

**LONG-TERM DYNAMICS IN PLANT ABUNDANCE AND SPATIAL
VARIATION IN RESPONSE TO GRAZING SYSTEMS, PRECIPITATION AND
MESQUITE COVER**

by

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DEDICATION

To my daughter Anotida Nicole.

TABLE OF CONTENTS

LIST OF TABLES	9
LIST OF FIGURES	10
LIST OF FIGURES	10
ABSTRACT.....	11
ABSTRACT.....	11
INTRODUCTION	13
Grazing management theory on rangelands	13
Precipitation and mesquite influence vegetation dynamics in grazed ecosystems 21	
<i>Precipitation gradient</i>	22
<i>Mesquite abundance</i>	24
<i>Fire regime, grazing history, and soil characteristics</i>	26
Analytical challenges and future directions in studying grazing systems	27
<i>Statistical assumptions and analytical approaches</i>	28
<i>Long-term data</i>	32
<i>Measures of spatial variation</i>	33
<i>Future directions for grazing system studies</i>	33
Research problem in context	35
<i>History of grazing in the southwestern United States</i>	35
<i>Grazing system research on the SREER</i>	36
<i>Current research and analytical approach</i>	38
Dissertation format	43
PRESENT STUDY.....	45
REFERENCES	55
APPENDIX A: SHORT- AND LONG-TERM VEGETATION CHANGE RELATED TO GRAZING SYSTEMS, PRECIPITATION AND MESQUITE COVER.....	76
ABSTRACT.....	77
INTRODUCTION	80
MATERIALS AND METHODS.....	83
Study area	83
Grazing systems	84
Vegetation variables	85
Covariates	86
Analytical approach	86
RESULTS	90
Grass density	90
Shrub density and cover	91
Grass cover	92
DISCUSSION.....	93
Grazing systems	93
Precipitation and mesquite covariates	95

TABLE OF CONTENTS (Continued)

Temporal dynamics	97
Maintaining and improving long-term grazing system studies	100
IMPLICATIONS	101
LIST TABLES	111
LIST OF FIGURES	115
APPENDIX B: USING VARIANCE TO DETECT SPATIAL VARIATION OF GRASS ABUNDANCE UNDER YEARLONG AND SEASONAL ROTATION GRAZING SYSTEMS.....	119
INTRODUCTION	122
MATERIALS AND METHODS.....	125
Study area	125
Grazing systems	125
Precipitation covariate	126
Response variables	126
Analytical approach	127
RESULTS	130
DISCUSSION	131
Grazing systems	131
Precipitation gradient	132
Variance and spatial variability	133
IMPLICATIONS	135
AKNOWLEDGEMENTS.....	136
LIST OF TABLES	143
LIST OF FIGURES	145

LIST OF TABLES

Table 1. Summary of analytical methods applied to studies evaluating grazing system effects on rangeland vegetation.	31
Table 2. Size, elevation range, number of ecological sites, percent of sandy loam upland (SLU) and sandy loam deep (SLD) ecological sites, long-term stocking rate, stocking density, and annual precipitation for pastures experiencing yearlong and seasonal-rotation grazing treatments over 34 years (1972-2006). Parenthetical values are one SE of the mean.	41
Table 3. Pasture size, elevation range, proportion of sandy loam upland (SLU) and sandy loam deep (SLD) ecological sites, stocking rate in ha/animal unit year (\bar{x} , SE), annual precipitation (\bar{x} , SE) and mesquite cover (\bar{x} , SE) in the seven study pastures over the 12-y (short) and 34-y (long) time periods in relation to grazing systems treatment (yearlong and seasonal rotation).	111
Table 4. Pearson product-moment correlation coefficient (r) between plant variable and type of precipitation (mm). 2- and 3-y represent cumulative 2- and 3-y values leading to vegetation measurement. Level of significance: $*P < 0.05$. ¹ Precipitation parameter with the greatest correlation with the response variable and was selected as the precipitation covariate for that response variable in the analysis of variance.	112
Table 5. P-values from the split-plot ANOVA of vegetation density and cover during short-term ((- or 12-y) and long-term (31- or 34-y) study periods with grazing systems (GS) main effect, precipitation (PPT) and mesquite cover (MESQ) covariates, year (YR) as the split, and their interactions. (+) and (-) adjacent to P-values of covariates shows the direction of correlations with the response variable.	113
Table 6. P-values from the split-plot analysis of grass basal cover over 22-y (1984-2006) with grazing system (GS) main effect, precipitation (PPT) and mesquite cover (MESQ) covariates, year (YR) as the split, and their interactions. (+) and (-) adjacent to P-values of covariates shows the direction of correlation with the response variable.	114
Table 7. Size, elevation range, number of ecological sites, percent of sandy loam upland (SLU) and sandy loam deep (SLD) ecological sites, long-term stocking rate, stocking density, and annual precipitation for pastures experiencing yearlong and seasonal-rotation grazing treatments over 34 years (1972-2006). Parenthetical values are one SE of the mean.	143
Table 8. P-values from the split-plot analysis of the variance of grass density over 34 years (1972-2006) and of grass cover over 22 years (1984-2006) with grazing system (GS) main effect, precipitation (PPT) covariate, year (YR) as the split, and their interactions. * = non-significant interaction with PPT which was excluded from the final model. (+) = positive correlation with precipitation gradient.	144

LIST OF FIGURES

- Figure 1. Annual summer (solid bar) and winter (open bar) precipitation on the seven study pastures on Santa Rita Experimental Range, 1971-2006. Precipitation year is October to September, summer months are June through September and winter months are October through May. Dashed line is average precipitation for the same period. 48
- Figure 2. Standardized difference for seasonal precipitation on the seven study pastures on Santa Rita Experimental Range, 1972-1973 to 2005-2006. Precipitation year is October to September, summer months are June through September. Standardized difference is the individual year value minus long-term (1922-2006) average (winter mean = 158 mm, summer mean = 213 mm) divided by the standard deviation (winter SD = 61.0, summer SD = 64.2). 115
- Figure 3. Density of perennial grasses, native grasses, forage grasses, *Eragrostis lehmanniana*, *Aristida* spp., *Bouteloua rothrockii*, *Digitaria californica* and *Isocoma tenuisecta* in the two grazing systems (seasonal rotation SR = solid circles, and yearlong YL = open circles) between 1972-2006. The vertical broken line shows the end of the short-term period in 1985. Different letters above the single SE bars indicate years with significantly different ($P < 0.05$) plant density after combining grazing treatments..... 116
- Figure 4. Percent cover of total shrubs, *Isocoma tenuisecta* and *Prosopis velutina* in the two grazing systems (seasonal rotation SR = solid circles, and yearlong YL = open circles) 1975-2006. The vertical broken line shows the end of the first nine years. Different letters above the single SE bars indicate years with significantly different ($P < 0.05$) cover after combining grazing treatments. 117
- Figure 5. Basal cover for four perennial grass groups in the two grazing systems (seasonal rotation SR = solid circles, and yearlong YL = open circles), 1984-2006. Different letters above the single SE bars indicate years with significantly different ($P < 0.05$) cover after combining grazing treatments. 118
- Figure 6. Relationship between annual precipitation and log variance of density and cover of native, forage, and non-native grasses for seasonal rotation (SR, open circle) and yearlong grazing (YL, solid circle) pastures. Lines represent correlation between log variance (LV) and precipitation (PPT) within pastures in each grazing system (SR and YL). Solid lines are significant ($P < 0.05$) relationships and dotted lines are not significant. Vertical bars are 1+SE of the mean. 145
- Figure 7. Log variance of cover for perennial grass groups in the two grazing systems (seasonal rotation SR = open circles, and yearlong YL = solid circles), over 22 years (1984-2006). Different letters above the 1+SE bars indicate years with different ($P < 0.05$) log variance when grazing treatments are combined..... 146

ABSTRACT

Higher stocking density under seasonal-rotation grazing is expected to increase plant abundance because expanded animal distribution and reduced selective grazing on forage species will reduce the spatial variation and competitive advantage of non-forage species compared to yearlong grazing. Rangeland scientists struggle with how long rangeland experiments must continue in order to detect grazing treatment effects, particularly in semi-arid ecosystems with slow responses and high spatio-temporal variability. My first study investigated grazing system effects on plant abundance (cover and density) over the short-term (12yrs) or long-term (22 or 34yrs) after accounting for covariates (mesquite and precipitation gradients). My second study assessed how grazing systems affected spatial variation in grass abundance over 22 or 34 years after accounting for precipitation gradient. The first study was a coarse resolution approach, looking at grazing impacts on plant abundance. The second study was a finer resolution assessment of the underlying assumption that rotational grazing systems reduce selective grazing. Using split-plot analysis of variance, with year as the split, changes in mean plant abundance and variance in grass abundance were compared between two grazing systems (yearlong vs. seasonal rotation), after accounting for covariate(s). Variance of grass abundance among sample locations within an experimental pasture was the measure of spatial variability and was expected to increase with selective grazing. Grazing systems did not influence plant abundance or spatial variation of grasses. The absence of grazing effect may be due to overriding influences of grazing intensity, large pasture sizes, temporal variation in

precipitation, and few replicates. Specific to spatial variation, the absence of grazing system effect may be due to discrepancies in transect representation across ecological sites and spatial variation of grasses occurring at scales different than the 30-m transect size. Like earlier research, my studies failed to substantiate the fundamental premise for implementing rotational grazing systems. This exposes challenges that confront rangeland scientists when implementing grazing studies in spatio-temporally heterogeneous ecosystems. I recommend that research shift from comparing rigid schedule-driven grazing systems to more adaptive management approach where there are comparisons between different levels or different designs of flexible systems.

INTRODUCTION

Grazing can either have positive or negative effects on the ecosystem depending on management practices used in relation to the potential and current condition of the rangeland. The potential and current conditions of a rangeland impose an upper limit to ecosystem productivity that cannot be overcome by management (Briske and Heitschmidt 1991). Ecosystem potential and current conditions of rangelands are a function of many factors including climate, soils type, topography, history of grazing and fire regime. Critical to note however, is that rangelands are not static systems, but are very dynamic and heterogeneous over space and time. This spatial and temporal variation introduces complexity when evaluating the response of rangeland resources to management practices. When assessing management effects on rangeland resources it becomes imperative to look at different scales, have multiple indicators as response variables, account for non-treatment variation (e.g. precipitation and woody species abundance) as covariates and recognize that different ecosystems may have different rates of response to management.

Grazing management theory on rangelands

Grazing management is the manipulation of grazing intensity, season and duration of grazing to achieve optimum and sustained plant, land, environmental and economic results (Heady and Child 1994). These factors influence the seed bank, root mass, residual leaf area and meristematic tissue, which in turn influence recruitment, growth

and persistence of plants (Briske 1991). Grazing drives plant dynamics directly through effects on the physiology of plants e.g. influencing photosynthetic efficiency and primary productivity depending on residual leaf area and meristems after grazing (Briske 1991) and indirectly through ecosystem function e.g. changes in rates of erosion and primary production associated with changes in spatial variation in plant distribution (Archer and Smeins 1991; Thurow 1991).

Grazing intensity is a function of stocking rate (animals/area/time), which influences the level of utilization of forage species. Grazing effects can range from positive to negative depending on grazing intensity and the growing conditions of plants (Belsky 1986). A primary factor determining the balance between negative and positive effects is the removal of old leaf area as grazing intensity increases and the positive effects of increasing photosynthetic efficiency by new leaves that regrow after defoliation (Parsons et al. 1983). By altering the age structure of leaves within plant canopies, grazing has direct consequences to the photosynthetic capacity of plants because leaves exhibit maximum photosynthetic rates at about the time of full expansion and decline thereafter (Caldwell 1984). There is some evidence that under ideal plant growing conditions low to moderate grazing intensity can increase biomass production, which then declines at higher grazing intensities creating a unimodal response to grazing intensity termed the grazing optimization hypothesis (Parsons et al. 1983; McNaughton 1983a; Noy-Meir et al. 1989). However biomass production tends to be negatively associated with grazing intensity because of the increased dependence on photosynthetically-inefficient leaf sheath and older leaves, more so for plants growing in

resource limited environments because regrowth of new leaves is less certain (Mathew et al. 2000).

Grazing intensity also influences below ground productivity. Root initiation and development are supported by photosynthetic material from aboveground plant parts and the roots in turn supply aboveground parts with nutrients and water. Therefore a positive feedback exists between aboveground and belowground productivity. Grazing intensity that causes a net loss in plant productivity will result in a decline in net belowground productivity and sometimes root mortality (Troughton 1981; Biondini et al. 1998), which subsequently reduces plant regrowth and persistence as the potential for nutrient and water uptake is lost. Two species showed a gradual decline in belowground plant production when grazing intensity exceeded 20% in sub-humid grasslands (Oesterheld 1992) and net primary belowground productivity gradually declined from no grazing, to moderate grazing to heavy grazing in a semi-arid area (Gao et al. 2008).

Timing (season) of grazing relative to the phenological stage of development of different species influences plant sensitivity to grazing intensity, subsequently affecting competitive interaction among species and future species composition (Briske 1991). As a result similar levels of grazing intensity produce different outcomes in the same plant community depending on the season of grazing. For example, a study assessing the negative impacts of season of grazing on next season's plant development found that undefoliated plants or plants defoliated during the early vegetative stage had more active buds at the end of the season than plants that were defoliated after internode elongation, likely because limited productivity after clipping compromised photosynthate

replenishment to sustain metabolic activity (Becker et al. 1997). One basic principle for grazing management is to allow for plant growth prior to and regrowth following defoliation to maintain photosynthetic material and the energy needed to support important physiological processes of a plant. However, because the species used in this experiment were tolerant to grazing due to long history of grazing, new meristems had established by the beginning of the following growing season.

Grazing tends to be more detrimental to future growth, development and seed production if done later in the growing season when potential for regrowth is limited and apical meristems are elevated. Heavy grazing on *Agropyron desertorum*, a grazing-tolerant grass, prior to apical meristems elevation during culm elongation seldomly affected tiller replacement, but heavy grazing during or after culm elongation increased overwinter mortality of fall-produced tillers and reduced the number and heights of replacements (Olson and Richards 1988). Grazing just prior to seed head development causes a decline in seed production and subsequently the seed bank (Sternberg et al. 2003).

Ungrazed, or rest periods that coincide with the plants' active growing season tend to have positive results. For example, under tropical climate spring-summer rest promotes establishment and persistence of warm season plant species because they are protected during the period of maximum growth and may even improve the reproductive rate of cool season species that establish in fall (Hidalgo and Cauhepe 1991). Conversely, on a rangeland with a Mediterranean climate dominated by annuals, spring grazing produced no significant differences in primary production and plant cover compared to

continuous grazing, but fall grazing reduced foliar cover and the number of taxa in the community (Bartolome and McClaran 1992). Because rangeland plant communities are often a mixture of species with different phenologies, consistently resting during one season will create a competitive advantage to the species that are actively growing during the rest period while suppressing other species. Periodically changing the season of grazing will likely improve the competitive interaction among species, thus maintaining or increasing species diversity.

The primary goal of grazing systems is typically to minimize negative impacts of grazing and optimize the opportunities to maintain ecological potential and livestock productivity. A grazing system is grazing management that employs alternate periods of grazing, deferment and rest in at least 2 pastures (Society for Range Management 1989). Generally, grazing systems are expected to improve seed production, plant recruitment, abundance of palatable species, herbivore distribution, uniformity in forage utilization and subsequently rangeland condition compared to yearlong (YL) grazing (Heady 1961). It is assumed that because of higher rates of regrazing, YL grazing lacks time for vegetation to regrow without regrazing, thereby compromising rangeland productivity. The lower stocking density and continued livestock presence in YL grazing systems result in greater patch level selective grazing (Norton 1998; Teague and Dowhower 2003). This pattern of patchy use can promote a more heterogeneous landscape that provides a greater opportunity for a variety of plants to persist especially when coupled with low to moderate stocking densities (McNaughton 1983b; Loeser et al. 2007).

Livestock grazing systems that employ alternate periods of use, rest or deferment by increasing stocking density and grazing intensity without reducing long-term stocking rates are expected to improve vegetation productivity compared to YL grazing by allowing for periods of regrowth without regazing by periodically removing grazing during critical periods of plant growth and by creating more uniform spatial distribution of forage use (Heady 1961). Greater stocking density in rotational grazing systems is expected to reduce patch-level selective grazing and thus the competitive advantage of less preferred species as well as plant spatial variation compared to YL grazing (Cassels et al. 1995; Kirkman and Moore 1995; Weber et al. 1998; Teague and Dowhower 2003). Evidence for less selective grazing under seasonal-rotation grazing includes reduced number and sizes of patches over time and as distance from water sources increased (Cassels et al. 1995; Cid and Brizuela 1998; Weber et al. 1998) and more random distribution of neighboring plants (Teague and Dowhower 2003). In semi-arid ecosystems, rotational grazing can increase basal cover and decrease bare ground compared to continuous grazing (Teague et al. 2004).

Most studies investigating grazing system effects on vegetation have used some measure(s) of plant abundance as the response, based on the expectation that rotational grazing systems will facilitate plant growth, but not much work has been done on grazing system effects on spatial variability of forage plants (Table 1). This happens despite the documented association between spatial distribution of plants and ecosystem function and sustainability of rangeland resources even when average plant abundances are not different. Soil erosion and water runoff can increase when plant distribution becomes

more heterogeneous (Ludwig et al. 1994; Hart and Frasier 2003), plant productivity in drier locations can decrease when the distribution becomes more uniform (Aguiar and Sala 1999), and plant diversity and ecosystem stability can decrease as distribution becomes more homogeneous (Rietlerk et al. 2004). More heterogeneous plant distribution may increase plant production by redistributing water from the bare patches (source) to vegetated patches (sink), resulting in lower effective precipitation threshold compared to when plant distribution is homogenous (Noy-Meir 1973; Ludwig 1994). In arid ecosystems, islands of fertility and higher infiltration rates often associated with individual plants or vegetation patches tend to enhance productivity due to greater nutrient availability (Burke et al. 1998; McClaran et al 2008).

