PERENNIAL GRASS COMMUNITY RESPONSE TO SEVERE DROUGHT, TOPO-EDAPHIC VARIATION, AND LONG-TERM HERBIVORY ON THE EDWARDS PLATEAU OF TEXAS

A Thesis

by

COLIN SCOTT SHACKELFORD

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2004

Major Subject: Rangeland Ecology and Management

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ABSTRACT

Perennial Grass Community Response to Severe Drought, Topo-Edaphic Variation, and Long Term Herbivory on the Edwards Plateau of Texas. (August 2004)

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Perennial grass vegetation dynamics of heavy grazing, moderate grazing and ungrazed treatments were analyzed during two extreme drought events: the drought of 1951 to 1956 and the drought events centered on the year 2000. Analysis of each drought event from weather records and Palmer Drought Severity Index values showed that the intensity, duration and pattern of each drought event were structurally unique. Grazing intensity was the primary driver of perennial grass species composition and community structure both during and between each drought event. Total basal area for each drought event was driven primarily by variation in precipitation pattern. Basal area per plant dynamics were significantly influenced by grazing intensity while plant density was driven by both precipitation and grazing intensity.

Topo-edaphic variation significantly influenced the persistence and distribution of perennial grass species during an extreme drought event centered on the year 2000. The presence of large or abundant surface rock features facilitated the survival of perennial grasses during this drought event by creating a positive soil microenvironment. Sites with large surface rock features acted as drought refugia for perennial grass populations. Sites with abundant surface rock features had 10 times greater perennial grass basal area and 5 times greater plant density than sites with few surface rock features. Grazing intensity was the primary driver of species composition and community structure within both refugia and non-refugia sites. Grazing intensity had no effect on perennial grass basal area. However, grazed treatments had two times greater perennial grass density than non-grazed treatments. Species response to grazing intensity and surface rock cover was individualistic. Grazing response groups (intolerant, intermediate, and tolerant) separated along a gradient of surface rock cover and grazing intensity. Abundant surface rock features act as refugia for perennial grasses by facilitating their persistence during extreme drought events on the Edwards Plateau.

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Sincere thanks goes to my committee chair, Dr. Fred Smeins, for his insight, guidance and friendship over the last three years. His curiosity, good nature, and passion for ecology have been an inspiration. I am grateful to the other members of my committee, Dr. Charles "Butch" Taylor, Dr. Larry White, and Dr. Raghavan Srinivasan for their guidance, input and support throughout this project.

Special thanks go to my friends, John and Jeanne Anne, whose home acted as my own private B&B and respite during the stressful moments of my graduate career. Extra thanks goes to Jeanne Anne for coming out to Sonora, braving the summer heat and acting as my GPS wrangler, gate monkey and goat herder. You truly are a dangerous woman and no, you're wrong, the shade index is a 2 and not a 3, so quit arguing. Thanks to Isaac, Adam, Peter, Eric and Katie as well. Support from my Houston cohort has been invaluable and the friendship and generosity from each of you knows no end.

I am grateful for the friendships with the faculty and my fellow graduate students in the Department of Rangeland Ecology and Management. These friendships contributed significantly to my professional education, broadened my understanding of ecology, and enriched my life while here at Texas A&M. Thanks to all who made my graduate career at Texas A&M the important and worthwhile learning experience it has been.

TABLE OF CONTENTS

Page

CHAPTER

CHAPTER Page

LIST OF FIGURES

LIST OF TABLES

CHAPTER I

INTRODUCTION

Justification

Grazing by large herbivores and variable precipitation are two primary forces driving temporal shifts in herbaceous species composition and community structure in semi-arid grasslands (O'Connor 1995). Conflicting arguments have been made as to the relative impact of one variable over the other (O'Connor 1985, Milchunas et al. 1988, Belsky 1992, Behnke and Scoones 1993).

Over the past 50-plus years the Texas A&M University Sonora Experiment Station on the southwestern edge of the Edwards Plateau Land Resource Area in central Texas (Hatch et al. 1990) has experienced two major and several minor droughts as well as several above normal precipitation periods. The station has vegetation records from permanent plots for over 50 years from a variety of different grazing regimes, as well as precipitation and temperature records for over 80 years. These long-term records of vegetation response to herbivory and weather variation provide an ideal opportunity to investigate the interaction of these two variables on vegetation dynamics in the region and, in particular, the impacts of drought on the survivability and response of plant species under different grazing regimes.

Past research has shown that herbaceous community response to grazing and drought can be patch specific (Fuls 1992a, b, Hodgkinson 1996). This patch specific response is driven by both the inherent spatial heterogeneity of semi-arid landscape features as well as variation in grazing intensity across a coarse scale landscape due to patch grazing (Ludwig and Tongway 1995, Ludwig et al. 1997).

This thesis follows the style and format of Ecology.

A recent major drought event beginning in the mid-1990's offered an opportunity to examine patch specific response to both grazing and extreme drought at the Sonora Experiment Station. Initial observations of plant community dynamics in response to this drought event showed that some patch types experienced greater perennial grass mortality than others. This differential mortality provided an ideal opportunity to characterize patch features that facilitate the survival of perennial grass in extreme drought events.

Hypothesis and Objectives

Hypothesis 1: Recent severe drought events (1995 – 2002) are no different than past severe drought events (1950 – 1956) in intensity, duration or pattern.

Objective 1: Evaluate long-term annual and seasonal rainfall, temperature, and Palmer Drought Severity Index for the Sonora Experiment Station in order to reconstruct past and current drought intensity and duration.

Hypothesis 2: Perennial grass community response to drought will not be influenced by variation in long-term grazing intensity.

Objective 1: Evaluate long-term (53 years) records of perennial grass basal diameter, density and composition across 2 major and several minor droughts for three long-term grazing regimes: heavy, moderate, and no grazing.

Hypothesis 3: Perennial grass community response to extreme drought on the Edward's Plateau major land resource area will not differ between patches with high and low densities of large surface rock fragments within and between long-term grazing intensity treatments.

Objective 1: Characterize the soil resources, surface rock features, and landscape position of patches with high and low densities of large surface rock fragments for heavy, moderate, and no grazing long-term grazing treatments.

Objective 2: Characterize the perennial grass composition, basal area, and density of patches with high and low densities of large surface rock fragments for heavy, moderate, and no grazing long-term grazing treatments.

Objective 3: Test for the influence of patch features, grazing intensity, and the interaction of these two variables as they relate to the perennial grass community composition, basal area and plant density for heavy, moderate, and no grazing long-term grazing treatments during the extreme drought of 2000 to 2002.

Literature Review

Semi-Arid Environments

Examinations of climatic variation across the continental United States have shown that the longest and driest drought periods as well as a majority of surplus rainfall periods have taken place in the arid and semi-arid landscapes of the western United States (Diaz 1983). These prolonged periods of surplus or deficit moisture are not abnormal events and should be considered part of the normal climatic landscape for much of the western United States (Glantz and Katz 1977, Diaz 1983).

The distribution of rainfall events in arid and semi-arid landscapes are typically positively skewed with small amounts of rainfall occurring more frequently than large amounts (Glantz and Katz 1977). Measures of normal rainfall can be artificially inflated by a small number of large rainfall events. Deviation from normal conditions are thus not the best tool for defining or describing periods of drought in arid and semi-arid landscapes (Glantz and Katz 1977, Hodgkinson and Freudenberger 1997, Thurow and Taylor 1999).

