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Scaling effects of grazing in a semi-arid grassland

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Abstract. Previous studies have demonstrated relationships between spatial scale and spatial pattern and developed general hypotheses of scaling effects. Few studies, however, have examined the interactive relationship between scale and pattern-driving processes such as grazing. The goal of this study is to evaluate scale-dependent patterns across three spatial scales for three grazing intensities over 45 yr and to identify some mechanisms that may be associated with scale related differences. Correlation analysis and analysis of the coefficients of variation indicate that the relationships between units are dependent upon spatial scale and treatment. Across all grazing treatments, the relationship between units of the same scale becomes stronger as the spatial scale is increased. However, the rate of increase in the correlation coefficient is different for each treatment. The coefficient of variation responded inversely across scales with the greatest variation between small-scale units and little difference between the intermediate- and large scales. In addition to different relationships between units at each scale, differences in heterogeneity within treatments over time is illustrated by the relationship between small-scale units within each treatment and their associated larger scale units. The strongest relationship occurred in the heavily grazed treatments where correlation coefficients of small-scale units with intermediate- and large-scale units were ca. 0.60, indicating similar dynamics across scales. For the moderately grazed and ungrazed treatments this relationship varied from 0.40 to 0.47.

Results from this study suggest that grazing alters scaling effects. Variability between small-scale units was greatest in the ungrazed treatment which had greater heterogeneity and less predictability than grazed treatments because of the influence of grazing on plant morphology, demography and composition. At the intermediate scale, relationships between units were fairly similar with the least variation occurring in the moderately grazed treatment. Alternatively, variation between large-scale units was greatest in the moderately grazed treatment because of the relationship between rest cycles, weather patterns, and patch grazing. Therefore, grazing can have a positive, a negative, or no influence on heterogeneity between units depending upon the scale of observation. Evaluation of long-term dynamics across these treatments at the same small spatial scale results in different variances within each treatment which may violate assumptions of some statistical and experimental designs. Therefore, evaluations of temporal dynamics should consider scale relative to the relationship between plant size, density and longevity (relative scale).

Keywords: Herbivory; Heterogeneity; Hierarchy; Savanna; Scale; Stability; Succession; Temporal pattern; Vegetation dynamics.

Nomenclature: Hatch et al. (1990).

Introduction

Dynamic patterns are variable when observed across different organizational levels and spatio-temporal scales because they are driven by different processes (Carlile et al. 1989; O'Neill et al. 1989; Wiens 1989; Menge & Olson 1990). Therefore, no proper scale exists to collectively describe population, community and landscape patterns (Greig-Smith 1983; Wiens 1989; Levin 1992). Development of specialized quantitative methods (Turner et al. 1992) and quantitative studies at different scales (e.g. Sugihara & May 1990; Glenn et al. 1992; Fuhlendorf & Smeins 1996; Jonsson & Moen 1998) suggest that analysis of multiple scales is necessary to accurately describe temporal and spatial patterns and processes. These approaches have demonstrated relationships between spatial scale and spatial pattern (Turner 1990; Costanza & Maxwell 1994) and general hypotheses have been developed (Wiens 1989), but few studies have examined the interactive relationship between scale and pattern driving processes.

Several approaches have been developed to deal with analyses of variability across spatial scales and description of scale dependent patterns (Kershaw 1957; Greig-Smith 1983; Horne & Schneider 1995). They include (1) analyses of data sets at several spatial scales so that results can be compared and reported across multiple scales, (2) matching environmental variation with population/community variance patterns from different spatial scales, and (3) explicit treatment of measurement scale in experimental design (Horne & Schneider 1995). Incorporating the appropriate scale of observation within the design of experiments would require extensive knowledge and possibly pilot studies. Obviously, this approach is the most appropriate for studying patterns associated with spatial scales, but few, if any, long-term (> 10 yr) data sets are available to specifically evaluate scaling effects over time. Therefore, we will focus on the first and second approaches and apply them to long-term data from several grazing treatments to determine relationships between vegetation dynamics, heterogeneity, and grazing across several scales.

