

CLIMATE AND HERBIVORY IN STRUCTURING THE VEGETATION OF THE MALPAI BORDERLANDS

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Arid ecosystems in *La Frontera* have undergone unprecedented change during the past 125 years (Bahre 1991; Buffington and Herbel 1965; Hastings and Turner 1965; Humphrey 1987). While most of this change is attributed to the later part of the nineteenth century (Bahre 1991; Cooke and Reeves 1976; Grover and Musick 1990), many areas appear to have undergone accelerated increases in woody vegetation since the 1970s (Betancourt 1996; Brown et al. 1997). These changes follow a widespread decline in woody vegetation in the middle of this century linked to the 1950s drought (Allen and Breshears 1998) (Archer personal communication 1999; Swetnam and Betancourt 1998) and have been documented at all elevations and across habitat types ranging from pinyon-juniper woodlands (Davenport et al. 1996; Gottfried et al. 1995), to savannas and shrublands (Archer 1995; Betancourt 1996), to arid grasslands (Brown et al. 1997).

Arid ecosystems are affected by the interaction of four major variables: soils and topography, climate, fire, and herbivory, which determine their basic structure and function (Crawford and Gosz 1982; Noy-Meir 1973; Schlesinger et al. 1990). Here, we investigate the effects of grazing and climate on the vegetational composition of the borderlands of Chihuahua/Sonora and Arizona/New Mexico (figure 6.1). This area was selected because it has high plant and animal diversity and has been the site of numerous ecological studies.

Effects of Climate in Arid and Semiarid Ecosystems

Traditionally, overgrazing, drought, and fire suppression have been cited as major causes of desertification (defined here as increases in shrubs and declines in grasses) in *La Frontera* (Bahre 1991; Bahre and Shelton 1993; Buffington and Herbel 1965; Gehlbach 1981). Yet variation in timing and intensity of rainfall can have equally important implications for the structure and function of arid and semiarid ecosystems, potentially leading to large reorganization of floral and faunal components of these systems (Brown et al. 1997; Neilson 1986).

Variation in the distribution of rainfall can have considerable impacts on plant life-form distribution, with the later resulting from fundamental constraints associated with different life history strategies (Holdridge 1947; Neilson et al. 1992b; Veblen and Lorenz 1988; Walter 1973; Wilcox and Breshears 1995). While woody vegetation requires deep soil moisture, grasses only need sufficient surface moisture to support growth and reproduction during the summer growing season (Neilson 1993; Woodward 1987). Vegetation stature, rooting depth, and

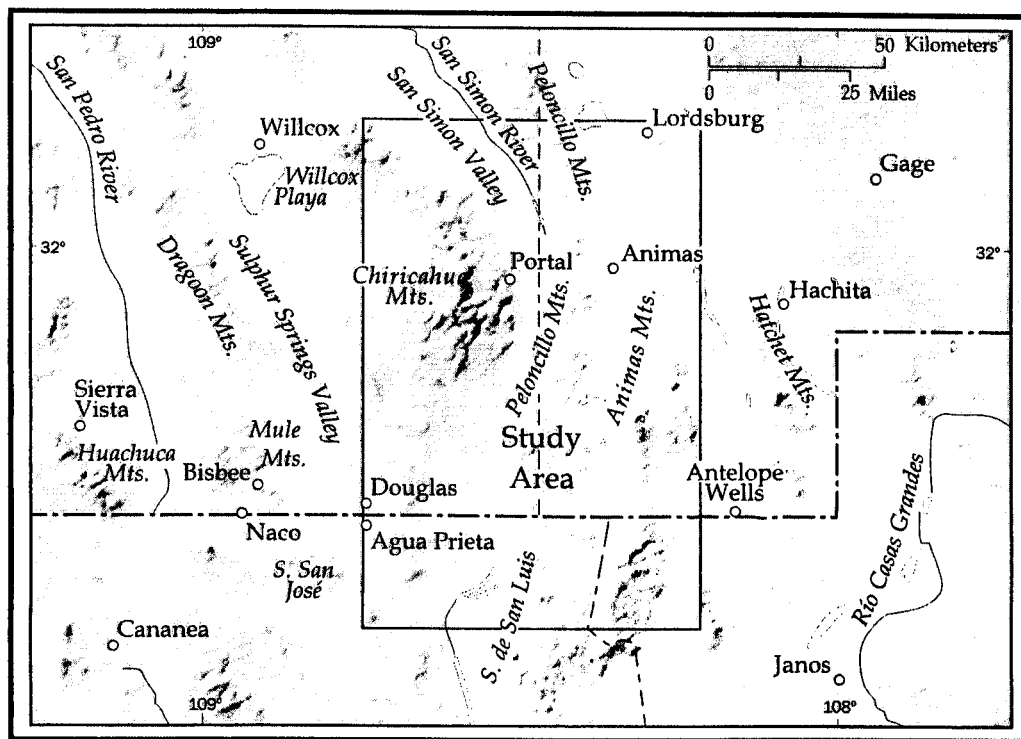


FIG. 6.1
Map of the Malpai
Borderlands.

leaf area therefore represent a balance between precipitation inputs and evaporation withdrawals with periods of wet winters and dry summers favoring deep-rooted woody vegetation over relatively shallow-rooted summer-active grass species (Brown et al. 1997; Neilson 1986; Neilson et al. 1992b).

