Herbaceous vegetation change in variable rangeland environments: The relative contribution of grazing and climatic variability

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Abstract. A 44-yr record of herbaceous vegetation change was analysed for three contrasting grazing regimes within a semi-arid savanna to evaluate the relative contribution of confined livestock grazing and climatic variability as agents of vegetation change. Grazing intensity had a significant, directional effect on the relative composition of short- and mid-grass response groups; their composition was significantly correlated with time since the grazing regimes were established. Interannual precipitation was not significantly correlated with response group composition. However, interannual precipitation was significantly correlated with total plant basal area while time since imposition of grazing regimes was not, but both interannual precipitation and time since the grazing regimes were established were significantly correlated with total plant density. Vegetation change was reversible even though the herbaceous community had been maintained in an altered state for ca. 60 yr by intensive livestock grazing. However, ca. 25 yr were required for the mid-grass response group to recover following the elimination of grazing and recovery occurred intermittently. The increase in mid-grass composition was associated with a significant decrease in total plant density and an increase in mean individual plant basal area. Therefore, we failed to reject the hypotheses based on the proportional change in relative response group composition with grazing intensity and the distinct effects of grazing and climatic variability on response group composition, total basal area and plant density. Long-term vegetation change indicates that grazing intensity established the long-term directional change in response group composition, but that episodic climate events defined the short-term rate and trajectory of this change and determines the upper limit on total basal area. The occurrence of both directional and non-directional vegetation responses were largely a function of (1) the unique responses of the various community attributes monitored and (2) the distinct temporal responses of these community attributes to grazing and climatic variation. This interpretation supports previous conclusions that individual ecosystems may exist in equilibrial and non-equilibrial states at various temporal and spatial scales.

Keywords: Climate; Grazing; Herbivory; Plant-animal interaction; Rangeland evaluation; Resilience; Stability; State and transition model; Vegetation change; Vegetation monitoring.

Nomenclature: Hatch et al. (1990)

Introduction

The relative contribution of grazing and climatic variability to vegetation change are difficult to assess because both occur over numerous spatio-temporal scales and may produce various interactive effects (McNaughton 1983; Archer & Smeins 1991; O'Connor 1995; Fuhlendorf & Smeins 1999). Communities may also possess considerable biological inertia such that vegetation change may lag behind episodic environmental events to obscure the nature of the cause-effect relationships (Westoby 1980; Milchunas & Lauenroth 1995). Therefore, it is not surprising that some investigators have concluded that grazing is the primary agent of vegetation change on rangelands (Tomanek & Albertson 1953, 1957; Belsky 1992), while others have emphasized climatic variability as the primary change agent (Westoby 1980; Clarkson & Lee 1988; Milchunas et al. 1989; O'Connor 1991; 1995; Allen et al. 1995; Biondini et al. 1998). We contend that much of the uncertainty associated with the relative impacts of grazing and climate resides in the lack of long-term data to discriminate between these two change agents (Connell & Sousa 1983; O'Neill et al. 1986; Franklin 1989).

The relative contribution of grazing and climate to vegetation change resides at the very center of the debate regarding the appropriate paradigm for managing and interpreting vegetation change on rangelands. The traditional paradigm based on the assumption that community composition will show a proportional response to grazing intensity has been criticized as being overly simplistic (Westoby et al. 1989; Laycock 1991; Behnke & Scoones 1993). In contrast, over emphasis on climatic variability as an agent of vegetation change minimizes the influence of grazing on semi-arid rangelands (Ellis & Swift 1988; Ellis 1994). The relative contribution of grazing intensity and climatic variability to rangeland vegetation change has far reaching ecological and managerial implications and merits a thorough conceptual evaluation

(Illius & O'Connor 1999; Fernandez-Gimenez & Allen-Diaz 1999). In addition, the plant or community attributes measured i.e., composition, basal area, density or production, may yield distinct interpretations of vegetation change in response to grazing and climate.

This investigation evaluated the response of herbaceous vegetation change to grazing intensity and climatic variability within a semi-arid oak-juniper savanna over a 44-yr period (1949-1993). It was designed to extend and verify conclusions derived from a multivariate analysis of this community (Fuhlendorf & Smeins 1997) by distinguishing between the relative effects of grazing intensity and climatic variability on response group composition, plant density and total basal area. The previous results indicated that grazing had a greater effect on community composition than did discrete climatic events and that short- and mid-grass response groups were an appropriate means of vegetation analysis in this system. Three distinct grazing regimes were implemented in this community in 1949 and the subsequent 44-yr period was punctuated with substantial climatic variability, including the severe long-term drought of the 1950s, and a severe episodic freeze in December 1983. Our goal was to evaluate changes in not only relative composition of perennial short-grass and mid-grass response groups, but also total plant density, and total and individual plant basal area among grazing intensities and through time to establish whether grazing was more or less important than climatic variability in driving these changes (O'Connor 1991, 1995). We reasoned that as vegetation change deviated from a directional and proportional relationship with grazing intensity it would indicate a greater relative contribution of climatic variability as an agent of vegetation change. We further assumed that vegetation change would occur erratically and intermittently, if climatic variability was a more important change agent than grazing. We hypothesized that (1) grazing intensity would produce a directional and proportional change in the relative composition of short-grass and mid-grass response groups, and (2) that response group composition, plant density, and total basal area would show distinct responses to grazing and climatic variability.