The influence of herbivores may be expressed at landscape-, community-, population-, individual-, and plant part levels of organization (Senft et al. 1987; Brown & Allen 1989; Archer & Smeins 1991; Fuhlendorf & Smeins 1997, 1998). Across various spatio-temporal scales grazing influences are confounded by other factors, such as climate patterns, altered disturbance regimes and competitive interactions (Archer 1994; Briske & Richards 1995; Fuhlendorf et al. 1996; Fuhlendorf & Smeins 1997). Because of variable influences across scales, and multiple pattern-driving processes, description of vegetation dynamics and grazing influences on rangelands requires a multi-scale approach.

Vegetation dynamics of an ungrazed semi-arid grassland were dependent upon spatio-temporal scales of evaluation (Fuhlendorf & Smeins 1996). Large-scale (pasture) dynamics following removal of grazing was characterized by low variation between units (synchronous movement through time), high variation within units, high predictability, and apparent movement toward a relatively stable state although fluctuating with precipitation. At the small-scale (within pasture, i.e. quadrat), dynamics were described as highly variable between units, little or no predictability, and no indication of movement toward a stable state. Small-scale units with similar starting points followed divergent trajectories through time (asynchronous movement). This approach identified different patterns for the same data at two different scales within an ungrazed grassland. The current study extends this analysis to three spatial scales within three grazing intensities over nearly a 50-yr period and discusses the relationships between spatial scale and plant size, longevity, grazing history and weather patterns.

Study area

The Sonora Research Station is located within the Edwards Plateau Vegetation Area (Hatch et al. 1990), ca. 56 km south of Sonora, Texas. Average annual precipitation (1919-1993) is ca. 600 mm and has varied from 156 mm in 1951 to 1054 mm in 1937. Rainfall is bimodal with peaks occurring in the spring and fall; seasonal and annual droughts are common. A severe and prolonged drought occurred from 1951 to 1956 with an average annual precipitation for that period of ca. 300 mm. The growing season is ca. 240 days. Temperatures average 30 °C in July and 9° C in January (Fuhlendorf & Smeins 1997).

Elevation of the station is ca. 730 m a.s.l. The landscape has gentle slopes of 3 - 4 % and is a heterogeneous mixture of soil depths, rock outcrops, and topographic positions. Dominant soils are Tarrant stony clays of the thermic family of Lithic Haplustolls. Soils formed over fractured Edwards and Buda Cretaceous limestones, are generally 15 - 30 cm deep, and contain 5 - 70 % limestone fragments with frequent limestone outcrops.

Vegetation is a savanna/parkland with individuals or clusters of woody species interspersed within a mid- and shortgrass matrix (Kuchler 1964; Smeins & Merrill 1988). Important herbaceous species include the stoloniferous shortgrass *Hilaria belangeri* and the bunchgrasses *Aristida purpurea*, *Bouteloua curtipendula* var. *caespitosa*, *B. trifida*, *B. hirsuta*, *Stipa leucotricha* and *Erioneuron pilosum,* while woody species include *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei*, *J. pinchotii*, and *Diospyros texana* (Smeins & Merrill 1988). Current woody canopy cover may be as high as 40 %, but varies greatly with topo-edaphic features, and grazing and fire history. No fires have occurred in the area over the past 100 yr. In the absence of fire these communities can eventually change to a nearly closed-canopy woodland with low herbaceous species diversity and low production (Fuhlendorf et al. 1996; Fuhlendorf et al. 1997).

In 1948, the 1402-ha station was fenced into several study units to investigate the effects on the vegetation of livestock/wildlife stocking rates, kinds and mixtures of animals, and grazing systems. An attempt was made in 1948 to remove all *Juniperus* plants on the station by hand cutting. Since other woody species (*Quercus*, etc.) were not removed, many small *Juniperus* plants present under their canopies, as well as small seedlings/saplings throughout the grassland portion of the station, may have escaped detection.