Seasonal patterns of precipitation have changed substantially in the Malpai Borderlands study area during the past several decades (Betancourt 1996; Brown et al. 1997). While relatively small, these shifts in patterns of rainfall with summer precipitation remaining around the 100-year mean and winter precipitation several times the 100-year mean represent a significant perturbation to this system.

In the vicinity of our study area, these changes in rainfall patterns to wet winters and dry summers have primarily been associated with El Niño Southern Oscillation (ENSO) events. Analysis of climatic records and models of vegetation response to climate in the 1980s (Neilson 1986) show accelerated increases in woody vegetation across the American Southwest in the last several decades (Archer 1996; Betancourt 1996; Brown et al. 1997; Gottfried et al. 1995). Based on work in savanna ecosystems in Africa and Australia, Walker (1991) also predicted that climatically-induced vegetation change "in general will be most marked in those ecosystems where the structure and composition are strongly influenced by limiting conditions of temperature or rainfall." Grassland and savanna systems in *La Frontera* are just such systems.

Effects of Herbivory in Arid and Semiarid Ecosystems

Herbivory and livestock grazing have important interactions with climate that result in dynamic, nonlinear responses within these ecosystems. These increases in woody plants are

often associated with livestock grazing and fire suppression (Archer 1994; Bahre 1991). These effects occur in a number of self-reinforcing ways, including: dispersal of woody plant seeds, decreases in grass leaf area and cover (which increases the germination potential for woody plants), soil compaction (which favors deep rooted organisms), and increases in nutrients available to woody species (Archer 1995).

However, many grassland and savanna systems evolved with grazing (Milchunas and Lauenroth 1993). While high grazing levels may degrade range lands, light to moderate grazing may be essential in maintaining the structure and composition of range ecosystems (Archer 1995; Milchunas et al. 1988). While much of the large herbivore community that once roamed the American Southwest has been extirpated from the region (Van Devender 1986a, this volume), smaller rodents continue to play a pivotal role in structuring the grassland and savanna ecosystems. For example, prairie dogs (*Cynomys* spp.), prior to extirpation early in the twentieth century, were once widespread in western ecosystems (Miller et al. 1994; Stapp 1998). In addition to soil perturbation, prairie dogs reduce woody shrub cover through girdling woody vegetation and seed and pod predation (Weltzin et al. 1997). These documented effects of prairie dogs on vegetation composition suggest that some of the shrub increases in *La Frontera* may be the result of prairie dog extirpation (C. Oakes, personal communication 1998).

Kangaroo rats (*Dipodomys* spp.) and other granivorous rodents now play a crucial role in structuring arid and semiarid ecosystems. Brown and Heske (1990) demonstrated that kangaroo rats, by significantly reducing grass cover in experimental removal plots, play a keystone or engineering role in some ecosystems (Jones et al. 1994). Kangaroo rats have also been shown to increase local diversity (Hawkins and Nicoletto 1992) and to facilitate shrub establishment through soil structure modification (Chew and Whitford 1992). Studies in preparation by Curtin and Kelt suggest that the effects of this keystone guild are climatically mediated and vary with rainfall patterns. This results in kangaroo rats grazing grasses disproportionately in wet years (when grass growth is greater) and shrubs in wet winter-dry summer years (when shrub growth is greater).

Environmental Change and the Malpai Borderlands

In this chapter, we address three basic questions: (1) How climate affects these arid and semiarid ecosystems, (2) How herbivory alters the impacts of climate in these arid and semiarid ecosystems, and (3) How different grazing regimes, resulting from different land tenure systems north and south of the international boundary, affect vegetation change.

In the following pages we will examine the interaction of these factors in grassland, shrubland, and savanna communities, at lower elevation sites (< 1,700 m) and at higher elevation sites (> 1,700 m). Studies range in size from 5 x 10 m plots (in experimental manipulation) to 1 km² plots measured from aerial photos over 12–60 years.

Our study area is the greater Malpai Borderlands extending along the Chihuahua/Sonora-Arizona/New Mexico borders (figure 6.1). The Malpai Borderlands, according to Arizona and New Mexico Heritage Databases, is perhaps the most biologically diverse region in North America. The area has > 40 rare and endangered species including the northern aplamado falcon (*Falco femoralis septentrionalis*), New Mexican ridgenose rattlesnake (*Crotalus willardi*), Mexican long-nosed bat (*Leptonycteris nivalis*), white-sided jack rabbit (*Lepus callotis*), and jaguar (*Panthera onca*). The primary economic activity in the region is ranching.