Study area and grazing regimes

Research was conducted on the Texas A&M University Agricultural Research Station, which is located within the Edwards Plateau Land Resource Area (Hatch et al. 1990) 56 km south of Sonora, Texas. Elevation of the station is ca. 730 m. Dominant soils are Tarrant stony clays of the thermic family of Lithic Haplustolls (Wiedenfield & McAndrew 1968). Soils formed over fractured Edwards and Buda Cretaceous limestone are generally 15 to 30 cm deep, contain 5 to 70% limestone fragments, and have gentle slopes of 3 to 4%.

The growing season is ca. 240 days; temperatures average 30 °C in July and 9 °C in January (Station Records). Average annual precipitation (1919-1993) is ca. 600 mm and has varied from 156 mm in 1951 to 1054 mm in 1937 (Fig. 1). Precipitation is bimodal with distribution peaks in the spring and fall and periodic droughts are common. A severe prolonged drought occurred from 1951 to 1956 with an average annual precipitation for that period of ca. 300 mm (Herbel et al. 1972; Stahle & Cleaveland 1988; Smeins & Merrill 1988). An unusually severe freeze occurred in December 1983, where record low temperatures (– 17 °C) occurred for 7 to 10 days (Lonard & Judd 1985; Station Records). This severe freeze was preceded by moderate temperatures which had maintained growth of most grasses beyond their normal growing season which made them more susceptible to the rapid decrease in temperature. The freeze was followed by a dry period through the following spring which further limited vegetation recovery.

Vegetation is a savanna/parkland with individuals or clusters of woody species interspersed within a mid- and short-grass matrix (Kuchler 1964; Smeins & Merrill 1988). Woody canopy cover may be as high as 40%, but varies
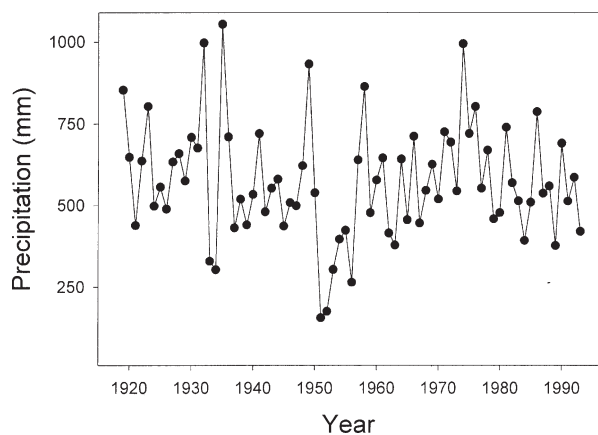

Fig. 1. Annual precipitation from 1919 to 1994 at the Sonora Research Station near Sonora, Texas.

greatly with topo-edaphic features, grazing and fire history (Fuhlendorf et al. 1996). Dominant woody species include *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei*, and *J. pinchotii*. Dominant short-grasses are *Hilaria belangeri*, *Erioneuron pilosum* and *Bouteloua trifida,* while dominant caespitose mid-grasses are *Aristida purpurea*, *Bouteloua curtipendula* var. *caespitosa*, and *Eriochloa sericea* (Fuhlendorf & Smeins 1997).

Prior to 1948, stocking rates on the station were up to six times the current average stocking across all grazing regimes (Youngblood & Cox 1922; Smeins et al. 1997). Approximately 80 yr (1870-1950) of heavy grazing and cessation of fire caused a decrease in mid-grasses and an increase in woody plants (Smeins & Merrill 1988). In 1948, three grazing regimes were established within this heavily grazed community. The heavily grazed regime was continued in two 32-ha treatment units that were stocked with cattle, sheep and goats at a stocking rate that ranged from 4.8-5.4 ha/auy (animal unit year = 4314 kg of above-ground herbaceous biomass or the amount of forage consumed by a 450 kg animal for one year) until 1983 when the stocking rate was reduced to moderate levels. The moderately grazed regime consisted of four 24-ha treatment units from a four-pasture, three-herd deferred rotational system grazed by cattle, sheep and goats at a stocking rate that varied from 6.0-10.4 ha/auy. Stocking rates have been variable since 1948, but the grazing intensity in the heavily grazed regime has always been 1.5 to 2 × greater than in the moderately grazed regime until 1983. Both grazing regimes have been moderately grazed since 1983 (see Fuhlendorf & Smeins 1997 for detailed description). The ungrazed regime consisted of 2-12 ha exclosures that have not been grazed by livestock since 1948. One of the exclosures also excluded large, free-roaming native herbivores, primarily white-tailed deer (*Odocoileus virginianus* L.).

Methods

Vegetation sampling

In 1948, three transect lines (ungrazed and moderate = 800 m, heavy = 1050 m) were established along the long axis of each of the eight treatment units, and 12 permanently marked 30.5 cm × 30.5 cm quadrats were established on each line (36 quadrats/treatment unit). Plant density and diameter at the soil surface of each rooted perennial grass plant was measured annually from 1949 to 1965 within each quadrat and converted to a circular area for each plant. Since 1965, sampling intervals have been sporadic and not all treatment units were evaluated during each sampling period. Basal dia-

meters were converted to an area basis for each plant. Plant density and basal area were recorded if the plants were at least partially rooted within a quadrat.