Arid and semi-arid landscapes have been described as “water-controlled ecosystems with infrequent, discrete, and largely unpredictable water inputs” (Noy-Meir 1973). Precipitation events are variable both temporally and spatially. Stochastic variation of precipitation event size and timing combined with the spatial variability of individual events create a complex and unpredictable landscape mosaic of rainfall distribution across space and time (Noy-Meir 1973).

Herbivory, Climatic Variation and Vegetation Response

Variation in rainfall has been identified by many as a primary driver of directional shifts in species composition in semi-arid plant communities (Westoby 1980, Milchunas et al. 1989, O'Connor 1991, 1994, 1995, O'Connor and Roux 1995, Biondini et al. 1998). Periods of drought can result in decreased plant production, alteration of species composition and changes in vegetation community structure (Herbel et al. 1972, Gibbens and Beck 1988, Smeins and Merrill 1988, Tilman and Elhaddi 1992). Seasonal precipitation patterns within a given year have also been found to influence vegetation composition (Herbel et al. 1972).

Gazing, in turn, has also been shown to be a primary modifier of species composition within a plant community (O'Connor 1995). A model of plant community response to grazing based on an extensive survey of the literature across a global scale shows grazing to be the primary driver of plant diversity based on the grazing evolutionary history of a site and its position along a moisture gradient (Milchunas et al. 1988). Grazing intensity in this model alters the physiognomy and competitive relationships for light, space and soil resources of a plant community in favor of plants that tolerate or avoid a given intensity of herbivory. Experimental studies in the African Serengeti have shown that grazing and physical disturbance had the greatest impact on plant cover and diversity compared to competition from dominant species or fire (Belsky 1992).

It has been shown that grazing intensity and climatic variation drive change in the composition and structure of semi-arid vegetation communities at different temporal scales. Grazing intensity is the primary driver of coarse scale, long-term (decadal) directional change with climatic variation driving the short-term rate and trajectory of these changes (Fuhlendorf et al. 2001).

Individual plant response to herbivory may result in an increase, decrease or no net change in basal area or plant longevity depending on the frequency and intensity of herbivory (Butler and Briske 1988, Briske 1991). However, changes in individual plant basal area in response to herbivory are seldom associated with a corresponding change in total basal area at the community level. This suggests a community level interaction of plant density and basal area in response to herbivory (Sala et al. 1986). The primary modification of perennial bunch-grass species population structure in response to herbivory is a decrease in individual plant basal area resulting in a shift from a community of low density, large basal area plants to a community of high density, low basal area plants (Butler and Briske 1988, Fuhlendorf et al. 2001).

Decreases in individual basal area per plant can increase the susceptibility of a plant community to the impacts of severe drought (Butler and Briske 1988, Briske 1991). Significantly higher mortality has been documented for grazed versus ungrazed perennial grasses during periods of drought (Box 1967). Lag effects of drought induced mortality have been documented along a grazing gradient. Perennial grass mortality in semi-arid Australian rangelands occurred earlier and at higher rates in treatment units with higher stocking rates during a series of drought years (Hodgkinson 1996).

Patch Specific Response to Herbivory and Drought

Vegetation response to herbivory and drought is often patch specific. A lag effect of drought induced perennial grass mortality was documented at the patch scale in a pasture lightly stocked with sheep (Hodgkinson 1996). The cumulative percentage of annual mortality over a six-year period for the perennial grass *Monachather paradoxa* differed significantly depending on patch type and landscape position. Vegetation patches with structural characteristics and landscape positions favorable for capturing and maintaining water resources persisted for longer and had lower rates of mortality during successive drought events. Perennial grass mortality occurred earlier and with a higher cumulative percentage of mortality in less favorable resource patches (Hodgkinson 1996). This patch specific response to drought is driven by both the inherent spatial heterogeneity of arid and semi-arid landscape features as well as variation in grazing intensity across a coarse scale landscape due to patch grazing (Ludwig and Tongway 1995, Ludwig et al. 1997).

Herbivore foraging behavior interacts with patch heterogeneity to create alternating heavily grazed, lightly grazed, and ungrazed sites both within and between vegetation patches (Bakker et al. 1984, Fuls 1992a). Long term heavily grazed patches may be more susceptible to drought induced plant mortality due to an alteration of soil water relations and a reduction in individual plant basal area (Fuls 1992a, b).

As vegetation retreats to more favorable sites in response to drought, herbivores are forced to utilize smaller patches of drought persistent vegetation. This can result in a positive feedback cycle of drought induced mortality and patch overgrazing (Fuls 1992b, Koppel et al. 1997, Koppel et al. 2002).

Grazing and Drought Refugia

This positive feedback may be absent in patches where herbivore access is restricted. Landscape or vegetation features that reduce patch utilization or restrict the movement of herbivores act as refugia from herbivory and can moderate the impacts of overgrazing. Refugia may be biotic or geologic in origin (ex: cacti or thorny shrubs versus rock outcrops or mesas) and small or large in size, number, or geographic extent within the larger landscape (Milchunas and Noy-Meir 2002).

These refugia often act as repositories of biological diversity within a coarse scale landscape (Clements 1934, Ludwig et al. 1997). A survey of refugia showed that 93% of small refugia and 41% of large refugia showed higher plant diversity than non-refugia sites (Milchunas and Noy-Meir 2002). Refugia may be important as recruitment loci or dispersal patches due to the protection offered to plants that promote seed production. Refugia sites have been shown to have 78% to 128% greater seed production in comparison to non-refugia sites (Milchunas and Noy-Meir 2002).

Refugia that are small in size but of large geographic extent may be more important as repositories of biotic diversity than large refugia of a small geographic extent during recovery from landscape scale disturbance (Forman 1995). Mosaics of small patches across large geographic extents act as loci for seed dispersal into the larger landscape.

The importance of refugia sites as dispersal patches within a larger landscape may be determined by stochastic climatic events. The timing and intensity of rainfall can influence the importance of geologic refugia sites as depositories of biotic diversity. Germination rates of the annual grass *Triticum turgidum* var. *dicoccoides* during periods of light rainfall occurring early in the growing season were significantly higher in geologic refugia than non-refugia sites. Heavy rainfall occurring late in the season resulted in more widespread germination that was, in some cases, greater outside of non-refugia sites (Noy-Meir et al. 1991a).

Features of geologic refugia such as the arrangement and size of rock fragments may provide positive microenvironment conditions in addition to protection from herbivory (Milchunas and Noy-Meir 2002). These structural characteristics can enhance soil moisture as well as modify grazing pressure and competition (Noy-Meir et al. 1991b). Surface rock fragments have been shown to create a positive microenvironment by a) protecting soil structure from rainfall impact (Wilcox et al. 1988, Poesen and Ingelmo-Sanchez 1992, Brakensiek and Rawls 1994, Poesen and Lavee 1994, Moustakas et al. 1995), b) concentrating runoff by slowing overland flow (Poesen and Ingelmo-Sanchez 1992), c) increasing infiltration and percolation (Wilcox et al. 1988, Poesen et al. 1990, Poesen and Ingelmo-Sanchez 1992, Brakensiek and Rawls 1994, Moustakas et al. 1995), and d) decreasing soil moisture evaporation (Kosmas et al. 1993, Poesen and Lavee 1994, Moustakas et al. 1995).

