RESEARCH ARTICLE

Multi-scale factors and long-term responses of Chihuahuan Desert grasses to drought

Jin Yao · Debra P. C. Peters · Kris M. Havstad · Robert P. Gibbens · Jeffrey E. Herrick

Abstract Factors with variation at broad (e.g., climate) and fine scales (e.g., soil texture) that influence local processes at the plant scale (e.g., competition) have often been used to infer controls on spatial patterns and temporal trends in vegetation. However, these factors can be insufficient to explain spatial and temporal variation in grass cover for arid and semiarid grasslands during an extreme drought that promotes woody plant encroachment. Transport of materials among patches may also be important to this variation. We used long-term cover data (1915–2001) combined with recently collected field data and spatial databases from a site in the northern Chihuahuan Desert to assess temporal trends in cover and the relative importance of factors at three scales (plant, patch, landscape unit) in explaining spatial variation in grass cover. We examined cover of five important grass species from two topographic positions before, during, and after the extreme drought of the 1950s. Our results show that dynamics before, during, and after the drought varied by species rather than by topographic position. Different factors were related to cover of each species in each time period. Factors at the landscape unit scale (rainfall, stocking rate) were related to grass cover in the pre- and post-drought periods whereas only the plant-scale factor of soil texture was significantly related to cover of two upland species during the drought. Patch-scale factors associated with the redistribution of water (microtopography) were important for different species in the pre- and post-drought period. Another patch-scale factor, distance from historic shrub populations, was important to the persistence of the dominant grass in uplands (*Bouteloua eriopoda*) through time. Our results suggest the importance of local processes during the drought, and transport processes before and after the drought with different relationships for different species. Disentangling the relative importance of factors at different spatial scales to spatial patterns and long-term trends in grass cover can provide new insights into the key processes driving these historic patterns, and can be used to improve forecasts of vegetation change in arid and semiarid areas.

Keywords Arid grasslands · Desertification · Drought · Grazing · Perennial grasses · Transport processes

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Introduction

Environmental factors operating across a range of spatial and temporal scales are known to influence ecosystem dynamics (Whittaker 1975). A major

challenge in ecology is to identify the dominant factors, out of the many possibilities, that explain vegetation patterns and dynamics (Steffen et al. 2002). Pattern analyses based on a hierarchical approach are often used to infer causal relationships and to develop hypotheses about the relative importance of these dominant factors to vegetation dynamics under different conditions, either in time or space (e.g., Powers et al. 1999; Heyerdahl et al. 2001; Abrahamson and Layne 2003). These analyses often examine factors that vary at broad scales, such as climate, and at fine scales, such as soil texture, that influence local processes at the scale of individual plants (e.g., competition). Processes associated with transport of materials, such as water, seeds, and soil, at patch to landscape unit scales can also be important to vegetation dynamics, although the ecological importance of these processes has not been well studied (Tongway et al. 2001; Ludwig et al. 2005). Long-term observations combined with spatially distributed data are often required to examine these relationships for infrequent extreme events, such as prolonged drought, within the context of responses to climate variability (Parshall et al. 2003).

In arid and semiarid regions, severe to extreme droughts can have large negative impacts on grasses over a broad spatial extent, however cover is often spatially variable at fine scales because grass species respond differently to variation in site conditions (Peters and Gibbens 2006). A number of fine- and broad-scale factors can influence variation in local site conditions. Fine-scale factors associated with individual plants, such as soil texture and depth, can affect plant available water with implications for plant growth, survival, and spatial distribution (Wondzell et al. 1990; Hochstrasser and Peters 2004; Peters and Gibbens 2006). Other factors, such as precipitation and grazing by cattle, have broad-scale spatial variation in characteristics, such as amount and seasonality, that can influence local site conditions with consequences for patterns in vegetation (Herbel 1972; Schlesinger et al 1990; Archer 1994; Fredrickson et al. 1998).

In many cases, fine- and broad-scale factors are insufficient to explain patterns in perennial grass cover through time and across space, in particular in the presence of extreme events that promote woody plant encroachment (Conley et al. 1992; Peters et al.

2006). For example, the extreme drought of the 1950s combined with intense livestock grazing has often been implicated as a key driver in the demise of perennial grasslands, and in particular the dominant upland species *Bouteloua eriopoda* in the Chihuahuan Desert. However, not all grasslands have converted to shrublands (Gibbens et al. 2005), and factors affecting spatial and temporal variation in grass loss have not been examined (Peters et al. 2006). Nonlinear decreases in grass cover and increases in shrub cover have been suggested to be related to a sequence of processes that change in importance through time and across space (Peters et al. 2004). The expansion of woody plants into adjacent livestock exclosures provides another example where fine-scale factors within an exclosure are insufficient to explain local patterns and dynamics (Peters et al. in press).

Factors at intermediate scales, such as microtopography at the patch scale and topography within landscape units, can also be important to patterns in grass cover. These factors influence transport processes that redistribute water, nutrients, soil particles, and seeds within and among patches or parts of the landscape with important effects on perennial grass dynamics (Tongway et al. 2001). These transport processes may be particularly important in systems with low precipitation where even a small localized increase or decrease in plant available water can have important consequences for plant growth (Ludwig et al. 2005).

Because precipitation is uniformly low with few large rain events during a drought, we expected that transport processes related to water movement are also negligible during drought. Thus, factors that influence local processes were expected to be more important than transport processes to grass cover during a drought. Before and after a drought when rainfall amounts are sufficient to generate run-on and run-off events, we expected that patch-scale factors that influence transport processes are important to dynamics of species in different topographic positions. Thus, we had two specific objectives: (1) to examine temporal variation in cover of five important grass species in the Chihuahuan Desert for three major time periods that bracket the drought of the 1950s (pre-drought: 1915–1950, drought: 1951–1956, post-drought: 1957–2001), and (2) to examine spatial variation in cover of these species in each time period

as related to factors at one of three spatial scales (plant, patch, landscape unit) that influence either local or transport processes. Although spatial scales are arbitrary and factors can operate across a continuum of scales, the designation of a spatial scale or extent over which a factor is homogeneously distributed is a useful and practical approach that allows comparative analyses to be conducted.