Data analysis

Perennial grass responses were analyzed as short-grass and mid-grass response groups to simplify vegetation responses to more clearly assess the relative impact of grazing and climatic variability on vegetation change. These response groups were each dominated by a relatively small number of species. The stature of perennial grasses has long been recognized to affect grazing resistance (Branson 1953; Arnold 1955; Dyksterhuis 1949; Noy-Meir et al. 1989) and exploratory investigations of this data set have indicated that these response groups would effectively describe vegetation responses to grazing (Fuhlendorf & Smeins 1997, 1998).

Analyses were conducted on short- and mid-grass response groups, total basal area and total density to determine the relative importance of grazing and precipitation on vegetation change. The three grazing treatments provided discrete vegetation variables that were confounded through time because all treatments were heavily grazed prior to 1948. Therefore, vegetation responses between grazing treatments were tested with repeated measures analysis of variance. Vegetation response to grazing intensity was also correlated with time so that it could be directly compared to the correlations between vegetation response and inter-annual precipitation. Vegetation change in the heavily grazed treatment was anticipated to have a weak correlation with time because it represented a continuation of the historical grazing regime while the moderate and ungrazed treatments were anticipated to have stronger correlations with time as vegetation responded to a relaxation of grazing. Precipitation is a continuous variable that is more appropriately analyzed with correlation through time, rather than with analysis of variance. The strength of correlation between vegetation response variables and interannual precipitation would be indicative of the importance of precipitation on vegetation change. The relationship between community attributes and annual precipitation was examined for precipitation during the year of the vegetation response and for each of 4 yr preceding the vegetation response, as well as running mean windows including annual precipitation during the past 2 to 6 yr.

Relative composition of species response groups was based on relative total basal area of short-grass and mid-grass species and differences between response groups were examined with the Wilcoxon Signed-Rank test to avoid the assumption of normality (Conover 1980). This test assessed differences between grazing regimes

by ranking the relative composition of short- and mid-grasses among treatments and years. The ranks were standardized with a mean of zero for each response group and then tested to determine if the ranks were significantly different than zero for each grazing regime. In addition, correlation analyses were also used to evaluate the strength of the relationship between compositional trends in species groups with time and precipitation.

Total plant density and basal area were calculated by summing values for individual grasses across all species within 36 quadrats for each treatment unit and then converted to a m^2 basis. Preliminary analyses indicated that total basal area and total density were normally distributed and that parametric statistics could be used without data transformation. Analysis of variance was used to evaluate the significance of changes in vegetation structure through time within a grazing regime. Analyses of the influence of time, grazing intensity and their interaction were conducted using a repeated measures design (Stroup & Stubendeick 1983) to determine the importance of grazing intensity on basal area and density. To minimize difficulties associated with missing sample dates in some treatment units, basal area and density data were pooled across years for analysis of variance as follows: 1949-1960, 1961-1982, and 1982-1993.

The first hypothesis which indicated that grazing intensity would produce a directional and proportional change in relative response group composition was tested by comparing response group composition among grazing regimes with the Wilcoxon Signed-Rank procedure and by the strength of the correlation between response group composition and time since the grazing treatments were imposed. The absence of a significant, inverse relationship between response group composition and grazing intensity by either analyses would determine that hypothesis one be rejected. The second hypothesis which indicated that community attributes would show distinct responses to grazing and climatic variability was tested by determining whether grazing or climatic variability had significant effects on response group composition, total basal area and plant density. The effect of grazing on response group composition was tested as indicated in hypothesis one and the effects of grazing intensity on total basal area and plant density were tested with ANOVA. The effect of climatic variability on the response of community attributes was tested by determining the strength of the correlation between these attributes and interannual precipitation. The absence of unique, significant responses by all three community attributes to grazing intensity and climatic variability would determine that hypothesis two be rejected.

Results

Species response groups

All grazing regime plots had been heavily grazed for over 60 yr prior to 1948 and as a result short-grasses comprised over 80% of the grass composition at the initial sampling in all treatments (Fig. 2a). Relative composition of short-grass and mid-grass plant response groups was significantly different among all three grazing regimes over the 44-yr period (Wilcoxon Signed-Rank test; $p < 0.001$) (Fig. 2a,b). The ungrazed regime showed the greatest increase in mid-grasses ($r = 0.90$) and decrease in short-grasses ($r = -0.87$, $p < 0.01$). Short-grasses steadily decreased to ca. 20% of the total grass composition by 1993. In the moderately grazed regime, short-grasses gradually decreased to ca. 50-70% of the
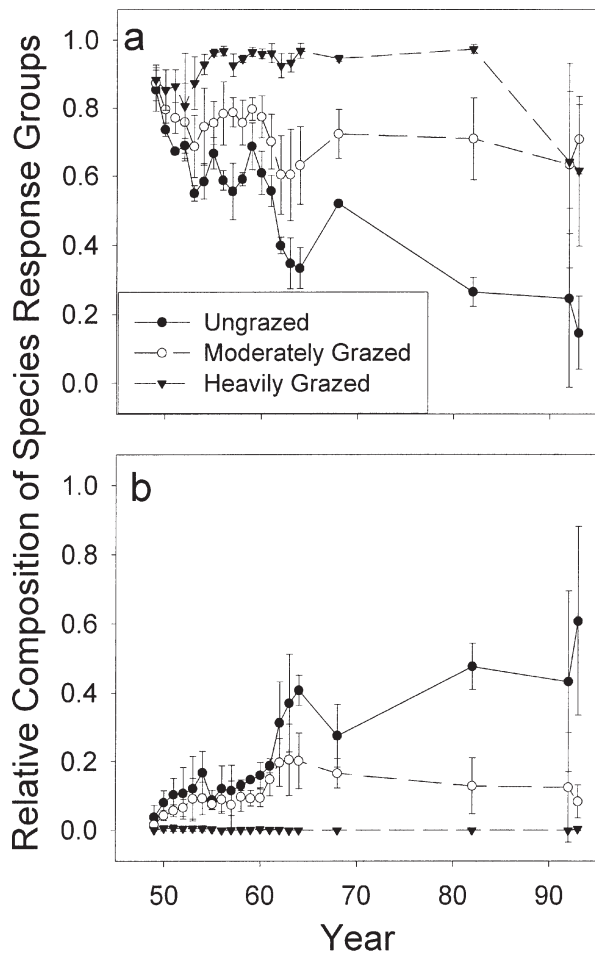

