Baisan, C.H. and T.W. Swetnam. 1990. Fire history on a desert mountain range: Rincon Mountain Wilderness, Arizona, USA. Can. J. For. Res. 20:1559-1569.

Bazzaz, F.A. 1990. The response of natural ecosystems to the rising global CO_2 levels. Ann. Rev. Ecol. Syst. 21:167-196.

Beatley, J.C. 1974. Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55:856-863.

Belsky, A.J. 1984. Role of small browsing mammals in preventing woodland regeneration in the Serengeti National Park, Tanzania. Afr. J. Ecol. 22:271-279.

Belsky, A.J. 1991. Tree/grass ratios in East African savannas: a comparison of existing models, pp. 139-145. *In:* P.A. Werner (ed), Savanna ecology and management: Australian perspectives and intercontinental comparisons. Blackwell Scientific Publications, London.

Berdowski, J.J.M. 1987. Transition from heathland to grassland initiated by the heather beetle. Vegetatio 72:167-173.

Betancourt, J.L., T.R. Van Devender, and P.S. Martin. 1990. Synthesis and prospectus, pp. 435-447. *In:* J.L. Betancourt, T.R. Van Devender and P.S. Martin, (eds), Packrat middens: the last 40,000 years of biotic change. University of Arizona Press, Tucson.

Blackburn, W.H. and P.T. Tueller. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. Ecology 51: 841-848.

Bogusch, E.R. 1952. Brush invasion of the Rio Grande Plains of Texas. Texas J. Sci. 4:85-91.

Booth, C.A. and P.J. Barker. 1981. Shrub invasion on sandplain country west of Wanaaring, New South Wales. Soil Conservation Service of New South Wales. 37:65-70

Box, E.O. 1981. Microclimate and plant forms: an introduction to predictive modeling in phytogeography. Dr. W. Junk Publishers, The Hague, Netherlands.

Bragg, T.B. and L.C. Hulbert. 1976. Woody plant invasion of unburned Kansas bluestem prairie. J. Range Manage. 29:19-23.

Branson, F.A. 1985. Vegetation changes on western rangelands. Range Monograph No. 2, Soc. Range Management, Denver, CO.

Briske, D.D. 1991. Developmental physiology and morphology of grasses, pp. 85-108. *In:* R.K. Heitschmidt and J.W. Stuth. (eds), Grazing management: an ecological perspective. Timber Press, Inc. Portland, OR.

Brown, A.L. 1950. Shrub invasions of southern Arizona desert grasslands. J. Range Manage. 3:172-177.

Brown, J.R. and S. Archer. 1987. Woody plant seed dispersal and gap formation in a North American subtropical savanna woodland: the role of domestic herbivores. Vegetatio 73:73-80.

Brown, J.R. and S. Archer. 1989. Woody plant invasion of grasslands: establishment of honey mesquite (*Prosopis glandulosa var. glandulosa*) on sites differing in herbaceous biomass and grazing history. Oecologia (Berl.) 80:19-26.

Brown, J.R. and S. Archer. 1990. Water relations of a perennial grass and seedling versus adult woody plants in a subtropical savanna, Texas. Oikos 57:366-374.

Brown, J.H. and E.J. Heske. 1990. Control of a desert-grassland transition by a keystone rodent guild. Science 250:1705-1707.

Bryant, N.A., L.F. Johnson, A.J. Brazel, R.C. Balling, C.F. Hutchinson and L.R. Beck. 1990. Measuring the effect of overgrazing in the Sonoran Desert. Climate Change 17:243-264.

Bryson, R.A. 1974. A perspective on climatic change. Science 184:753-760.

Bucher, E.H. 1987. Herbivory in arid and semi-arid regions of Argentina. Revista Chilena de Historia Natural 60:265-273.

Buffington, L.D. and C.H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1958 to 1963. Ecol. Monogr. 35:139-164.

Burke, I.C., T.G.F. Kittel, W.K. Lauenroth, P. Snook, C.M. Yonker, and W.J. Parton. 1991. Regional analysis of the central Great Plains: sensitivity to climate variability. Bio-Science 41:685-692.

Burkhardt, J.W. and E.W. Tisdale. 1969. Natural and successional status of western juniper vegetation in Idaho. J. Range Manage. 22:264-270.

Burrows, W.H., I.F. Beale, R.G. Silcock, and A.J. Pressland. 1985. Prediction of tree and shrub population changes in a semi-arid woodland, pp. 207-211. *In:* J.C. Tothill and J.J. Mott (eds), Ecology and management of the world's savannas. Australian Academy of Science, Canberra.