Three grazing intensity treatments that were established in 1948 were used in this study (see Fuhlendorf & Smeins 1997 for a detailed description). The heavily grazed treatment included two 32-ha units that have had a stocking rate of 4.8 - 8.1 ha/auy[1] in a year-long continuous grazing system. The moderately grazed treatment includes four pastures (24 ha each) stocked with cattle, sheep, and goats at a stocking rate that varied from 6.0 - 10.4 ha/auy from 1949 to 1993. Moderately grazed pastures were a part of a Merrill 4-pasture grazing system where each pasture was grazed for a year and then rested for 4 months. Stocking rates have been variable since 1948, but until 1983 the stocking rate in the heavily grazed treatment was always 1.5 to 2 times the moderate stocking rate. Since 1983, the stocking rates of both the heavily and moderately grazed treatments have been

[1]auy = animal unit year = 4314 kg or the amount of forage consumed by 450 kg animal for one year.

moderately stocked. The ungrazed treatment consists of two 12 ha units that have not been grazed by livestock since 1948. One unit of this treatment also excluded large, free-roaming wildlife (primarily white-tailed deer).

All treatments had essentially the same composition in 1949 due to a previous long history of heavy grazing (Smeins & Merrill 1988). Thus, the ungrazed and moderately grazed treatments were not representative of their current treatment designation when initially established in 1948. This past heavy utilization and absence of fire resulted in many structural and functional changes still evident today, namely increase in woody plants and reduction of productive midgrasses (e.g. *B. curtipendula* and *Eriochloa sericea*) which reduced livestock carrying capacities.

Methods

Vegetation sampling

In 1948, 12 permanently marked 30.5 cm × 30.5 cm quadrats were established on each of three sample lines (ungrazed and moderate = 800 m, heavy = 1050 m) in the eight units (36 quadrats/unit). Quadrats were originally evenly spaced along the sample line and located at least 4 m from the nearest woody species, and in sufficient soil to sustain perennial grasses. Since 1948, some of the 36 quadrats have become shaded by woody plants or covered by their litter which has resulted in the loss of two to five quadrats within each treatment unit. 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, intervals between sampling have been sporadic and not all treatment units were sampled each year.

Quantitative methods

Vegetation dynamics were evaluated at three spatial scales and three grazing treatments to evaluate the relationship between spatial scale differences within three grazing regimes. Large-scale dynamics were analyzed by summing the 36 individual quadrats within each treatment unit (ungrazed $n = 2$, moderately grazed $n = 4$, heavily grazed $n = 2$). Intermediate scales were evaluated by summing the 12 quadrats along each of the three sampling lines within each treatment unit (ungrazed $n = 6$, moderately grazed $n = 12$, heavily grazed $n = 6$) and the small scale assessed the dynamics of individual quadrats (ungrazed $n = 38$, moderately grazed $n = 117$, heavily grazed $n = 56$). Basal area variation of *H. belangeri*, the most abundant species, was used to describe scale-dependent behavior on long-term temporal dynamics of this ecosystem because of its dominance across all treatments (Fuhlendorf & Smeins 1996, 1997). Prior to statistical analysis, quadrats that did not contain *H. belangeri* for more than 10 of the 21 sampling years were removed from analyses. In the ungrazed treatment 34 quadrats were removed which left 38 quadrats for small-scale analysis. 16 quadrats were removed from heavily grazed treatments which left 56 quadrats for small-scale analysis. In the moderately grazed treatment, 27 quadrats were removed which left 117 for analysis. All treatments were sampled annually from 1949 to 1964, then in 1968, 1982, 1984, 1987, 1992 and 1993 (21 samples over 44 yr). Several of the sampling times since 1982 are limited to one treatment unit within each treatment.

Analyses of the influence of scale on vegetation dynamics over time were conducted with a technique that is similar to autocorrelation which was developed for analysis of spatial patterns (Turner et al. 1992; Fuhlendorf & Smeins 1996). For this study, correlation analyses (Turner et al. 1992; Miller et al. 1995) and coefficients of variation were used to quantify differences between dynamic patterns at three spatial scales for three grazing intensity treatments (heavily grazed, moderately grazed, and ungrazed).