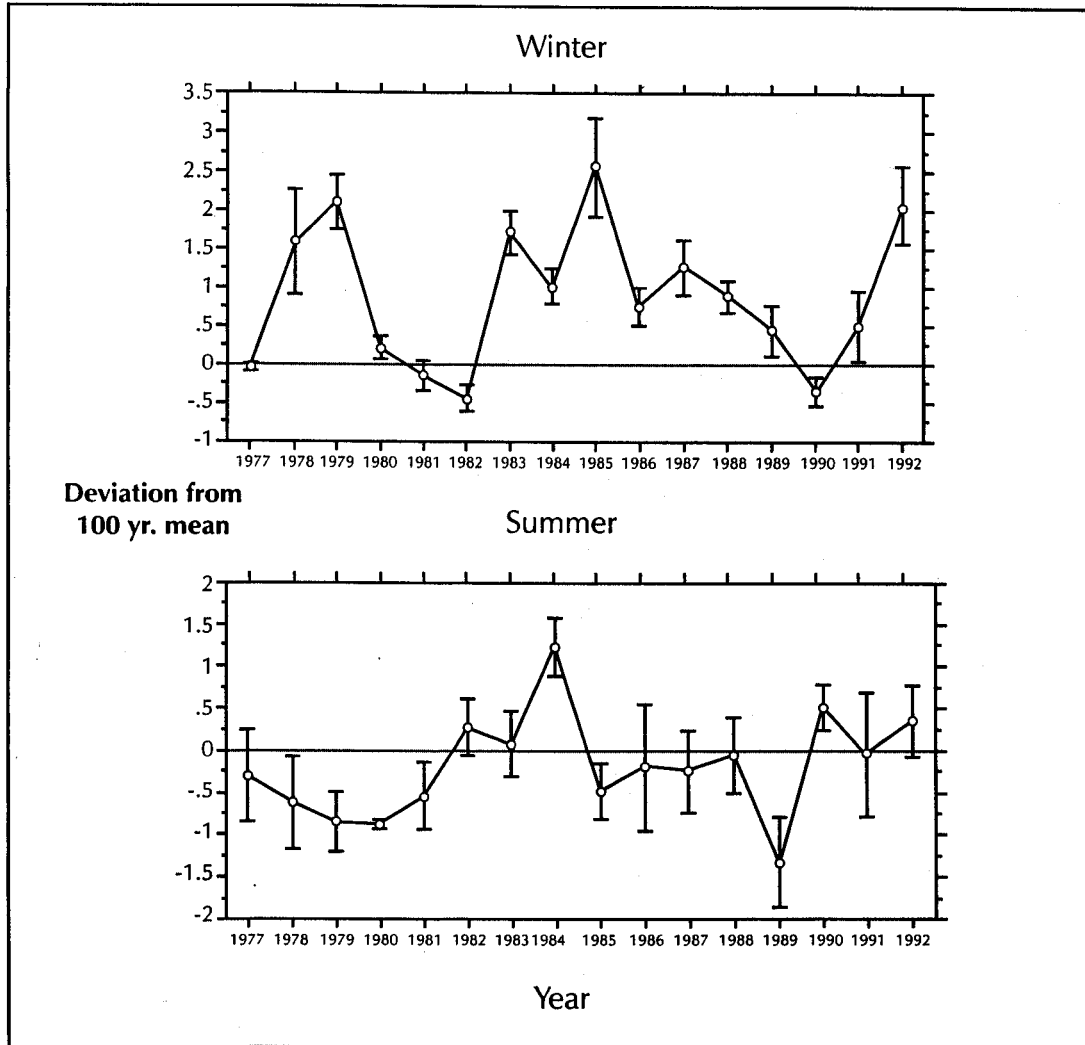


FIG. 6.2
Rainfall deviation from the 100-year mean from five stations surrounding the Malpai Borderlands (Douglas, Safford, Tombstone, Tucson, and Jornada) (after Brown et al. 1997).