Methods

Site description

Our study was conducted at the Jornada Experimental Range USDA-ARS and Jornada Basin Long-Term Ecological Research Site in southern New Mexico, USA (32°37′ N, 106°40′ W, 1260 m a.s.l.). The Jornada is a 78,266 ha research site located within the northern extent of the Chihuahuan Desert. Long-term (1915–2001) mean annual precipitation was 246 mm (Fig. 1a), more than half of the annual precipitation occurs from July to October. Mean monthly average temperatures over the same time period were highest in June (26 °C) and lowest in January (4 °C) (Hochstrasser et al. 2002). Similar to other arid and semiarid regions, severe drought (Palmer Drought Index between −3 and −4) of 2–4 years duration occurs, on average, every 20–25 years whereas extreme drought (Palmer Index < −4) occurs every 50–60 years (Woodhouse and Overpeck 1998). At the Jornada, extreme drought occurred between 1951 and 1956 (Fig. 1b, Herbel et al. 1972).

Grasslands at the Jornada occur on one of two topographic positions that are dominated or codominated by characteristic grass species, and are often associated with a particular soil type (Peters and Gibbens 2006): (1) uplands are dominated by *Bouteloua eriopoda* (Torrey) Torrey (black grama), *Sporobolus flexuosus* (Thurb. ex Vasey) Rydb. (mesa dropseed) and *Aristida* spp. (threeawns) on deep loamy sand soils, (2) lowlands are dominated by *Pleuraphis mutica* Buckley (tobosa) and *Scleropogon brevifolius* Phil. (burrograss) on heavy, clay soils that may or may not receive run-on water during large rain events. Over the past century, large areas of upland grasslands have converted to shrublands dominated by *Prosopis glandulosa* Torrey (honey mesquite) or *Larrea tridentata* (Sess. & Moc. ex DC.)

(creosotebush). Some areas of lowland grasslands have converted to shrublands dominated by *L. tridentata* and *Flourensia cernua* DC. (tarbush) (Buffington and Herbel 1965; Gibbens et al. 2005). Thus, dynamics of grasses need to be considered within the context of woody plant expansion, and account for differences between uplands and lowlands.
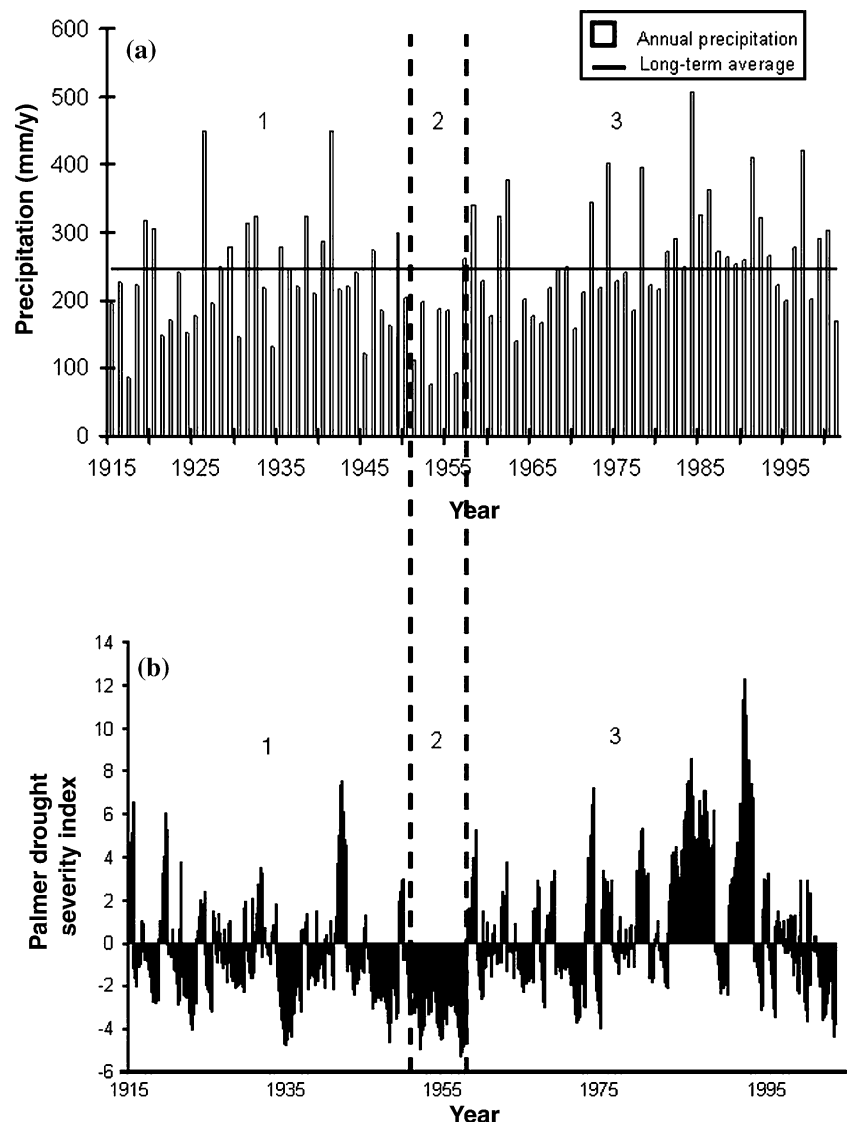
Vegetation sampling