Correlation analysis was conducted to determine relationships between *H. belangeri* basal area and precipitation (three-year running average) (Fuhlendorf & Smeins 1997) for three grazing treatments. Correlations and coefficients of variation between the aggregated units, within each treatment, across sampling years were used to evaluate large-scale dynamics and the variability between units over time. Intermediate dynamics were evaluated by conducting these analyses on the aggregated quadrats for each of the three lines within each treatment unit. Correlations and coefficients of variation across time for all combinations of individual quadrats (ungrazed $n = 703$, moderately grazed $n = 6888$, heavily grazed $n = 1544$) were used to evaluate small-scale dynamics and determine the relationships between small-scale units. These high n-values reduce the value of presenting p-values but result in a normal distribution for the correlation coefficients which are presented as averages (Fuhlendorf & Smeins 1996). Variation within large and intermediate-scales was determined through correlations between small-scale units (quadrats) and the large-scale aggregates over time. Also, coefficients of variation were calculated between small-scale units, within each grazing treatment, for each year to determine how the variation within each treatment changed over time. Analyses of small-scale units results in stochastic patterns (Fuhlendorf & Smeins 1996) so units were separated by soil depth classes (Fuhlendorf & Smeins 1998) and correlation coefficients were calculated to determine if units with similar soil depths had similar dynamics.

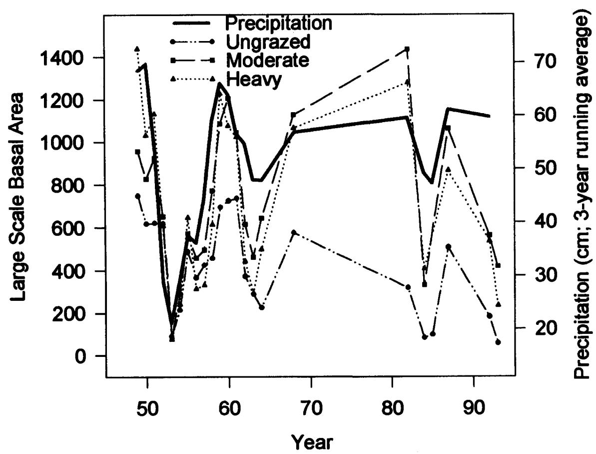

Fig. 1. Large-scale temporal dynamics of *H. belangeri* basal area for heavily grazed, moderately grazed, and ungrazed treatments. The solid line represents the corresponding three-year running average of precipitation. For years with missing basal area data, precipitation data was also excluded in order to better illustrate the relationship between precipitation and basal area.

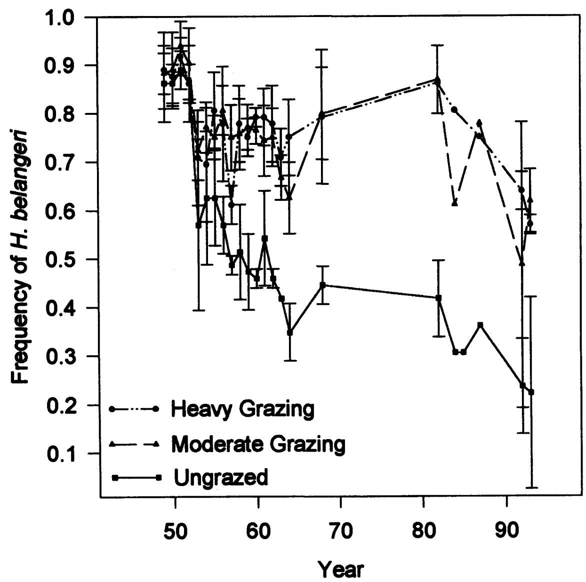

Fig. 2. Frequency (%) of quadrats that contain *H. belangeri* within heavily grazed, moderately grazed and ungrazed treatments over time.