Munn et al. (1987) concluded that the effect of soil rock volume on plant productivity changed along a moisture gradient from humid to arid environments. Productivity is negatively impacted by soil rock volume in humid climates due to restricted rooting space but is positively influenced in semi-arid and arid climates due to favorable soil moisture conditions. In a hill-slope hydrology study, soils with large rock fragments had higher plant production than similar plots without large rock fragments (Moustakas et al. 1995). Similar results were found when the effect of rock fragments on the production of rain-fed wheat was examined on Mediterranean hill slopes (Kosmas et al. 1993, Danalatos et al. 1995).

CHAPTER II

STUDY AREA

Research was conducted at the 1401 ha Texas A&M University Sonora Experiment Station roughly 56 km south of Sonora, Texas in Sutton and Edwards county. The station is located on the southwestern edge of the Edwards Plateau Land Resource Area (Hatch et al. 1990). Rainfall distribution is bimodal with peaks in the fall and spring. Average annual precipitation is highly variable, ranging from a low of 156 mm in 1951 to a high of 1055 mm in 1935 with a 1919 to 2002 annual mean of approximately 570 mm (Fig. 1). Median annual rainfall, which may be a better indicator of long term rainfall patterns in semi-arid climates (Thurow and Taylor 1999), is approximately 425 mm. The growing season is roughly 240 days with average July temperatures of 34^{o} C and January temperatures averaging $16\,^{o}$ C (Station Records).

Average elevation of the station is 730 m. The topography has gentle slopes of 3 to 4% with a heterogeneous mix of soil depths, rock outcrops and topographic position. Dominant soils are Tarrant stony clays of the thermic family of Lithic Haplustolls. Soils range in depth from 5 to 30 cm with 30 to 60% of the profile consisting of limestone rock fragments (Wiedenfeld and McAndrew 1968). Soils are formed over limestone from the Buda formation of the Washita geologic division and the Segovia member of the Edwards formation of the Fredericksburg geologic division (McKalips and Barnes 1981).

Historical vegetation is a juniper-oak savanna with a mid- or short-grass matrix interspersed with individuals or groupings of woody species (Kuchler 1964, Smeins and Merrill 1988). Woody vegetation composition and canopy cover varies significantly with topography and soils as well as with fire and grazing history (Fuhlendorf et al. 1996). Common woody species include *Quercus virginiana*, *Q. pungens* var. *vaseyana*, *Juniperus ashei*, *J. pinchotii*, and *Diospyros texana*.

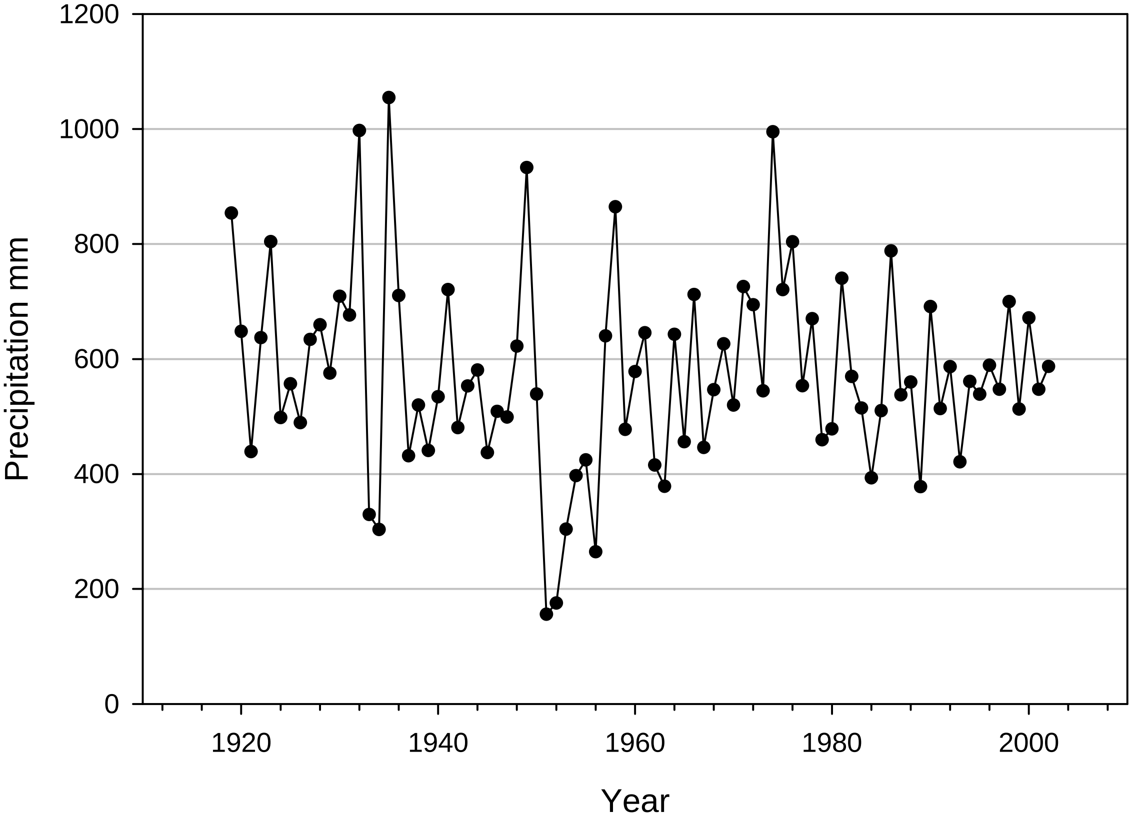


Fig. 1. Sonora Experiment Station total annual precipitation from 1919 to 2002.

Dominant herbaceous vegetation includes the bunch-grasses *Aristida purpurea*, *Bouteloua curtipendula* var. *caespitosa, B. trifida, B. hirsuta, Eriochloa sericea, Erioneuron pillosum*, *Stipa leucotricha,* and the stoloniferous short-grass *Hilaria belangeri* (Smeins and Merrill 1988). Nomenclature follows Hatch *et al.* (1990).

The Station was established in 1916 for the study of management, breeding, and disease issues of cattle, sheep, and goats. In 1948, research at the station was shifted to grazing management studies. Stocking rates prior to the establishment of the grazing treatments were continuous and heavy across all treatment units. The 1402 ha area was fenced into 25 pastures and assigned different grazing intensity regimes. Three of the grazing regimes established in 1948 were utilized for this study.

The heavy grazing treatment consists of two 32 ha replications. Each replication had a stocking rate of 5.4 ha/auy (animal unit year = 4314 kg of aboveground biomass or the amount of forage consumed by a 450 kg animal for one year) when established in 1948. A 60:20:20 ratio of cattle, sheep, and goats was stocked on one replication from 1949 to 1970. The other replication was stocked with sheep only from 1949 to 1969. The stocking rate of both replications was increased in 1970 to a rate of 4.8 ha/auy with a stocking ratio of 50:25:25 cattle, sheep, and goats. In 1983 the grazing regime was changed from a heavy continuous grazing regime to a high-intensity, low-frequency regime. Stocking rates of both treatment replications were reduced to a moderate stocking rate around 8.1 ha/auy. The stocking rate was reduced in 1986 to 10.4 ha/auy and again in 1998 to 16.2 ha/auy (Heitschmidt and Taylor 1991). Since 1983, the heavy grazing treatment stocking rate has been reduced to that of the moderate grazing treatment.

The moderate grazing treatment consists of four 24 ha replications with a 4-pasture, 3-herd deferred rotational grazing system (grazing system specifics can be found in (Heitschmidt and Taylor 1991). Stocking rate from 1949 to 1986 varied from 6.0 – 8.1 ha/auy with a 60:20:20 or 50:25:25 ratio of cattle, sheep, and goats. The stocking rate was reduced in 1986 to 10.4 ha/auy and again in 1998 to 16.2 ha/auy (Heitschmidt and Taylor 1991).