Burrows, W.H., J.O. Carter, E.R. Anderson, and M.P. Bolton. 1986. Prickly acacia (*Acacia nilotica*) invasion of Mitchell grass (*Astrebla* spp.) plains in central and northern Queensland. Proc. 4th Bienn. Conf. Australian Rangeland Soc., Armidale, pp. 104-106.

Burrows, W.H., J.O. Carter, J.C. Scanlan, and E.R. Anderson. 1990. Management of savannas for livestock production in north-east Australia: contrasts across the tree-grass continuum. J. Biogeography 17:503-512.

Bush, J.K. and O.W. Van Auken. 1989. Soil resource levels and competition between a woody and herbaceous species. Bul. Tor. Bot. Club 116:22-30.

70

Grime, P.J. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York.

Gross, F.A. and W.A. Dick-Peddie. 1979. A map of primeval vegetation in New Mexico. Southwestern Naturalist 24:115-122.

Grover, H.D. and H.B. Musick. 1990. Shrub land encroachment in southern New Mexico, USA: an analysis of desertification processes in the American Southwest. Climate Change 17:305-330.

Grubb, P.J. 1977. The maintenance of species richness in plant communities: the importance of the regeneration niche. Biol. Rev. 52:107-145.

Hallmark, C.T. and B.L. Allen. 1975. The distribution of creosotebush in west Texas and eastern New Mexico as affected by selected soil properties. Soil Sci. Soc. Amer. Proc. 39:120-124.

Hanselka, C.W. and Kilgore, D.E. 1987. The Nueces River valley: the cradle of the western livestock industry. Rangelands 9:195-198.

Hara, M. 1987. Analysis of seedling banks of a climax beech forest: ecological importance of seedling sprouts. Vegetatio 71:67-74.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

Harrington, G.N. 1979. The effects of feral goats an sheep on the shrub populations in a semi-arid woodland. Australian Rangeland Journal 1:334-345.

Harrington, G.N. 1991. Effects of soil moisture on shrub seedling survival in semi-arid grassland. Ecology 72:1138-1149.

Harrington, G.N. and K.C. Hodgkinson. 1986. Shrub-grass dynamics in mulga communities of eastern Australia, pp. 26-28. In: Rangelands: a resource under siege. P.J. Joss, P.W. Lynch, and O.B. Williams (eds), Australian Academy of Science, Canberra.

Harrington, G.N., R.E. Oxley, and D.J. Tongway. 1979. The effects of European settlement and domestic livestock on the biological system in poplar box (Eucalyptus populnea) lands. Australian Rangeland Journal 1:271-279.

Hastings, J.R. and R.I. Turner. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semi-arid region. University of Arizona Press, Tucson.

Haynes, C.V. Jr. 1982. Great Sand Sea and Selima Sand Sheet, eastern Sahara: geochronology of desertification. Science 217:629-633.

Heddle, E.M. and R.L. Specht. 1975. Dark Island heath (Ninety-Mile Plain, South Australia). VIII. The effects of fertilizers on composition and growth, 1950-1972. Aust. J. Bot. 23:151-164.

Heitschmidt, R.K., D.L. Price, R.A. Gordon and J.R. Frasure. 1982. Short duration grazing at the Texas experimental ranch: effects on above-ground net primary production and seasonal growth dynamics. J. Range Manage. 35:367-372.

Hennessy, J.T., R.P. Gibbens, J.M. Tromble and M. Cardenas. 1983. Vegetation changes from 1935 to 1980 in mesquite dunelands and former grasslands of southern New Mexico. J. Range Manage. 36:370-374.

Henry, G.H.R., B. Freedman and J. Svoboda. 1986. Effects of fertilization on three tundra plant communities of a polar desert oasis. Can. J. Bot. 64: 2502-2507.

Herbel, C.H. 1979. Utilization of grass and shrublands of the southwestern United States, pp. 161-203. In: B.H. Walker (ed), Management of semi-arid ecosystems. Elsevier, New York.

Herbel, C.H., F.N. Ares, and R.A. Wright. 1972. Drought effects on a semi-desert grassland. Ecology 53:1084-1093.

Hobbs, R.J. and H.A. Mooney. 1986. Community changes following shrub invasion of grassland. Oecologia (Berl.) 70:508-513.

Hogberg, P. 1989. Root symbiosis of trees in savannas, pp. 121-136. In: J. Proctor, (ed), Mineral nutrients in tropical forest and savanna ecosystems. Blackwell Scientific Publ., London.

Holdridge, L.R. 1947. Determination of world plant formations from simple climatic data. Science 105:367-368.