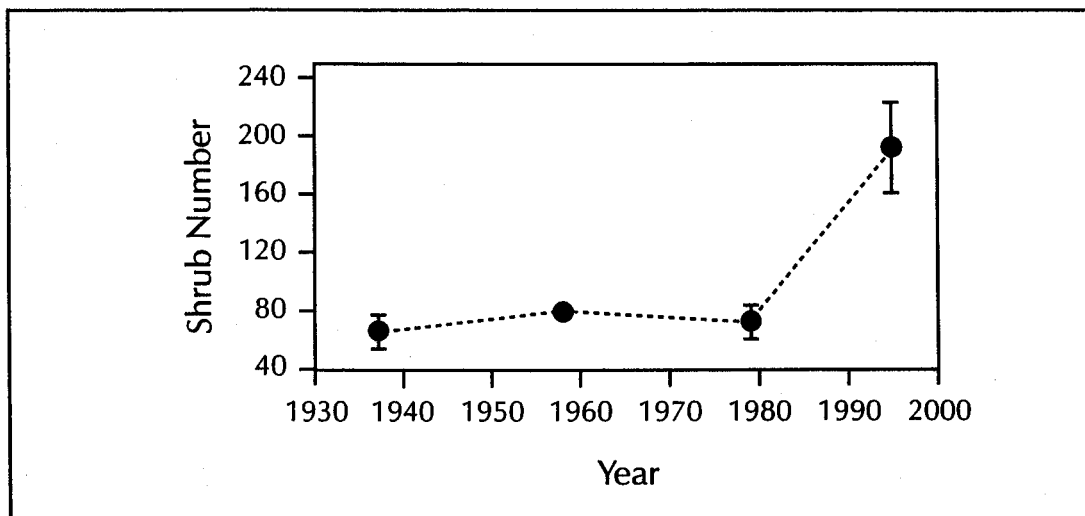


FIG. 6.3
Increase in the number of long-lived woody shrubs ($P > 0.5$ m) at the Portal study site.

Long-term studies from 1977 to the present on the interaction of desert granivore species (ants, birds, and rodents) have been conducted on a bajada 10 km east of Portal, Arizona. A 20-ha area was fenced to exclude cattle and permit manipulations of the small mammal and ant populations within the study area (Brown 1997; Brown et al. 1986). Recently these studies have focused on the interaction between climate and herbivory in this Chihuahuan desert/arid grassland ecotone (Brown et al. 1997).

Because historical survey records, photographs, and paintings indicate that the region was grassland prior to the 1900s, but primarily a shrubland by the 1920s, we believe that some combination of heavy grazing and drought was probably responsible for reorganizing the ecosystem at this site.

Since the 1970s, the region has undergone a profound shift in climate that has continued until the present with winter precipitation several times the 100-year average and summer precipitation near normal (Brown et al. 1997) (figure 6.2). While subshrubs such as snake-weed (*Gutierrezia* spp.) have undergone extensive short-term population fluctuations in response to yearly climatic variation, long-lived woody plants such as *Acacia*, *Ephedra*, *Flourensia*, and *Prosopis* have experienced three-fold increases since the 1970s (figure 6.3). These changes have occurred at two other sites in the valley in both grazed and ungrazed locations. Ground studies by Kelt and Valone (1995) failed to show discernible differences in fence-line contrasts, and we also documented little or no differences in vegetation or native animal communities across the fence line between our ungrazed study site and other areas, suggesting that they cannot be attributed to current grazing practices.

The increasing shrub cover, in turn, has had cascading effects on the rest of the system. The second most common rodent on the site, the mound-building banner tail kangaroo rat went locally extinct. At the same time another rodent, typical of shrub habitats, *Chaetodipus bayleii*, which was never on the site in the previous 17 years, has become common over the last several years. Some of the most common mound-building seed-harvester ants (*Pogonomyrmex rugosus* and *Aphaenogaster cockerellii*) have also gone locally extinct. In association with the decline of these mound-building rodents, several other large, predatory species have declined or become locally extinct. These include the Mojave green rattlesnake (*Crotalus scutulatus*), whose numbers have decreased an estimated 15–25%, and the burrowing owl (*Athene cunicularia*) whose populations “collapsed in the 1980s” in the valley and many surrounding portions of the region (Brown et al. 1997).

The results of previous grazing and herbivory studies have led us to examine in greater detail, and at a larger scale, the impacts of grazing and climate in structuring the vegetation of the Malpai Borderlands. To analyze these processes, we have used aerial photography. We believe that the value of aerial images as a resource for understanding environmental change has been underused. These images provide a relatively long-term record, in many regions back to the 1930s, of environmental change at scales appropriate for understanding local and regional processes.

While past analysis of aerial images has principally relied on manual counts of vegetation change or complex computer-driven algorithms, we have taken a middle-of-the road approach of devising a simple protocol for analyzing vegetation cover changes on a personal computer using commonly available and inexpensive software (Adobe Photoshop and NIH Image) coupled with extensive ground truthing (Frey and Curtin 1997). This low-tech approach allows us to relatively quickly quantify changes in vegetation cover.

Effects of Herbivory and Climate in Experimental Plots near Portal, Arizona

These studies, conducted at long-term study sites near Portal (Brown 1997; Brown et al. 1986) ask: (1) How different guilds of herbivores impact arid ecosystems, and (2) How herbivory affects climatically-induced vegetation change?

To understand the relative impacts of herbivory, we examined 14- and 18-year old experimental treatments that excluded various herbivore guilds from our study area. Excluded organisms included birds (primarily black-throated sparrow [*Amphispiza bilineata*] and scaled quail [*Callipepla squamata*])—5 × 10 m enclosures); folivores (including deer [*Odocoileus hemionus*], rabbits [*Sylvilagus auduboni* and *Lepus californicus*], and javelina [*Tayassu tajacu*])—5 × 10 m enclosures); granivores (primarily kangaroo rats [*Dipodomys* spp.]—50 × 50 m enclosures), ants ([*Pogonomyrmex* and *Pheidole* spp.]—50 × 50 m enclosures); and cattle (inside and outside our 20 ha study area). Details of these experimental enclosures can be found in Guo et al. (1995).