Until the stocking rate reduction in 1983, the grazing intensity of the heavy grazed treatment has always been greater than the moderate grazing treatment. The stocking rates of the heavy and moderate treatments have been the same since 1983.

The ungrazed treatment consists of two 12 ha replications. These replications have not been grazed since 1948. One replication was established with a high fence in order to exclude large wildlife, primarily white-tailed deer. A relatively small number of deer access this replication and are hunted ever 2 or 3 years as needed.

In 1948 hand cutting was used to eliminate most *Juniperus* species across the Experiment Station. Other woody species such as *Quercus virginiana* were left in place. Estimated canopy cover of *Juniperus* species following the cutting was <1% in 1949 (Smeins and Merrill 1988). No manipulation of woody species has taken place since 1948 within the grazing treatment units examined in this study. More recently, *Juniperus* species cover has increased to roughly 30% canopy cover (Smeins and Merrill 1988, Fuhlendorf 1992, Smeins et al. 1994).

CHAPTER III

LONG-TERM WEATHER AND VEGETATION DYNAMICS: PERENNIAL GRASS COMMUNITY RESPONSE TO TWO DROUGHT EVENTS

Introduction

Over the past 50-plus years the Sonora Experiment Station has experienced two major and several minor droughts as well as several above normal precipitation periods. The station has vegetation records from permanent plots for over 50 years from a variety of different grazing regimes, as well as precipitation and temperature records for over 80 years. These long-term records of vegetation response to herbivory and weather variation provide an ideal opportunity to investigate the interaction of these two variables on vegetation dynamics in the region and, in particular, the impacts of drought on the survivability and response of plant species under different grazing regimes.

Previous analysis of the perennial grass community examined the role of grazing and weather on the long term vegetation dynamics for the entirety of this data set (Fuhlendorf and Smeins 1997). The current analysis is focused specifically on the perennial grass community response to two drought events: 1) the drought of 1951 to 1956, characterized by year round drought conditions continuous for over five years and 2) the pattern of abundant cool season precipitation followed by growing season drought that began around 1994 and continued through 2002.

Methods

Analysis of Drought Pattern and Intensity

Long term daily precipitation and temperature records of the Sonora Experiment Station for the period 1919 to 2002 were examined at increasing temporal scale for patterns of drought or abundant moisture. A Walter climate graph (Walter and Breckle 2002) of mean monthly temperature and precipitation as well as median precipitation was plotted in order to examine the temporal distribution of precipitation and temperature across the 83 years of weather records for the Sonora Experiment Station.

Three major droughts have occurred during this 83 year long period: the dustbowl drought of 1933 to 1935, the long term drought of 1951 to1956 and a shorter more intermittent drought from 1997 to 2002. Past analysis of herbaceous vegetation response to weather variation showed the strongest correlation between perennial grass basal area and three year running averages of precipitation (Fuhlendorf and Smeins 1997). The years 1953 and 2001 had the lowest basal area across a long term vegetation monitoring data set began in 1948. In light of this relationship of basal area and three year running averages of precipitation, weekly temperature and precipitation was plotted for the time intervals 1951 to 1953 and 1999 to 2001 in order to examine the similarities and differences of these two drought events.

The Palmer drought severity index (Palmer 1965) was utilized to examine patterns of drought or surplus moisture for the entirety of the 83 years (1919 to 2003) of weather records for the Sonora Experiment Station. Palmer drought severity index values were calculated for the Sonora Experiment Station using the PDSI software package developed for the National Agricultural Decision Support Center at the University of Nebraska, Lincoln (Palmer 1965, PDSI 2003). The Palmer drought severity index (PDSI) is widely used as an indicator of regional drought conditions (Palmer 1965, Karl and Koscielny 1982, Diaz 1983, Alley 1984).

The Palmer drought severity index measures the accumulated effect of deficit or surplus rainfall relative to the rainfall needed to maintain adequate soil water content for normal (water stress free) growth of plants for a region on a monthly or weekly scale (Palmer 1965). The calculation of PDSI values begins with a water balance model using historic records of weekly or monthly precipitation and temperature. Soil moisture storage is calculated by dividing the soil into two layers, a surface layer and an underlying layer. The calculations of the Palmer index assumes a surface layer storage capacity of 25 mm of water regardless of soil texture (Palmer 1965, PDSI 2003). Storage for the underlying layer is dependent on the soil characteristics of the site being considered.

The water balance equation is composed of eight different variables in four sets of two: potential evapotranspiration (PE) and actual evapotranspiration (ET), potential recharge (PR) and actual recharge (R), potential runoff (PRO) and actual runoff (RO), potential loss (PL) and actual loss (L). The PE for each month or week is calculated from historic temperatures using a variation of the Thornwaite equation (Alley 1984).

These sets of variables are used to calculate the following coefficients included in the PDSI calculation:

$$\alpha = {}^{\sum ET}\!\big/_{\sum PE} \qquad \beta = {}^{\sum R}\!\big/_{\sum PR} \qquad \lambda = {}^{\sum RO}\!\big/_{\sum PRO} \qquad \delta = {}^{\sum L}\!\big/_{\sum PL}$$

When calculated, these variables are used to derive the departure from normal moisture level *d*:

$$d = P - \overline{P} = P - [\alpha \bullet PE + \beta \bullet PR + \gamma \bullet PRO + \delta \bullet PL]$$

The departure from normal moisture level d is used to calculate the moisture anomaly index Z. The Z index is an expression of the relative departure of the weather of a particular week or month and location from the average moisture conditions of that week or month (Alley 1984). This is adjusted by a weighing factor for a given region called the climatic characteristic and is denoted by *K*. The Z index is calculated from the equation

$$Z = d \bullet K$$

The final computation of the Palmer index uses one of three intermediate variables. X1 is the index for wet periods before they become established and is always greater than 0. X2 is the index for all dry periods before they become established and is always less than 0. X3 is the index for any established wet or dry period. The indices are calculated with the formula

$$X_i = p \bullet X_{i-1} + q \bullet Z$$

where $p = 0.897$ and $q = 1/3$. For the self calibrating version of the Palmer index that is part of the PDSI software package from the National Agricultural Decision Support Center at the University of Nebraska, Lincoln, p and q are adjusted to the time scale as well as the characteristics of the climate at the location of interest (Palmer 1965, PDSI 2003). For a more detailed examination of the equations, assumptions and limitations involved in the calculation of the Palmer index see Palmer (1965) and Alley (1984).

Daily precipitation records for the Sonora Experiment Station were complete. Daily temperature records were incomplete for some time intervals. Weekly and monthly averages were calculated from these daily temperature records. No measures were made for weekly temperature averages if more than three missing records were recorded for a given week. Total weekly and monthly measurements were calculated from daily rainfall measurements. Weekly and monthly long-term means for temperature and rainfall were calculated from the 83 years of daily measurements. All temperature and rainfall records were complete for the time periods of interest for this analysis.