Results

Large-scale (the sum of 36 30.5 cm × 30.5 cm quadrats within each pasture) temporal dynamics of *H. belangeri* basal area are highly variable and dependent upon precipitation patterns and long-term grazing treatments (Fig. 1). Large-scale dynamics were similar for heavily and moderately grazed treatments throughout the study and variation was largely accounted for by correlation with a three-year running average of precipitation ($r = 0.72$ and $r = 0.69$, respectively). In the ungrazed treatment, precipitation was significant ($r = 0.47$) but not as important as in other treatments because directional successional changes associated with the removal of domestic herbivory altered patterns following the drought of 1951-1956 (Fig. 1). Since 1965, the ungrazed treatment has never been above 600 cm^2 basal area whereas both grazed treatments fluctuated but had maximum values > 1000 cm^2. In 1982, basal area increased in all replications of both grazed treatments to the highest level for the temporal extent of this study. By 1984, all treatments had the lowest basal area since the 1951-1956 drought because of an episodic freeze (Fuhlendorf & Smeins 1998). Due to weather driven variation over time, the ungrazed treatment was only different from the grazed treatments between 1965 and 1982. Basal areas of all treatments have decreased over the past 10 yr, perhaps in response to an increased abundance of the trees/shrubs, particularly *Juniperus ashei* (Fuhlendorf et al. 1996), and concomitant root and canopy competition.

At the large-scale, long-term treatment differences in basal area were confounded by weather patterns. However, the number of quadrats without *H. belangeri* increased through time for the ungrazed treatment (Fuhlendorf & Smeins 1996) and temporal patterns of frequency were different among treatments. Frequency was more dependent upon grazing treatment than weather patterns (Fig. 2). As with basal area, frequency of the two grazed treatments were similar throughout the 45 yr. However, the ungrazed treatment has expressed a downward trend in the frequency of *H. belangeri* since 1953. For grazed treatments, no trend was evident prior to 1982, but since then all treatments have decreased at about the same rate (0.2/10 yr) probably due to increases in woody plants which has occurred across all grazing treatments (Fuhlendorf et al 1996; Fuhlendorf & Smeins 1997).

Correlation analysis (Fig. 3) and analyses of the coefficients of variation (Fig. 4) indicate that the relationships between units are dependent upon spatial scale and treatment. Across all grazing treatments, the relationship between units becomes stronger as the spatial scale is increased. However, the rate of the increase in the correlation coefficient is different for each treatment. For the ungrazed treatment, the correlation between units increased from 0.22 at the small-scale (quadrat) to 0.86 at the large-scale (treatment) with 60 % of the change occurring between the small- and intermediate-scale (sample line). For the heavily grazed treatment, the total difference was less, ranging from 0.40 at the

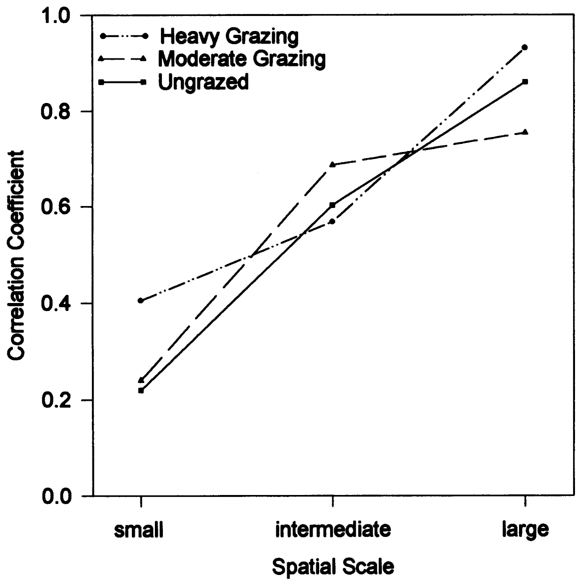

Fig. 3. Average correlation coefficients between units at each spatial scale (small = quadrat, intermediate = sample line, and large = treatment) for each grazing treatment. These coefficients represent the degree of synchronous movement through time at each scale and each treatment.