We measured vegetation cover using low-altitude (75–100 m above ground) aerial images taken during March of 1995. All measurements were taken at least 0.5 m away from fences to reduce edge effects. Results were contrasted with those of Guo et al. (1995) and by ground truthing to check for accuracy. Statistical comparisons were conducted using a one-factor ANOVA. The experimental exclusion of different animal consumer groups resulted in highly significant differences between treatments ($P < 0.0002$, $SE = 2.3$ – 5.5). Vegetation cover in rodent enclosures was greatest for folivores ($P < 0.001$, $SE = 2.3$), followed by granivores ($P < 0.004$). No significant differences could be found between ant and bird enclosures and adjacent control areas or in fence-line contrast between cattle-grazed and ungrazed areas. This meant that in the absence of grazers and seed-eating rodents, shrubs and winter annuals increased.

While the differences in treatment design and extent make this less than a definitive study, at the same time the results are consistent with other studies in the region (Guo et al. 1995; Kelt and Valone 1995) and provide a direct comparison of the relative effects of herbivores in Chihuahuan Desert ecosystems. The results illustrate the importance of small mammals within these systems and illustrate that after 100 years of grazing, cattle had an imperceptible impact on vegetation cover in lowland shrubland communities following 18 years of enclosures, while native herbivores and folivores had highly significant effects.

Given the apparent importance of rodents as engineering organisms within our study system, we next asked how herbivory affected the climatically-induced vegetation change discussed in an earlier section. We again used analysis of low-elevation aerial photographs (75–100 m above the ground) but this time contrasted vegetation in the 50 × 50 m rodent experiment plots and adjoining control plots, using aerial images flown in 1979 (before changes in rainfall patterns) and 1995 (after > 10 years of wet winters had altered the shrub community) (Brown et al. 1997).

Using a three-factor ANOVA, we again measured the percentage cover of woody shrubs, winter annuals, summer annuals (grasses), and open ground within six rodent removal, six kangaroo rat removal, and six control plots. While there was a significant effect of time (due to vegetation change) with woody shrubs increasing and grasses decreasing, the percentage of open ground remained constant. While vegetation changed across all treatment types, the change was significantly greater in the rodent removal plots ($P < 0.0001$). The results suggest that herbivores play a significant role in mitigating climatically-induced vegetation change. For example, while the mean patch size of vegetation (reflecting mostly growth of existing

shrubs [*Acacia*, *Ephedra*, *Flourensia*, and *Prosopis*] and recruitment of new ones) in control plots during our study period increased three-fold, it increased six-fold in the absence of rodent activity ($P < 0.0009$).

Effects of Grazing on Woody Vegetation in Uplands

The results of the previous studies led us to hypothesize that in the face of climatically driven increases in woody vegetation, grazing by cattle might also play an important role in mitigating the effects of climate on vegetation. To this end, we ask to what extent can results derived from small-scale manipulative studies be extrapolated to apply to real landscapes.

Here we examine the effect of winter grazing on vegetation change at higher elevations, on sites with oak savanna. Post Office Canyon, 20 km southeast of Portal, is an east-west running canyon in the Peloncillo Mountains at an elevation of ca. 1,700 m. The area has a 100-year grazing history with browsing by goats the dominant land use in the early years of this century and cattle grazing since at least the 1950s (Moir 1979) (W. Miller, personal communication 1997). In the late 1960s, the eastern portion of the valley was removed from grazing while the western portion continued to be winter grazed (W. Miller and R. Scholes, personal communications 1997). This contrast between grazed and ungrazed landscapes with similar slope, aspect, elevation, topography, and soils, provides a good opportunity to investigate vegetation change in upland sites and the effects of cattle grazing within these areas.

Using the same image analysis technique discussed above (Frey and Curtin 1997), we measured the percentage of cover by woody vegetation (primarily *Quercus* spp.) in twelve 50 × 50 m plots, six on each side of the fence line. Plot size and locations were determined using ground control (roads and fences). Comparisons were conducted using aerial images flown in 1946, 1957, 1976, and 1992. Images at scales of 1:15,000 and 1:28,000 were acquired through a database at the Earth Data Analysis Center (EDAC) at the University of New Mexico. Statistical analysis of vegetation change was conducted using a one-factor ANOVA.