Data files were created for the weekly and monthly temperature averages, the cumulative weekly and monthly precipitation measurements, and the long-term weekly and monthly temperature mean. A parameter file utilized by the PDSI software was created with measurements of the available water holding capacity of the underlying soil layer and the negative tangent of the latitude of the Sonora Experiment Station. The PDSI software assumes two soil horizons, a surface layer and an underlying layer. It is assumed that the surface layer has a storage capacity of 25 mm of water. Water storage capacity for the underlying soil layer was calculated from the Sutton county soil survey (Wiedenfeld and McAndrew 1968). Total available water holding capacity of the Tarrent soil series was calculated as 32 mm of water. This was derived from the average depth of the Tarrent soil series and the water holding capacity per inch of stony clay soil (Wiedenfeld and McAndrew 1968). A measurement of $32mm - 25mm = 7mm$ of water was used as the available water holding capacity of the underlying soil horizon in the PDSI parameter input file.

PDSI values were calculated for all years from 1919 to 2002. Since the emphasis of this investigation is a comparison of the two major drought events, only two 10 year periods, 1949 to 1959 and 1992 to 2002 are presented here to illustrate conditions prior to, during and post-drought.

Quarterly PDSI values were generated by taking the mean of the following 3 month intervals: 1) December, January, and February 2) March, April, and May 3) June, July, and August 4) September, October, and November.

The key to interpreting PDSI values is as follows: 4.0 and above = extreme moist spell, 3.0 to 3.9 = very moist spell, 2.0 to 2.9 = unusual moist spell, 1.0 to 1.9 = moist spell, 0.5 to 0.9 = incipient moist spell, 0.4 to -0.4 = near normal, -0.5 to -0.9 = incipient drought, -1.0 to -1.9 = mild drought, -2.0 to -2.9 = moderate drought, -3.0 to -3.9 = severe drought, -4.0 and below = extreme drought (Palmer 1965).

Vegetation Sampling

Permanent vegetation sampling plots were established within the grazing treatment units in 1948. Three lines were established on the long axis of each of the 8 grazing units. Twelve permanently marked 30.5 cm X 30.5 cm (originally measured as 1 ft^2) quadrats were established on each line for a total of 36 quadrats per treatment unit. Each quadrat was established at least 4 m from the nearest woody plant and located in an area with sufficient soil resources to support herbaceous vegetation. Rock outcrops and very shallow soil sites were excluded.

Basal diameter of all perennial grasses was measured within each quadrat annually from 1949 to 1964 and periodically from 1964 to the present. Sample dates were variable throughout the history of the data set. Past analysis has shown that current season rainfall has no significant effect on current year basal area measurements thus legitimizing comparisons between data sets with seasonally variable sample dates (Herbel et al. 1972).

Basal diameter measurements for each individual perennial grass were converted into circular basal area measurements. All perennial grasses rooted within the quadrat were measured. A total of 21 years of data spanning a period of 53 years exist for this data set.

Vegetation Data Analysis

Detrended Correspondence Analysis (DCA; (Hill 1979, Hill and Gauch 1980, Gauch 1982) was performed on the 21 years of data for the 10 most abundant perennial grass species using the default options in the software package PC-ORD (McCune and Mefford 1999). Detrended Correspondence Analysis has been demonstrated to be a robust method of extracting gradients predicting species abundance (Ejrnaes 2000).

Ordination techniques such as DCA perceive rare species as outliers. This can obscure the analysis of data and mask directional shifts in species composition across time. The elimination or down rating of rare species is common practice in DCA and other ordination techniques in order to minimize the stochastic influence of these species on the analysis (Hill and Gauch 1980, Gauch 1982, Jongman et al. 1995). Precedence is also set for the removal of abundant species with relatively even distributions (Gemborys and Hodgkins 1970, Ware 1988, Fuhlendorf 1996, Fuhlendorf and Smeins 1996, 1997). The perennial grass *Hilaria belangeri* was omitted from the analysis due to its even abundance across years and grazing treatment units.

The ten perennial grass species used in this analysis were: *Aristida purpurea*, *Bouteloua curtipendula*, *Bouteloua hirsuta*, *Bouteloua trifida*, *Bothriochloa barbinodis*, *Digitaria cognatum*, *Erioneuron pillosum*, *Eriochloa sericea*, *Panicum hallii*, and *Stipa leucotricha*. Past analysis of this data set and suite of species included only species with summed basal area >500 cm^2 across all years and treatments (Fuhlendorf and Smeins 1997). Species included in this iteration of the analysis did not meet this past selection criteria due to limited plant production during the current drought study period. Failure to meet this past selection criteria did not impact the outcome or interpretation of the analysis. Correlation analysis was utilized to examine the relationship of DCA axes to both grazing intensity and the distribution of perennial grass species basal area.

Detrended correspondence analysis is an eigenvector technique based on reciprocal averaging. DCA corrects the “arch effect” common in other types of reciprocal averaging ordinations by detrending data with the criteria that second and higher axis have no systematic relations with lower axis. Reciprocal averaging techniques also have the problem of compression of the ends of the first axis relative to the middle of the axis. DCA corrects this problem through axis rescaling based on standardization to unit within-sample variance (Hill and Gauch 1980, Gauch 1982, Jongman et al. 1995).

Comparisons across grazing intensities between the drought years 1953 and 2002 were made for differences in perennial grass basal area, density and basal area per plant with the non-parametric Scheier-Ray-Hare analysis of variance and Wilcoxon signed rank tests. Analysis of variance was used to test for differences in treatment unit summations of perennial grass basal area and density between drought years. A natural log transformation was used for the perennial grass density summation data set in order to meet the assumptions of normality and equality of variance. The years 1953 and 2002 were chosen because they had the lowest basal area measurements across a long term vegetation monitoring data set of permanently marked quadrats that began in 1948 as well as the most complete data set with the fewest missing quadrats.

Results

Drought Pattern and Intensity

Mean and median rainfall distribution was bimodal with peaks in the fall and spring. Mean annual rainfall was approximately 570 mm while median annual rainfall was approximately 425 mm, a difference of 145 mm (Fig. 2). The differences between mean monthly rainfall and median monthly rainfall were greatest during the growing season months of April through September with the largest differences occurring for the months of July and August. The difference between the mean and median rainfall curves for the second mode in September (14.5 mm) was much greater than the differences for the first mode in May (8.7 mm) (Fig. 2).

Quarterly and monthly Palmer drought severity index values were markedly different in intensity, duration, and pattern for the time periods of 1949 to 1959 and 1992 to 2002 (Fig. 3). Index values for the six year drought event of 1951 to 1956 were continuously below the moderate drought level (< -2.00) for all years. The subset of years 1951 to 1953 were at extreme drought levels (< -4.00) year round with some monthly values of -5.00, the lowest recorded PDSI values for the 83 years of weather data for the Sonora Experiment Station.

The pattern of quarterly Palmer drought severity index values that emerges for the time period 1992 to 2002 was that of an increasing sinusoidal curve starting in 1994 and increasing in amplitude until the year 2001. The general pattern was alternating years of surplus precipitation followed by deficit precipitation. And perhaps more importantly, during years of surplus precipitation, a majority of the precipitation fell during the cool season with lower amounts or deficit precipitation during the growing season (Fig. 3).

The timeline of climatic events leading to the significant perennial grass mortality of 2001 and 2002 generally followed an annual pattern of October through September. Climatic events for the three years proceeding 2002 swung wildly from above normal conditions to severe drought back to above normal conditions again. August 1998 through July 1999 was marked by abundant precipitation and normal to below normal temperatures as reflected in the monthly Palmer drought severity index values for this time period (2.0 to 2.5). August 1999 through September 2000 was marked by deficit precipitation and above normal temperatures with the lowest continuous PDSI values for the Sonora Experiment Station for any 12 month time period outside of the drought of the 1950's and the dust bowl drought of 1934. October 2000 through May 2001 was marked by abundant precipitation with continuous PDSI values ranging from unusual moist spells (2.0) to very moist spells (3.9). PDSI values dropped significantly from an unusual moist spell (2.5) to mild drought (-1.0) from May 2001 to June 2001.