Although rotational grazing is often proposed as a solution to rangeland degradation, many empirical studies have not provided evidence to support such claims because many studies fail to find differences between YL and rotational grazing systems (see reviews by Heady 1961; Van Poolen and Lacey 1979; Briske et al. 2008). For example studies found similar frequency of defoliation (Gammon and Roberts 1978) and plant abundance under continuous and rotational grazing systems especially when large pastures were used (Hart et al. 1993; Norton 1998). Results that show rotational grazing systems performing better than continuous grazing systems occur more during periods of above average precipitation or in wetter areas (Manley et al. 1997; Gillen et al. 1998; McCollum and Gillen 1998; Teague et al. 2004).

Laca (2009) suggests scientists take a different approach to analyzing grazing management systems by paying particular attention to 1) different scales at which spatial

heterogeneity in plant growth and defoliation occur, 2) event driven dynamics instead of emphasizing equilibrium or trend dynamics, and 3) nonlinear scaling effects of pasture sizes, herd size and grazing period. Grazing system studies miss opportunities to detect real treatment effects when they base their analytical approaches on assumptions that responses will be homogenous across spatial and temporal scales (Parson and Dumont 2003). Measuring multiple response variables at multiple levels of biological organization (Pellant et al. 2000; Dale and Beyeler 2001), improves the chance of detecting treatment effects when variables target different stages of ecological processes and scales of ecosystem response (Noss 1990). For example, chances of detecting treatment effects improve when measurements are done at multiple scales e.g. individual plants, populations, plant community, patches, pastures and landscape. In arid and semi-arid areas non-equilibrium changes in response to treatment, management or rare environmental events occur and ecosystems transition to a state that is not reversible to the previous state or may change in a direction different than some predictions (Westoby et al. 1989; Briske et al. 2003; Bestelmeyer et al. 2009).

High temporal and spatial variability that characterizes rangeland ecosystems introduces complex and non-linear response patterns. Therefore large scale grazing studies need to account for differences in ecological sites under different treatments and account for grazing patterns that change with size of pasture, topography and vegetation communities (Herrick et al. 2006). Ecological sites are strong drivers of ecosystem potential in terms of plant composition, productivity and grazing resilience, and therefore grazing response, will vary among ecological sites. Some examples of non-linear

response patterns that require attention when designing studies include livestock distribution that tends to be more uniform in 1) smaller pastures than larger pastures (Norton 1998); 2) where species interspersions are more random than clustered (WallisDeVries et al. 1999; Rutter 2006); and 3) on flat versus undulated terrain even when stocking densities are similar.

It is becoming more apparent that many factors interact to influence vegetation abundance and spatial variation in grazed ecosystems (Fynn and O'Connor 2000). Inconsistent responses to grazing systems have been largely attributed to ecosystem complexity. Many abiotic (e.g. precipitation regime and soils) and biotic (e.g. vegetation components and type of herbivores) factors interact with (Milchunas *et al.* 1994) and/or override the influence of grazing management on vegetation dynamics (Ellis and Swift 1988). The interactions between grazing and environmental factors cause vegetation response patterns (Belsky 1986; Ludwig and Tongway 1995; Fuhlendorf and Smeins 1998) that cannot be explained by grazing alone. Therefore, analytical approaches that directly account for these non-treatment factors have greater potential to detect grazing effects (Milchunas *et al.* 1994).

Precipitation and mesquite influence vegetation dynamics in grazed ecosystems

Although many factors like precipitation, plant-to-plant interactions, fire regime, grazing history, soil characteristics, topography and temperature have potential to influence vegetation dynamics in grazed ecosystems, many grazing system studies do not account

for their effects. I will focus on the effects of precipitation and mesquite cover gradients on vegetation dynamics as confounding factors in more detail because they are two of the major factors that are likely to influence vegetation abundance, species composition, spatial variation and rates of response to grazing on my study site. In addition, I will briefly highlight the potential influences of fire regime, grazing history, and soil characteristics on the spatial and temporal dynamics of vegetation.

Precipitation gradient

Differences in precipitation across the environment (precipitation gradient) is one of the major drivers for different plant communities occurring across the landscape (Brown 1994). The spatial pattern of plant communities across the landscape is represented in hierarchical land classifications (Herrick et al. 2006) that identified in the broader categories of Major Land Resources Areas (MLRA) and the finer resolution categories of ecological sites. Precipitation is one of the main considerations in both of these classifications (USDA NRCS 2003). MLRAs are designated based on climate (including average precipitation) among other factors like physiography, geology, soils and land use. For example, the Santa Rita Experimental Range (SRER) spans across two Major Land Resource Areas (MLRA) 40 and 41. The zones on the SRER are the 250-325mm precipitation zone of the MLRA 40 (Upper Sonoran Desert), the 300-400mm precipitation zone of the MLRA 41-3 (Southern Arizona Grassland) and 400-500mm precipitation zone of the MLRA 41-1 (Mexican Oak Savanna) (Breckenfield and

Robinett, 2003). On a finer scale, precipitation is a major input when delineating ecological sites because it interacts with other environmental factors to influence the kind, proportion, and production of the overstory and understory vegetation (USDA NRCS 2003).

It is critical to account for precipitation gradient because of potential differences in plant abundance and rates of response to grazing effects in different precipitation zones and such variation can interfere with detecting treatment effects if not explained. Also as aridity increases, ecosystems become less resilient compromising the system's ability to recover after disturbance due to slower turnover of resources, resulting in slower responsiveness to changes in management (Bork et al. 1998; Havstad et al. 1999). Inter-annual variation in precipitation tends to increase with declining average annual precipitation and vegetation dynamics may become even more responsive to stochastic inter-annual precipitation events than grazing management practices (Ellis and Swift 1988; Ellis 1995). Species composition, biomass productivity, plant vigor and rate of plant recovery change as average annual precipitation changes (Martin and Severson 1988; Augustine 2003). The ultimate question becomes whether the small directional changes caused by grazing treatments accumulate to detectable levels over time even when the effects of precipitation may override the grazing treatment effects in any year (O'Connor and Roux 1995).

Generally spatial distribution of vegetation becomes more homogenous as mean annual precipitation increases along a precipitation gradient. In arid areas, patchiness

results from an increase in bare ground and the concentration of resources in vegetated areas. Interactions between runoff and aggregation of plants that trap runoff generate spatial variation in form of 5-100 m wide strips or 1-100 m diameter circular shaped patches of alternative grasses and bare ground (Soriano et al. 1994; Klausmeiser 1999). The vegetation clusters that intercept runoff enhance within-patch plant growth (Montana 1992; Bromley et al. 1997) and induce regular patterns of vegetation alternating with bare soil and can maintain plant abundance at coarse scale (HilleRisLambers et al. 2001). This process tends to increase with aridity as the water absorption levels of soils become more limiting and plant life becomes heavily dependent on the presence of vegetation to concentrate limiting resources and promote infiltration (Ludwig and Tongway 1995; Aguiar and Sala 1999). Plant abundance that increases with precipitation may interact with patterns of selective grazing subsequently influencing patch sizes across the precipitation gradient (Wallisdevries 1996; Weber et al. 1998; Aguiar and Sala 1999).

Mesquite abundance

Mesquite, like other woody plants has potential to generate unique patterns of understory vegetation through localized interactions (Scholes and Archer 1997; Reid et al. 1999; McClaran and Angell 2007). Seedling establishment and subsequent persistence of mesquite is highly insensitive to grazing management practices evidenced by the lack of differences in mesquite abundance under a variety of grazing intensities (Brown and Archer 1999; Jurena and Archer 2003; McClaran 2003). On the other hand, herbaceous plants tend to be more sensitive to grazing management. Although germination and

survival of mesquite increases when herbaceous plants are defoliated, and does not decline in response to grazing management especially after a height of ~0.9m (Glendening 1952; Brown and Archer 1999), it is unclear how the herbaceous-mesquite relationship varies with grazing system practices.

Accounting for effects of plant-plant interactions between mesquite trees and understory vegetation components is important because the influence of mesquite can vary from inhibition, facilitation to neutral relationships depending on grass species and annual precipitation (Cable 1971; Scholes and Archer 1997; House et al. 2003; McClaran and Angell 2007). Facilitation by mesquite trees occurs when they act as nurse plants for understory vegetation. Shrubs in semi-arid ecosystems are often associated with islands of fertility (Burke et al. 1998; McClaran et al. 2008). Islands of fertility are created by: 1) biotic processes when water and minerals are absorbed from deeper soils and deposited into shallower soils during hydraulic lift and organic nutrient accumulated through leaf fall; and 2) abiotic processes when shrubs capture fine particles redistributed by wind and water. This together with attenuating harsh soil surface temperatures allows certain understory species like Arizona cottontop (*Digitaria californica*) and bush muhly (*Muhlenbergia porteri*) to establish and persist better under the mesquite canopy (Klemmedson and Tiedemann 1986; Gutierrez et al. 1993; Livingston et al. 1997). Small mesquite shrub canopies can protect herbaceous plants against grazing, and that protection may be critical because but because grasses under mesquite tend to remain greener longer, and have higher nitrogen concentrations (Tiedemann 1970). An inhibitive relationship has been reported between mesquite and Lehmann lovegrass (*Eragrostis*

lehmanniana), where *E. lehmanniana* is more abundant in open areas and compared to under the canopy (Tiedemann and Klemmedson 2004). Inhibitive relationships are more prevalent in mesic areas and limited in arid ecosystems where woody species abundance may be self-limiting before reaching levels that can reduce grass abundance (McClaran and Angell 2006).

Mesquite effect on grass persistence and production are contingent on elevation, amount of mesquite cover and age-group distribution of mesquite trees (Scholes and Archer 1997; McClaran and Angell 2007). For example, after a 90% reduction in mesquite cover on the SRER, grass productivity increased greatest and persisted longer at elevations that had higher initial mesquite densities (Cable 1971; Williams 1976). Over a 21-year period, production of both native grasses and Lehmann lovegrass (whose seeding coincided with mesquite removal) increased but then declined as mesquite density recovered, with native grass production declining faster (Cable 1975; 1976). The negative relationship between mesquite and grass abundance was not supported by the 1960-91 data on the SRER that showed grass cover increasing concurrently with mesquite cover (McClaran 2003), showing how tenuous these relationships can be.

Fire regime, grazing history, and soil characteristics

Frequent fire regimes have been important in the history of many herbaceous dominated rangeland ecosystems to prevent woody species encroachment (Scholes and Archer 1997). Fire has also been used as a tool to control non-native species invasion (Zouhar et al. 2008) and maintain spatial heterogeneity (Fuhlendorf and Engle 2004).

Plant communities that evolved under long histories of grazing by large herbivores tend to be more resilient to grazing compared to those on the other end of the spectrum. Under arid conditions, increases in grazing intensity will cause a limited decline in plant diversity and invasion by non-natives in areas with long histories of grazing, while the effect will be moderate in areas with a shorter history of grazing (Milchunas et al. 1988). As a result grazing in areas with long grazing history is likely to cause less change in species composition.

Soil characteristics affect species composition and productivity depending on water infiltration, moisture retention capacity, soil depth, and pH among other characteristics (USDA NRCS 2003). Soil characteristics therefore have a strong influence on a site's plant production potential and response to grazing disturbance.

Analytical challenges and future directions in studying grazing systems

Generating reliable information from experiments is a function of the experimental design, analytical procedure and interpretation of results. Experimental designs of grazing system studies have to consider existing interactions that may influence how the system works and responds to treatments, and select the relevant response variable(s) and secondary data to be collected. During analysis, selecting the best analytical model for the question being asked and upholding assumptions is critical. Scientists must at least acknowledge and take the caveats necessary when, for example, pseudoreplication has been committed, and make appropriate inferences without overextending the relevance of their results.

Statistical assumptions and analytical approaches

Parametric statistical analysis is mainly based on three assumptions; that the data are normally distributed, the variances are homogeneous across data sets, and sample units are independent (Ramsey and Schafer 2002). Upholding these statistical assumptions makes the inferences more reliable, assuming the appropriate experimental design was used. Violating the assumption of normality increases the chances of committing Type I or Type II errors, but several data transformations can be performed to normalize the data (Ramsey and Schafer 2002).

Of 38 empirical studies on effects of grazing systems whose methods I reviewed (Table 1), most do not report on the assumptions of data normality (81%) and homogeneity of variance (86%): no studies do this before 1992. Although it is difficult to conclude that the assumptions were violated in all these studies, it is unlikely that all their data were normally distributed and had homogenous variances.

Time series data are collected in most (55%) long-term experiments because they use permanent transects to study treatment effects over time (Table1). These data can be analyzed either by univariate or multivariate analysis of variance. Time series data are not independent across time and analyzing the data requires statistical models that correct for non-independence (McArdle 1996). Repeated measurements analysis of variance, a multivariate analysis procedure, assumes correlation between response variables over time and corrects for it (McArdle 1996). As a result, repeated measurements analysis of variance exploits the non-independence of time series data and capitalizes on sampling

efficiency instead of it being a weakness (McArdle and Blackwell 1988). On the other hand, univariate analysis like split-plot analysis assumes independence between data series, and no cumulative effect on the response over time (Wilm 1945). Therefore correcting for the non-independence (sphericity violations) of such data is imperative (Greenhouse and Geisser 1959; Algina and Keselman 1997). Twenty four percent (24%) of the studies that collected time series data used repeated measurement analysis or corrected for non-independence over time when univariate analyses were used (Table 1).

Pseudoreplication, is another statistical error committed when inferential statistics are used on data from experiments where either treatments are not replicated (though sample units may be) or experimental units are not statistically independent (Hulbert 1984). The implication of pseudoreplication is that chance events affecting one sample unit are more likely to affect other sample units within the same experimental unit than sample units in other treatment groups (Heffner et al. 1996). The lack of randomization across confounding factors causes biased results. Hulbert (1984) reported that of 176 ecological experiments that used inferential statistics he reviewed, 48% committed pseudoreplication. Pseudoreplication is more common in expensive field experiments requiring large areas that limit the number of replicates. Fewer replicates create a dilemma where scientists have to choose between pseudoreplication that increases statistical power to detect treatment effects because of larger “sample sizes”, but limits opportunity to extrapolate inferences to similar populations. This may be the case for many (54%) grazing system studies reviewed for methodological procedures that committed pseudoreplication especially before 1987 (Table 1).

To appropriately make inferences about other areas based on research result, the scale of study ought to be comparable. For example, results from a grazing system experiment are only appropriate for extrapolating to management practices if the scale of experimental units used was comparable to management units (Briske et al. 2008). Spatial variation in grazing increases with pasture size and distance to water (Bailey et al. 1996) implying that different outcomes are likely to occur if similar practices are implemented in different size units (Hart et al. 1993). However, many grazing system studies have used much smaller experimental units (<10 ha) than management pasture sizes (Gutman et al. 1990; Cassels et al. 1995).

Similarly, most previous research efforts have not systematically included non-treatment variables in the analysis as covariates. Covariates are random variables that cause temporal and spatial variation that cannot be explained by the variables under investigation (Ramsey and Schafer 2002). Most studies comparing grazing system effects on vegetation have used only the main effects as the explanatory variables (89%) with precipitation and other factors being included as covariates rarely (11%) after 1994 (Table 1). However, natural ecosystems have so many factors interacting with treatment effects that it is not possible to control all factors that have potential to influence vegetation dynamics. In such cases, including covariates becomes an important option.

Table 1. Summary of analytical methods applied to studies evaluating grazing system effects on rangeland vegetation.