Cover data were collected from permanently marked and geo-referenced 1 m × 1 m quadrats established between 1915 and 1932 in the two grassland types based on topographic position (Paulsen and Ares 1962; Wright and Van Dyne 1976; Gross 1984; Gibbens and Beck 1987, 1988). Quadrat locations were selected to represent typical species composition in each grassland type, and were usually placed at 0.8-km intervals along lines radiating from permanent water points (Nelson 1934). We used data from 98 quadrats in our analyses, including 64 upland quadrats (58 in *B. eriopoda* dominated grasslands, 6 in *Aristida* spp. grasslands), and 34 lowland quadrats (22 in *P. mutica* grasslands and 12 in *S. brevifolius* grasslands). Basal area of each perennial grass plant and location of each annual grass, forb, and shrub were charted, first using a decimeter grid (until 1925) and then a pantograph (Paulsen and Ares 1962). Most quadrats were charted annually until 1947, periodically until 1979, and were re-charted in 1995 and 2001. Because basal area was only charted for perennial grasses in each sample year, similar analyses were not possible for the other species. Basal area was converted to basal cover using the quadrat area. Because of the small quadrat size (1 m^2) relative to plant size, in particular for stoloniferous grasses, average cover may be over- or underestimated, and caution is required when extrapolating these quadrat-level measurements to the landscape. In addition, the small quadrat size precluded analyses for shrubs.

Environmental factors

We selected environmental factors for each of three spatial scales that were expected to be important to grass dynamics in different time periods defined by the 1950s drought: plant scale (<10 m^2), patch scale

Fig. 1 (**a**) Annual precipitation (mm/y) through time at the Jornada Experimental Range and (**b**) monthly average Palmer drought severity index in southern New Mexico (http://www.ncdc.noaa.gov/oa/climate/onlineprod/drought/xmgrg3.html). Time periods used in this study: 1. pre-drought (1915–1950), 2. drought (1951–1956), 3. post-drought (1957–2001)

(groups of plants) (1–10,000 m^2), and landscape unit scale (groups of patches) (>5000 m^2). Plant- and landscape unit-scales represent factors with different spatial extents that influence local processes primarily associated with plant available water and grazing impacts. Although broad-scale factors, such as precipitation, can vary over short distances (tens of meters to kilometers), data are not available to determine this fine-scale variation. Stocking rate is used as a broad-scale surrogate for average grazing intensity at the pasture scale. Similar to precipitation, data required to characterize within-pasture variability in grazing (e.g., plant scale) are unavailable. Thus, these factors are often considered

broad-scale factors with local impacts. Patch-scale factors influence transport processes that act to redistribute resources horizontally between patches within a landscape unit. For each factor, we determined a value for each quadrat using data either from existing spatial databases or collected as part of this study (Appendix A).

Factors measured at the plant scale that influence local processes

Soil texture was determined from a composite of at least three soil cores collected in 2001 from bare

interspaces between plants at a distance of 1 m from the edge of each quadrat (Appendix A). A separate set of cores was collected for each of two depths (0–5 cm, 5–20 cm). Gravel was removed from the air-dried samples using a 2 mm sieve; sand, silt, and clay were determined using the hydrometer method following dispersion in a sodium hexametaphosphate solution (Gee and Bauder 1986). Sand content was verified by wet sieving.

Soil depth to the petrocalcic horizon (indurated calcic horizon) was measured where present (Appendix A). This horizon is formed by deposits of calcium carbonate, and occurs at variable depths and stages of development in arid soils (Monger 2002). This horizon influences water available to plants because it is often less permeable to water and less easily penetrated by roots than other soil horizons (Hennessy et al. 1983). In 2001, we measured soil depth at each corner for each quadrat, and averaged these values to obtain one estimate. At each point, a 1 cm-diameter × 150 cm long steel rod was pounded vertically into the soil until resistance prohibited further insertion. We then measured the length of the rod remaining above the soil, and subtracted this length from the total rod length to obtain soil depth. We confirmed the existence of calcium carbonate by inspecting the rod tip for white, chalky material after its removal. If the rod did not encounter a resistant soil layer by 125 cm, then we recorded soil depth as >125 cm. We could not measure the depth at the 18 quadrats on rocky soils because of the difficulty in determining if the hard surface that stopped the rod was a rock or the petrocalcic horizon. Depth was not included as a variable in the analysis of lowland quadrats because petrocalcic horizons do not occur in these areas.

Factors measured at the landscape unit scale that influence local processes

Factors with spatial variation at the landscape unit scale include elevation, soil type, precipitation, and stocking rate of livestock. Elevation of each quadrat was obtained from a digital elevation model with an *x*- and *y*-resolution of 10 m, and a *z*-resolution (altitude) of 1 m (http://data.geocomm.com/dem/) (Appendix A). Soil type was obtained from a soil survey conducted in 1962 (Soil Conservation Service

unpublished report). Plant available water (PAW) was ranked and placed into one of six classes based on soil type using an established relationship with soil texture (Saxton et al. 1986) (Appendix A). Soil attributes were derived from the dominant soil map unit where the quadrat occurred. This approach is relatively accurate where the soils within a map unit are similar, or where the dominant soil covers most of the area within a unit. The approach can be inaccurate in units with a high diversity of soils. Consequently, lack of correlations with soils at broad scales often reflects the relatively low precision of soil maps, yet these maps are often used, in particular when detailed data are not available.

Two measures of precipitation were selected that were expected to influence plant available water differently by species: growing season (1 July–31 October) and non-growing season (1 January–30 June, and 1 November–31 December). Precipitation for each quadrat was interpolated from data collected monthly in rain gauges established between 1918 and 2001 (Appendix A). The number of rain gauges increased over time (one in 1915, four in 1918, 11 in 1926, 21 in 1937, 30 in 1965, and 34 in 2001). We first calculated seasonal precipitation for each quadrat for each year from 1918 to 2001 using data from the three closest rain gauges weighted by the inverse of their distance to that quadrat. Distances ranged from 2 m to 26 km with the longest distances occurring early in the time period when few rain gauges were in operation. We then calculated mean precipitation for each season for each time period (mean precipitation from 1918 to 1950 was used for the 1915–1950 period).