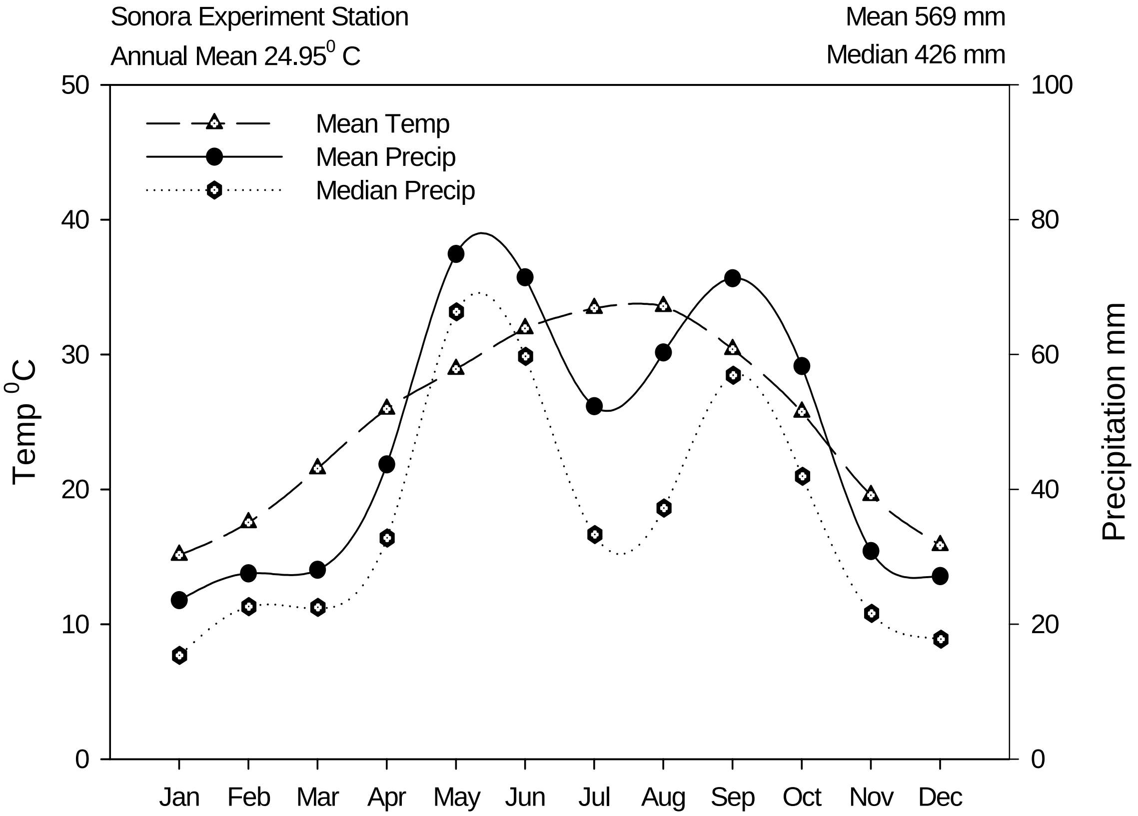


Fig. 2. Walter climate graph (Walter and Breckle 2002) of the Sonora Experiment Station for the years 1919 to 2002. Scale is a 1:2 ratio of the monthly mean temperature to the monthly mean precipitation.

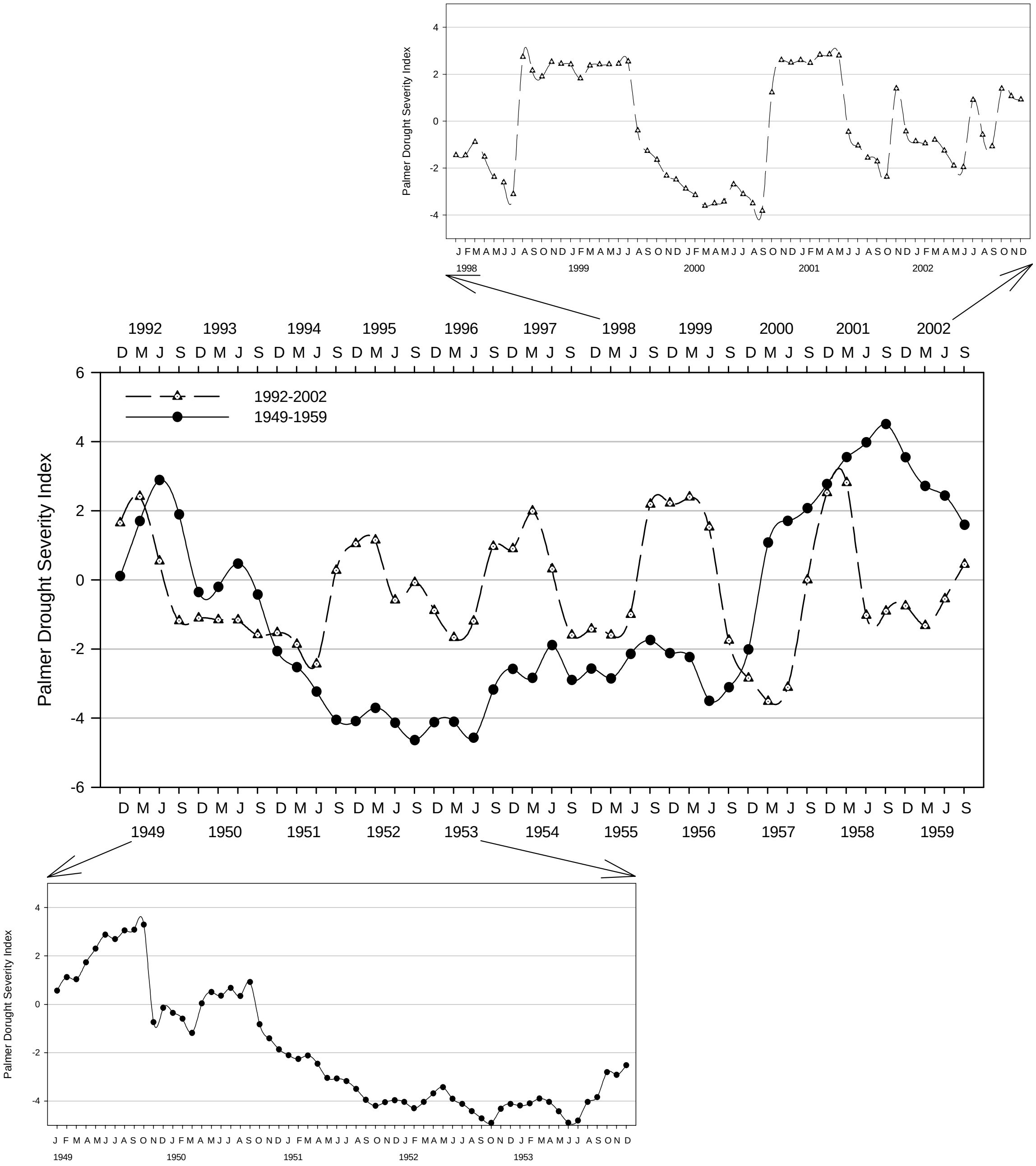


Fig. 3. Quarterly Palmer drought severity index values for the years 1949 to 1959 & 1992 to 2002. The overlay of lines is not meant for individual year pairing comparisons but is intended to show the long term climatic pattern of two different drought events. D = mean PDSI Dec, Jan, Feb. M = mean PDSI Mar, Apr, May. J = mean PDSI Jun, Jul, Aug. S = mean PDSI Sep, Oct, Nov. Insets are the monthly PDSI values for the years 1949 to 1953 & 1998 to 2002. See Methods for PDSI key.