Fig. 2. Relative composition (mean ± S.E.) of (**a**) perennial short-grass and (**b**) mid-grass response groups in response to three grazing regimes imposed by domestic livestock from 1948 to 1993 near Sonora, Texas.
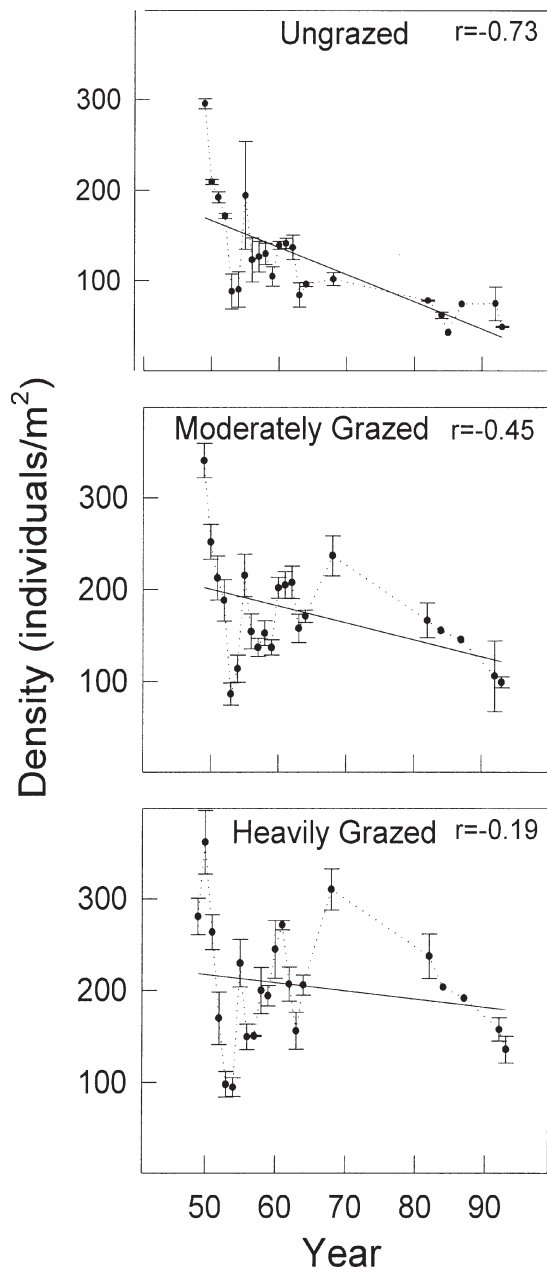
Fig. 3. Total density (mean ± S.E.) of perennial grasses (dotted lines) within three grazing regimes imposed by domestic livestock from 1949 to 1993 near Sonora, Texas. Simple linear correlations between time and plant density (solid lines) represent the long-term trend in each grazing regime.

Fig. 4. Total basal area (mean ± S.E.) of perennial grasses within three grazing regimes imposed by domestic livestock from 1949 to 1993 near Sonora, Texas. Simple linear correlations between time and total basal area were not significant ($p > 0.10$) in any grazing regime.