Methodological procedure	Action taken	Total and list of studies	Comment
Corrected for data normality	Yes	7 (^{20, 25, 27, 31, 32, 33, 35})	*Studies did not state whether they corrected for normality or not
	Not reported*	31 (^{1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 26, 28, 29, 30, 34, 36, 37, 38})	
Corrected for homogeneity of variance	Yes	5 (^{20, 25, 27, 32, 35})	*Studies did not state whether they corrected for equal variance or not
	Not reported*	33 (^{1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 21, 22, 23, 24, 26, 28, 29, 30, 31, 33, 34, 36, 37})	
Avoided pseudoreplication	Yes	8 (^{15, 21, 23, 27, 31, 36, 37, 38})	9 (^{1, 2, 3, 12, 18, 24, 25, 28, 34}) difficult to tell. * tested for sub-sample independence
	No	21 (^{4, 5, 6, 7, 8, 9, 10, 11, 13, 14, 16, 17, 19, 20, 22, 26, 29, 30, 32, 33, 35*})	
Included covariate(s)	Yes	4 (^{23, 31, 33, 38})	Blocking or analysis within e.g. ecosites was not considered including covariates
	No	34 (^{1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 24, 25, 26, 27, 28, 29, 30, 32, 34, 35, 36, 37})	
Measured Spatial variation only	Yes	5 (^{9*, 22*, 28, 32*, 34})	*Studies measured absolute abundance and spatial variation.
	No	33 (^{1, 2, 3, 4, 5, 6, 7, 8, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 23, 24, 25, 26, 27, 29, 30, 31, 33, 35, 36, 37})	
Study length ≥10yrs	Yes	9 (^{1, 7, 8*, 10, 17, 23, 26, 31, 36, 38})	* Data collected at the end of a 20 yr study.
	No	29 (^{2, 3, 4, 5, 6, 9, 11, 12, 13, 14, 15, 16, 18, 19, 20, 21, 22, 24, 25, 27, 28, 29, 30, 32, 33, 34, 35, 37})	
Data corrected for non-independence over time	Yes	5 (^{24, 25, 27, 35, 36})	The rest (17) did not use permanent plots: data not correlated over time.
	No	16 (^{1, 2, 3, 6, 7, 10, 11, 12, 14, 17, 18, 26, 28, 31, 32, 33})	

Key to list of studies in chronological order: ¹Hyder and Sawyer 1951, ²Fisher and Marion 1951, ³Merrill 1954, ⁴Smoliak 1960, ⁵Hazell 1967, ⁶Hanson et al.1970, ⁷Martin and Cable 1974, ⁸Reardon and. Merrill 1976, ⁹Smith and Owensby 1978, ¹⁰Gutman and Seligman 1979, ¹¹Laycock and Conrad 1981, ¹²Ratliff 1986, ¹³Kirby et al. 1986, ¹⁴Pitts and Bryant 1987, ¹⁵Heitschmidt et al. 1987, ¹⁶Anderson 1988, ¹⁷Martin and Severson 1988, ¹⁸Gutman et al. 1990, ¹⁹White et al. 1991, ²⁰Bartolome and McClaran 1992, ²¹Taylor et al. 1993, ²²Hart et al. 1993, ²³O'Connor and Roux 1995, ²⁴Cassels et al. 1995, ²⁵Biondini and Manske 1996, ²⁶Manley et al. 1997, ²⁷Gillen et al. 1998, ²⁸Cid and Brizuela 1998, ²⁹Bork et al. 1998, ³⁰Jacobo et al. 2000, ³¹Fuhendorf et al. 2001, ³²Teague and Dowhower 2003, ³³Teague et al. 2004, ³⁵Cipriotti and Aguiar 2005, ³⁶Jacobo et al. 2006, ³⁷Khumalo et al. 2007, ³⁸Isselstein et al. 2007, ³⁸Derner and Hart 2007

Long-term data

Detecting vegetation changes related to different rangeland management systems is at the core of rangeland science. Yet for management effects to be detected, they must be larger than the variability in the system and they must reach this size during the period of observation. Many rangeland scientists have struggled with the fundamental question of how long rangeland experiments must last in order to detect treatment effects, particularly in arid and semi-arid ecosystems characterized by high spatial and temporal variability and slow response to management practices (e.g. Westoby 1980; Ellis and Swift 1988; Milchunas et al. 1994; Milchunas and Lauenroth 1995; Havstad et al. 1999). This is a pressing issue for studies evaluating livestock grazing systems (Heady 1961; Briske et al. 2008).

Presumably, real treatment effects become apparent over time, even if the incremental year-to-year difference remains small or variable, because the low detection power is compensated for by allowing the effects to accumulate over many years. For example, in semi-arid rangelands many decades of observation were needed before some livestock grazing treatment effects were revealed (Gibbens et al. 1993; O'Connor and Roux 1995; Valone et al. 2002) whereas, studies with less than 13 years of observation found no treatment effects (Martin and Severson 1988; Taylor et al. 1993; Ward et al. 2004). Despite this, many (81%) grazing system studies had study periods of less than 10 years (Table 1). Therefore a study comparing short-term versus long-term vegetation

response to grazing management may shed some light into appropriate lengths of grazing system experiments in order to detect treatment effects in semi-arid environment.

Measures of spatial variation

Most studies of spatial variation in plants use analysis of spatially explicit measurement, like semi-variograms or Euclidean distance (Ludwig and Tongway 1995; Pastor et al. 1998; Augustine 2003) and distance to nearest neighbor (Teague et al. 2004) that can describe the size and distribution of vegetation patches (Kosala and Rollo 1991; Adler et al. 2001). However, these approaches require very intense sampling efforts that are impractical for evaluating management impacts on large pastures e.g. greater than 400 hectares used in this study. Fewer studies have used non-spatially explicit measurements to estimate spatial variation by comparing average values among locations within a management treatment (Gammon and Roberts 1978; Derner et al. 1994; de Bello et al. 2007), and the heterogeneity of variance among locations within a pasture (Barnes et al. 2008). Because spatially-explicit methods of measuring spatial variation are better accepted, but more cumbersome, very few (13%) grazing system studies have measured spatial variation (Table 1).

Future directions for grazing system studies

To improve the quality and reliability of information generated by grazing systems research, future studies must both report and uphold the major statistical assumptions. Upholding the assumptions of normality and equal variance will ensure that

unnecessary Type I or II errors are avoided and more reliable information is generated. The other important factor is either to avoid pseudoreplication so that results applicable to other similar environments or clearly state when interpreting the results that pseudoreplication was committed so results are not applicable outside the study area (Heffner et al. 1996).

Including confounding variables as covariates will be an improvement to studying grazing system effects. More reliable information can be generated if data about confounding variables are applied during analysis to separate the effects of interest from plausible alternatives (Huitema 1980; McArdle 1996; Ramsey and Schafer 2002). Including covariates improves the precision of estimating treatment effects by systematically reducing unexplained variation and widening the scope of inference to include other variables that influence vegetation dynamics (Ramsey and Schafer 2002). An analytical model with covariates is likely to generate results that better reflect the complex processes driving changes in plant abundance and spatial distribution. I propose that in field experiments, the difference between finding significant treatment effects or not could be defined by whether confounding variables are included in the statistical model as covariates.

The number of studies on changes in spatial variability in response to implementation of grazing systems may increase if more studies explore non-spatially explicit measures of variability of plant abundance among sub-plots within an experimental unit (Kosala and Rollo 1991) because these measures can be easily calculated from response variables measured in a typical experimental design. More

studies may end up using measurements made throughout the study period to measure changes in spatial variation over time rather than relying on initiating spatially-explicit measurements at the end of the experiment. Although non- spatially explicit measures may not provide precise, fine-scale measures of spatial patterns, they may be useful indicators of some change in spatial patterns that would initiate efforts to acquire more detailed short-term spatially-explicit measures if necessary.

Research problem in context

This section gives a very brief outline of the history of livestock grazing and management in the southwestern United States. It is intended to give more details about the evolution of grazing system studies on the Santa Rita Experimental Range (SRER) including the background, design and results of the experiment whose data I used 34 years later. I will then outline my analytical approach and present some justification for my research.

History of grazing in the southwestern United States

Livestock were introduced into southern Arizona in the late 1600s (Allen 1989). Beginning around 1800, the ranges were open access areas and were ‘fully stocked’ with cattle, sheep and goats until the 1900s (Ruyle 2003). Severe drought from 1891 to 1892 resulted in livestock deaths due to overstocking (Martin 1975). In 1903 the SRER was fenced and ungrazed until 1916 to allow vegetation recovery (Martin and Reynolds 1973). In 1916, yearlong (YL) grazing resumed. This history of heavy grazing among other factors led to changes in species composition, reduced species diversity and

declining forage production (Canfield 1948; Martin and Cable 1974). As a result concerted research efforts like grass seeding and woody species removal programs were initiated to reverse declining rangeland condition and soil erosion. Beginning around 1957 rotational grazing systems were introduced. Grazing systems included summer ‘closed periods’ and rotating access to water to alter pattern of heavy use around water points (Martin and Ward 1970; Cable and Martin 1975). However, utilization levels of up to 80% were accepted as proper use levels until the 1940s, after which 40-45% was recommended as the proper utilization on perennial grasses (Ruyle 2003).

Grazing system research on the SREER

In a continued effort to improve rangeland productivity, a plot-level trial was conducted between 1962 and 1969 where 15 grazing treatments; 14 rotational grazing systems, including a seasonal rotation (SR) grazing system that included 2 out of 3 spring-summer rest and one yearlong (YL) grazing system were compared (Martin 1973). The premise behind the long summer rests in the SR grazing system was the assumption that ~ 90% of the grass production in the southwestern U.S. occurred between mid through late summer and would therefore facilitate grass growth (Martin 1973, 1975). The treatments were applied to three replicates in 9.1 x 9.1m plots. Each of the 9.1 x 9.1m plots under rotational grazing system was excluded from grazing during the scheduled rest period by movable enclosures. Influences from other factors were controlled as much as possible by killing mesquite trees, removing shrubs and cacti and poisoning rodents and ants (Martin 1973). During each grazing period, stocking densities

in the rotational grazing plots were similar to those in the surrounding areas and plots grazed YL (Martin 1973), resulting in lower stocking rate (AUM/ha/yr) on rotational grazing treatment plots than the YL plots. The SR grazing system produced the highest perennial grass biomass and density compared to 13 other rest-rotation and YL grazing schedules (Martin 1973). These encouraging results from the plots led to a pasture level trial where the SR and YL grazing systems were compared, starting in 1972. A randomized block design with three blocks based on elevation (Block I = high, Block II = intermediate, Block III = low) because precipitation, grass production, and stocking rates increased with increasing elevation (Martin and Severson 1988). Each block had four pastures; one YL and three SR pastures, bringing the total to 12 pastures. The SR grazing system was a three-pasture 1-herd system, with a three year grazing cycle. Each of the three pastures had two grazing periods; March to October (spring-summer) and November to February (fall), with 12 months rest after every grazing period (Martin and Severson 1988). Stocking density (animals·ha⁻¹) was 3 times greater during grazing in SR pastures than would have occurred if grazed yearlong. Forage utilization at the end of each SR and YL grazing period was ~50% between 1972 and 1984 (Martin and Severson 1988; not measured after 1984).

Plant measurements were taken in ten transects per pasture starting in 1972 (Martin and Severson, 1988). An analysis using transects as experimental units, pastures grazed at different times as separate grazing treatments (SR1, SR2, SR3, and YL) and blocks showed no significant differences in vegetation response to grazing systems after 12 years (Martin and Severson 1988). Potential explanations for the inability to repeat

the significant grazing system effects found during the plot experiment include similar utilization rates between SR and YL pastures as a result of 3 times the stocking density during grazing periods in SR pasture, the failure to account for differences in mesquite cover across the study area and possibly the study period was not long enough for an arid ecosystem to respond to management effects. Contrary to the plot-level study where utilization was lower under SR, utilization rates were similar under SR and YL grazing in the pasture-level study because long-term stocking rates were similar (Martin 1973, Martin and Severson 1988).

In the 1930s, velvet mesquite started expanding into upland areas that were relatively free of mesquite and dominated by grasses. Mesquite densities increased to 200-450 plants/ha at 900m to 1,250m elevation from 1972 through 2000 (McClaran 2003). Prior to the implementation of the pasture level SR vs. YL grazing system study, some pastures had all or patches of mesquite removed from the permanent sampling transects while others were untreated (Martin and Cable 1974). However, Martin and Severson (1988) neither controlled for shrub abundance nor included shrub cover as a covariate. During the plot trial however, shrubs were removed to offset the confounding effect of differences in shrub abundance.

Current research and analytical approach

I could use only 7 of the 12 original pastures used by Martin and Severson (1988) in my research because the SR and YL grazing protocols were not continued in five pastures after 1984 (Table 2).

Data were collected in 10 sub-sample units per pasture and such intensive sampling improves interspersed samples within an experimental unit and may improve the precision of the estimated response by capturing spatial variation within the pastures especially in large pastures (experimental units). Data collected in points within the experimental units (pastures) provided an additional utility. I used the data to calculate variance within experimental units as an estimate of spatial variation in grass abundance. The assumption was that higher stocking density under SR grazing will reduce selective grazing, which will in turn reduce variation among sites in a pasture.

The data were collected at 3-yr intervals (Martin and Severson 1988). This interval matched the grazing cycle of the SR grazing system and this may have created some correlation with immediate grazing effect instead of response variables measuring cumulative effects of grazing over time. Standing biomass would likely be more sensitive to current year grazing effects under these circumstances. However, the response variables measured in this study (canopy for shrubs and cacti and basal cover for perennial grasses), are better measures of long-term trends because they are more stable attributes than biomass (Elzinga et al. 1998) and are not influenced heavily by the current season's grazing treatment. A comparison between density and basal cover as measures of long-term trend response to grazing is valid here. Grass cover might be a better measure of grazing impact, especially species-level selective grazing than density because grazing may not result in plant mortality or altered recruitment, but rather changes in plant vigor, expressed more as changes in plant cover (Fuhlendorf et al. 2001).

My study area was set along a 270 to 440 mm mean annual precipitation gradient that largely follows an 880 to 1400 m elevation gradient (McClaran 2003; Table 2). Plant communities, plant abundance, vigor and spatial variation change across the precipitation gradient (Cable 1976; Klemmedson and Tiedemann 1986). Precipitation gradient was treated as a continuous variable which made more degrees of freedom available than using three blocks (a nominal variable). These additional degrees of freedom enabled my analytical model to include the mesquite covariate.

Accounting for potential effects of mesquite cover on vegetation dynamics may be critical because the influence of mesquite cover on herbaceous understory varies across herbaceous species, elevation, abundance of cover and precipitation gradient (Cable 1975, 1976; Scholes and Archer 1997; Tiedmann and Klemmedson 2004; McClaran and Angell 2006). Gradual increases or tree diebacks during drought may have potentially elicited different response patterns among species that would not be explained by my analytical model. However for this analytical model I could not use values of precipitation or mesquite cover over time which limits my ability to systematically evaluate the influence of short-term temporal variation of these variables on the response variables.

Table 2. Size, elevation range, number of ecological sites, percent of sandy loam upland (SLU) and sandy loam deep (SLD) ecological sites, long-term stocking rate, stocking density, and annual precipitation for pastures experiencing yearlong and seasonal-rotation grazing treatments over 34 years (1972-2006). Parenthetical values are one SE of the mean.

Pasture	Pasture size (ha)	Elevation (m)	Ecological sites	Ecological site (%)		Stocking rate (10^{-2} AU \cdot ha $^{-1}$)	Stocking density (10^{-2} AU \cdot ha $^{-1}$)	Precipitation (mm \cdot y $^{-1}$)
				SLU	SLD			
YEARLONG GRAZING								
8	403	1165-1298	5	20	10	5.6 (0.11)	5.6	437 (41.1)
2N	1801	1065-1185	3	50	40	3.0 (0.03)	3.0	399 (40.2)
SEASONAL ROTATION GRAZING								
2S	1438	1054-1196	3	25	38	3.5 (0.34)	10.6	403 (39.6)
6A	1425	1178-1267	2	20	80	2.8 (0.23)	8.5	394 (37.0)
3	1728	956-1033	4	20	40	1.7 (0.18)	5.0	339 (32.7)
6B	1524	1017-1094	2	40	60	4.1 (0.44)	12.3	330 (29.5)
5S	1637	933-1008	4	25	25	1.3 (0.21)	3.9	326 (29.7)

Long-term data are instrumental in investigating the time needed for treatment effect to possibly accumulate to detectable levels especially in semi-arid ecosystems that respond slowly to changes in management (Bork *et al.* 1998; Havstad *et al.* 1999) and provide some evidence about the rate of response to changes in grazing management. Long-term data can be helpful in separating trends due to climatic variability from those associated with management because in short-term experiments environmental fluctuations may obscure directional trends caused by treatment effects.

For data analysis I upheld the assumptions of normality and homogeneity of variance; ensured the non-independence of samples over time was corrected for and that confounding variables were included as covariates. For the inferences to be applicable to similar rangelands I avoided pseudoreplication by making pastures the sample units. However, avoiding pseudoreplication reduced the replicates from possible 70 transects in seven pastures used by Martin and Severson (1988) to seven (7). The three seasonal rotation pastures were treated as one treatment because the overall goal of the study was to evaluate the effects of seasonal rotation (SR) and yearlong (YL) grazing systems on vegetation response and the three pastures per block received similar grazing schedules although at different times.

To compare grazing effects in the short- and long-term, I divided the analysis into two time periods: the short-term, the first 12 years (1972-1984) and the long-term, 34 years (1972-2006). The first period is the same period that was evaluated by Martin and Severson (1988). Using the same data as Martin and Severson (1988) enables comparison between their results and those generated by the analytical procedure used

in this study. This will give an insight into how upholding statistical fundamentals and including covariates influenced the research results. Detecting treatment effects over the long-term but not in the short-term will mean that it takes longer than 12 years for semi-arid ecosystems to respond to changes in management.

Dissertation format

The main goal of my dissertation was to evaluate how vegetation abundance and spatial variation over 34 years differed between yearlong (YL) and seasonal rotation (SR) grazing management. The analytical model included environmental gradients as covariates to reduce variation left unexplained by grazing systems, which would likely improve the power to detect a treatment effect and at the same time provide a more realistic picture of the factors that influence plant dynamics in semi-arid grazed ecosystems. In collaboration with two other coauthors we wrote two manuscripts, one was published (Mashiri et al. 2008) and the other is under review at *Rangeland Ecology and Management* (Mashiri and McClaran in review).

In the first article ‘Short- and long-term vegetation change related to grazing systems, precipitation, and mesquite cover’ (Mashiri et al. 2008), the goals were to investigate (i) how long grazing management studies should last in order to detect treatment affect in semi-arid ecosystems that are characterized by slow turnover of resources and response to changes in management and (ii) the effects of upholding statistical assumptions and including covariates on detecting grazing system effects. This article is being presented as Appendix A.

In the second manuscript ‘Spatial variation of grass abundance under yearlong and seasonal rotation grazing’ (Mashiri and McClaran in review), the goal was to evaluate how grazing systems influence the spatial variability of grass abundance measured by variance of grass cover and density within a pasture. This research evaluates the assumption that increasing spatial homogeneity of vegetation will follow from higher stocking densities under rotational grazing systems because it will reduce selective defoliation among grass species compared to yearlong grazing resulting. This article is presented as Appendix B.