The remainder of 2001 and 2002 was variable with a majority of these months having PDSI values of incipient to mild drought (-0.5 to -1.9) with no dominate pattern of severe drought or surplus moisture (Fig. 3).

It should be noted that the severe drought of 1999 to 2000 was not evident when examined at the yearly temporal scale (Fig. 1). Total annual precipitation for these years was close to the mean total annual precipitation at this scale of temporal resolution. Drought conditions in this instance were only seen at finer temporal scales of analysis.

Past analysis of herbaceous vegetation response to weather variation showed the strongest correlation between perennial grass basal area and three year running averages of precipitation (Herbel et al. 1972, Fuhlendorf and Smeins 1997). The years 1953 and 2001 had the lowest basal area across a long term vegetation monitoring data set that began in 1948. In light of this relationship of basal area and three year running averages of precipitation, weekly temperature and precipitation were plotted for the time intervals 1951 to 1953 and 1999 to 2001 in order to examine the similarities and differences of these two drought events.

Large differences in weekly mean high temperature were observed when comparing these two time periods. August 1999 to September 2000 was a period of high temperatures when compared to both the long term weekly mean as well as August 1951 to September 1952 (Fig. 4). Precipitation patterns for both of these time intervals were more similar than different. This was a period of continuous year round precipitation deficit for both time intervals (Fig. 5). There was a break in this continuous drought with the onset of spring rains in April and May with a greater amount of precipitation occurring in 2000 than in 1952. This pattern of deficit precipitation continued during the 1950’s drought while the pattern was broken with abundant precipitation in the winter months of October through December 2001 (Fig. 5). A similar pattern of deficit precipitation continued for the 1950’s drought until 1956. Higher temperatures persisted into the summer of 2001 with more abundant precipitation.

The general pattern was one of higher temperatures from 1999 to 2001 than in 1951 to 1953. The more recent drought had a shorter period of continuous deficit precipitation than found in the drought of the 1950's but with a strong pattern of abundant non-growing season precipitation.

Grazing Influence and Species Composition Between Drought Events

DCA ordination of the 10 dominant perennial grass species reduced the variation from these species to 3 DCA axes. The ordination accounted for 58.3% of the total species variation with 48.8% of this variation accounted for in the first two ordination axes (Table 1). Spearman's rank correlations of DCA axes scores to external environmental data showed strong significant relationships ($p < 0.01$) of axis 1 ($r = 0.67$) and axis 2 ($r = 0.23$) scores to grazing intensity (Table 1). Prior analysis of this data set showed similar results (Fuhlendorf and Smeins 1997).

Pearson's correlation analysis was utilized to examine the relationship of individual perennial grass species basal area to each DCA axis score. Significant relationships ($p<0.01$) were found for 7 of the 10 species utilized in the analysis and moderately significant relationships ($p<0.10$) for the other 3 species. Correlation coefficients ranged from absolute values 0.15 to 0.73 (Table 1).

The basal area of *Hilaria belangeri* was included in the correlation analysis but not in the ordination analysis. *Hilaria belangeri* has a broad ecological amplitude in this ecosystem but is known to have a positive correlation to increasing grazing intensity (Fuhlendorf and Smeins 1997). The positive correlation of *Hilaria belangeri* to the first DCA axis score adds further legitimacy to the interpretation of the first axis as a grazing gradient (Table 1).

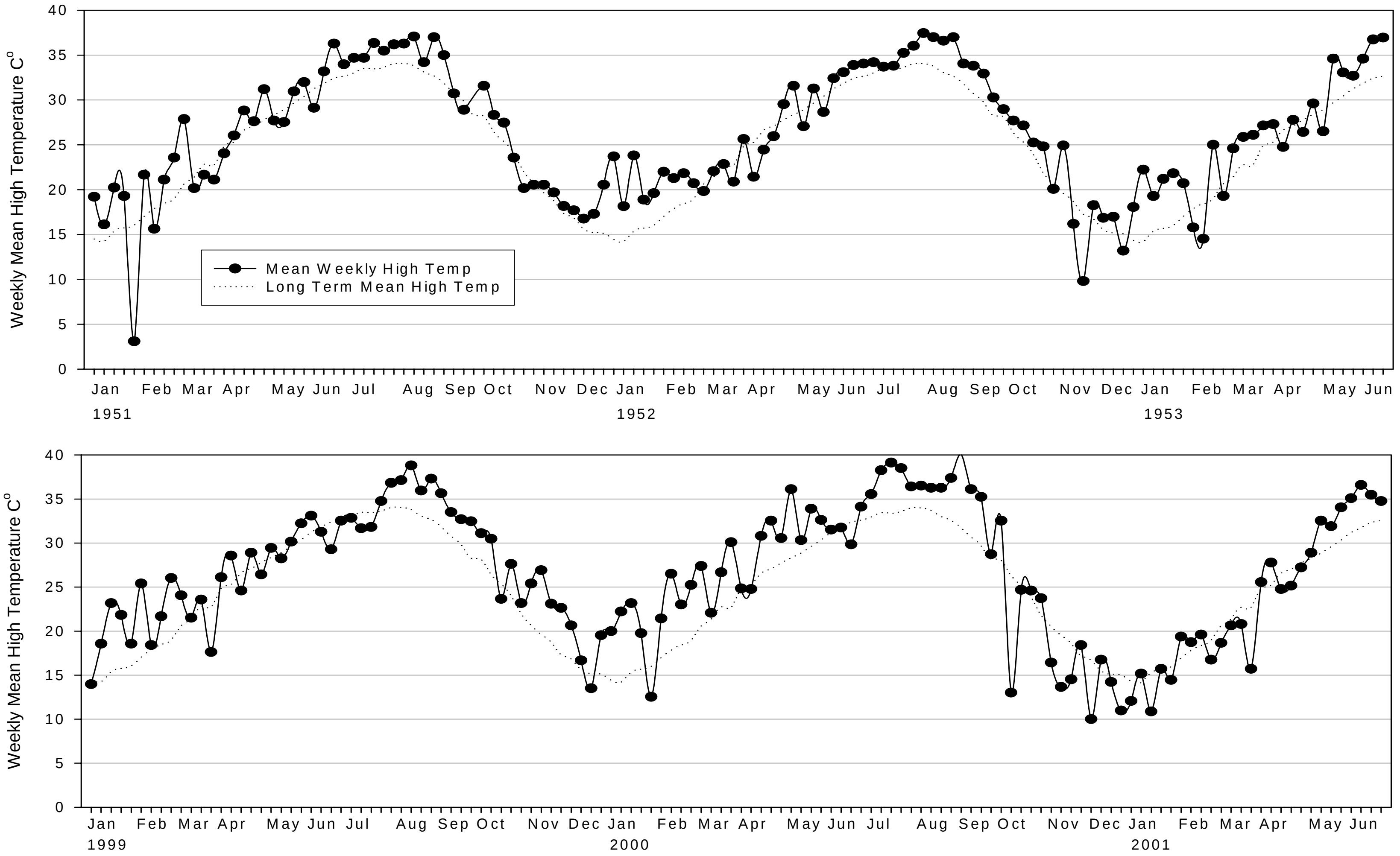


Fig. 4. Mean weekly high temperature for the years 1951 to 1953 and 1999 to 2001 and the long term (83 years) mean weekly high temperature.