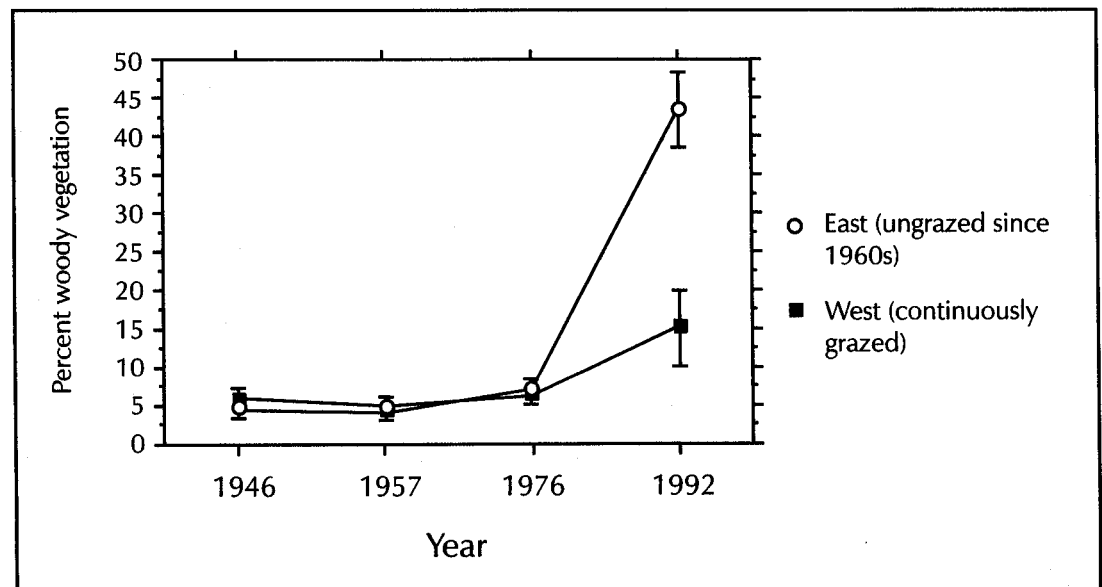


FIG. 6.4
Changes in woody
vegetation at Rodeo,
New Mexico.

The cover of woody vegetation was similar from the 1940s–1970s, but diverged from 1976–1992. Woody vegetation in the grazed area shifted from a mean cover of 6.6% (SE = 1.7) in 1976 to 15.3% (SE = 4.3) in 1992. In contrast, in the ungrazed area the mean woody cover went from 7.2% (SE = 0.9) in 1976 to 43.8% in 1992 (SE = 5.2). Thus, there was a significant difference in vegetation cover between 1976 and 1992 ($P < 0.0001$), and even greater difference in woody cover between land-use types ($P < 0.0006$) within this same time period (figure 6.4).

The two-fold increase in woody vegetation in the grazed area and six-fold increase in woody vegetation in the ungrazed area illustrates two points. First, the patterns of woody plant increase hold not just for grassland and shrub communities in the valley bottoms, but are also prevalent in upland areas. Second, grazing by cattle, as with herbivory by rodents at lower elevations, can serve an important role in reducing climatically-induced vegetation change. Third, in the absence of grazing or fire, woody vegetation increased at a significantly greater rate in ungrazed areas. While it should be noted that grass cover was also greater in the ungrazed landscapes, without the intervention of disturbance factors (such as fire) that can reduce the woody cover, grasses will eventually be eliminated from much of the system.