Stocking rate (animal unit month/ha) [AUM/ha] by cattle was used as an overall measure of livestock effects, including grazing, trampling, and seed and nutrient redistribution within each landscape unit. In most cases, a landscape unit corresponded to a pasture for this analysis. Monthly stocking rates were obtained from historical records available since 1915 by accounting for changes in fence locations. We used stocking rates from two time periods: growing season and non-growing season (Appendix A). Each intra-annual stocking rate was averaged for each time period. The range in stocking rates was low (0–0.05 growing season; 0–0.5 non-growing season) as a result of management decisions.

Factors measured at the patch scale that influence transport processes

Factors with spatial variation at the patch scale influence transport processes that redistribute water and seeds either into or out of a quadrat. These factors include distance to the nearest historic shrub community, topography, and distance to permanent water sources for cattle. Distance to the nearest historic shrubland was used as a measure of shrub seed availability through dispersal. The Euclidean distance to the nearest shrub-dominated pixel (2 m × 2 m) was calculated using vegetation maps from 1928–29 (Gibbens et al. 2005). These distance measures may over-estimate distances to small shrubs (<4 m^2) that may have also been seed sources. Similar results were found using distances to the nearest shrubland from the 1915 – 16 map in Gibbens et al. (2005). Distances were not calculated for the 1998 map because all quadrats were within 700 m of shrublands by that time.

Topographic factors related to water and nutrient redistribution were based on field observations in 2001, both for the microtopography of the patch surrounding each quadrat and for the surrounding area (20 m × 20 m) that represents topographic relief within the landscape unit (Appendix A). Microtopography measures provide estimates of redistribution of materials (primarily water, soil, nutrients) between plants and bare interspaces whereas topography measures provide estimates of material redistribution among patches or groups of plants. Both scales of redistribution can be important in arid systems (Wainwright et al. 2002). Microtopography and topography were classified independently for each quadrat using one of three categories: run-on area (depression relative to its surroundings), slope (run-on equals runoff), or runoff area (elevated area relative to surroundings).

Distance to the nearest permanent water source (e.g., wells, dirt tanks) for cattle was calculated for each time period as an estimate of livestock impact: cattle impacts tend to decrease with increasing distance from water sources (Arnold and Dudzinski 1978; Nash et al. 1999). We measured the distance between each quadrat and the nearest water source using coverages in ArcMap (Appendix A).

Statistical analyses

Objective 1. Temporal variation in responses

Persistence of *B. eriopoda* was defined as the number of years that plants of this species persisted in each upland quadrat from 1915 to 2001. We focused on *B. eriopoda* for this analysis for two reasons: (1) it is an important forage species in desert grasslands in the southwestern USA, and it is often used as an indicator of grass loss during shrub encroachment, and (2) recruitment by seed occurs infrequently, thus it is possible to differentiate persistent adults from short-lived seedlings. For the other grass species, seedling establishment occurs more frequently, and it is often difficult to separate small adults from large seedlings. We counted the number of quadrats where *B. eriopoda* went locally extinct (i.e., cover on a quadrat = 0) within each time period.

Response variables for each species were compared among the three time periods using a one-way ANOVA and either cover or frequency by species; upland and lowland quadrats were analyzed separately. Species cover was calculated from basal area measured in each quadrat. Mean basal cover in each year was calculated across all quadrats sampled in that year. Frequency was the percentage of quadrats with a species present out of all quadrats sampled in a year. Because not all quadrats were sampled every year, only data from sampled quadrats were used in the analyses. Frequency was the percentage of quadrats with a species present out of all quadrats sampled in a year.

Objective 2. Spatial variation

For *B. eriopoda* persistence, the response variable was the number of years the species persisted on each quadrat from 1915 – 2001. For cover of each grass species, the response variable was mean basal cover for a quadrat within a time period. Because the number of years that a quadrat was sampled within a time period varied by quadrat, we included in the analysis only those quadrats that had been sampled for more than ca. 50% of the number of years in that time period. Using this subset of quadrats ensured that a reasonable estimate of the average basal cover of a species within each time period was obtained. All

0 values in the response variables were excluded from the analyses because we were interested in explaining variation in cover for quadrats containing grasses.

Categorical independent variables (microtopography, topography) were converted into dummy variables for the analyses (run-on 0, 0; slope 1, 0; runoff, 0, 1). Because soil depth was measured in a subset of quadrats (46 out of 64), we examined the importance of soil depth using only those quadrats. The other data set containing all quadrats was used to examine the importance of the remaining 18 environmental variables. Because soil depth was not significant in these analyses, only results from the analyses without soil depth are shown.

We used hierarchical r^2 partitioning to identify the most likely causal factors (Chevan and Sutherland 1991; MacNally 2000, 2002). Hierarchical partitioning determines the independent contribution of each explanatory factor to the response variable for a data set with multiple explanatory factors. The potential independent contribution of an explanatory factor to a response variable was examined using Pearson's r, calculated as the average value of the variances explained by the factor in all regression models in which it appears. Variance in the response variable explained by all explanatory factors equals the sum of the independent contributions of all explanatory factors (MacNally 2000, 2002). A high pair-wise correlation between an explanatory factor and the response variable may be due to the explanatory factor's high joint contribution with other explanatory factors, but not due to its high independent contribution (MacNally 2000). Therefore, the explanatory factors with high independent contribution are the most likely causal factors.