In the first study my main role was selecting analytical approaches, organizing and compiling data from the Santa Rita Experimental Range archives, performing data analyses, interpreting the results, and writing the manuscript. For the second study, I conceived the idea of using variance among sub-sample locations within an experimental pasture as a measure of spatial variation of plant abundance. Variance in plant abundance estimates among transects within a pasture as a measure of levels of selective grazing, is expected to increase with increasing selective grazing. For both studies, my co-authors helped develop the original research idea, fine-tuned the analytical design, interpreted results, edited the manuscripts, and provided some financial support.

PRESENT STUDY

In this section, I present the summary of important findings from both studies, my perceived contributions of this work to the field of rangeland ecology and management, particularly the area of grazing management and recommendations for possible future improvements to methods of inquiry. Details about the methods, results, discussions and implications of my research are presented in the papers appended to this dissertation.

Detecting vegetation changes that result from different management of rangeland systems is at the core of rangeland science. One of the challenges rangeland management researchers face is to determine the relative importance of analytical methods and treatments in detecting a treatment effect. Sometimes, even when treatments induce different ecological processes and possibly different outcomes, analytical models may lack the power to detect these differences if they do not appropriately account for variation from non-treatment variables. Slow response to changes in management in semi-arid ecosystems adds another dimension to the already complex scenario by introducing the question about how long rangeland experiments should continue before the response accumulates to detectable levels.

Rotational grazing systems are recommended mainly because the periodic increases in stocking densities associated with rotational grazing systems should expand animal distribution thus facilitating more uniform forage utilization and less selective grazing compared to YL grazing. Spatial distribution of plants is important for sustaining rangeland resources even when total plant abundance is similar because it influences

ecosystem processes and functioning (Gutierrez et al. 1993; Ludwig et al. 1994; Aguiar and Sala 1999; Rietlerk et al. 2004).

The major goals of the two studies were to 1) investigate the effects of grazing systems on plant abundance (cover and density) in the short-term (12 years) vs. long-term (22 or 34 years) after accounting for mesquite and precipitation gradients and 2) determine if spatial variation of grass abundance (cover and density) differed between YL and SR grazing over 22 or 34 years after accounting for precipitation gradient. Variance of grass abundance among sample locations within an experimental pasture was the measure of spatial variability. The assumption was that variance increased with increasing selective grazing of grasses. These two studies complemented each other in assessing the effects of grazing system. The first investigation was the coarse resolution approach that looked at the final outcome of grazing impact (i.e. differences in plant abundance under SR and YL grazing systems); whereas the second study was focused at a finer resolution to assess the underlying assumption by which the rotational grazing systems are expected to cause changes in the spatial pattern of plant abundance (i.e. lower levels of selective grazing) compared to YL grazing.

Using split-plot analysis of variance, with year as the split, changes in the plant density, cover and variance of cover and density were compared between two grazing systems (YL vs. SR with similar long-term stocking rates), and covariate(s) (precipitation and mesquite gradients) over the different study periods on the Santa Rita Experimental Range, Arizona.

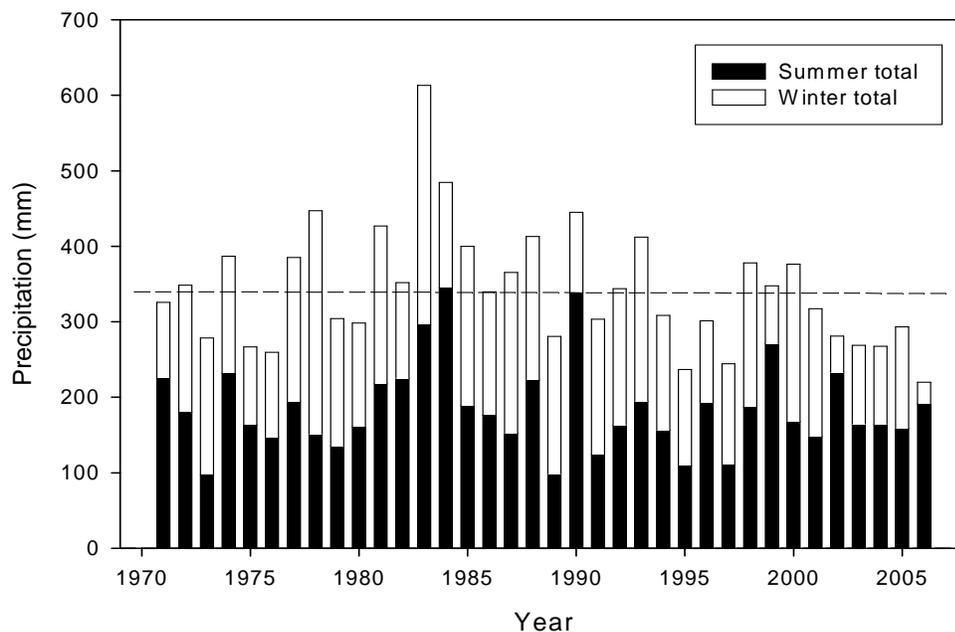
Grazing systems did not influence plant dynamics or spatial variation of grasses as shown by the lack of grazing system by year effect on all response variables in the different time periods. The absence of a detectable grazing effect on changes in plant abundance and spatial variation may be due to overriding influences of grazing intensity, large pasture sizes, temporal variation in precipitation, and few replicates. Additional reasons for lack of grazing system effects on spatial variation of grasses may be discrepancies in transect representation across ecological sites and spatial variation of grasses occurring at scales different than the 30-m transect size.

The SR vs. YL experiment was started following positive results from a plot-scale study where defoliation intensities were lower for SR than YL grazing (Martin 1973), but in this study defoliation intensity was 3.0 times greater during the grazing periods in the SR system than the YL system. It is likely that even the long rest periods following SR grazing may not have been sufficient to improve vegetation conditions after such long periods of intense defoliation (see review in Briske et al. 2008). Van Poollen and Lacey's (1979) conclusion that grazing intensity has a greater influence on vegetation response than seasonal rotation may apply here.

Theoretically, rotational grazing benefits the main forage species by reducing selective grazing (Kirkman and Moore 1995; Teague and Dowhower 2003), but the large pasture sizes in this study (400-1800 ha) may have limited the influence of the SR treatment on spatial variation (Hart et al. 1993; Norton 1998; Barnes et al. 2008) because this outcome is most apparent in small (<10 ha) pastures (Bailey et al. 1996).

The benefits of SR treatment are limited by recurring dry periods (Teague et al. 2004). Drought is common on this study area (Fig. 1) and during the prolonged drought since 1994, grass density and cover declined to similar values under both the SR and YL systems.

Figure 1. Annual summer (solid bar) and winter (open bar) precipitation on the seven study pastures on Santa Rita Experimental Range, 1971-2006. Precipitation year is October to September, summer months are June through September and winter months are October through May. Dashed line is average precipitation for the same period.



Avoiding pseudoreplication reduced the replicates from possible 70 transects in seven pastures used by Martin and Severson (1988) to only seven which is the number of

pastures that represent experimental units. The fewer replicates require larger differences between treatments to detect treatment effects. However, the avoidance of pseudoreplication permits inferences from this study to be applied to similar areas. The power to detect differences between grazing systems was low because of the few pasture replicates. For example, for the first study I performed a conservative power analysis for perennial grass density by quadrupling the number of pastures (increased from 2 to 8 YL and 5 to 20 SR pastures) by simply replicating values collected from the study pastures. I detected a significant grazing system by year interaction only in 1991 (SR $\bar{x} = 26.75 \text{ m}^{-2}$; YL $\bar{x} = 19.47 \text{ m}^{-2}$). This treatment effect would not have been detected in the short-term (1972-1984). In the second study, I applied a similar conservative power analyses at 5 times the replicates (YL = 10 and SR = 25), and found a significant grazing system by year interaction for perennial, native and forage grass cover with YL>SR in all cases. Power analyses from both studies produced results that were consistent with expectation of higher plant abundance and lower spatial variation under SR. This is evidence that differences between the two grazing systems would have been detectable at these levels of replication, but such levels of replication are not realistic for the pasture sizes that were used in this study.

Detecting spatial variation may be limited if patterns in plant distribution occur at spatial scales different than the 30-m transect used in this study (Keitt et al. 2002).

Vegetation patches can be 1-100 meters in diameter or width in similar environments (Belsky 1986; Bromley et al. 1997; WallieDeVries et al. 1999; HilleRisLambers et al. 2001), but no such analysis has been reported for the SRER.

The detected relationships between precipitation and mesquite covariates and the response variables provided an evaluation of a wider scope of factors influencing plant dynamics. The negative relationship between precipitation and native grass variance (after removing an outlier pasture) is consistent with the greater likelihood of clumped vegetation distributions in drier locations. Including these covariates also provided an opportunity for some predictive ability of potential changes that may be associated with climatic change. In addition the relationships between the abundance of certain response groups and the precipitation covariate may provide opportunities to predict vegetation responses to the climate changes predicted for the southwestern United States. The 5-10% less precipitation and 2-4° C increase by the end of this century predicted by recent climatic models (Christensen and Hewitsen 2007), may result in density of forage grasses, *D. californica*, and density and cover of the non-native *E. lehmanniana*, and cover of *P. velutina* declining at all elevations, and *I. tenuisecta* and *Aristida* spp. increasing at higher elevations.

Long-term experiments are an important component of arid to semi-arid research because responses to changes in management tend to be slow. The fact that temporal changes in the density of six grass species and groups, and grazing system effect on perennial grass density during the power analysis only became significant only in the long-term and not in the short-term, is consistent with changes that occur slowly in arid and semi-arid ecosystems (e.g. Havstad et al. 1999, Valone et al. 2002).

Although I did not find any grazing system effect, changes in variance of plant cover and density were related to the precipitation gradient and soil variability, and they

varied over time. Variance has the potential of being a simpler method to estimate spatial variation of vegetation than spatially-explicit methods. Simpler methods, like variance, may generate more research interest in evaluating changes in spatial variation in vegetation over time rather than applying spatially-explicit techniques at the end of long-term experiments.

The approach to the research of grazing systems has evolved over time as shown by more recent studies upholding statistical assumptions, including covariates, measuring spatial variation and avoiding pseudoreplication (Table 1). Studies that reported and corrected for normality and equal variance were all published after 1992, those using covariates were published after 1995, and measures of spatial variation became more common after 1993 with Smith and Owensby (1978) as the sole exception. All grazing system studies that avoided pseudoreplication were published after 1986, which is after Hulbert (1984) reported that many ecological papers committing pseudoreplication. This shows that the field of rangeland ecology and management, and particularly grazing management is evolving to meet these analytical challenges.

My research joins a large body of evidence failing to substantiate the fundamental premise for implementing rotational grazing systems by failing to detect greater plant abundance or reduced spatial variation in forage species that are expected to follow the application of periodic high-stocking density of livestock associated with SR grazing. This undermines one of the scientific bases for what has become a common management practice. Realistically, that body of evidence is constrained by the rules of scientific inquiry requiring the unwavering application of treatments over time.

These studies bring to light the many challenges that confront rangeland scientists as they design and implement grazing studies in spatially and temporally heterogeneous ecosystems. The challenges include the practicalities of implementing studies that have sufficient replications, uniform representation of environmental variable under different treatments (e.g. ecological sites, woody species abundance), multiple levels of intensities, and pasture sizes; and how these are representative of on-going management practices for which the research is intended to inform. Similarly, the strict application of treatments necessary in scientific experiments does not reflect the changes that managers apply when adapting to temporal heterogeneity of precipitation and growing conditions, invasive species, fire, and markets.

These challenges call for a re-assessment of how scientific inquiries on grazing system impacts are done. My proposition is for grazing management studies to take an adaptive management approach which would integrate learning with assessing response of resources to changes in management and environmental factors. An adaptive management approach to grazing system research involves cycles of problem identification, monitoring (measuring response), reflection and redefining the problem throughout the project life (Cundill and Fabricius 2009). Adaptive management requires flexibility and willingness to change the design, implementation, and evaluation phases of a project, when new information is obtained or changes in socio-ecologic conditions occur (Ludwig et al. 1993; Holling 2001; Olsson et al. 2004). This way research switches from focusing on outcomes of treatments in a rigid regime, and the focus becomes learning-by-doing and better responsiveness because of the complex and unpredictable

nature of rangeland resources and an appreciation for the fact that the available information is imperfect (Walters and Holling 1990; Olsson et al. 2004; Armitage et al. 2008).

Not all past grazing system experiments applied treatment regimes rigidly with no regard for any deviation from ‘ideal’ growing conditions. Some past grazing systems studies (e.g. Martin and Severson 1988; Teague et al. 2004), including this study, made adjustments to stocking rates or periods of grazing in response to changes in forage availability, but the question is whether this is enough to qualify as adaptive management. These adjustments are a step in the right direction because available past information about ecosystem carrying capacity was used to make decisions. However, it should not stop there. What is even more important is to take advantage of such isolated events to generate more information about how those environmental perturbations drive ecosystem processes by taking intensive measurements and evaluating responses during and after the event as the ecosystem recovers. This way there are better chances of capturing unexpected outcomes, and that information can be fed into future decision making processes. Adjustments can also be in response to poor spatial distribution of use across the pastures, which might require assessment of distribution of water sources or ecological sites within pastures.

Even with the built-in requirement for flexibility, adaptive management approaches still demand the same rigor to experimental design that are required by traditional scientific approaches when the evaluation criteria include biophysical characteristics. Adaptive management projects would require having enough replicates,

experimental controls and collecting secondary data to reduce unexplained variation and using traditional monitoring tools for measuring response variables (Conley and Moote 2003). When experimental controls are not available, causal links can only be determined by comparing biophysical response to baseline data especially where monitoring is done regularly or to long-term data from past carefully designed monitoring programs on the study area (Conley and Moote 2003).

Adaptive management approaches would serve both the scientific and ranching community better because goals would shift to assessing resources condition and generating knowledge about how ecosystems work and can be sustained under different conditions through swift interventions to impacts (Campbell et al. 2001). Such information will be a powerful tool for rangeland managers to understand potential impacts of management practices on rangelands and livestock production.

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APPENDIX A:
SHORT- AND LONG-TERM VEGETATION CHANGE RELATED TO
GRAZING SYSTEMS, PRECIPITATION AND MESQUITE COVER.

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ABSTRACT

Rangeland scientists struggle with how long rangeland experiments must continue in order to detect treatment effects, particularly in semi-arid ecosystems characterized by slow responses and high spatio-temporal variability. We compared changes in eight grass and three shrub categories to grazing systems (yearlong vs. seasonal rotation with equivalent long-term stocking rates), and covariates (precipitation and mesquite (*Prosopis velutina*) gradients) over 12 y (1972-1984) and 34 y (1972-2006) on the Santa Rita Experimental Range, Arizona, USA. We used split-plot analysis of variance, with year as the split, to make these comparisons. Grazing systems (GS) did not influence plant dynamics as shown by the lack of GS by year effect on all response variables in either time period. The absence of a detectable grazing effect on vegetation changes may be due to overriding influences of grazing intensity, pasture size, precipitation variability, and few replicates. Also, more time may be needed to detect the small accumulating, and potentially temporary effects from GS. The GS main effects present at the beginning and throughout the study, suggest that pastures assigned to each GS had different potentials to support vegetation. Nearly twice the number of response variables were related to the precipitation covariate than to mesquite cover, but only about half of all the relationships were consistent between time periods. The struggle to know how long to observe before detecting a grazing system effect was not resolved with the additional 22 y of observation

because we cannot definitively reject that either more time is needed to detect small but cumulative effects or that the two grazing systems are not different.

RESUMEN

Científicos en la ciencia de manejo de pastizales tienen dificultades al determinar la extensión de los proyectos sobre manejo de pastizales de forma que se puedan determinar los efectos debido a los tratamientos, especialmente en ecosistemas de zonas áridas que se caracterizan por una respuesta demasiado lenta y una alta variabilidad a nivel de espacio y tiempo. Se comparó los cambios de ocho gramíneas y tres arbustivas entre diferentes sistemas de pastoreo (continuo Vs. rotacional estacional, con cargas animales similares a largo plazo). Se utilizó la precipitación y el Mesquite (*Prosopis velutina*) como covariables sobre 12 años (1972-1984) y 34 años (1972-2006), en la estación experimental de Santa Rita, en Arizona USA. Se usó un análisis de varianza de parcelas-dividas utilizando los años como parcelas, para llevar a cabo estas comparaciones. Los sistemas de pastoreo (SP) no afectaron la dinámica de las plantas como pudo observarse por no haber efecto de año para todas las variables de respuesta en ninguno de los dos períodos. La falta de detección de los efectos del pastoreo en los cambios de la vegetación se puede haber debido a los efectos de la intensidad de pastoreo, tamaño de los potreros, variación en la precipitación y el resultado de pocas repeticiones. Además se requeriría más tiempo para detectar los pequeños efectos acumulativos así como los efectos temporales de los SP. Los efectos principales de los SP identificados al inicio y a través del estudio, sugieren que cada uno de los potreros

asignado a cada uno de los SP tenía un potencial diferente para mantener vegetación. Cerca del doble del número de variables de respuesta estuvieron relacionadas con las covariable de precipitación que con la cobertura del mezquite, pero solamente la mitad de la relación fue consistente entre los periodos del tiempo. La dificultad para saber que tanto tiempo hay que observar antes de poder detectar el efecto de un sistema de pastoreo no se pudo resolver con los 22 años adicionales debido a que no se pudo definitivamente rechazar que ya sea que más tiempo se requiera para detectar los pequeños efectos acumulativos o que los dos sistemas de pastoreo no son diferentes.