Holdridge, L.R. 1964. Life zone ecology. Tropical Science Center, San José, Costa Rica.

Humphrey, R.R. 1987. 90 years and 535 miles: vegetation changes along the Mexican border. Univ. New Mexico Press, Albuquerque.

Humphrey, R.R. and Mehrhoff, L.A. 1958. Vegetation change on a southern Arizona grassland range. Ecology 39:720-726.

Humphrey, R.R. 1958. The desert grasslands: a history of vegetational changes and an analysis of causes. Bot. Rev. 24:193-252.

Hunt, H.W., M.J. Trlica, E.F. Redente, J.C. Moore, J.K. Detling, T.G.G. Kittel, D. E. Walter, M.C. Fowler, D.A. Klein, and E.T. Elliott. 1991. Simulation model for the effects of climate change on temperate grassland ecosystems. Ecological Modelling 53:205-246.

Hunter, R.B., E.M. Romney and A. Wallace. 1980. Rodent-denuded areas of the northern Mojave Desert. Great Basin Naturalist Memoirs 4:208-211.

Huston, M. and T. Smith. 1987. Plant succession: life history and competition. American Naturalist 130:168-198.

Idso, S.B. 1992. Shrubland expansion in the American southwest. Climate Change 22:85-86

Inglis, J.M. 1964. A history of vegetation on the Rio Grande Plains. Texas Parks and Wildlife Dept. Bull. 45, Austin, 122 p.

Jameson, D.A. 1987. Climax or alternative steady states in woodland ecology, pp. 9-13. In: R.L. Everett (ed), Proceedings — pinyon-juniper conference. USDA Forest Service Gen. Tech. Rep. INT-215, Ogden, Utah. 581 pp.

Janzen, D.H. 1986. Chihuahuan Desert nopaleras: defaunated big mammal vegetation. Ann. Rev. Ecol. Syst. 17:595-636.

Johnson, H.B. and H.S. Mayeux. 1990. Prosopis glandulosa and the nitrogen balance of rangelands: extent and occurrence of nodulation. Oecologia (Berl.) 84:176-185.

Johnson, H.B., H.W. Polley and H.S. Mayeux. 1993. Increasing CO₂ and plant-plant interactions: effects on natural vegetation. Vegetatio 104-105:157-170.

Johnson, K.L. 1987. Sagebrush over time: a photographic study of rangeland change, pp. 223-252. In: E.D. McArthur and B.L. Welch (eds), Biology of Artemisia and Chrysothamnus. USDA For. Serv. Gen. Tech. Rep. INT-200, Ogden, Utah.

Johnson, R.W. and J.C. Tothill. 1985. Definition and broad geographic outline of savanna lands, pp. 1-13. In: J.C. Tothill and J.J. Mott (eds), Ecology and management of the world's savannas. Australian Academy of Science.

Johnston, M.C. 1963. Past and present grasslands of southern Texas and northeastern Mexico. Ecology 44:456-466.

Jordan, T.G. 1981. Trails to Texas: southern routes of western cattle ranching. Univ. Nebraska Press, Lincoln. 220 p.

Katz, R.W. and B.G. Brown. 1992. Extreme events in a changing climate: variability is more important than averages. Climatic Change 21:289-302.

Klemmedson, J.O. 1979. Ecological importance of actinomycete-nodulated plants in the western United States. Bot. Gaz. 140 (Suppl.):S91-S96.

Knight, D.H. 1991. Congressional incentives for landscape research. Ecol. Soc. Amer. Bul. 72:195-203.

Knoop, W.T. and B.H. Walker. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. J. Ecol. 73:235-253.

62

Kuchler, A.W. 1964. The potential natural vegetation of the conterminous United States. Amer. Geographical Soc. New York, NY.

Kuchler, A.W. 1978. Natural vegetation, pp. 16-17. *In*: E.B. Espenshade, Jr. and J.L. Morrison (eds), Goode's World Atlas, 15th ed. Rand-McNally, Chicago.

Kummerow, J., D. Krause and W. Jow. 1977. Root systems of some chaparral shrubs. Oecologia (Berl.) 29:163-177.

La Marche, V.C., Jr., D.A. Graybill, H.C. Fritts and M.R. Rose. 1984. Increasing atmospheric carbon dioxide: tree ring evidence for growth enhancement in natural vegetation. Science 225:1019-1021.

Lechowicz, J.J. and G.R. Shaver. 1982. A multivariate approach to the analysis of factorial fertilizer experiments in Alaskan arctic tundra. Ecology 63:1029-1038.