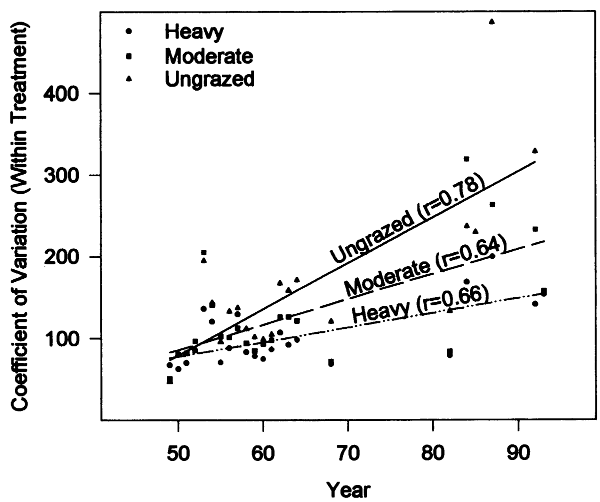

Fig. 4. Coefficients of variation within treatments (variation between small-scale units) over time. Lines represent the simple linear correlation between variation within each treatment and time.

small-scale to 0.93 at the large-scale and with only 32 % of the change occurring between the small- and intermediate scales. Correlation coefficients of the moderately grazed treatment ranged from 0.25 at the small-scale to 0.75 at the large-scale with almost all of the change (87 %) occurring between the small- and intermediate scales.

The coefficient of variation responded inversely across scales with the greatest variation between small-scale units and little change between the intermediate- and large-scales. At the small-scale the highest variation between units occurred in the ungrazed treatment (cv = 144) followed by the moderately (cv = 121) and heavily grazed (cv = 112) treatments, respectively. When temporal dynamics of the variation are considered within each treatment, differences in the coefficient of variation across time are variable, but more obvious patterns appear (Fig. 4). In the ungrazed treatment the coefficient of variation increased the most over time ($r = 0.78$), from < 80 in 1949 to the current level of > 300. The heavily grazed treatment had the slowest rate of increase in variation from near 80 to about 110 ($r = 0.66$) with most of this occurring after the reduction in grazing intensity in 1983. Moderate grazing had a similar starting point in 1949 to other treatments because of their previously similar grazing and an intermediate rate of increase in coefficient of variation over time ($r = 0.64$). There is an inverse relationship between grazing intensity and variation or heterogeneity within treatments.

In addition to different relationships between units at each scale, differences in heterogeneity within treatments over time is illustrated by the relationship between dynamics of small-scale units within each treatment and their associated intermediate and large scale

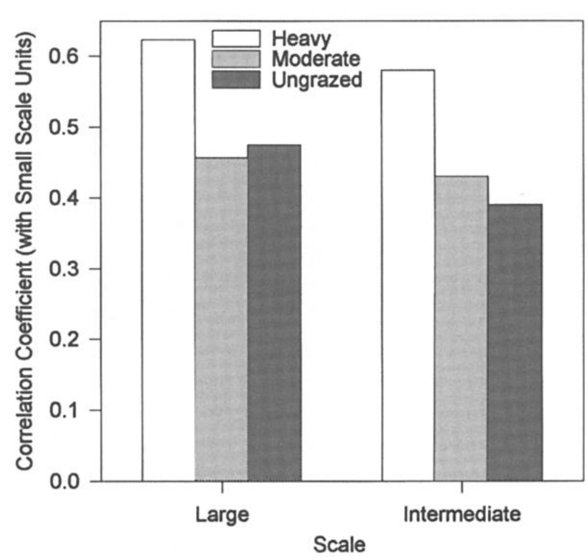

Fig. 5. Average correlation coefficients between small-scale units and their associated intermediate- and large-scale units for each treatment illustrating the similarity in dynamics across scales and the heterogeneity within each treatment.

units (Fig. 5). The strongest relationship occurred in the heavily grazed treatments where correlation coefficients of small-scale units with intermediate- and large-scale units were approximately 0.60, indicating similar dynamics across scales. For the moderately grazed and ungrazed treatments this relationship was less and ranged from 0.40 to 0.47 which suggests greater variation at smaller scales. Hence, there is less difference between scales and reduced heterogeneity within heavily grazed treatments.