Key words: plant cover and density, Santa Rita Experimental Range, seasonal rotation grazing, semi-arid grassland, yearlong grazing, long-term experimentation.

INTRODUCTION

Detecting vegetation changes that result from different management of rangeland systems is at the core of rangeland science. Yet for management effects to be detected, they must meet two criteria: the effects must be larger than the variability in the system and they must reach this size during the period of observation. Therefore, one fundamental question is how long rangeland experiments must last in order to detect real effects, particularly in arid and semi-arid ecosystems characterized by high temporal and spatial variability, slow response to management practices, and threshold-type changes in vegetation that may limit response to some management practices (e.g. Westoby 1980; Ellis and Swift 1988; Milchunas et al. 1994; Milchunas and Lauenroth 1995; Havstad et al. 1999). This is an especially pressing issue for studies evaluating seasonal rotation grazing of livestock (Heady 1961; Briske et al. 2008).

Presumably, real treatment effects become apparent over time, even if the incremental year-to-year difference remains small or variable, because the low detection power is compensated for by allowing the effects to accumulate (and thus increase in size) over many years. For example, on semi-arid rangelands many decades of observation were needed before some livestock grazing treatment effects were revealed (Gibbens et al. 1993; O'Connor and Roux 1995; Valone et al. 2002) whereas, studies with < 13 y of observation found no treatment effects (Martin and Severson 1988; Taylor et al. 1993; Ward et al. 2004).

Livestock grazing systems that employ alternate periods of use, deferment and rest, without reducing long-term stocking rates are thought to improve vegetation compared to yearlong grazing by creating a uniform spatial distribution of forage use and periodically removing grazing during critical periods of plant growth (Heady 1961). Rotating high stocking density is thought to create a more uniform defoliation across plant species thereby decreasing the competitive advantage of less preferred plant species (Kirkman and Moore 1995; Teague and Dowhower 2003), and periodic growing seasons without grazing are thought to allow recovery and recruitment of plants (Teague et al. 2004). However, any effects of seasonal rotation may be complicated by the interaction among grazing intensity, plant phenology, along with the length and quality of the growing season (Olson and Richards 1988; Briske 1991; Mathew et al. 2000; Briske et al. 2008).

Interpretations of the lack of grazing effects in arid and semi-arid systems often invoke *post hoc* influences of precipitation variability and neighboring non-forage species (Ellis and Swift 1988; Milchunas et al. 1994; Fynn and O'Connor 2000; Khumalo et al. 2007). Therefore, analytical approaches that directly account for these influences have the potential to improve the detection of grazing effects. For example, inter-annual and inter-decadal variability in precipitation which commonly increases or mitigates plant responses to different grazing systems (Westoby 1980; Hoffman et al. 1990; Palmer et al. 1990; Ellis 1994; Fynn and O'Connor 2000; Fuhlendorf et al. 2001) can be formally accounted for with a precipitation covariate in the statistical analysis. Similarly, the influence of shrubs on herbaceous species, especially when shrub abundance does not

respond to grazing management (Scholes and Archer 1997; Livingston et al. 1997; Tiedemann and Klemmedson 2004), can be accounted for with a shrub cover covariate. Furthermore, covariates are attractive compared to blocks or categories because they give a continuous representation of environmental variables and require only a single degree of freedom in the analytical model.

We applied this analytical approach to compare the vegetation changes under yearlong and seasonal rotation grazing systems that have been in place for 34 y. A previous analysis of the first 12 y of the experiment (Martin and Severson 1988) found no differences in vegetation due to the grazing systems, but used blocks to represent the precipitation gradient and did not account for shrub abundance as an explanatory variable. We expect the detection of differences in vegetation between the grazing systems will be more likely after 34 y than 12 y, and the use of covariates should improve the potential to detect those effects.

MATERIALS AND METHODS

Study area

The study was conducted on the 21,500 ha Santa Rita Experimental Range 40 km south of Tucson, Arizona, USA (McClaran 2003). Elevation increases from 880 to 1400 m; major landforms are fan terraces, flood plains, basin floors and hills and mountains; and soils are in the thermic temperature regime and Typic Aridic, Ustic Aridic and Aridic Ustic soil moisture regimes (Breckenfield and Robinett 2003). The major ecological sites are sandy loam deep and sandy loam upland (Table 1; USDA NRCS 2003). A 270-440 mm gradient of mean annual precipitation largely follows the elevation gradient (McClaran 2003; Table 1). Precipitation is characterized by high inter-annual variability of winter (October-May) and summer (June-September) precipitation with 45% and 31% coefficient of variation, respectively (Fig. 1; McClaran 2003).

Vegetation is a mixture of shrubs, cacti, forbs, and C₄ grasses (McClaran 2003). The common native perennial grasses are *Digitaria californica* (Benth) Chase (Arizona cottontop), *Bouteloua rothrockii* Vasey (Rothrock grama), and *Aristida* spp. (threeawns) comprised of *Aristida glabrata* (Vasey) Hitchc, *Aristida hamulosa* Henr and *Aristida fendleriana* Steud.). *Eragrostis lehmanniana* Nees (Lehmann lovegrass) is the major non-native perennial grass species introduced from the 1930s to the 1970s. The most common shrub species is *Prosopis velutina* Woot. (velvet mesquite), and half shrub *Isocoma tenuisecta* Greene (burroweed). *Opuntia spinisior* (Engelm) Toumey (cane cholla),

Opuntia fulgida Engelm. (chainfruit cholla) and *Opuntia engelmannii* Salm-Dyck (Engelmann prickly pear) are the common cactus species.

Grazing systems

Only 7 of the 12 original pastures used by Martin and Severson (1988) could be analyzed because the seasonal rotation (SR) and yearlong (YL) grazing systems did not continue in the other pastures after 1985 (Table 1). Pastures receiving the SR treatment were grazed twice by a cow-calf herd (March-October and November-February) during a 3-y grazing cycle with 12 mo rest between each use. Average stocking rates ($\text{ha}\cdot\text{AU}\cdot\text{Y}^{-1}$) were calculated over the 12- and 34-y periods, and for SR pastures these were based on 3-y values that encompassed the entire rotation because short-term stocking rates were 3.0 times greater during the 4- and 8- month grazing periods. Average (and SE) stocking rates ($\text{ha}\cdot\text{AU}\cdot\text{Y}^{-1}$) were calculated over the 12- and 34-y periods in 3-y increments to encompass the complete rotation among pastures because an individual year may have stocking rates that were 3.0 times greater during the 4- and 8- month grazing periods. Stocking rate variability was greater in the long-term because there was inconsistent stocking immediately following the short-term period (1984-1987), but rates then stabilized to minor adjustments during dry conditions to prevent utilization > 50% (Table 1). Stocking rates were slightly less (more $\text{ha}\cdot\text{AU}\cdot\text{Y}^{-1}$) than the average for the region. Average utilization between 1972 and 1984 was 50% (Martin and Severson 1988), but was not measured from 1984 through 2006. Average precipitation (mean of two closest

rain gages) and mesquite cover was based on measures from each of the permanent transects in each pasture.

Vegetation variables

Vegetation response variables were measured on 10 permanent transects per pasture, except there were 8 transects in Pastures 2S and 5S (Martin and Severson 1988). Basal grass and shrub canopy cover were measured along a 30.5 m transect, and plant density was measured in a 0.305 m wide belt along the same 30.5 m transect (total 9.3 m²). Plant density was measured every three years from 1972 through 1984, and 1991 through 2006; shrub canopy cover measurements followed this schedule starting in 1975; and grass basal cover measurements began in 1984.

We lumped grasses into five categories: perennial (all perennial species), native, non-native (*Eragrostis lehmanniana* and *E. curvula* (Shrod.) Nees), long-lived forage (*D. californica*, *Bouteloua curtipendula* (Michx.) Torr, *Setaria macrostachya* H.B.K., *Muhlenbergia porteri* Scribn. and *B. eriopoda* Torr.; based on palatability and longevity from Ruyle and Young 1997), and threeawns (three *Aristida* sp. because of field identification problems). Species-level analysis of density was performed on only the most common grasses (*D. californica*, *B. rothrockii* and *E. lehmanniana*) because zero values were too common for other species; and zero values for cover were very common for all grass species. Analysis of canopy cover was performed for total shrubs, *P. velutina* and *I. tenuisecta*; but shrub density was analyzed only for *I. tenuisecta* because zero values were too common for other species.

Covariates

Each pasture had separate precipitation and mesquite (*P. velutina*) cover covariates for the 12-y short-term, 34-y long-term and 22-y grass cover only, observation periods (Table 1). The value for each covariate was the average of the 10 transects in the pasture over each observation period.

A separate type of precipitation covariate was used for each vegetation response variable because grasses are expected to respond most strongly to current summer and preceding winter precipitation (Cable 1975), whereas shrubs appear to respond more strongly to winter precipitation (McClaran 2003). We used six precipitation parameters: current summer (June-September) and current annual (12 mo) prior to vegetation measurements; and 2- and 3-y cumulative summer and annual precipitation prior to vegetation measurement. The parameter with the strongest correlation between the vegetation variable over the 34-y study period was selected as the covariate for both observation periods (Table 2). For these correlations, the sample unit was the pasture (average of 10 permanent transects), and precipitation for each transect was estimated as the average of the two closest (range of 0.1-4.0 km) rain gages.

Analytical approach

To assess the relationship between vegetation change and grazing systems while accounting for variation associated with precipitation and mesquite cover, we used a split-plot ANOVA with year as the split (Wilm 1945), grazing system (YL and SR) as the

main effect and precipitation and mesquite cover as covariates. To avoid pseudoreplication (*sensu* Hulbert 1984), the pastures were the experimental units, and vegetation values were the average of the 10 transects per pasture. Separate analyses were performed for the short-term period (1972-1984 for density and 1975-1984 for shrub cover) and the long-term period (1972-2006 for density and 1975-2006 for shrub cover), and for the 22-y period (1984-2006) for grass basal cover. The mesquite covariate was not included in the analyses of *P. velutina* and total shrubs because it was not independent of those response variables.

We used the split-plot analysis instead of the multivariate repeated measurements analysis because it preserved enough degrees of freedom to include two covariates. This decision resulted in an analysis that was not only conservative but also rigorous and fully supported by upholding statistical assumptions of independence, correcting for sphericity violations (Algina and Keselman 1997) and avoiding pseudoreplication.

Based on the Shapiro-Wilk W-test on the residuals (Shapiro and Wilk 1965), response variables became normal after a log ($Y + 1$) transformation except for non-native grass density which was instead square-root transformed. Total shrub and mesquite cover needed no transformation. All data met the homogeneity of variance assumptions using the Brown-Forsythe test (Sall et al. 2005). We used the Mauchly test for sphericity and made adjustments for violations using the Greenhouse-Geisser correction method (Greenhouse and Geisser 1959).

In our analytical approach, the grazing system by year interaction was most important because it indicates that values for a response variable became different

between the grazing systems at some time after the study started (implying an accumulation of effects). Whereas, a simple grazing system main effect without a grazing system by year interaction, indicates that the overall mean value of the response variable differed throughout the study period, suggesting that the differences were not affected by implementing the rotational grazing systems (implying a pre-existing difference and a lack of cumulative effects). Significant covariate terms indicate a linear relationship between the response variable and the precipitation or mesquite cover covariates. A significant covariate by year interaction term indicates that the relationship between the covariate and vegetation variable was not consistent over time. A simple year effect, without a grazing system by year or covariate by year interaction, indicates that values for the response variable differed between at least two dates.

When grazing system by year interaction or year effects were significant ($P \leq 0.05$), we used Tukey-Kramer HSD (Honestly Significant Difference) multiple comparisons test (Sall et al. 2005) to determine which system-year combinations and which years differed. Simple linear regression was used to describe the direction of significant relationships between the covariates and response variables. When the covariate by time interaction was significant, separate regression analyses were performed for each year to identify differences in the relationship among years.

Data analyses were performed using JMP IN 5.1 statistical package (Sall et al. 2005). We used $P \leq 0.05$ to reject the null hypothesis of no difference between grazing treatments, among years, relationship with covariates and interactions in split-plot analysis; multiple comparisons of means among years; and regression for covariates and

interactions. We reported actual values of plant density and cover in the text and figures, but all statistical results were based on data transformed for normality.

RESULTS

Grass density

The application of different grazing systems did not correspond to changes in grass density in either the 12-y short-term (1972-1984) or the 34-y long-term (1972-2006) periods as shown by the absence of any significant grazing system by year interactions (Table 3). However, in both the short- and long-term periods, there were differences in the density of *Aristida* spp. between the grazing systems that predated and persisted through their application as shown by a significant grazing system main effect. *Aristida* spp. was greater for SR than YL in the short-term period (SR \bar{x} = 4.71 m⁻², SE = 0.15; YL \bar{x} = 1.91 m⁻², SE = 0.27), and long-term period (SR \bar{x} = 2.71 m⁻², SE = 0.09; YL \bar{x} = 0.99 m⁻², SE = 0.11). A grazing system main effect was detected only in the short-term period for perennial grasses (SR \bar{x} = 16.49, SE 0.10; YL \bar{x} = 22.60, SE = 0.19) and in the long-term period for native grasses (SR \bar{x} = 10.68 m⁻², SE = 0.09; YL \bar{x} = 7.43 m⁻², SE = 0.12).

Across both time periods, the precipitation and mesquite cover covariates were positively correlated with perennial grasses, but non-native grasses and *E. lehmanniana* were positively correlated with precipitation only (Table 3). Native grass was negatively correlated with both covariates in the short-term period, but only with mesquite cover in the long-term. In the long-term period only, both covariates were positively correlated with forage grasses and *D. californica* and negatively correlated with *Aristida* spp.; but *B. rothrockii* had a negative relationship with precipitation only.

Changes over time (year effects) were never significant in the short-term period, but significant changes occurred in the long-term period for all species and groups except *B. rothrockii* (Table 3). Between 1991 and 2006, overall densities decreased to very low values for all these species and groups; but in the short-term (1972-1984) values remained relatively stable (Fig. 2). The largest increase in *E. lehmannina* occurred between 1984 and 1991.

Shrub density and cover

I. tenuisecta density was not related to the application of different grazing systems in either the 12-y (1972-1984) or the 34-y (1972-2006) periods as shown by the lack of a significant grazing system by year interaction, and the density did not differ between grazing systems in either time period based on the lack of a significant grazing system main effect (Table 3). *I. tenuisecta* density had a negative correlation with both covariates only in the short-term (Table 3). Changes over time (year effects) were significant in the long-term period only, when density declined to near zero by 2006 (Fig. 2).

Changes in total shrub, *P. velutina*, and *I. tenuisecta* cover were not related to the application of different grazing systems in either the 9-y short-term (1975-1984) or the 31-y long-term (1975-2006) periods as shown by the lack of a significant grazing system by year interaction (Table 3). However, in the short-term period, *I. tenuisecta* cover was greater in the SR than YL grazing system (SR $\bar{x} = 7.33\%$, SE = 0.06; YL $\bar{x} = 4.91\%$, SE = 0.11). Precipitation was positively correlated with *P. velutina* cover in both the short- and long-term period, but only with total shrub cover in the short-term (Table 3). *I.*

tenuisecta cover was negatively correlated with both covariates (precipitation and mesquite cover) in the short-term, but had a mesquite by year interaction in the long-term where the slope was positive in 1975, 2003, and 2006, but negative in all other years (Table 3). In both the short- and long-term periods, cover of total shrub, *P. velutina*, and *I. tenuisecta* changed over time (Table 3). Between 1975 and 1991, total shrub and *P. velutina* cover increased, but remained relatively stable thereafter, but *I. tenuisecta* increased through 1984 and then declined to near zero by 2006 (Fig. 3).

Grass cover

The application of different grazing systems did not correspond to changes in grass cover over the 22-y period (1984-2006), as shown by the lack of a significant grazing system by year interaction (Table 4). However, perennial grass cover was less in the SR than YL grazing system (SR $\bar{x} = 2.04\%$, SE = 0.06; YL $\bar{x} = 2.96\%$, SE = 0.11), as shown by a significant grazing system main effect (Table 4). Non-native grass cover was positively correlated with precipitation (Table 4). Cover in all four groups changed over time (Table 4), where cover increased from 1984 to 1991 and declined to 1984 values between 1994 and 2006 (Fig 4).

DISCUSSION

Grazing systems

There were no detectable differences in vegetation between the seasonal rotation (SR) and yearlong (YL) grazing systems in either the short-term (12-y) or long-term (34-y) periods even after accounting for spatial gradients of precipitation and mesquite cover. Either the grazing systems do not produce different effects or the effects are small and have not yet accumulated to a detectable level.

The absence of a detectable rotational grazing effect on vegetation changes may result from the overriding influences of grazing intensity, length of grazing periods, pasture size, precipitation variability and few replicates. The SR system was based on positive results from a short-term, plot-scale study where defoliation intensities were lower for seasonal rotation than for yearlong grazing (Martin 1973). However as applied to this study, defoliation intensity was 3.0 times greater during the grazing periods in the SR system than the YL system. Even though generous rest periods followed SR grazing, the rest may not have been sufficient to improve vegetation conditions after such long periods of intense defoliation (see review in Briske et al. 2008). Van Poollen and Lacey's (1979) conclusion that grazing intensity has a greater influence on vegetation response than seasonal rotation may apply here. Rotational grazing is expected to benefit forage species because it reduces their selected use (Kirkman and Moore 1995; Teague and Dowhower 2003), but our large pastures (400-1800 ha) may have precluded that benefit (e.g. Bailey et al. 1996; Norton 1998) despite the periodic intense use.