Effects of Grazing along the International Boundary

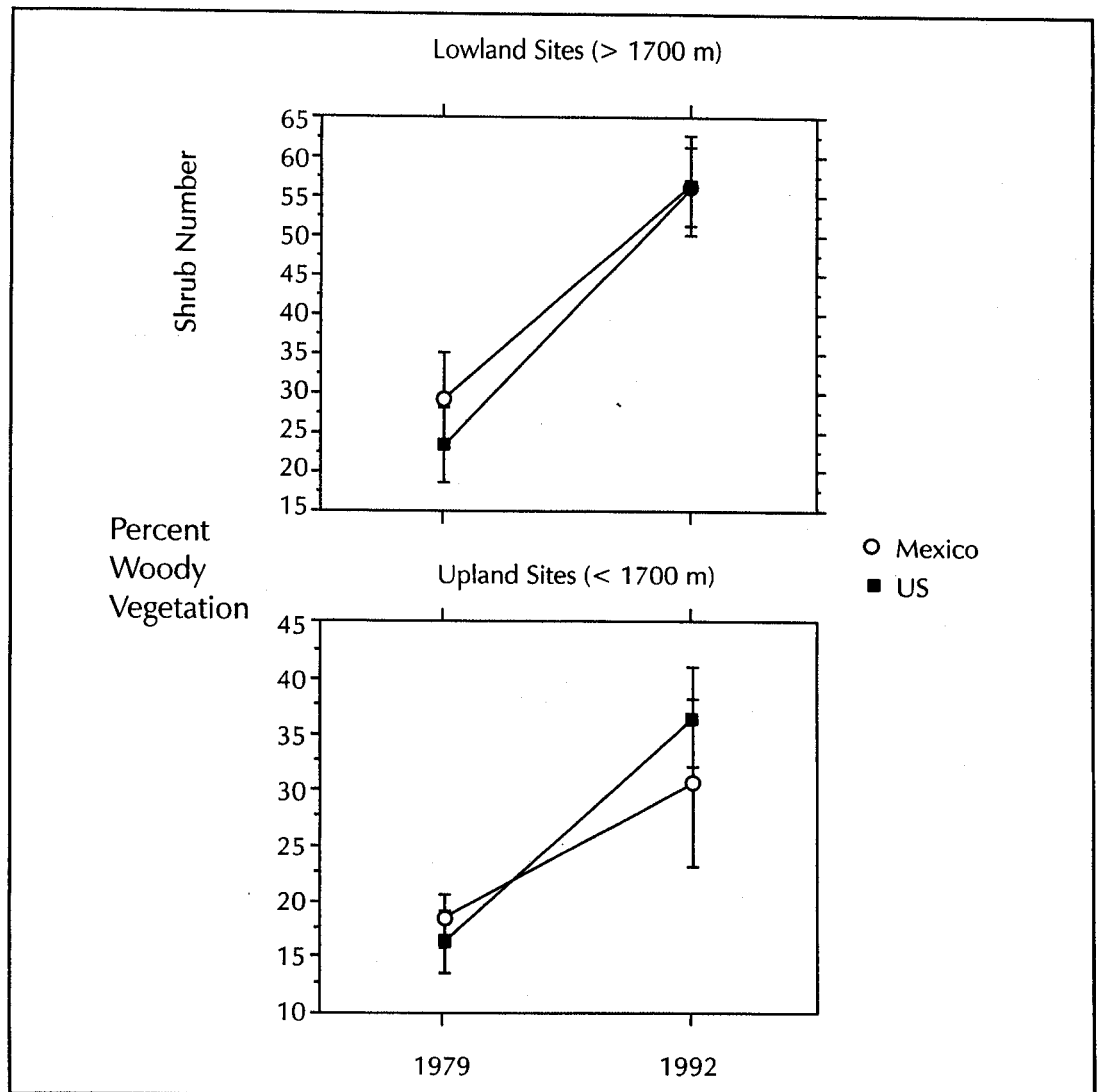
It has been frequently noted that a “grazing line” exists between the U.S./Mexico boundary. Here, we investigate the extent to which this represents a permanent environmental perturbation, versus relatively short-term and reversible changes in grass basal area, in the Malpai Borderlands.

While grass and subshrub cover vary dramatically from year to year and thus is relatively ephemeral on the landscape, cover by woody shrubs or trees can persist for decades or centuries (Brown 1997; Goldberg and Turner 1986; Hastings and Turner 1965; Schlesinger et al. 1990; Webb 1996;). The biological feedbacks associated with conversion of grassland to shrubland result in extensive, and often irreversible, changes in the system (Schlesinger et al. 1990). These include increased erosion rates and loss of soil cover (Buffington and Herbel 1965); reorganization of soil resources (Crawford and Gosz 1982; García-Moya and McKell 1970; Kieft et al. 1998; Schlesinger et al. 1996); changes in above-ground microclimates (Breshears et al. 1998; Tiedemann and Klemmedson 1977); changes in water relationships (Crawford and Gosz 1982); and reorganization of plant and animal communities in response to biotic and abiotic interactions (Brown et al. 1997; Chew and Whitford 1992). Therefore, measurement of relative rates of increase in woody vegetation across the international boundary has fundamental implications for ecosystem structure and composition.

The study area stretches 80 km from Douglas/Agua Prieta east to the Animas Valley. This area was selected primarily because overlapping aerial photographs exist for both sides of the border in this region of the Malpai Borderlands. Because most aerial photography of the Mexican portion of the border was blacked-out or deleted for many time periods, this represented a significant constraint on photo availability and the geographic extent of this portion of the project. Interviews with local ranchers indicate that, at least in the recent past, the grazing regime north of the border has been typified by rotational programs, while south of the border has had almost entirely year-round stocking. While land does change hands, the landscape has typically been held by seven or eight land holders on each side of the border (W. Glenn, personal communication 1998).

In this study, we focused on the 1980s and early 1990s when recent records indicate that

FIG. 6.5
Changes in woody
vegetation cover
across the international
boundary between
Douglas/Agua Prieta
and the Animas Valley.



vegetation and climate change was most pronounced (Swetnam and Betancourt 1998; Brown et al. 1997). As with the previous study in the Peloncillo Mountains, aerial photographs from 1979 and 1992 were selected and 1:20,000-scale images were used. Aerial imagery was located through databases at EDAC at the University of New Mexico. One km² plots were placed at 3 km intervals at adjacent locations north and south of the boundary. We analyzed 14 plots on each side of the boundary; seven were in upland sites (> 1,700 m) and seven in lowland sites (< 1,700 m). Statistical analysis was conducted using a one-factor ANOVA (figure 6.5).