The hierarchical partitioning analyses were carried out using the hier.part package in R (Walsh and MacNally 2004). This package currently will run for no more than 12 explanatory factors, but we found some discrepancies in values for more than nine explanatory factors. Thus, we initially included all explanatory factors into the routine in groups of nine at a time in the order of their pair-wise correlation coefficients with each response variable. We found that the rank order of at least the first five factors with the highest independent contributions did not change with order, and significance tests showed that only the first one, two, or three factors with the highest contributions were significant. We then selected the nine factors with the highest pair-wise correlation coefficients with each response variable to run the partition routine. An explanatory factor was considered significant when its independent contribution was greater than the upper 95% confidence limit of the independent contribution values generated from 500 randomizations (MacNally 2002; Walsh and MacNally 2004). We compared the r^2 values from the regression analyses using all possible subsets of the nine explanatory variables to determine the set with the most explanatory power.

Results

Objective 1. Temporal variation in responses

Persistence of B. eriopoda

The 1950s drought was associated with the quadrat-level extinction of *B. eriopoda* in 39% of the upland quadrats during the drought (1951–1956). Cover of this species went to zero in a large percentage of quadrats (21%) prior to the drought, and this species remained on 10% of the upland quadrats until at least 2001. Cover on the remaining 18 quadrats (30%) went to zero during the post-drought period (1957–2001). The number of years that *B. eriopoda* persisted in a quadrat from 1915 to 2001 ranged from 4 to 87, with a mean of 43 and a standard deviation of 20.

Cover and frequency by species

Cover and frequency of occurrence on quadrats varied by species rather than by topographic position. Cover of two upland species, *B. eriopoda* and *Aristida* spp., decreased during the drought and remained at low average values throughout the post-drought period (Fig. 2). The frequency of quadrats containing *B. eriopoda* decreased through time. By contrast, the frequency of quadrats with *Aristida* spp. decreased during the drought, but increased during the post-drought period to a level that is still lower than the pre-drought period. Cover and frequency of quadrats containing the remaining upland species, *S. flexuosus*, and the lowland species, *P. mutica*, decreased during the drought, but returned to pre-drought values during the post-drought period (Figs. 2, 3). Cover of the other lowland species, *S. brevifolius*, was unaffected
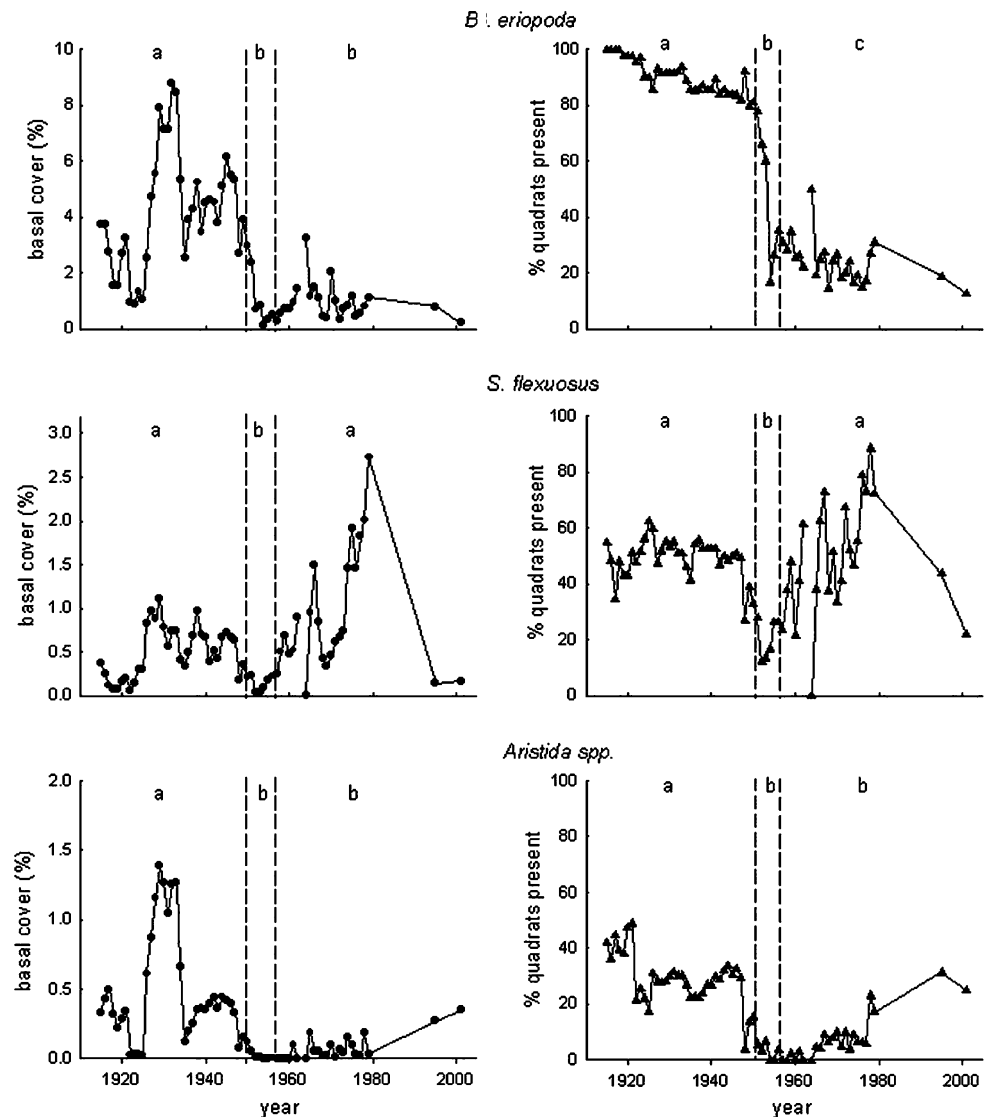
Fig. 2 Mean basal cover (%) and percentage of quadrats where a species was present through time for upland quadrats: (**a**) *B. eriopoda*, (**b**) *S. flexuosus*, and (**c**) *Aristida* spp. Different letters indicate significant differences in average values among time periods and within species and measurement type.

by the drought, and the percentage of quadrats containing this species increased during the drought (Fig. 3). Cover of *S. brevifolius* increased initially following the drought, but returned to pre-drought values during the post-drought period.