The impacts of the recurring dry periods on vegetation may have limited the influence of the seasonal rotation treatment because when dry periods become droughts, there may be little benefit of seasonal rotation grazing systems (Teague et al. 2004). Drought is common on our study area (Fig. 1) and during the prolonged drought since 1994, grass density and cover declined equally under both the SR and YL systems.

The power to detect differences between grazing systems was low because there were few pasture replicates. For example, we performed a conservative power analysis for perennial grass density by quadrupling the number of pastures (increased from 2 to 8 YL and 5 to 20 SR pastures) through the simple replication of values collected from the study pastures. In spite of this conservative estimate of variance, we detected a significant grazing system by year interaction only in 1991 (SR $\bar{x} = 26.75 \text{ m}^{-2}$; YL $\bar{x} = 19.47 \text{ m}^{-2}$), but that difference did not persist during the dry period beginning in 1994.

It remains a possibility that more time is needed to detect the small but accumulating grazing system effect, and those situations where the effects do not persist through dry conditions. In nearby arid locations, Valone et al. (2002) reported vegetation differences between grazed and ungrazed areas 39 y after livestock exclusion but not after 20 y. Whereas in observations over 56 y, there were temporary (persisting for 1, 6, or 20 y) differences in some vegetation attributes that occurred as early as 9 y and as late as 50 y after grazing exclusion (Havstad et al. 1999). In arid and semi-arid ecosystem, the detection of management influences on vegetation dynamics arises from the inherently slow rates of vegetation response due to slow turnover of resources, and rapid but temporary responses to high inter-annual variability of precipitation (e.g. Milchunas et al.

1994; Milchunas and Lauenroth 1995; O'Connor and Roux 1995). Frequently measuring numerous replicates over many years may be the only means of detecting responses to management practices in these ecosystems.

The significant grazing system main effects we found were remnants of the pastures being different before the research began, and those differences persisted through the application of the grazing treatments. We concentrate our interpretation at the soil-ecological site level (Taylor et al. 1993) because precipitation and mesquite cover effects are already accounted for as covariates in our analytical model. The transects in the SR pastures were predominantly (50%) on sandy-loam deep ecological sites, whereas YL pastures were dominated by (35%) sandy-loam upland sites (Table 1). Greater density of the short-lived *Aristida* spp. in SR pastures is consistent with the lower water holding capacity and drought-prone conditions on sandy-loam deep sites; whereas, greater perennial grass cover in YL pastures is consistent with the greater persistence of soil moisture on sandy loam upland sites (Martin and Severson 1988; USDA NRCS 2003).

Precipitation and mesquite covariates

The precipitation and mesquite cover covariates improved our analyses by accounting for previously unexplained variation. Even though the two covariates were correlated (R^2 of 0.70 in short-term and 0.76 in long-term), we retained both in our analysis because the proportion of explained variance increased by up to 24% with the addition of the second

covariate and there are strong theoretical bases that these environmental factors influence vegetation dynamics through different mechanisms.

The persistent long-term positive relationships with both covariates (precipitation and mesquite cover) and density of perennial grass, forage grass and *D. californica*, most likely reflect the stronger influence of increasing precipitation at higher elevation pastures because maximum mesquite cover was < 25% (Martin and Severson 1988; McClaran and Angell 2006). Similarly, the persistent negative relationships between the covariates and *Aristida* spp. density and *I. tenuisecta* cover reflects a long-observed pattern of greater abundance in drier settings and little response to mesquite cover of < 25% (Martin and Severson 1988; McClaran and Angell 2006).

The relationship between the covariates and eight vegetation variables changed between the short- and long-term periods: from negative to no relationship for native grass and *I. tenuisecta* densities, from no relationship to positive for forage grass and *D. californica* densities and total shrub cover, and from no relationship to negative for *Aristida* spp and *B. rothrockii* densities. The long-term decline of native grass species and *I. tenuisecta* may have contributed to the absence of any relationship in that period. In contrast, the detection of any relationships with covariates in the long-term may occur from the additional degrees of freedom from seven additional years of observation (e.g. Ramsey and Schafer 2002).

Relationships with the precipitation covariate provide opportunities to estimate responses to the climate changes predicted for the southwestern United States. Recent climate models (Christensen and Hewitsen 2007) predict 5-10% less precipitation and 2-

4° C increase by the end of this century, suggesting that the density of forage grasses, *D. californica*, and density and cover of the non-native *E. lehmanniana*, and cover of *P. velutina* will decline at all elevations, but *I. tenuisecta* and *Aristida* spp. may increase at higher elevations. We cannot comment on any differences in the outcome of vegetation response to grazing systems under different climatic conditions because our analytical model did not have enough degrees of freedom to include a grazing system by precipitation interaction.

Temporal dynamics

Detectable temporal changes (as shown by year effects without interactions) in the density of six grass species and groups only after long-term observation is consistent with changes that occur slowly in arid and semi-arid ecosystems (e.g. Havstad et al. 1999, Valone et al. 2002). For grass density and cover, the clear trend was a reduced abundance since 1984-1991. This was independent of grazing treatment, and the mesquite cover and precipitation covariates. The simultaneous decline of native grasses and increase of *E. lehmanniana* between 1984 and 1991 is the result of highly successful lovegrass recruitment (invasion) rather than the hastened death of adult native grasses (Angell and McClaran 2001). Whereas, the decline of nearly all grasses since 1991 may be the result of dry summer conditions since then (Fig. 1), possibly combined with reduced nitrogen availability because nitrogen use-efficiency is low for *E. lehmanniana* (Fernandez-Gimenez and Smith 2004). These patterns were probably not strongly influenced by the

increase of mesquite cover because it has not reached levels thought to strongly inhibit grasses (McClaran and Angell 2006, 2007).

Temporal changes in shrub cover were observed in both the short- and long-term periods, suggesting that these changes are more rapid and more persistent than changes in grass density. The slow or lack of increase of *P. velutina* cover since 1991, compared to its steady increase earlier, may signal a landscape carrying capacity that is constrained by precipitation (e.g. Glendening 1952; House et al. 2003; Sankran et al. 2005; Browning et al. in press). The increase and then decline of *I. tenuisecta* density and cover may begin with wet winters and end when death results from dry conditions or old age, because neighboring grass and *P. velutina*, and livestock grazing have not prevented new eruptions (McClaran 2003). The cyclic pattern is similar to short-lived *Gutierrezia sarothrae* (Pursh) Britt. & Rusby (snakeweed) in the Chihuahuan Desert grasslands of New Mexico (Torrel et al. 1992).

It is not surprising that the abundances of *P. velutina* and the non-native *E. lehmanniana* were unrelated to grazing management systems because they are examples of threshold-type changes that are not likely to respond to the application of new grazing management practices (Westoby et al. 1989; Briske et al. 2003). *P. velutina* has increased in density and cover following cessation of fire and the ubiquitous dispersal of seed by livestock beginning around 1880, and the subsequent manipulation of livestock has not altered this pattern (see review in McClaran 2003). The presence of livestock grazing may hasten the spread of *E. lehmanniana* (Bock et al. 2007), but the eventual abundance

will be independent of livestock use or use intensity (McClaran and Anable 1992; Angel and McClaran 2001).

Our ability to distinguish equilibrium from non-equilibrium dynamics is limited by our analytical model, the structure of the covariates, and similar grazing pressures in the yearlong (YL) and seasonal rotation (SR) treatments. Evidence supporting non-equilibrium dynamics include high inter-annual variation in precipitation, *B. rothrockii* and *E. lehmanniana* dynamics that were related to precipitation (external driver) but not mesquite (internal competition), and the absence of a grazing system by time interaction (weak coupling of plant-herbivore interaction) (Ellis and Swift 1988, Briske et al. 2003). However, because of limited degrees of freedom, our analytical model did not include grazing by precipitation or grazing by mesquite interactions, and the covariates (precipitation and mesquite) represent multi-year spatial gradients rather than inter-annual variation. Therefore, we are not able to distinguish the relative influence of inter-annual precipitation versus grazing system (plant-herbivore coupling) or mesquite (internal competition). This is particularly true for the dynamics of *D. californica*, *Aristida* spp., and *I. tenuisecta* which were related to both precipitation and mesquite. Our ability to distinguish the relative influence of biotic (grazing pressure) versus abiotic (precipitation) factors on vegetation dynamics is limited because utilization was similar at ~50% for both SR and YL grazing treatments. A more relevant design would include measures along a gradient of grazing intensities.

Maintaining and improving long-term grazing system studies

This 34-y grazing system study is unusually long (Briske et al. 2008), but the re-assignment of 5 of the 12 original pastures to different studies shows that maintaining the full study design was not the highest priority for pasture allocations on the Santa Rita Experimental Range. We believe that the continued allocation of 7 original pastures occurred because 1) grazing rotations and vegetation measurements were simple and infrequent, 2) abundant opportunities were available to establish new research projects in alternative locations, and 3) a livestock cooperator and a succeeding rangeland scientist were willing to continue the protocols established by others.

Increasing the number of pastures and strategic location of sample transects relative to ecological sites and distance to water could improve the ability to detect differences in vegetation created by these grazing systems. If more pastures were created by reducing pasture size, then some attention will be needed to establish a minimum pasture size that will not affect grazing behavior (Bailey et al. 1996; Norton 1998). Improved detection may also occur if more transects were established to account for the spatial variation related to ecological sites (i.e. soils) and grazing intensity at increasing distances from water developments (Briske et al. 2008).

IMPLICATIONS

Based on vegetation change, there was no detectable advantage to using the seasonal rotation grazing system over the yearlong grazing. From the land manager's perspective, it does not matter whether the absence of a detectable effect is because the systems do not differ or the effect is too small and has yet to reach a detectable level. In either case, the extra effort of implementing a seasonal rotation grazing system did not produce a change in the vegetation within 34 y.

In addition to planning for the long-term maintenance of grazing systems studies, the power to detect treatment effects would be increased by including co-variates such as precipitation and overstory vegetation because of their conservative use of degrees of freedom, and by strategically locating sample transects to account for spatial variation due to ecological sites and distance from livestock water developments.

Different short- and long-term relationships between vegetation and the precipitation and mesquite cover covariates have implications for vegetation classification systems and predicting response to mesquite management. For example, differences in the strength of the precipitation gradient between the short- and long-term periods can help define the range of variability incorporated into ecological site descriptions.

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LIST TABLES

Table 3. Pasture size, elevation range, proportion of sandy loam upland (SLU) and sandy loam deep (SLD) ecological sites, stocking rate in ha/animal unit year (\bar{x} , SE), annual precipitation (\bar{x} , SE) and mesquite cover (\bar{x} , SE) in the seven study pastures over the 12-y (short) and 34-y (long) time periods in relation to grazing systems treatment (yearlong and seasonal rotation).

Pasture	Pasture size (ha)	Elevation (m)	Ecological site (%)		Stocking rate (ha·AUY ⁻¹)		Precipitation (mm)		Mesquite cover (%)	
			SLU	SLD	12-y	34-y	12-y	34-y	12-y	34-y
YEARLONG GRAZING										
2N	1801	1065-1185	50	40	34.0 (0.0)	33.8 (1.6)	435 (65.2)	399 (40.2)	10 (2.6)	15 (2.0)
8	403	1165-1298	20	10	19.2 (0.0)	17.8 (0.7)	474 (61.8)	437 (41.1)	10 (1.2)	13 (0.9)
SEASONAL ROTATION GRAZING										
2S	1438	1054-1196	25	38	28.6 (4.4)	28.2 (2.4)	434 (62.4)	403 (39.6)	14 (2.6)	15 (1.9)
3	1728	956-1033	20	40	55.1 (0.6)	60.3 (5.3)	360 (53.1)	339 (32.7)	8 (1.6)	9 (0.9)
5S	1637	933-1008	25	25	57.5 (5.8)	77.5 (11.2)	339 (45.8)	326 (29.7)	2 (0.7)	4 (0.5)
6A	1425	1178-1267	20	80	28.3 (4.4)	35.1 (3.1)	425 (54.9)	394 (37.0)	11 (2.2)	13 (1.4)
6B	1524	1017-1094	40	60	26.6 (1.4)	24.4 (1.6)	348 (46.3)	330 (29.5)	5 (1.0)	7 (1.0)

Table 4. Pearson product-moment correlation coefficient (r) between plant variable and type of precipitation (mm). 2- and 3-y represent cumulative 2- and 3-y values leading to vegetation measurement. Level of significance: $*P \leq 0.05$. ¹ Precipitation parameter with the greatest correlation with the response variable and was selected as the precipitation covariate for that response variable in the analysis of variance.

Response variable	Precipitation parameter					
	Current summer	2-y summer	3-y summer	Current Annual	2-y annual	3-y annual
PLANT DENSITY						
Perennial grasses	-0.08	0.12	0.08	0.34* ¹	0.19*	0.16
Native grasses	-0.15 ¹	-0.12	-0.09	0.09	0.02	-0.04
Forage grasses	0.22	0.11	0.14	0.32*	0.46* ¹	0.40*
<i>Digitaria californica</i>	0.08	0.00	0.03	0.30*	0.39* ¹	0.32*
<i>Aristida</i> spp.	0.02	-0.05	0.08	0.07	0.15 ¹	0.14
<i>Bouteloua rothrockii</i>	-0.29* ¹	-0.23*	-0.26*	-0.06	-0.20	-0.25*
Non-native grasses	0.06	0.26*	0.18	0.30* ¹	0.20	0.22
<i>Eragrostis lehmanniana</i>	0.06	0.26*	0.18	0.30* ¹	0.20	0.22
<i>Isocoma tenuisecta</i>	-0.08	0.08	-0.18 ¹	-0.04	0.00	-0.04
PLANT COVER						
Total shrubs	0.47*	0.56*	0.56*	0.61* ¹	0.51*	0.53*
<i>Isocoma tenuisecta</i>	0.40*	0.39*	0.33*	0.57*	0.59* ¹	0.52*
<i>Prosopis velutina</i>	0.20	0.31*	0.35* ¹	0.19	0.08	0.17
Perennial grasses	-0.30* ¹	0.02	-0.08	0.17	0.07	0.05
Native grasses	-0.39* ¹	-0.15	-0.24	0.23	-0.03	-0.08
Forage grasses	-0.24	0.04	-0.08	0.35* ¹	0.12	0.08
Non-native grasses	-0.05	0.22	0.17	0.20	0.23	0.25 ¹

Table 5. P-values from the split-plot ANOVA of vegetation density and cover during short-term ((- or 12-y) and long-term (31- or 34-y) study periods with grazing systems (GS) main effect, precipitation (PPT) and mesquite cover (MESQ) covariates, year (YR) as the split, and their interactions. (+) and (-) adjacent to P-values of covariates shows the direction of correlations with the response variable.

Response variable	Study Period (Yrs)	Explanatory Variables						
		GS	PPT	MESQ	YR	GS x YR	PPT x YR	MESQ x YR
DENSITY								
Perennial grass	12	<0.01	<0.01 (+)	<0.01 (+)	0.85	1.00	1.00	0.94
	34	0.58	<0.01 (+)	<0.01 (+)	<0.01	0.99	0.31	0.71
Native grass	12	0.22	0.01 (-)	<0.01 (-)	0.38	0.97	0.95	0.95
	34	0.03	0.07	<0.01 (-)	<0.01	1.00	0.84	0.99
Forage grass	12	0.32	0.08	0.96	0.24	0.98	0.99	0.97
	34	0.81	<0.01 (+)	<0.01 (+)	<0.01	1.00	1.00	0.90
<i>Digitaria californica</i>	12	0.89	0.22	0.23	0.90	0.88	0.97	0.95
	34	0.68	<0.01 (+)	<0.01 (+)	<0.01	0.99	0.83	0.85
<i>Aristida</i> spp.	12	0.05	0.62	0.60	0.36	0.99	0.98	0.94
	34	0.01	<0.01 (-)	0.04 (-)	<0.01	0.98	0.98	0.87
<i>Bouteloua rothrockii</i>	12	0.38	0.27	0.02	0.56	0.96	0.96	0.96
	34	0.24	<0.01 (-)	0.26	0.08	0.98	0.98	1.00
Non-native grass	12	0.54	0.03 (+)	0.53	0.73	1.00	0.97	1.00
	34	0.33	<0.01 (+)	0.68	<0.01	0.98	0.14	0.32
<i>Eragrostis lehmanianna</i>	12	0.54	0.03 (+)	0.61	0.73	1.00	0.99	1.00
	34	0.50	<0.01 (+)	0.53	<0.01	1.00	0.12	0.31
<i>Isocoma tenuisecta</i>	12	0.53	0.01 (-)	0.05 (-)	0.13	0.96	0.98	1.00
	34	0.64	0.46	0.97	0.03	1.00	0.75	0.95
SHRUB COVER								
Total shrubs	9	0.73	0.68		<0.01	0.99	0.92	
	31	0.38	0.03 (+)		<0.01	0.98	0.73	
<i>Prosopis velutina</i>	9	0.72	<0.01 (+)		0.01	0.81	0.55	
	31	0.47	<0.01 (+)		<0.01	0.74	0.85	
<i>Isocoma tenuisecta</i>	9	0.02	<0.01 (-)	<0.01 (-)	<0.01	0.74	0.11	0.22
	31	0.73	0.03 (-)	0.05 (-)	<0.01	0.82	0.11	0.02

Table 6. *P*-values from the split-plot analysis of grass basal cover over 22-y (1984-2006) with grazing system (GS) main effect, precipitation (PPT) and mesquite cover (MESQ) covariates, year (YR) as the split, and their interactions. (+) and (-) adjacent to *P*-values of covariates shows the direction of correlation with the response variable.