While no differences in vegetation change were detected across the international boundary, there were highly significant changes in vegetation occurring concurrently on both sides of the boundary. In lowland sites, there was a change in woody cover from 26.2% in 1979 to 56.0% in 1992 ($P < 0.022$), while in the upland sites woody cover expanded from 17.3% in 1979 to 33.2% in 1992 ($P < 0.0001$). Thus, while lowland sites started and ended with higher woody cover, both lower and upper elevational sites exhibited about a two-fold increase in woody vegeta-

tion. These increases were comparable to grazed sites in Post Office Canyon in the Peloncillo Mountains, indicating that this magnitude of increase is pervasive in this region.

A "grazing line" denoted by lighter colored vegetation occurred on the Mexican side of the boundary in lowland portions of the study area and in valleys in upland areas. These changes, often visible in satellite imagery, have been documented to dramatically change albedo and surface microclimates (Ray 1995). In our studies of the Malpai Borderlands area, while changes in albedo were evident even to the naked eye, these changes in timing or intensity of grazing did not produce detectable changes in woody vegetation cover. This suggests that, at least in this region, increased soil exposure (apparently due to a reduction in basal cover for grasses and forbs) has not been associated with increases in shrub density and therefore probably do not represent long-term, irreversible system changes.

Conclusions

Our studies of the Malpai Borderlands ecosystem indicate that across our study area relatively greater winter precipitation (since the 1970s) is correlated with increases in woody vegetation and declines in grasses. Experimental studies of herbivores indicate that folivores (such as rabbits, javelina, and deer), and granivorous rodents (such as kangaroo rats) had the greatest impact on vegetation structure, with cattle having little detectable effect. Additional studies indicate that rodents play a key role in mitigating climatically-induced vegetation change, with shrub and winter annual increases greater in rodent exclosures.

These results led us to examine vegetation change in nearby grazed and ungrazed landscapes where we found that ungrazed areas experienced, in the absence of fire, significant increases in shrubs. This resulted in our examining vegetation change on both sides of the international boundary to determine whether different grazing regimes have led to divergent patterns of vegetation change north and south of the border. While a "grazing line" is visible in aerial photographs and significant increases in shrub cover occurred from the 1970s–1990s, our measurements of shrub cover did not detect significant differences in vegetation change across the border.

The interaction of climate, grazing, and herbivory by native species leads to a series of complex, nonlinear interactions in which the precise outcome is probably impossible to determine. At the same time, the above studies suggest that several basic patterns emerge. First, in the face of wet-winter and dry-summer climatic cycles, shrubs and other woody vegetation will expand. Second, herbivory by native species and livestock grazing, in the face of recent climatic conditions, can serve an important role in mitigating or compensating for climatically-driven vegetation change.

At the same time, current climatic effects and the role of herbivores must be looked at in the context of longer term, larger scale processes. The unprecedented changes in vegetation and the current role of the present herbivores as stabilizing agents probably also result from the loss of other controlling processes that previously organized the system. Perhaps most important of these is fire. Prior to intensive settlement and fire suppression over the past 80 years, regular fire was a common and integral part of these systems (Bahre and Shelton 1993; Ffolliott et al. 1996; Gottfried et al. 1995; McClaran and Van Devender 1995). Fire represents a resource dissipater that redistributes resources and nutrients across the landscape, creating spatial and temporal heterogeneity within the system. Upland areas with relatively high moisture and thus rich resource accumulations become carbon sinks

composed of dense woody vegetation; fires periodically release nitrogen and carbon that are then, in turn, carried down slope and distributed across bajadas and eventually into riparian areas. Lowland fires redistribute carbon in woody shrubs and facilitate the dynamic interaction of shrubs and grasses.

Prairie dog towns also once covered much of the American Southwest including much of the lowlands within the Malpai Borderlands (J. Frey and C. Oaks, personal communications 1998). Prairie dogs are resource concentrators that organize energy and nutrients into a complex of burrows and disturbance gradients. These concentrations of nutrients and structured habitat are hotspots for biodiversity. Although these organisms are gone, in places once occupied by prairie dog towns, kangaroo rats and cattle continue the role of disturbance agents, resource dispersers, and nutrient concentrators within the system. Thus, it is not so much that particular organisms represent distinct organizing species, but more that they fill certain invariant niches that maintain the continuity of the system. Thus, the final message of this chapter is that when one is looking at processes such as herbivory and climate, they must be observed in the context of the system. Without the historical agents within the system (such as fire, prairie dogs, or Pleistocene fauna in the more distant past), shrubs have come to dominate and small mammals and cattle have come to mediate.

In summary, it is not so much the particular agents that currently are in place in the system but the processes they represent that can lead to a fundamental understanding of the basic properties organizing the Malpai Borderlands ecosystem. To maintain the borderlands ecosystem, particularly in the face of current climatic patterns, an understanding of the fundamental structuring processes, without getting bogged-down in the management of the current actors on the scene, is crucial to the maintenance of the long-term health and integrity of dynamic physical, biological, social, and economic systems.

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