total grass composition during the first 10-15 yr, while in the heavily grazed regime, short-grasses actually increased to greater than 90% of the total grass composition during the drought of 1951-1956 and then remained fairly constant for the next 27 yr (1956-1983). Short-grasses then decreased to ca. 60% by 1993 following a stocking rate reduction in 1983 (Fig. 2a).
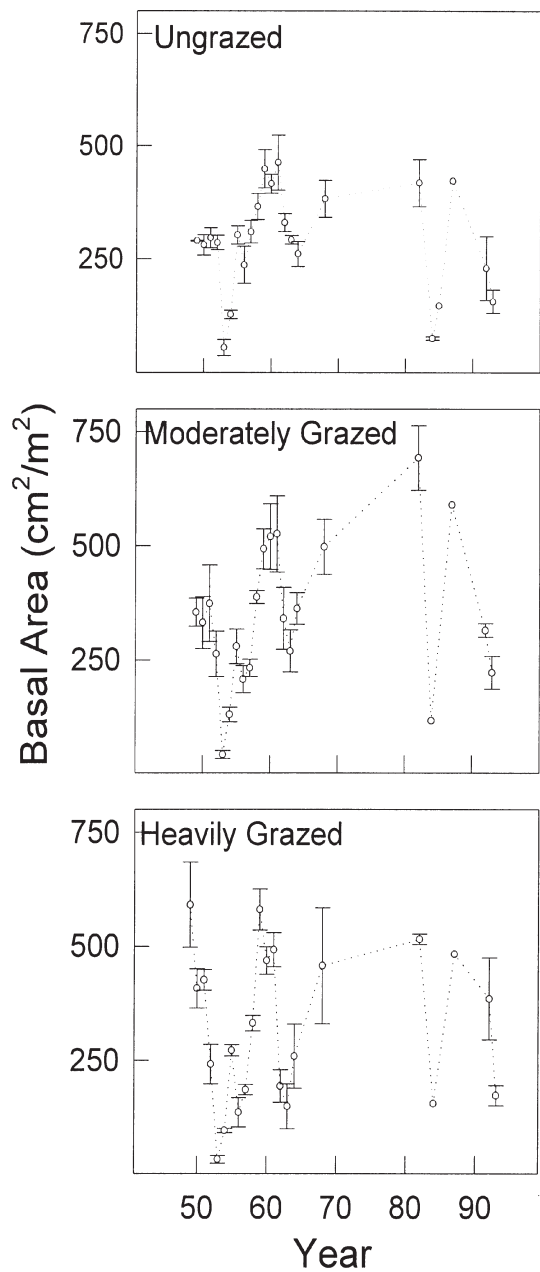
Response group composition was similar in the moderately and heavily grazed regimes during the last decade of the study period following this reduction in stocking rate. The mid-grass response group showed the inverse response of the short-grass response group (Fig. 2b). Response group composition was not significantly correlated with precipitation.

Density and basal area

Time, grazing regime, and their interaction were all significant ($p < 0.10$) for plant density, but not for total basal area (Figs. 3 and 4). This indicates that density responded differently among the three grazing regimes while total basal area did not. Total basal area was not significantly correlated with time in any of the grazing regimes to further substantiate the absence of a response for this variable to changes in grazing intensity.

Plant density showed a strong negative correlation with time in the ungrazed regime ($r = -0.73$, $p < 0.01$), an intermediate negative correlation in the moderate regime ($r = -0.45$, $p < 0.10$), and a weak correlation in the heavily grazed regime ($r = -0.19$, $p < 0.20$), respectively. This proportionality of change demonstrates that plant density, which had been maintained at high levels by prior long-term intensive grazing, was readily reversed when grazing was reduced or eliminated at the onset of these treatments. Total grass density decreased rapidly from about 300 plants/m^2 across all grazing regimes in 1949 to about 75 plants/ m^2 during the severe 1950s drought (Fig. 3). Following the drought, plant density increased to a high of 225 and 300 plants/m^2 in the moderately and heavily grazed regimes, respectively. The ungrazed regime experienced a temporary increase in plant density after the drought, but then decreased to current densities of less than 50 plants/m^2. The heavily grazed regime showed a decrease in plant density from 1983 to 1993 following the reduction of stocking rate in 1983.

Total plant basal area was variable through time and showed no long-term response in any grazing regime which indicated that it primarily responded to climatic variability (Fig. 4). The coefficient of variation for total plant basal area was lowest in the ungrazed regime (40 ± 1.5) followed by the moderately (45.5 ± 1.0) and heavily grazed regimes (53 ± 2.2), respectively. Total basal area ranged from approximately 30 cm^2/m^2 during the drought of the early 1950s and again following an extreme freeze in 1983, to about 450 cm^2/m^2 prior to and following these episodic climatic events (Fig. 4).

The strongest correlations between precipitation and plant density and total plant basal area (basal area $p < 0.05$; density $p < 0.10$) occurred with a running mean window of 3-yr (current and previous 2-yr) (Fig. 5). Significant correlations also occur between plant density and basal area for annual precipitation the year of data collection and for annual precipitation each of the two previous years (Fig. 6). Correlative relationships between all mean running precipitation windows was 30% lower for density than for basal area. Plant density and total basal area were only weakly correlated with monthly and seasonal precipitation.
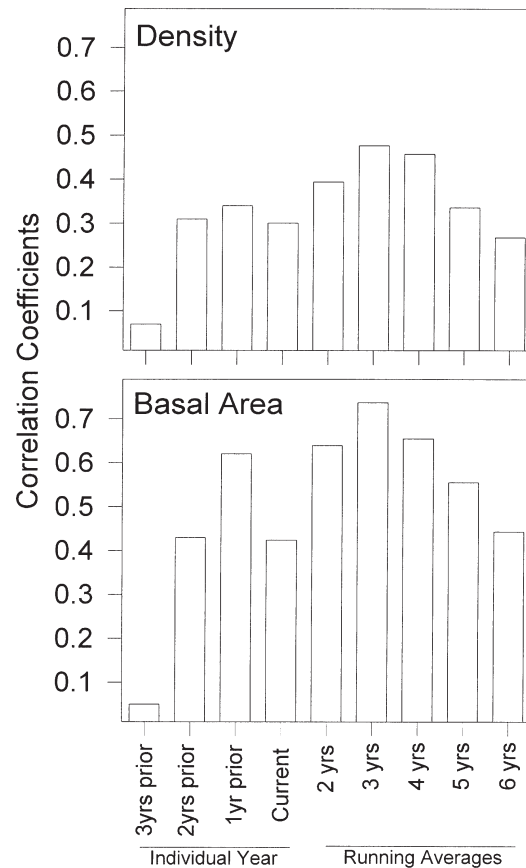

Fig. 5. Correlation coefficients (r) for precipitation and total density and total basal area of perennial grasses through time across all grazing regimes imposed by domestic livestock near Sonora, Texas. Precipitation variables are:
3yrs prior = annual precipitation at a three-year lag;
2yrs prior = a two-year lag;
1yr prior = a one-year lag;
Current = annual precipitation;
2yrs = a running two-year average;
3yrs = a running three-year average;
4yrs = a four-year running average;
5yrs = a running five-year average; and
6yrs = a running six-year average.
All correlations were significant ($p < 0.10$) except for those based on *3yrs prior*.