Grass response variables	Explanatory Variables						
	GS	PPT	MESQ	YR	GS x YR	PPT x YR	MESQ x YR
Perennial	<0.01	0.94	0.27	<0.01	0.49	0.88	0.74
Native	0.07	0.13	0.28	<0.01	0.96	0.96	1.00
Forage	0.11	0.37	0.95	<0.01	0.77	0.82	1.00
Non-native	0.92	<0.01 (+)	0.43	<0.01	0.95	0.23	0.13

LIST OF FIGURES

Figure 2. Standardized difference for seasonal precipitation on the seven study pastures on Santa Rita Experimental Range, 1972-1973 to 2005-2006. Precipitation year is October to September, summer months are June through September. Standardized difference is the individual year value minus long-term (1922-2006) average (winter mean = 158 mm, summer mean = 213 mm) divided by the standard deviation (winter SD = 61.0, summer SD = 64.2).

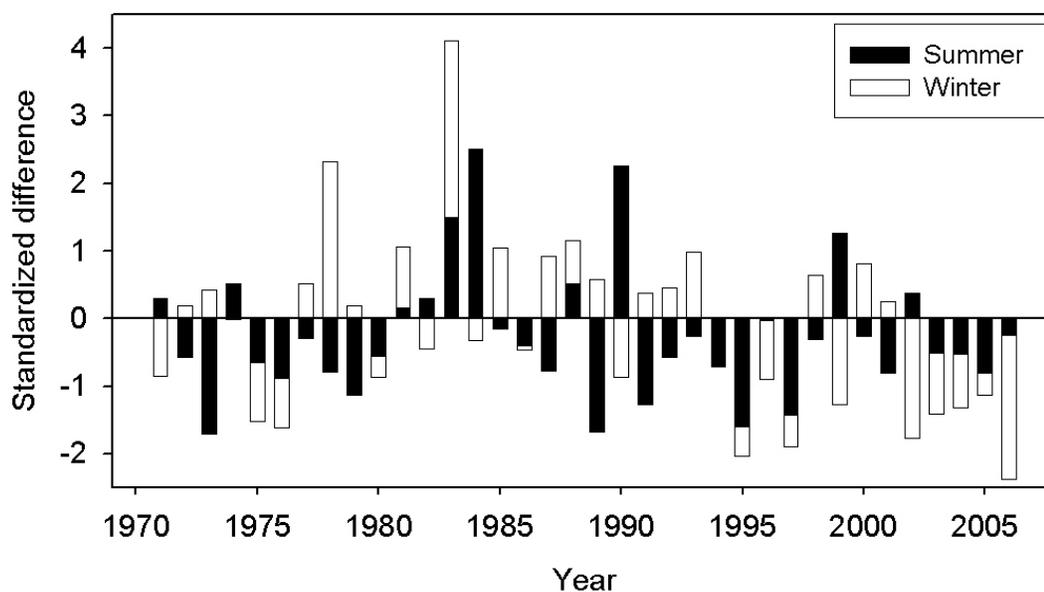


Figure 3. Density of perennial grasses, native grasses, forage grasses, *Eragrostis lehmanniana*, *Aristida* spp., *Bouteloua rothrockii*, *Digitaria californica* and *Isocoma tenuisecta* in the two grazing systems (seasonal rotation SR = solid circles, and yearlong YL = open circles) between 1972-2006. The vertical broken line shows the end of the short-term period in 1985. Different letters above the single SE bars indicate years with significantly different ($P \leq 0.05$) plant density after combining grazing treatments.

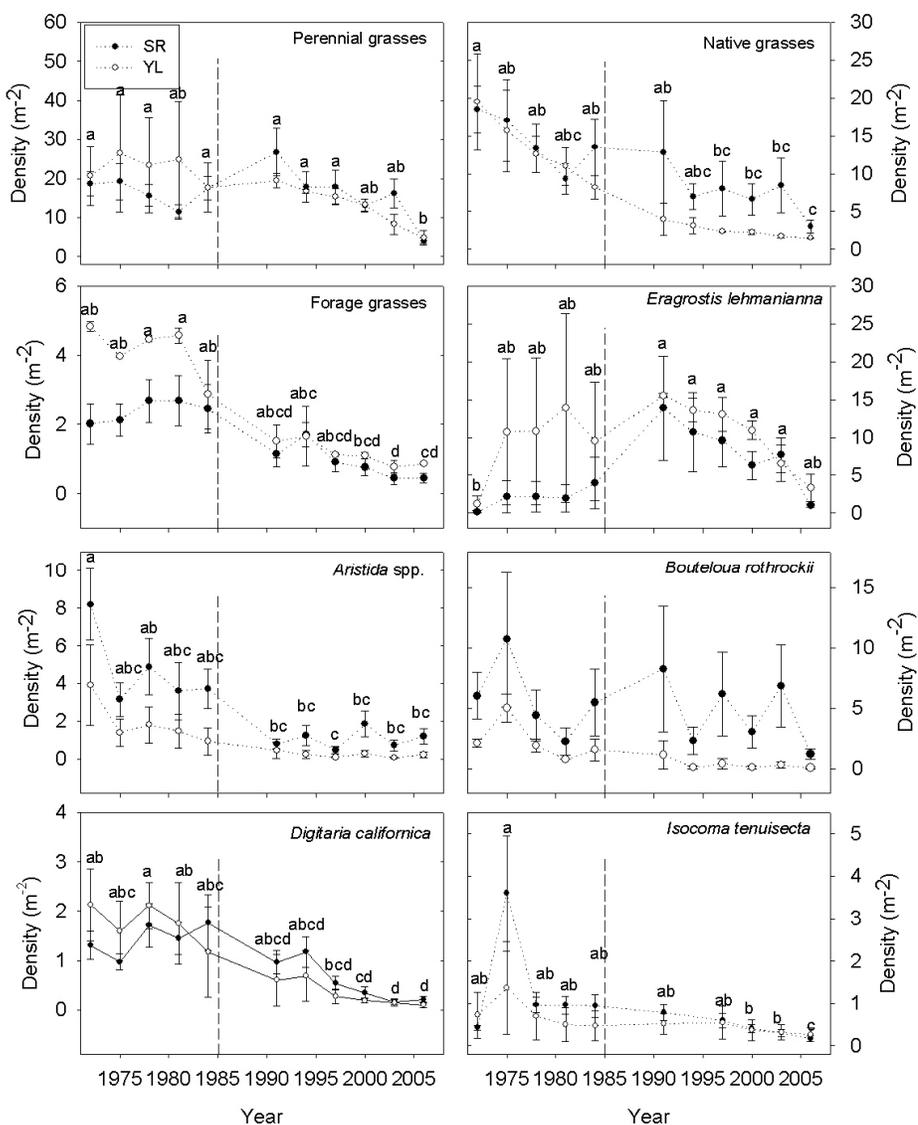


Figure 4. Percent cover of total shrubs, *Isocoma tenuisecta* and *Prosopis velutina* in the two grazing systems (seasonal rotation SR = solid circles, and yearlong YL = open circles) 1975-2006. The vertical broken line shows the end of the first nine years. Different letters above the single SE bars indicate years with significantly different ($P \leq 0.05$) cover after combining grazing treatments.

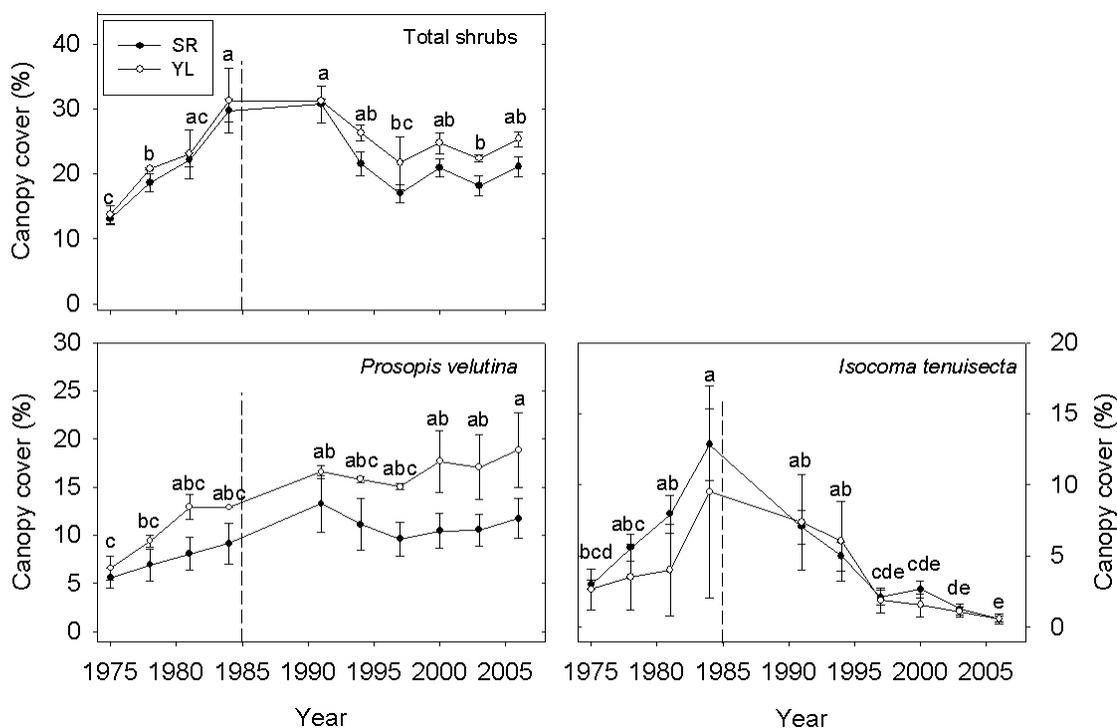
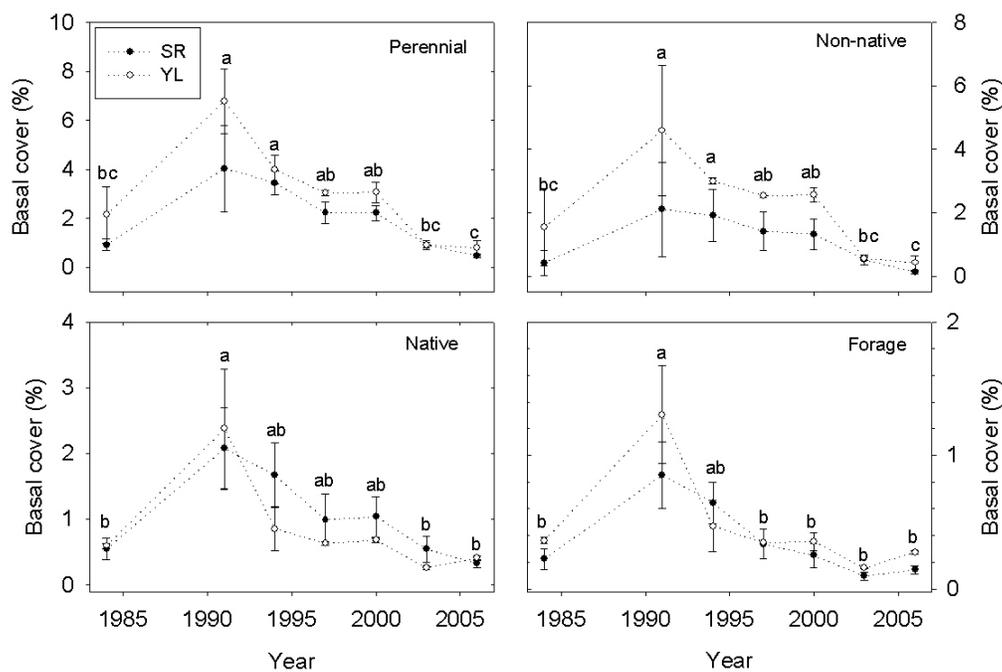


Figure 5. Basal cover for four perennial grass groups in the two grazing systems (seasonal rotation SR = solid circles, and yearlong YL = open circles), 1984-2006. Different letters above the single SE bars indicate years with significantly different ($P \leq 0.05$) cover after combining grazing treatments.



APPENDIX B:
USING VARIANCE TO DETECT SPATIAL VARIATION OF GRASS
ABUNDANCE UNDER YEARLONG AND SEASONAL ROTATION GRAZING
SYSTEMS

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ABSTRACT

Higher stocking density under seasonal-rotation (SR) grazing is expected to reduce selective grazing among forage species and expand animal distribution thereby reducing spatial variation in vegetation compared to yearlong (YL) grazing. Our goal was to determine if spatial variation of perennial grass abundance (cover and density) differed between YL and SR grazing after accounting for a precipitation gradient. We estimated spatial variability using variance of grass abundance among sample locations within seven experimental pastures on the Santa Rita Experimental Range (SRER) in southeastern Arizona. We used a split-plot ANOVA with year as the split, grazing system (YL and SR) as the main effect and precipitation as a covariate over 34-years (1972-2006) for grass density, and 22-years (1984-2006) for grass basal cover. We found no grazing system effect on variance of grass abundance, but variance was sensitive to changes of grasses abundance along a precipitation gradient and over time. Lack of grazing system effects may reflect an insufficient stocking density in the SR treatment, an overriding influence of temporal variation in precipitation, too few pasture replicates, large pasture sizes and spatial variation of grasses occurring at scales different than the 30-m transect size. A negative relationship between precipitation and variance of native grass abundance (after removing an outlier pasture) is consistent with the greater likelihood of more clumped vegetation distributions in drier locations. The positive relationship between variance of non-native grass abundance and precipitation may be due to their scarcity on drier locations and greater variability at wetter locations where the

species are aggressively spreading. Using within-pasture variance to represent spatial variation allows the analysis of the entire series of long-term data, instead of waiting to apply spatially explicit techniques towards the end of an experiment to detect differences in spatial pattern.

Key words: plant cover, plant density, precipitation gradient, selective grazing, variance

INTRODUCTION

Higher stocking density under seasonal-rotation (SR) grazing is expected to reduce spatial variation in vegetation compared to yearlong (YL) grazing when long-term stocking rates do not differ between SR and YL (Heady 1961; Kirkman and Moore 1995; Teague et al. 2004). This would occur because increased stocking density associated with SR grazing should expand animal distribution thus facilitating more uniform forage utilization and less selective grazing compared to YL grazing (Stuth 1994; Bailey et al. 1996). Evidence for less selective grazing under SR grazing includes the reduction in size and persistence of vegetation patches (Cid and Brizuela 1998; Weber et al. 1998), and more random distribution among neighboring plants (Teague and Dowhower 2003).

Spatial distribution of plants is important for sustaining rangeland resources even when total plant abundance does not decline. Soil erosion and water runoff can increase when plant distribution becomes more patchy (Ludwig et al. 1994), plant productivity in drier locations can decrease when the distribution becomes more uniform (Aguiar and Sala 1999), and plant diversity and ecosystem stability can decrease as distribution becomes more homogeneous (Gutierrez et al. 1993; Rietlerk et al. 2004). Despite such implications, most investigations of grazing effects on vegetation overlook changes in spatial variation, most likely because it can be time consuming.

The spatial distribution and size of vegetation patches can be described from spatially explicit measurement using semi-variograms or Euclidean distance (Ludwig and Tongway 1995; Pastor et al. 1998; Adler et al. 2001; Augustine 2003) and distance to

nearest neighbor (Teague et al. 2004). However, these approaches require very intense sampling efforts that are impractical for evaluating management impacts on large (>400 ha) pastures. Other studies have used non-spatially explicit measurements to estimate spatial variation of vegetation by comparing average values among areas receiving different intensities of use within a treatment replicate (Gammon and Roberts 1978; Derner et al. 1994; de Bello et al. 2007), and average deviation from the mean within a replicate (Barnes et al. 2008).

We used a non-spatially explicit approach by calculating the variance of grass cover and density within an experimental pasture (Kosala and Rollo 1991). Variance was used as the response variable to compare the influence of YL vs. SR on the spatial variation of grass. This allowed us to compare measurements made throughout the 34-year history of the experiment rather than relying on spatially-explicit measurements performed at the end of the experiment.

Including the precipitation gradient as a covariate is a useful tool in the analytical model to account for differences in plant variability among pastures that vary in elevation, especially in arid and semi-arid ecosystems (Mashiri et al. 2008). For example, in drier locations small-scale clusters of vegetation exist between large bare areas due to pooling of run-on water and nutrients from nurse-plant associations (Montana 1992; Bromley et al. 1997; Klausmeier 1999; HilleRisLambers et al. 2001); whereas in wetter locations the bare areas are less extensive and distance between vegetation patches is reduced (Ludwig and Tongway 1995; Aguiar and Sala 1999).

The potential to detect a grazing system effect may improve if grasses are assigned to homogeneous groups based on their ecological traits. For example, highly palatable grasses should be more sensitive to grazing management than less palatable grasses because they are more likely to be defoliated. Also, spatial variation of recently introduced and spreading non-native grasses may differ from other grasses, and be more independent of grazing management (Angell and McClaran 2001).

Our objective was to determine if spatial variation of grass abundance (cover and density) differs as expected between YL and SR grazing management, when accounting for the influence of a precipitation gradient. We performed this analysis using pastures where there was no significant difference in the overall (without regard for spatial pattern) plant abundance between YL and SR grazing systems (Mashiri et al. 2008).

MATERIALS AND METHODS

Study area

We used 7 pastures on the 21,500 ha Santa Rita Experimental Range (SRER), 40 km south of Tucson, Arizona, USA., along a $111 \text{ mm}\cdot\text{y}^{-1}$ precipitation gradient (Table 1). Precipitation is bimodal, with approximately 57% arriving from late June through September (Mashiri et al. 2008). Sandy loam deep (SLD) and sandy loam upland (SLU) are the major ecological sites (Table 1; USDA NRCS 2003), and vegetation is a mixture of shrubs, cacti, forbs, and C_4 grasses (Mashiri et al. 2008).