Discussion

Several hypotheses of scaling effects proposed by Wiens (1989) were previously quantified for two spatial scales in the ungrazed treatment of this semi-arid grassland (Fuhlendorf & Smeins 1996). Small-scale dynamics were highly variable, asynchronous across units, and unpredictable, while large-scale dynamics were predictable, synchronous, and driven by weather patterns and successional changes in composition. For the current study, the influences of scale were extended to three spatial scales and compared across three grazing intensities to identify the relationships between spatial scale and grazing. For all grazing treatments, correlations between large-scales (the sum of 36 quadrats within each pasture) were strong ($r >$ 0.70) followed by intermediate-scales (the sum of 12 quadrats along each sampling line; r = 0.50 - 0.70), with little or no relationship between small-scale units (individual quadrats; $r <$ 0.45). This is in agreement with other studies (O'Neill et al. 1986; Wiens 1989; Fuhlendorf & Smeins 1996) in that as spatial scale increases, relationships between units become stronger and variation between units decreases.

The cause for highly variable dynamics within small-scale units is difficult to isolate. Similar starting points for small-scale units at the time of establishment (1948) do not indicate potential or direction of dynamics for any grazing treatment. These rangelands possess high levels of inherent heterogeneity (Miller et al. 1995; Fuhlendorf & Smeins 1998) that is variable with soil depths and geomorphological characteristics associated with landscape position. This variability produces a shifting mosaic of variable soil dependent successional states across the landscape that prior to settlement was enhanced by variable weather patterns and disturbance regimes (Fuhlendorf & Smeins 1998). However, when quadrats were paired by soil depth classes within treatments, correlations between small-scale units did not increase and dynamics remained asynchronous. Lack of dependence upon weather patterns and topo-edaphic features suggests that small-scale dynamics are probably influenced by biotic factors associated with plant populations and communities.

Though the general relationship between scales was similar for all treatments, grazing alters heterogeneity at multiple spatial scales (Brown & Allen 1989; Fuls 1992; Fuhlendorf & Smeins 1998), so some differences in scaling effects would be expected across grazing treatments. In the heavily grazed treatment, small-scale units were more strongly correlated with other heavily grazed small-scale units, as well as heavily grazed large-scale units, than occurred in other treatments. This indicates lower heterogeneity and reduced differences across scales within the heavily grazed treatment. Alternatively, within moderately grazed and ungrazed treatments, dynamics of an individual quadrat is no indication of dynamics of other small-scale units or large-scale units indicating greater heterogeneity. Heavy grazing by livestock overrides local heterogeneity that is inherent in ungrazed communities and reduces the variability across different soil and landscape positions.

Decreased heterogeneity between small-scale heavily grazed units is associated with the influence of heavy, repeated defoliation on morphological and life history traits of each individual, as well as decreased species diversity and altered species composition (Briske & Richards 1995; Fuhlendorf & Smeins 1997). Heavy livestock grazing can cause fragmentation of large plants and an associated decrease in basal area of individuals (Butler & Briske 1988). Similarly, for these plant communities, removal of grazing or reduction in intensity resulted in an increase in basal area of individuals and a four- to five-fold decrease in density (Fuhlendorf et al. unpubl.). Grazing alters the demography and structure of all species collectively, as well as dominant individual species, such as *H. belangeri*. Heavy grazing resulted in small-scale units that contained as many as 50 rooted individual *H. belangeri* plants. Following 40 yr without grazing, the same quadrats generally contain < 5 individuals with no major changes in collective basal area within the quadrat because of an increase in their average basal area per individual. In addition to morphological structure, grazing alters plant longevity (Butler & Briske 1988; Briske & Richards 1995) which could influence variability of small scales when plant densities are low. These different scaling effects in each grazing treatment indicate that similar spatial scales (on an area basis) are not ecologically equivalent across treatments. When one of the many small plants die in a heavily grazed quadrat, the influence on the basal area within that quadrat remains relatively unaffected because of the high density and small basal area of individuals. However, mortality of larger individuals in ungrazed quadrats results in dramatic shifts in the total basal area within quadrats, increased heterogeneity at the small scale, and stochastic dynamics that may not be related to any measured factors. Therefore, structural changes in the morphological characteristics of plants within these treatments result in differential relationships between plant size, plant density, plant longevity and quadrat size which alters the relative scale of observation.