Lehman, V.W. 1969. Forgotten legions; sheep in the Rio Grande Plains of Texas. Texas Western Univ. Press, Univ. Texas, El Paso.

Leps, J., J. Osbornova-Kosinova and M. Rejmanek. 1982. Community stability, complexity and species life history strategies. Vegetatio 50:53-63.

Lewin, R. 1985. Plant communities resist climatic change. Science 228:165-166.

Liang, Y.M., D.L. Hazlett and W.K. Lauenroth. 1989. Biomass dynamics and water use efficiencies of five plant communities in the shortgrass steppe. Oecologia (Berl.) 80:148-153.

Lieth, H. 1972. Modelling the primary productivity of the world. Nature and Resources 8.5-10.

Lonard, R.I. and F.W. Judd. 1985. Effects of a severe freeze on native woody plants in the Lower Rio Grande Valley, Texas. Southwestern Naturalist 30:397-403.

Lonsdale, M. and R. Braithwaite. 1988. The shrub that conquered the bush. New Scientist 15:52-55.

Loomis, L.E. 1989. Plant-soil relationships in grassland-to-woodland succession. PhD Dissertation, Texas A&M University, College Station.

Lowe, C.H. and D.E. Brown. 1982. Introduction, pp. 8-16. *In*: D.E. Brown (ed), Biotic communities of the American Southwest-United States and Mexico. University of Arizona Press, Tucson (Special Issue of Desert Plants, vol. 4).

Lundelius, E.L. 1976. Vertebrate paleontology of the Pleistocene: an overview. Geoscience and Man 13:45-59.

MacMahon, J.A. 1980. Ecosystems over time: succession and other types of change, pp. 27-58. *In*: R. Waring (ed), Forests: fresh perspectives from ecosystem analyses. Oregon State Univ. Press, Corvallis.

Madany, M.H. and N.E. West. 1983. Livestock grazing-fire regime interactions within montane forests of Zion National Park, Utah. Ecology 64:661-667.

Malin, J.C. 1953. Soil, animal, and plant relations of the grassland, historically recorded. Scientific Monthly 76:207-220.

Martin, P.S. and P.J. Mehringer Jr. 1965. Pleistocene pollen analysis and biogeography of the Southwest, pp. 433-451. *In*: H.E. Wright, Jr. (ed), The late Quaternary of the United States. Yale University Press, New Haven.

Martin, S.C. 1975. Ecology and management of southwestern semidesert grass-shrub ranges: the status of our knowledge. USDA/For. Serv. Res. Paper RM-156.

Martin, S.C. and R.M. Turner. 1977. Vegetation change in the Sonoran Desert region, Arizona and Sonora. Arizona Acad. Sci. 12:59-69.

Mayeux, H.S., Johnson, H.B. and H.W. Polley. 1991. Global change and vegetation dynamics, pp. 62-74. *In*: L.F. James, J.O. Evans, M.H. Ralphs, and B.J. Sigler (eds), Noxious range weeds. Westview Press, Boulder, CO.

63

McArthur, E.D., E.M. Romney, S.D. Smith and P.T. Tueller. 1990. Cheatgrass invasion, shrub die-off and other aspects of shrub biology and management. USDA/Forest Service Gen. Tech. Rep. INT-276, Ogden, Utah. 351 pp.

McAuliffe, J.R. 1988. Markovian dynamics of simple and complex desert plant communities. Am. Nat. 131:459-490.

McBride, J.R. and H.F. Heady. 1968. Invasion of grassland by *Baccharis pilularis* DC. J. Range Manage. 21:106-108.

McCraw, D.J. 1985. Phytogeographic history of *Larrea* in southwestern New Mexico illustrating the historical expansion of the Chihuahuan Desert. MA Thesis, University of New Mexico, Albuquerque, USA.

McGraw, J.B. and F.S. Chapin III. 1989. Competitive ability and adaptation to fertile and infertile soils in two *Eriophorum* species. Ecology 70:736-749.

McLaughlin, S.P. and J.E. Bowers. 1982. Effects of wildfire on a Sonoran Desert plant community. Ecology 63:246-248.

McNaughton, S.J. 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. Ecol. Monogr. 53:291-320.

McMaster, G.S., W.M. Jow and J. Kummerow. 1982. Response of *Adenostoma fasciculatum* and *Ceanothus greggii* chaparral to nutrient additions. J. Ecology 70:745-756.

McPherson, G.R. and H.A. Wright. 1987. Factors affecting reproductive maturity of redberry juniper (*Juniperus pinchotii*). Forest Ecol. & Manage. 21:191-196.