Correlative relationships between interannual precipitation and plant density and total plant basal area also varied among grazing regimes (Fig. 6). The weakest correlations between precipitation and plant density and basal area were in the ungrazed regime (density $r = 0.23$, $p > 0.10$; basal area $r = 0.57$, $p < 0.05$); the strongest in the heavily grazed regime (density $r = 0.69$, $p < 0.01$; basal area $r = 0.78$, $p < 0.01$); and intermediate in the moderately grazed regime (basal area $r = 0.69$, $p < 0.01$; and density $r = 0.46$, $p < 0.10$). Precipitation-density correlations were consistently weaker than cor-
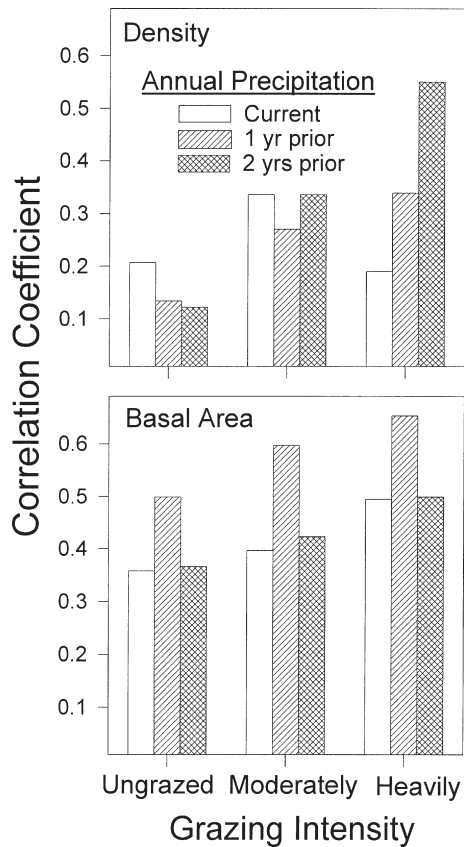
Fig. 6. Correlation coefficient (*r*) for precipitation and total density and total basal area of perennial grasses through time for three grazing regimes imposed by domestic livestock near Sonora, Texas. Precipitation variables represent annual (*Current*), annual with a one-year lag (*1 yr prior*), and annual with a two-year lag (*2 yrs prior*).

relations between precipitation and basal area. Lowest plant densities occurred following 44 years of protection from domestic herbivores and not during extreme climatic events. Disproportionate responses occurred among structural community attributes following the elimination of livestock grazing in 1949 (ungrazed treatment) (Fig. 7). Total plant basal area did not change directionally following the removal of grazing. In contrast, individual plant basal area increased and plant density decreased in response to the removal of grazing.

Discussion

Interpretations of vegetation change

Analysis of these long-term data indicate that both grazing and climatic variability are important agents of herbaceous vegetation change in this semi-arid savanna. Grazing intensity had a significant, directional effect on the relative composition of short- and mid-grass response groups and response group composition was significantly correlated with time since the various grazing regimes were established. Therefore, we failed to reject hypothesis one that grazing would produce a directional and proportional change in the relative composition of short- and mid-grass response groups. These results support the initial interpretation of compositional responses to grazing in this community based on multivariate analysis (Fuhlendorf & Smeins 1997). In contrast to grazing intensity, interannual precipitation was not significantly correlated with response group composition. However, interannual precipitation was
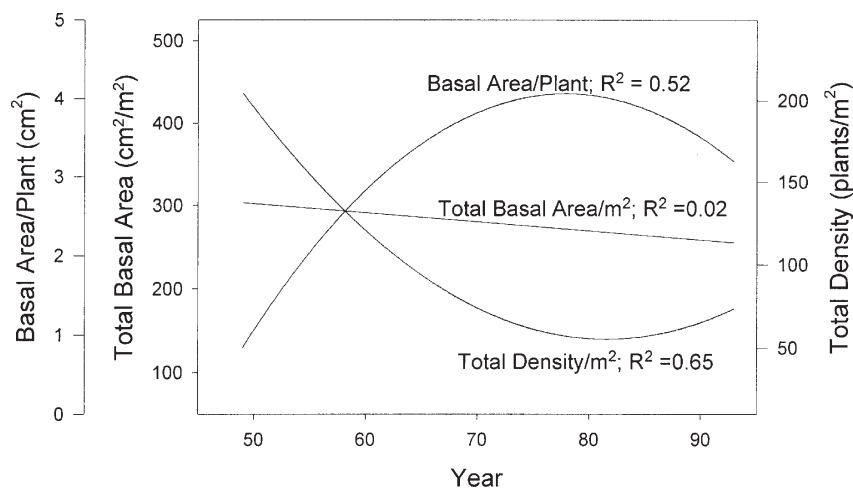

Fig. 7. Regression fitted responses for mean basal area of individual plants, total basal area, and total density for perennial grasses in response to the elimination of grazing by domestic livestock (ungrazed regime) in 1948 near Sonora, Texas. Total basal area and total density represent the average of all quadrats within each replication on a m² basis. Regression lines for mean total density and mean basal area of individual plants were significant (*p* < 0.01) through time following the removal of grazing.

significantly correlated with total plant basal area, while time since imposition of grazing regimes was not, but both interannual precipitations and time since imposition of grazing regimes were significantly correlated with plant density. Consequently, we also failed to reject hypothesis two that response group composition, plant density, and total basal area would show distinct responses to grazing intensity and climatic variability.