Objective 2. Spatial variation in responses

Persistence of B. eriopoda

The number of years that *B. eriopoda* persisted in each quadrat was related to a patch (distance to the nearest historic shrublands in m) and a landscape unit factor (non-growing season stocking rate):

Number of years persistence

$$= 28.1 + 0.006 \times \text{ (distance to shrublands)}$$
$$+ 98.3 \times \text{ (non-growing season stocking rate}$$
$$\text{during the drought)}$$
$$(N = 61, \ r^2 = 0.28, \ p{<}0.001).$$

This species persisted longer in quadrats that were located farther away from historic shrublands, and
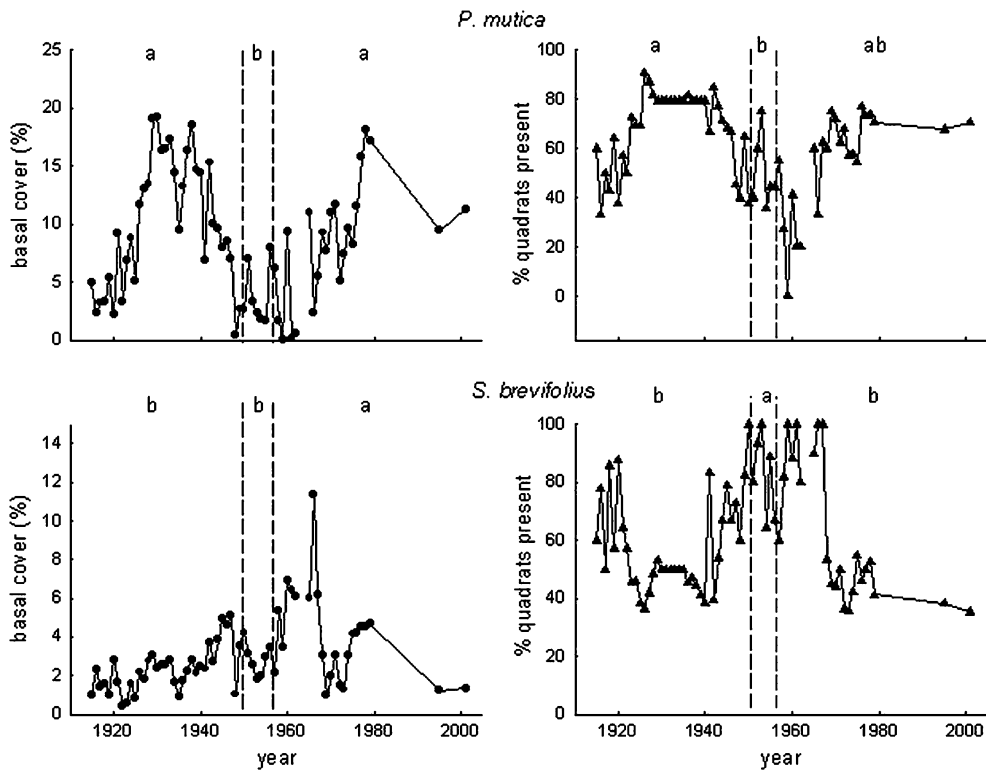
Fig. 3 Mean basal cover (%) and percentage of quadrats where a species was present through time for lowland quadrats: (**a**) *P. mutica*, and (**b**) *S. brevifolius*. Different letters indicate significant differences in average values among time periods and within species and measurement type.

that experienced higher stocking rates during the drought. These results were confirmed by the hierarchical partitioning procedure.

Cover by species

Different factors were related to cover for each species in each time period based on the hierarchical partitioning of variance (Table 1). Stocking rate and precipitation were most frequently related to cover, but soil depth, distance to water, topography, and soil type were not significant in these analyses. Patch-scale factors of distance to historic shrubland and microtopography were related to cover in only 3 of the 15 analyses conducted; all of which occurred during the pre- or post-drought periods. Plant-scale variation in soil texture was related to cover during the drought.

Prior to the drought, cover of the upland species, *B. eriopoda*, was higher in quadrats farther away from historic shrublands and experienced higher livestock grazing in both seasons (Table 1). For *S. flexuosus*, pre-drought cover was higher in quadrats with lower stocking rates during the growing season. For *Aristida* spp., pre-drought cover was higher in quadrats with lower growing season and non-growing season precipitation. For the lowland species, *P. mutica*, pre-drought cover was higher in quadrats with lower growing season stocking rates and in quadrats located in run-on areas than on slopes (no quadrats were located in runoff areas). For *S. brevifolius*, cover was higher when growing season precipitation was lower.

During the drought, upland species cover was higher on quadrats with high clay content, either at the surface (*S. flexuosus*: 0–5 cm) or at depth (*B. eriopoda*: 5–20 m depth); sample sizes of *Aristida* spp. cover values >0 were too small during the drought for analyses to be conducted. Cover of the two lowland species (*P. mutica*, *S. brevifolius*) were not related to any factors during the drought.