McPherson, G.R. and H.A. Wright. 1990. Effects of cattle grazing and *Juniperus pinchotii* canopy cover on herb cover and production in western Texas. Am. Midl. Nat. 123:144-151.

McPherson, G.R., H.A. Wright and D.B. Wester. 1988. Patterns of shrub invasion in semiarid Texas grasslands. The American Midland Naturalist 120:391-397.

Merrill, L.B. and V.A. Young. 1959. Effect of drouth on woody plants. Texas Agricultural Progress 5:9-10.

Merino, J., C. Field and Mooney, H.A. 1984. Construction and maintenance costs of mediterranean-climate evergreen and deciduous leaves. Oecologia Plantarum 5:211-229.

Merz, R.W. and S.G. Boyce. 1956. Age of oak "seedlings". J. Forestry 54:774-775.

Mitchell, J.F.B. and D.A. Warrilow. 1987. Summer dryness in northern mid-latitudes due to increased CO_2. Nature 330:238-240.

Mitchell, J.M. 1980. History and mechanisms of climate, p. 31-42. *In*: H. Oeschger, B. Messerli and M. Svilar (eds), Das Klima-analysen und modelle, geschichte und zukunft. Springer-Verlag, Berlin.

Mooney, H.A., Drake, B.G., Luxmore, R.J., Oechel, W.C. and Pitelka, L.F. 1991. Predicting ecosystem responses to elevated CO_2 concentrations. BioScience 41:96-104.

Morison, C.G.T., A.C. Hoyle and J.F. Hope-Simpson. 1948. Tropical soil-vegetation catenas and mosaics. J. Ecology 36:1-84.

Neftel, A., E. Moor, H. Oeschger, and B. Stauffer. 1985. Evidence from polar ice cores for the increase in atmospheric CO_2 in the past two centuries. Nature 315:45-47.

Nelson, R.P. 1986. High resolution climatic analysis and southwest biogeography. Science 232:27-34.

Neilson, R.P. and Wullstein, L.H. 1985. Comparative drought physiology and biogeography of *Quercus gambelii* and *Quercus turbinella*. Am. Midl. Nat. 114:259-271.

Nelson, E.W. 1934. The influence of precipitation and grazing upon black grama grass range. USDA Tech. Bul. 409, 32 p.

Nelson, J.T. and P.L. Beres. 1987. Was it grassland? A look at vegetation in Brewster County, Texas through the eyes of a photographer in 1899. Texas J. of Agric. and Nat. Res. 1:34-37.

Van Auken, O.W. and J.K. Bush. [...] petition on seedling growth o[...] 117:438-444.

Van Devender, T.R. 1980. Holo[...] Canyon, Eddy County, New M[...]

Van Devender, T.R. and W.G. S[...] in the southwestern United Sta[...]

Van Vegten, J.A. 1983. Thornbu[...] Vegetatio 56:3-7.

Vasek, F.C. 1980. Creosote bus[...] Botany 67:246-255.

Verstraete, M.M. 1986. Definin[...] invasion of [...]

Wagner, F.H. 1989. Grazers, pa[...] Mooney (eds), Grassland stru[...] Academic Publishers, Boston.

Wagoner, J.J. 1949. History of t[...] Sciences Bul. 20, Univ. Arizo[...]

Walter, H. 1979. Vegetation of [...] Springer-Verlag, New York.

Weltzin, J.F. 1990. The role of p[...] ulation dynamics of the woo[...] University, College Station.

West, N.E. 1988. Inter-mountai[...] M.G. Barbour and W.D. Billin[...] Univ. Press, New York.

West, N.E., K.H. Rea and R.O[...] grass communities in southea[...]

West, N.E. and N.S. Van Pelt. [...] pp. 43-52. *In*: R.L. Everett (e[...] Serv. INT-215, Ogden, Utah.

Western, D. and C. Van Praet. [...] African ecosystem. Nature 24[...]

Whicker, A.D. and J.K. Detli[...] bances. BioScience 38:778-7[...]

Whicker, A.D. and J.K. Detlin[...] ten processes by North Ame[...] P.J.M. van der Aart, H.J. Dur[...] structure. SPB Academic Pub[...]

Whitowski, E.T.F. 1989. Respo[...] plain lowland fynbos, South [...]

Whittaker, R.H. 1975. Commu[...]

Whittaker, R.H., L.E. Gilbert [...] in a mesquite grassland, Tex[...]

Williams, K., R.J. Hobbs and [...] Northern California by *Bac[...] 461-465.

Wondzell, S.M. 1984. Recover[...] 36 years of protection from g[...] University, Las Cruces.