Both grazing and climatic variability are important agents of vegetation change in this semi-arid system, but they appear to operate on distinct temporal scales. Grazing intensity establishes the long-term direction of compositional and structural change, but episodic climatic events substantially influence the short-term rate and trajectory of this change. For example, the 1950s drought reduced plant density to similarly low values in all three grazing regimes, but plant density recovered following drought and eventually became proportional with grazing intensity during the following decade. The intermittent influence of variable precipitation on vegetation dynamics has previously been recognized by Wiegand & Milton (1996) and Walker et al. (1997). The less persistent response of community composition to precipitation variability than to grazing intensity is partially a function of the non-selective, intermittent effects of drought compared to the more continuous, selective influence of grazing on individual species or species groups (Illius & O'Connor 1999).

Simultaneous reductions in individual plant basal area and increases in plant density with increasing grazing intensity were anticipated and have been widely documented in mesic grasslands and savannas (Sala et al. 1986; Vorontzova & Zaugolnova 1985; Butler & Briske 1988; O'Connor 1994; Pfeiffer & Hartnett 1995). Similar changes in density-basal area relationships in response to grazing intensity over this 44-yr period verify that these are critical demographic processes associated with herbivore-induced modifications of population structure for perennial bunchgrasses (Butler & Briske 1988; Briske & Anderson 1990; Briske & Hendrickson 1998). The inverse relationship between density and individual plant basal area is partially confounded by the relative composition of plant response groups among the three grazing regimes through time. An increase in mid-grass abundance in the moderately grazed and ungrazed regimes reduced total density because mid-grasses possess a potentially larger individual plant basal area than do short-grasses. In addition, the 1950s drought significantly contributed to the decrease in plant density, as did the reduction or elimination of grazing.

In contrast to density and response group composition, total plant basal area remained similar among the three grazing regimes through time and was highly correlated with interannual precipitation. The strongest correlation occurred with a running 3-yr mean window for annual precipitation suggesting the occurrence of a several year lag in the influence of precipitation on total plant basal area (Allen et al. 1995). This lag may partially reflect the time required for tiller recruitment and the occurrence of tiller turnover at approximately 2-yr intervals (Butler & Briske 1988; Briske & Hendrickson 1998). Sala et al. (1986) have previously found that grazing did not affect the total basal area of grasses in a more productive grassland in the flooding pampas of Argentina. The occurrence of a relatively constant total basal area among grazing regimes, while mid-grasses increased and short-grasses decreased, indicate a reciprocal replacement of basal area between the two plant response groups. The reciprocal replacement of basal area between these two species response groups is probably mediated by competitive interactions for below-ground resources (e.g. Derner & Briske 1999).

Periodic drought had a more detrimental effect on vegetation change in the heavily grazed regime than in the other two grazing regimes, as indicated by greater coefficients of variation for total basal area and density over time and stronger correlations with precipitation than in the less intensively grazed regimes (e.g. Allen et al. 1995). Greater fluctuation of total plant basal area in the heavily grazed compared to more lightly grazed regimes may have been associated with two distinct, but interrelated processes. First, a comparable reduction in net annual primary productivity associated with a prolonged drought would be expected to exacerbate grazing severity to the greatest extent in the heavily grazed regime (Fuhlendorf & Smeins 1999). Second, population structure characterized by high densities of plants with small basal areas in intensively grazed communities exhibit greater drought-induced mortality than plants with larger basal areas in ungrazed or lightly grazed communities (O'Connor 1995; Hodgkinson 1995). One of the dominant mid-grasses in the ungrazed regime, *Bouteloua curtipendula*, had 50% mortality in the heavily grazed regime, but minimal mortality in the moderate and ungrazed regimes during a short-term drought from 1993-1995 (Briske & Hendrickson 1998). General agreement between this long and short-term data suggests that reductions in mean plant basal area and increases in plant density may be valuable indicators of pending compositional changes that may be initiated by episodic climatic events in communities subjected to heavy grazing.

Implications for vegetation monitoring and management

The combined effect of grazing and climatic variation on vegetation change supports the inference that stochastic climatic variation does not maintain a system in

a perpetual non-equilibrium state (Weins 1984), but rather superimposes fluctuations on an otherwise directional response of community composition to grazing intensity. Vegetation change did exhibit a rapid, short-term deviation from this directional response following severe drought or an episodic freeze, but vegetation attributes established a similar trajectory following these events as previously recognized by Wiegand & Milton (1996) and Walker et al. (1997). The directional response of vegetation to grazing intensity for much of this 44-yr period supports the hypothesis of Illius & O'Connor (1999) that the occurrence of climatic variability does not justify the assumption that grazing intensity has a negligible impact on vegetation change. We found that both grazing and climatic variability influenced vegetation change in a system where the coefficient of variation for interannual (1949-1998) precipitation was the same value (33%) as that proposed to distinguish between equilibrial and non-equilbrial systems (Ellis 1994). This response confirms that total annual precipitation, as well as the variability of interannual precipitation, influences vegetation change in variable rangeland environments (Behnke & Scoones 1993; Ellis 1994; Fernandez-Gimenez & Allen-Diaz 1999).