Table 1 Factors identified by hierarchical partitioning as being significant independent contributors to variation in the response variable and their Pearson's coefficient with the response variable

Time period	Response variable	Explanatory variable	Pearson's r	Spatial scale
	B. eriopoda persistence	Distance to shrubland	0.42***	Patch
		Non-growing season stocking during drought	0.47***	Landscape unit
Pre-drought	B. eriopoda cover	Non-growing season stocking	0.44***	Landscape unit
		Growing season stocking	0.40**	Landscape unit
		Distance to shrubland	0.35**	Patch
	S. flexuosus cover	Growing season stocking	−0.42**	Landscape unit
	Aristida spp. cover	Non-growing season precipitation	−0.47**	Landscape unit
		Growing season precipitation	−0.45**	Landscape unit
	P. mutica cover	Growing season stocking	−0.44*	Landscape unit
		Microtopography	−0.66***	Patch
	S. brevifolius cover	Growing season precipitation	−0.58*	Landscape unit
Drought	B. eriopoda cover	Clay content (5–20 cm)	0.51***	Plant
	S. flexuosus cover	Clay content (0–5 cm)	0.39	Plant
Post-drought	S. flexuosus cover	Microtopography	0.38*	Patch
	S. brevifolius cover	Elevation	0.54	Landscape unit

*** $p<0.001$; ** $0.001<p<0.01$; * $0.01<p<0.05$

In the post-drought period, no factors were significant contributors to cover of two upland species (*B. eriopoda, Aristida* spp.); cover of *S. flexuosus* was higher in quadrats on slopes than on run-on areas. No factors were significantly related to post-drought cover for the lowland species *P. mutica*; higher cover of *S. brevifolius* was found on quadrats at higher elevation.

Discussion

In the northern Chihuahuan Desert, the extreme drought of the 1950s and historic overgrazing by livestock are often implicated in the loss of perennial grasses during woody plant expansion (Humphrey 1958; Buffington and Herbel 1965). However, these two factors can not explain patterns in perennial grass cover through time and across space, particularly at spatial extents smaller than a landscape unit (Peters et al. in press). In our study using 1 m² quadrats, temporal variation in grass cover was species-specific. Most species decreased in cover during the drought, and cover of one species was unaffected by the drought. Some species have recovered to pre-drought cover values while other species maintain low cover values to present. Spatial variation in perennial grass cover was related to different factors measured at different spatial scales before, during, and after the

drought. In general, fine-and broad-scale factors that influence local processes at the plant scale were important during the drought. A combination of local processes and patch-scale factors that influence transport processes were important before and after the drought. Our results support the need for a multi-scale approach and long-term data that can examine the changing importance of factors through time.

Temporal variation in responses

In our study, temporal changes in grass cover related to drought varied among species. Drought was an important factor driving the loss of two species of grasses from upland quadrats (*B. eriopoda, Aristida* spp.). However, one upland (*S. flexuosus*) and one lowland species (*P. mutica*) returned to pre-drought cover values within 10 years following the end of the drought, and one lowland species (*S. brevifolius*) had high cover throughout the time period. In addition, persistence of the dominant species, *B. eriopoda*, was not related just to the drought: a large percentage of quadrats (21%) lost this species prior to the drought while this species remains on 10% of the original quadrats.

Spatial variation in responses

Prior to the 1950s drought, precipitation and stocking rate of cattle were correlated with spatial

variation in grass cover. However, the relationships varied by species and were different than expected. Lower cover of two species (*Aristida* spp., *S. brevifolius*) under conditions of higher precipitation suggest that other characteristics not considered here, such as timing of precipitation or indirect effects of precipitation that affect competition for soil water by other plants, may be important to cover of these species. The positive relationship between cover and persistence of *B. eriopoda* and annual stocking rate is most likely a result of management decisions that increased stocking rate in response to cover of this important forage species rather than a response of plants to higher stocking rates. By contrast, higher cover of two species (*S. flexuosus*, *P. mutica*) with lower stocking rates may reflect grass responses to grazing and other impacts of cattle. It is important to recognize that stocking rates at the Jornada have been generally light to moderate since the research site was established in 1912; thus grass cover relationships with chronically high intensity grazing can not be examined.

In addition, livestock grazing was viewed as a broad-scale factor in this study because of the resolution of data at the pasture scale; finer-scale grazing data may have shown stronger relationships with grass cover through time. Livestock movement patterns often reflect spatial and temporal heterogeneity in habitat characteristics, including forage availability (Kie et al. 2002). Large herbivores interact with their environment across a range of spatial scales, from individual plants to feeding stations, patches, and topographic units within a pasture (Senft et al. 1987; Bailey et al. 1996). Heterogeneity in vegetation at each scale influences foraging behavior with feedbacks to the vegetation (van de Koppel 2002). Determining effects of grazing depends on the scale at which responses and impacts are measured (Brown and Allen 1989). Thus, a scale-dependent analysis of grazing intensity and vegetation responses is needed to examine these interactions and their influences on perennial grass dynamics. In addition, a number of factors influence the distribution of livestock, including distance to water, and forage quality and quantity, which vary at different scales. The lack of a relationship between distance to water and grass cover in our study likely reflects the long distances

between water sources and quadrats (100 m to >5000 m).

During the drought, soil texture was the only factor related to grass cover. Thus, drought acted as a broad-scale driver, but the effects were filtered by plant-scale variation in soil texture that can affect plant available water. Higher cover of two upland species during the drought (*B. eriopoda*, *S. flexuosus*) on soils with high clay content likely reflects retention of water in the grass rooting zone for longer periods during drought (McAuliffe 1994). Lowlands on fine-textured soils with a small range in variation in texture did not exhibit spatial variation in cover during the drought. In addition, soil surface texture measurements in this study may not reflect texture during the time of evaluation: in dynamic systems, such as during woody plant encroachment into perennial grasslands, extensive changes in both vegetation and soils can occur, particularly in surface soils (0–20 cm) (Gibbens et al. 1983; Schlesinger et al. 1990). Examination of deeper soils less affected by the erosive properties of wind and water that often accompany woody plant encroachment may have resulted in stronger vegetation–soil relationships. The lack of a relationship between soil depth and grass cover, in particular for upland species, was surprising given that observations suggest that soils with a shallow depth to calcium carbonate have slower rates of mesquite encroachment (Teaschner 2001) and continue to support upland grasses (R.P. Gibbens pers comm.). More focused studies on areas with similar soil surface texture and variable depth to calcic horizons, together with soil water measurements, are needed to determine the effects of soil depth on plant community dynamics.