Grazing systems

Five pastures received SR and two pastures received YL grazing (Table 1). SR pastures were grazed twice (March-October and November-February), during a 3-y grazing cycle with 12 mo rest between each use (Martin and Severson 1988). Stocking density ($\text{animals}\cdot\text{ha}^{-1}$) was 3.0 times greater during grazing in SR pastures than would have occurred if grazed yearlong. Forage utilization at the end of each SR and YL grazing period was ~50% between 1972 and 1984 (Martin and Severson 1988; not measured after 1984). Therefore, greater stocking density under SR resulted in more quickly reaching 50% utilization (8 months including the summer growing season and 4 months in the winter dormant season) than under YL (12 months, measured in June). This rapid use should provide less opportunity for selective defoliation among grass species under SR than YL. Stocking rates targeted $\leq 50\%$ utilization of available forage in a pasture,

occasional adjustments were made during dry years, and stocking was slightly less than the regional average (Martin and Severson 1988; Mashiri et al. 2008).

Precipitation covariate

Average annual precipitation ($\text{mm}\cdot\text{y}^{-1}$) for each pasture during the 34-year period was used as the precipitation covariate. It was calculated as the mean of precipitation for the population of vegetation transects in each pasture, and transect estimates were based on precipitation received at two nearest rain gauges (range of 0.1-4.0 km) on the SRER (Mashiri et al. 2008).

Response variables

We used variance ($S^2 = (\Sigma(X-\mu)^2)/N$) of grass abundance (density and cover separately) among permanent transects in a pasture to represent spatial variation for each pasture (experimental unit) at each measurement date. Perennial grass cover and density were measured in 10 permanent transects per pasture (except in Pastures 2S and 5S that had 8 transects) on 30.5-m line intercept transect and 0.305 m wide belt along the same 30.5 m transect (total 9.3 m²) respectively (Mashiri et al. 2008). Grass density was measured every three years from 1972 through 1984, and 1991 through 2006; measurements of grass basal cover followed this schedule starting in 1984.

We calculated spatial variation of basal cover and density for four groups of perennial grasses: perennial (all perennial native and non-native grass species), and subsets native, non-native and long-lived native forage. Non-native grasses were

Lehmann lovegrass (*Eragrostis lehmanniana*) and Boer's lovegrass (*E. curvula* (Shrod.) Nees). Long-lived native forage grasses (hereafter forage grasses) were Arizona cottontop (*Digitaria californica* (Benth.) Henr.), sideoats grama (*Bouteloua curtipendula* (Michx.) Torr), plains bristlegrass (*Setaria macrostachya* H.B.K.), bush muhly (*Muhlenbergia porteri* Scribn.) and black grama (*Bouteloua eriopoda* Torr.) based on Ruyle and Young (1997).

Analytical approach

To assess the relationship between the spatial variation and grazing systems while accounting for the influence of precipitation, we used a split-plot ANOVA with year as the split (Wilm 1945), grazing system (YL and SR) as the main effect, and precipitation as the covariate. The analysis was done in two stages to avoid including non-significant interactions with the covariate (Engqvist 2005). First, the model included all 2- and 3-way interactions with the covariate, and we retained all covariate interaction terms that were significant. Second, if the interactions were not significant, we removed them from the final model. Analyses were performed for the 34-y period (1972-2006) for density, and 22-y period (1984-2006) for basal cover.

We used the split-plot analysis instead of the multivariate repeated measurements analysis because it preserved enough degrees of freedom to include the covariate and interactions. This analytical model was not only conservative, but also rigorous and fully supported by upholding statistical assumptions of independence and correcting for sphericity violations (Algina and Keselman 1997).

Our response variables became normal after a \log_{10} transformation except for non-native grass density that was instead $\log_{10}(Y + 1)$ transformed (Shapiro-Wilk W-test on residuals, Shapiro and Wilk 1965). All data met the homogeneity of variance assumptions (Brown-Forsythe test, Sall et al. 2005). The Mauchly test was used for sphericity and adjustments for violations were made using the Greenhouse-Geisser (1959) correction.

A significant 2-way interaction (grazing system by year) was most important because it indicates that spatial variation differed between the grazing systems at some time after the implementation of the grazing systems. A significant grazing system main effect without the 2-way interaction indicates that the same difference in spatial variability existed between the pastures assigned to the treatments both before and after starting the treatments. A significant precipitation covariate term indicates a linear relationship with spatial variation of grass abundance, and a significant grazing system by precipitation interaction indicates that the relationships differ between grazing systems. A significant year effect, without a grazing system by year or precipitation by year interaction, indicates that spatial variation of grass abundance (all treatments combined) differed between at least two years.

Data analyses were performed using JMP IN 5.1 statistical package (Sall et al. 2005). We used $P \leq 0.05$ to reject the null hypotheses. We used the Tukey-Kramer HSD (Honestly Significant Difference) multiple comparisons test (Sall et al. 2005) to determine which grazing system by year combinations or which years differed when interactions with year or simple year effects were significant. We used simple linear

regression to describe the relationships between response variables and the precipitation covariate when precipitation or the grazing systems by precipitation interaction were significant.

RESULTS

The application of SR and YL grazing systems did not influence variance of grass density or cover measured within pastures as shown by the absence of any significant grazing system by year interaction (Table 2). It is not possible to determine if the greater spatial variation of total perennial grass cover under YL represents a response to the treatments or the persistence of a pre-existing difference because cover measurements did not begin until 12 years (1984) after applying the treatments.

There was a significant grazing system by precipitation interaction for variance of both density and cover of native and forage grasses, and only cover of non-native grasses (Table 2). Precipitation was negatively correlated with variance of density and cover of native grasses, and positively correlated with variance of non-native grass cover under SR grazing, but the relationships were not significant under YL grazing (Fig. 1). Variance of forage grass cover and density was positively correlated with precipitation under YL grazing, but there was no significant relationship under SR grazing. The significant precipitation by year interaction for variance of total perennial grass reflected a significant (negative) correlation with precipitation only in 1984. There was a positive correlation between variance of non-native grass density and precipitation. Significant differences in variance over time (year effects) without interactions occurred for both cover and density of native, forage and non-native grasses, but only variance of density of total perennial grasses (Table 2). Variance generally peaked in 1991 and declined through 2006 (Fig. 2).

DISCUSSION

Grazing systems

The absence of a SR grazing effect on the spatial variation of grass abundance may reflect an insufficient stocking density in the SR treatment and the overriding influences of temporal variation in precipitation. Much greater stocking densities may be needed to affect a response because Ruyle et al. (1988) found no difference in grazed patch size among stocking densities on the SRER that were 19 to 41 times greater than our densities. Large inter-annual variation in precipitation may also limit the influence of grazing management on spatial variation because grass abundance declined during the drought conditions that persisted since 2000 (Ellis and Swift 1988; Teague et al. 2004, Mashiri et al. 2008).

The absence of a SR grazing effect could also be the result of large within-treatment variation, large pasture size, scale of spatial variation different than transect length, and the absence of grass cover data for the first 11 years of the experiment (1972-1983). The large within-treatment variation (Fig. 2) is at least partly associated with the few replicates in each treatment (YL = 2 and SR = 5), and possibly differences in ecological sites among the replicates (Table 1). Unfortunately, we did not have sufficient representation of ecological sites across all pastures or degrees of freedom to include that term in the model. However, when we performed a conservative power analyses (without changing error) at 5 times the replicates (YL = 10 and SR = 25), we found a significant

grazing system by year interaction for perennial, native and forage grass cover with YL>SR in all cases.

The large pasture sizes in this study (400-1800 ha) may have limited the influence of the SR treatment on spatial variation (Hart et al. 1993; Norton 1998; Barnes et al. 2008) because this outcome is most apparent in small (<10 ha) pastures (Bailey et al. 1996). Detecting spatial variation may be limited if patterns occur at a spatial scale different than the 30-m transect used in this study (Keitt et al. 2002). Vegetation patches can be 1-100 meters in diameter in similar environments (Belsky 1986; Bromley et al. 1997; WallieDeVries et al. 1999; HilleRisLambers et al. 2001), but no such analysis has been reported for the SRER.

Without initial (1972-1983) data for grass cover, it is impossible to know conditions at the start of the experiment and whether treatment effects occurred in the first 11 years. Finally, it is also possible that >10 transects per pasture may have more precisely documented spatial variation in these large pastures.

Precipitation gradient

The different precipitation-grass relationships between SR and YL grazing systems (GS x PPT interaction) is more likely an artifact of Pasture 8 (~437 mm·y⁻¹; Fig. 1) being an outlier because the second YL pasture (2N) has variance values that are similar to the SR pastures with equivalent precipitation (~400 mm·y⁻¹). Pasture 8 is smaller, wetter, and has more total ecological sites, and therefore fewer transects in the SLU and SLD sites than any other pasture (Table 1). The greater heterogeneity of ecological sites in Pasture 8

may be maintaining the higher spatial variance in spite of the opposite expectation for smaller pastures to be more fully utilized by herbivores than larger pastures (Laca 2009).

Ignoring the data point for the outlying Pasture 8, reveals a more general set of patterns, where increased variance of native grass in drier locations may reflect the greater likelihood of contagious distributions of vegetation and nutrients (Ludwig and Tongway 1995; McClaran and Angell 2007; McClaran et al. 2008). Full ANOVA analysis without Pasture 8 was not possible because there would not be replicates for YL grazing. The inverse relationship of native grass variance and precipitation may be more representative of short-lived less palatable (non-forage) native grasses because the variance of forage grasses in the six pastures was not related to the precipitation gradient. The increasing variance of non-native cover with precipitation is consistent with very low abundance on the drier areas and high variability at the wetter locations where the species are aggressively spreading (Mashiri et al. 2008).

Splitting grasses into more homogeneous categories was critical for detecting patterns between spatial variability and precipitation (Fynn and O'Connor 2000) which was not significant in the most diverse category, total grasses.

Variance and spatial variability

Variance calculated from the within-pasture population of sample transects appears to be a good measure of the spatial variation of vegetation because our results detected the patterns of spatial variability expected for native and non-native grasses in relation to the precipitation gradient and increased heterogeneity of soils. However, this simple

estimation of spatial variation will not describe the spatial distribution or patch size of grass abundance, and therefore will not be a substitute for the spatially-explicit measurements needed to perform more sophisticated analyses such as semi-variograms that describe the decline of autocorrelation with distance.

IMPLICATIONS

Our findings have implications for the design and analysis of grazing systems studies. Our ability to detect treatment effects was limited by a design that had insufficient stocking density, pastures (experimental unit) that were too large and had too few replicates, and an inequitable distribution of ecological sites among pastures. An improved design would include at least a second and higher stocking density in the SR treatment to ensure some vegetation response, smaller pastures to improve sensitivity to treatments and greater uniformity of soils, and more replicates. However, the applicability of findings gained from this improved design will decline in proportion to the differences between the new approaches and the typical types of livestock management practices and policies. Applicability will also be limited by the infrastructure investments needed to adopt the findings.

In contrast, the implications regarding analysis of such studies are more optimistic. Using within-pasture variance to represent spatial variation has the advantage of being compatible with the normal data collection protocols using distributed transects and plots. In addition, this approach can be used retroactively on a long-term archive of measurements, which is not possible when spatially explicit measurements are applied at or near the end of an experiment to detect differences in spatial pattern.

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LIST OF TABLES

Table 7. Size, elevation range, number of ecological sites, percent of sandy loam upland (SLU) and sandy loam deep (SLD) ecological sites, long-term stocking rate, stocking density, and annual precipitation for pastures experiencing yearlong and seasonal-rotation grazing treatments over 34 years (1972-2006). Parenthetical values are one SE of the mean.

Pasture	Pasture size (ha)	Elevation (m)	Ecological sites	Ecological site (%)		Stocking rate (10^{-2} AU \cdot ha $^{-1}$)	Stocking density (10^{-2} AU \cdot ha $^{-1}$)	Precipitation (mm \cdot y $^{-1}$)
				SLU	SLD			
YEARLONG GRAZING								
8	403	1165-1298	5	20	10	5.6 (0.11)	5.6	437 (41.1)
2N	1801	1065-1185	3	50	40	3.0 (0.03)	3.0	399 (40.2)
SEASONAL ROTATION GRAZING								
2S	1438	1054-1196	3	25	38	3.5 (0.34)	10.6	403 (39.6)
6A	1425	1178-1267	2	20	80	2.8 (0.23)	8.5	394 (37.0)
3	1728	956-1033	4	20	40	1.7 (0.18)	5.0	339 (32.7)
6B	1524	1017-1094	2	40	60	4.1 (0.44)	12.3	330 (29.5)
5S	1637	933-1008	4	25	25	1.3 (0.21)	3.9	326 (29.7)

Table 8. *P*-values from the split-plot analysis of the variance of grass density over 34 years (1972-2006) and of grass cover over 22 years (1984-2006) with grazing system (GS) main effect, precipitation (PPT) covariate, year (YR) as the split, and their interactions. * = non-significant interaction with PPT which was excluded from the final model. (+) = positive correlation with precipitation gradient.

Ecological category	Explanatory Variables					
	GS	PPT	GS x PPT	YR	GS x YR	PPT x YR
DENSITY						
Perennial	0.48	0.95	0.21*	<0.01	1.00	0.42*
Native	0.13	0.97	0.01	<0.01	0.99	0.12*
Forage	0.25	<0.01	<0.01	<0.01	0.96	0.27*
Non-native	0.57	<0.01 (+)	0.31*	0.01	0.92	0.11*
COVER						
Perennial	0.03	0.51	0.34*	<0.01	0.36	0.05
Native	0.05	<0.01	0.02	<0.01	0.82	0.93*
Forage	0.02	0.01	<0.01	0.01	0.89	0.27*
Non-native	0.06	<0.01	<0.01	<0.01	0.41	0.19*

LIST OF FIGURES

Figure 6. Relationship between annual precipitation and log variance of density and cover of native, forage, and non-native grasses for seasonal rotation (SR, open circle) and yearlong grazing (YL, solid circle) pastures. Lines represent correlation between log variance (LV) and precipitation (PPT) within pastures in each grazing system (SR and YL). Solid lines are significant ($P \leq 0.05$) relationships and dotted lines are not significant. Vertical bars are $1 \pm SE$ of the mean.

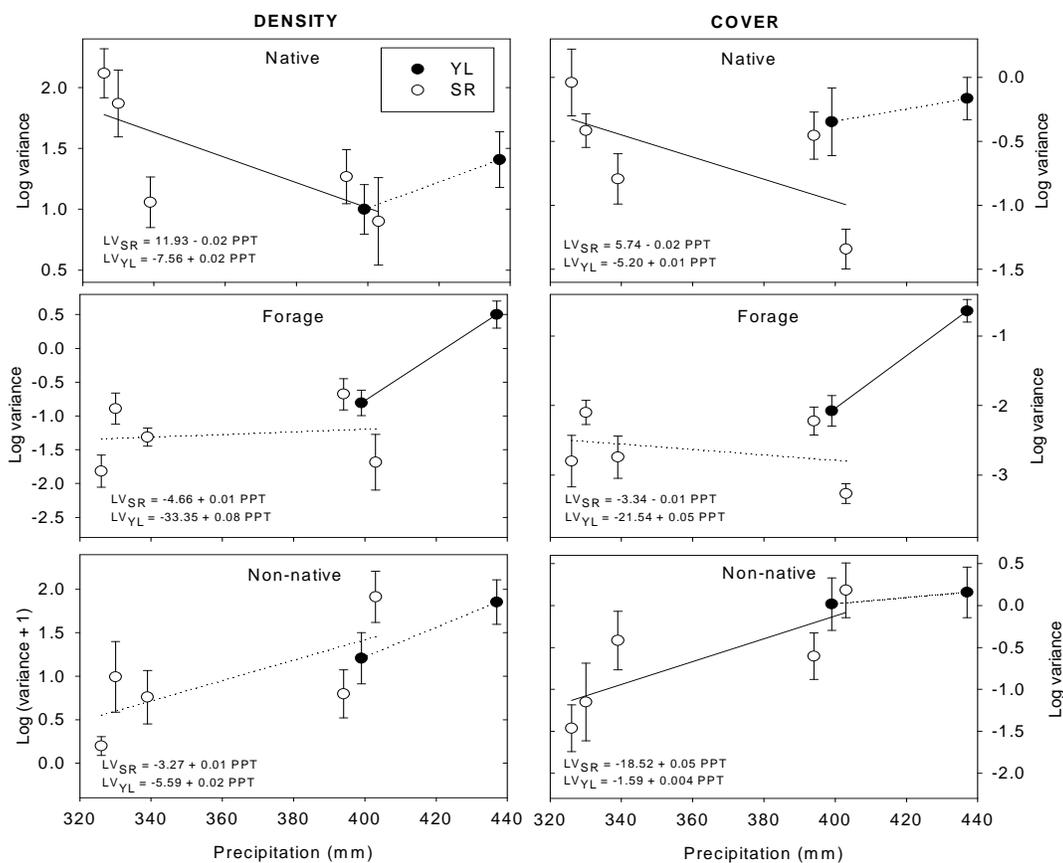


Figure 7. Log variance of cover for perennial grass groups in the two grazing systems (seasonal rotation SR = open circles, and yearlong YL = solid circles), over 22 years (1984-2006). Different letters above the $1 \pm SE$ bars indicate years with different ($P \leq 0.05$) log variance when grazing treatments are combined.