Although grazing intensity was associated with directional vegetation change in this semi-arid community, it is important to recognize that these changes often occurred intermittently over relatively long time periods, rather than continuously on annual time steps. Much of the data is characterized by intervals of static to very gradual change in vegetation composition and structure indicating that vegetation dynamics occur on prolonged temporal scales in semi-arid rangelands, especially in reference to managerial time frames (Wiegand & Milton 1996). Recovery of the mid-grass response group required approximately 25 yr following the elimination of grazing, but this period was very likely protracted by the drought of the 1950s. The reciprocal response between the mid-grass and short-grass response groups following the reduction or elimination of livestock grazing demonstrates the resilience of this community to long-term intensive grazing in combination with substantial climatic variation (Walker et al. 1997).

Minimal change in community composition following the removal of grazing has been interpreted as evidence of suspended vegetation stages (Laycock 1991) or vegetation thresholds capable of retarding or halting the reversibility of vegetation change (Friedel 1991). These two interpretations have been used to argue that directional vegetation change is inappropriate for evaluating and managing vegetation change on semi-arid rangelands (Laycock 1989; Westoby et al. 1989). However, data presented here demonstrate that vegetation change was reversible even though the herbaceous com-

munity was maintained in an altered state for ca. 60 yr by intensive livestock grazing that reduced the midgrass response group to a very small percentage of the total herbaceous composition. We acknowledge that non-reversible or slowly reversible vegetation change and vegetation thresholds may be more likely to occur in this system when there is a compositional shift from herbaceous to long-lived arborescent growth forms (Archer 1989; Fuhlendorf et al. 1996; Fuhlendorf & Smeins 1997), soil seed banks are depleted (Kinucan & Smeins 1992), or low residual densities of late-seral grasses constrain the reversibility of vegetation change (Hendrickson & Briske 1997; Briske & Hendrickson 1998). These effects would be exacerbated and the recovery times increased as climatic conditions become more limiting and variable (Laycock 1991; Fernandez-Gimenez & Allen-Diaz 1999).

Non-uniform responses among the various vegetation attributes to grazing and climatic variability has very likely contributed to the confusion and uncertainty regarding the primary agents of vegetation change. In this record of vegetation change, response group composition was affected by grazing intensity, total plant basal area was affected by interannual precipitation, and density was significantly affected by both change agents. This demonstrates that total basal area would not be an effective indicator of grazing intensity and suggests that the use of plant basal area as a reliable attribute of grassland structure may have partially contributed to the interpretation that vegetation change is more responsive to climate than to grazing. Response group composition and mean basal area per plant on the other hand, were much more responsive to grazing intensity than to interannual precipitation over the long-term suggesting that these structural attributes would be more sensitive indicators for monitoring vegetation change in response to grazing. Distinct responses of various community attributes to grazing and climatic variability supports the conclusion of Fernandez-Gimenez & Allen-Diaz (1999) that evaluation of a broader set of vegetation variables, including individual species attributes or specific functional groups, may lead to the conclusion that vegetation change is impacted by both grazing and climatic variability, rather than solely by climatic variability.

This pattern of long-term vegetation change occurred in response to the managerial constraints imposed in a commercial ranching operation characterized by the confinement of livestock grazing to specific areas at relatively constant stocking rates with minimal supplemental feeding of animals. We recognize that the relative contribution of grazing intensity and climatic variability to vegetation change may be system specific and is likely to be influenced by the degree of managerial in-

volvement imposed on a system (Milchunas et al. 1988; Augustine & McNaughton 1999; Fynn & O'Connor 2000). Free-roaming herbivores have the ability to access various plant communities within a landscape, including key resource areas, to optimize nutrient intake (Illius & O'Connor 1999). However, this is clearly not the case in commercial systems. Commercial ranching systems impose various management options to minimize fluctuations in livestock numbers in contrast to subsistence, nomadic livestock systems, which makes it difficult to directly compare these two livestock management systems (e.g. Ellis & Swift 1988; Behnke & Scoones 1993). However, it is the relative consistency of grazing in commercial systems that allows a clear distinction to be made between grazing and climatic variability as agents of vegetation change.

These analyses of long-term herbaceous vegetation change indicate that semi-arid grasslands respond to both grazing and climatic variability, but that episodic climatic events induce short-term fluctuations on the directional patterns of vegetation change established by grazing. Consequently, directional and non-directional vegetation change do not necessarily represent mutually exclusive responses and neither response independently provides a complete assessment of herbaceous vegetation change on semi-arid rangelands. The occurrence of both directional and non-directional vegetation responses within this system were largely a function of (1) the unique responses of the various community attributes monitored and (2) the distinct temporal responses of these community attributes to grazing and climatic variation. This interpretation supports previous conclusions that individual ecosystems may exist in equilibrial and non-equilibrial states at various temporal and spatial scales (Allen & Star 1982; Connell & Sousa 1983; Wiens 1984; O'Neill et al. 1986).

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