Factors measured at the patch scale had significant relationships with cover of two species prior to the drought (*B. eriopoda*, *P. mutica*), one species following the drought (*S. flexuosus*), and for the persistence of *B. eriopoda*. The importance of transport processes among patches to broader-scale patterns and dynamics has been recognized previously for a number of systems, including arid and semiarid grasslands and woodlands (Ludwig et al. 1997; Breshears et al. 2003). Most studies have focused on relationships between water redistribution and vegetation patterns, either along elevation gradients or within and among landscape units

(e.g., Wondzell et al. 1990). In our study, local topography that affected fine-scale water redistribution was related to cover for both an upland (*S. flexuosus*) and a lowland species (*P. mutica*). Wind redistribution of soil and nutrients is another process that can have significant effects on ecosystem processes related to desertification, but it has been less well-studied (Okin and Gillette 2001). In addition, less attention has been directed to the importance of landscape context and the dispersal of seeds from adjoining areas to woody plant invasion dynamics. Seed dispersal is often viewed as a constraint to vegetation dynamics (e.g., McEuen and Curran 2004); however, for invasive species, seed availability provides opportunities for broad-scale expansion (Mack et al. 2000). In our study, the tendency for remnant *B. eriopoda* quadrats to be found at large distances from historic shrublands provides an important explanation for vegetation patterns that can not be explained using current spatial data bases of environmental factors. Our results support the need for a landscape ecology approach to understanding and predicting the spread of native and invasive species (With 2002).

Long-term studies combined with multiple spatial scale analyses are increasingly used to address ecological questions as the availability of temporal and spatial datasets increases (Hobbie et al. 2003). In our study, this approach allowed us to examine variation in grass cover during an infrequent, extreme event (drought) within the context of long-term climate variability, similar to previous studies on large, infrequent events (Foster et al. 1998; Turner et al. 2003). Although the 1950s drought was the most severe one recorded in southern New Mexico over the past 350 years (Fredrickson et al. 1998), drought occurs on 20–60 year cycles with variable effects that depend, at least in part, on the severity and length of the dry period interacting with the physiological status of the plants (Herbel et al. 1972; Woodhouse and Overpeck 1998; Reynolds et al. 1999; Gibbens et al. in press). Less severe and short-duration droughts occurred within the long-term recovery period (1957–2001) that were interspersed with periods of average and above-average annual precipitation. Grass cover often mirrored this climatic variability with short-duration adverse periods followed by short-term recovery, although time lags may also be important (Anderson and Inouye 2001). In addition, variability in cover increased during the drought for upland quadrats, and this variability was subsequently maintained through time (Peters et al. 2004). The long lasting, legacy effect of broad-scale drivers on variability in cover has been observed previously for broad-scale disturbances, such as fire, hurricanes, and floods (Foster et al. 1998), as well as for drought regardless of grazing pressure (Biondini et al. 1998).

Conclusions

Our results demonstrate the need to account for spatial and temporal variation in environmental factors across a range of scales in order to understand perennial grass persistence and cover during woody plant encroachment. Drought is the overriding broad-scale driver shaping the structure and dynamics of arid and semiarid grasslands. However, plant, patch, and landscape unit factors that affect local and transport processes can either ameliorate or extend the effects of a drought. Our results also show that the position of a site within a landscape relative to water and seed movement, patterns in precipitation, and surface soil texture have important effects on long-term spatial variation in perennial grass cover. Understanding past dynamics is critical to our ability to manage these systems as well as to predict future dynamics under changing climatic and land use regimes.

Appendix A

Table A1 Spatial variation in environmental factors for quadrats located in uplands and lowlands

Factor	Upland quadrats				Lowland quadrats			
	N	Mean	Std	CV	N	Mean	Std	CV
Factors measured at the plant scale								
Soil texture (%)								
0–5 cm depth								
Sand	64	85	8	9	28	53	24	45
Silt	64	10	6	62	28	32	16	51
Clay	64	5	2	40	28	15	9	59
5–20 cm depth								
Sand	62	83	8	9	31	48	18	37
Silt	62	10	5	53	31	31	11	36
Clay	62	7	3	39	31	21	8	38
Soil depth (cm)	46	87	23	27				
Factors measured at the patch scale								
Distance to historic it Shrublands (m)	64	806	690	86	34	640	628	98
Topography	Run-on	Slope	Run-off		Run-on	Slope	Run-off	
Microtopography (# quadrats)	5	35	24		26	8	0	
Landscape unit topography (# quadrats)	9	49	6		26	7	1	
Distance to permanent water source (m)								
Pre-drought (1915–1950)	64	3320	1842	55	34	2551	1106	43
Drought (1951–1956)	64	2470	1398	57	34	2551	1106	43
Post-drought (1957–2001)	64	2289	1185	52	34	2551	1106	43
Factors measured at the landscape unit scale								
Elevation (m)	64	1327	17	1	34	1323	10	1
Precipitation (mm)								
Pre-drought (1915–1950)								
Growing season	64	146	6	4	34	146	8	6
Non-growing season	64	80	4	5	34	81	5	6
Drought (1951–1956)								
Growing season	64	87	7	8	34	86	8	10
Non-growing season	64	35	4	12	34	35	4	11
Post-drought (1957–2001)								
Growing season	64	160	7	4	34	159	6	4
Non-growing season	64	91	4	4	34	93	2	2
stocking rate (AUM/ha)								
Pre-drought (1915–1950)								
Growing season	64	0.06	0.02	33	34	0.07	0.02	23
Non-growing season	64	0.29	0.12	42	34	0.20	0.08	41
Drought (1951–1956)								
Growing season	64	0.02	0.01	70	34	0.02	0.01	46
Non-growing season	64	0.08	0.05	64	34	0.05	0.03	66
Post-drought (1957–2001)								
Growing season	64	0.03	0.01	34	34	0.04	0.01	28
Non-growing season	64	0.12	0.07	55	34	0.14	0.05	35

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