At the large scale, dynamics of *H. belangeri* was relatively predictable in that all replications within each treatment responded similarly and were primarily influenced by weather patterns, long-term grazing intensity, and the increase in invasive woody plants. Large-scale units in the moderately grazed treatment had the greatest variation between units. The correlation between moderately grazed large-scale units was only slightly higher than the correlation between intermediate-scale units suggesting that large-scale dynamics of this treatment was not as predictable as in other treatments. The moderately grazed treatment included four large-scale units from a rest/rotation grazing regime where each unit is grazed for a year and rested for four months. Spatial and temporally variable patterns of herbaceous biomass production and grazing within each unit results in a feedback that leads to divergent behavior where treatments may become more divergent over time. In addition, the timing of rainfall events relative to the rest/rotation cycles can result in variable levels of grazing intensity which can alter productivity during subsequent years. Within these units, moderate grazing can result in biomass that is less limited than with heavy grazing, so grazing patterns become spatially variable. Uneven distribution of grazing in space and time results in variable community structure within- and between-treatment units where some areas resemble heavily grazed communities while other, less accessible areas may be similar to ungrazed communities (Bakker et al. 1983; Fuls 1992). Therefore, moderate grazing increased large-scale heterogeneity by creating conditions that lead to patch grazing. Because of limited forage, heavy grazing forces livestock to utilize most of the landscape evenly reducing the inherent heterogeneity of ungrazed communities.

Conclusions

Grazing can alter plant density/size (Butler & Briske 1988; Fuhlendorf & Smeins 1998), plant longevity (Briske & Richards 1995), community composition and diversity (Fuhlendorf & Smeins 1997), vegetation response to climate patterns (Fuhlendorf & Smeins 1997), and vegetation response to other abiotic factors such as soil depth (Fuhlendorf & Smeins 1998). Results from this study suggest that grazing can also alter scaling effects and heterogeneity at several levels. Variability between small-scale units (individual quadrats) was greatest in the ungrazed treatment suggesting greater heterogeneity and less predictability than grazed treatments because of the influence of grazing on plant morphology and demography. At the intermediate-scale (the sum of 12 quadrats along each 800 - 1050 m sampling line), relationships between units were fairly similar with the least variation occurring between units in the moderately grazed treatment. Alternatively, large-scale units (the sum of 36 quadrats within each pasture) were most variable in the moderately grazed treatment because of the relationship between rest cycles, weather patterns, and patch grazing. Therefore, grazing can have a positive, a negative, or no influence on heterogeneity between units depending upon grazing intensity and the scale of observation.

Even across three very different communities, this study agrees with general theories that patterns of within- and between-unit variability are dependent upon the scale of observation (Wiens 1989; Levin 1992). As a result of these generalizations, single scale comparisons are generally considered invalid if observations are not on the same scale for each treatment (Horne & Schneider 1995). However, different scaling effects within each grazing treatment, suggest that area-based spatial scales are actually different in an ecological and statistical context when compared across treatments. Evaluation of long-term dynamics across these treatments at the same spatial scale suggests that variances are different within each treatment violating assumptions of some common statistical and experimental designs. Typically, ecological scale is defined in terms of grain and extent. Extent refers to the area of interest and the upper limits of understanding (treatment), while grain refers to the resolution or the sample unit size of the study (quadrat). This study indicates that analyses of vegetation dynamics should define scale relative to the relationship between plant size, density and longevity (relative scale). Alternative techniques should be developed to consider relative scale as a co-variable instead of erroneously assuming that scale is constant across treatments. Future research is needed to evaluate factors that alter scaling effects, such as grazing, and attempt to quantify relationships between scaling effects and dominant environmental gradients.

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