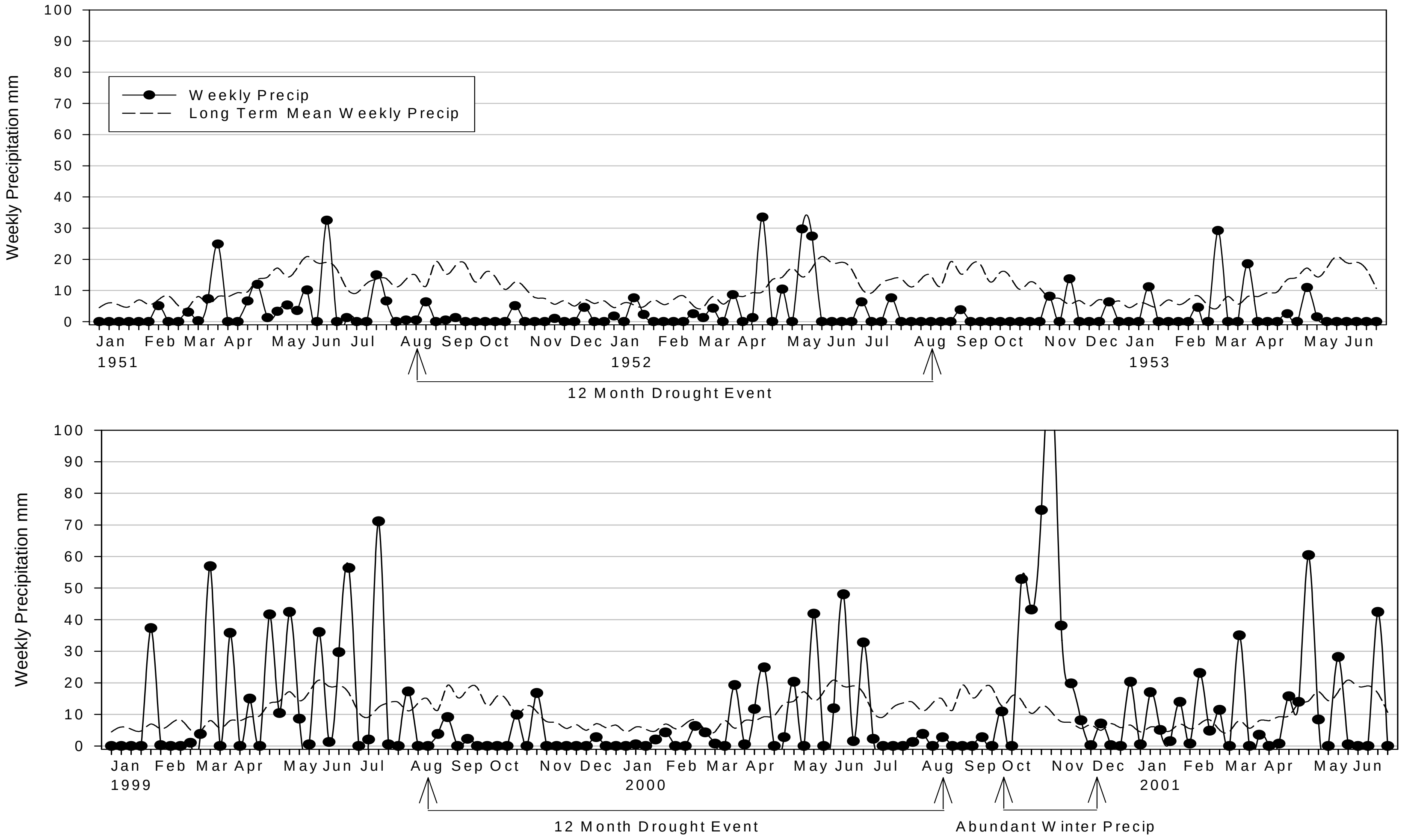


Fig. 5. Weekly precipitation for the years 1951 to 1953 and 1999 to 2001 and the long term (83 years) mean weekly precipitation.

Table 1. Results of the detrended correspondence analysis of the 13 most abundant perennial grass species within the heavy (n = 2), moderate (n = 4), and no grazing (n = 2) treatments across 53 years at the Sonora Experiment Station.

Variable	DCA Axis		
	1	2	3
Total species variance (inertia) in the species data: 1.252			
Eigenvalue	0.404	0.207	0.119
Cumulative percentage of variance from the species data	32.3	48.8	58.3
Pearson's Correlation of species with ordination axes			
Aristida purpurea	-0.15 #	0.58 **	0.45 **
Bothriochloa barbinodis	-0.34 **	-0.40 **	0.43 **
Bouteloua curtipendula	-0.54 **	-0.23 **	-0.24 **
Bouteloua hirsuta	-0.25 **	0.26 **	0.23 **
Bouteloua trifida	0.73 **	-0.03	0.11
Digitaria cognatum	-0.18 *	-0.56 **	-0.25 **
Erioneuron pilosum	0.24 **	-0.31 **	0.27 **
Eriochloa sericea	-0.55 **	-0.19 *	0.01
Hilaria belangeri	0.21 **	-0.07	0.25 **
Panicum hallii	-0.19 *	-0.55 **	0.00
Stipa leucotricha	-0.37 **	-0.37	-0.27 **
Spearman's Rank Correlation with Grazing intensity	0.67 **	0.23 **	0.07
#p<0.10 *p<0.05 **p<0.01			

The temporal trajectory of species composition for each of the three grazing treatments at the Sonora Experiment Station can be seen in the mean score for each DCA axis plotted by year and grazing intensity (Fig. 6). Grazing intensity for all replications was similar prior to the establishment of the 3 grazing treatments in 1948. This was seen in the overlapping positions of all treatment units in 1949, the first year of analysis. All three treatments followed similar trajectories from 1949 until the drought of 1951 to 1956. While all three treatments moved to positions higher on the grazing gradient (DCA axis 1) during the drought, the heavy grazing treatment separated from the parallel trajectories of the moderate grazing and no grazing treatments in 1953 and stabilized at the highest position on the grazing gradient (DCA axis score around 300) where it remained until 1983 (Fig. 6).

The moderate grazing and no grazing treatments remained on parallel trajectories throughout the drought of 1951 to 1956. The trajectories for these two treatments diverged beginning in 1963 with the no grazing treatment moving to lower positions along the grazing gradient and the moderate grazing treatment moving to positions between the no grazing and heavy grazing treatments (Fig. 6).

The greatest separation of the three grazing treatments occurred in 1983. The heavy grazing treatment maintained a position high on DCA axis 1 with a score around 300. The moderate grazing treatment maintained the same position found in 1963 around 125, while the no grazing treatment moved to the lowest position on DCA axis 1 around 50 (Fig. 6).

The moderate grazing and heavy grazing treatments began to converge in the early 1990’s with the greatest movement occurring with the heavy grazing treatment moving from a score around 300 to around 200. A statistical overlap of the positions for the moderate grazing and heavy grazing treatments occurred in 1993 suggesting that these treatments were converging in species composition.

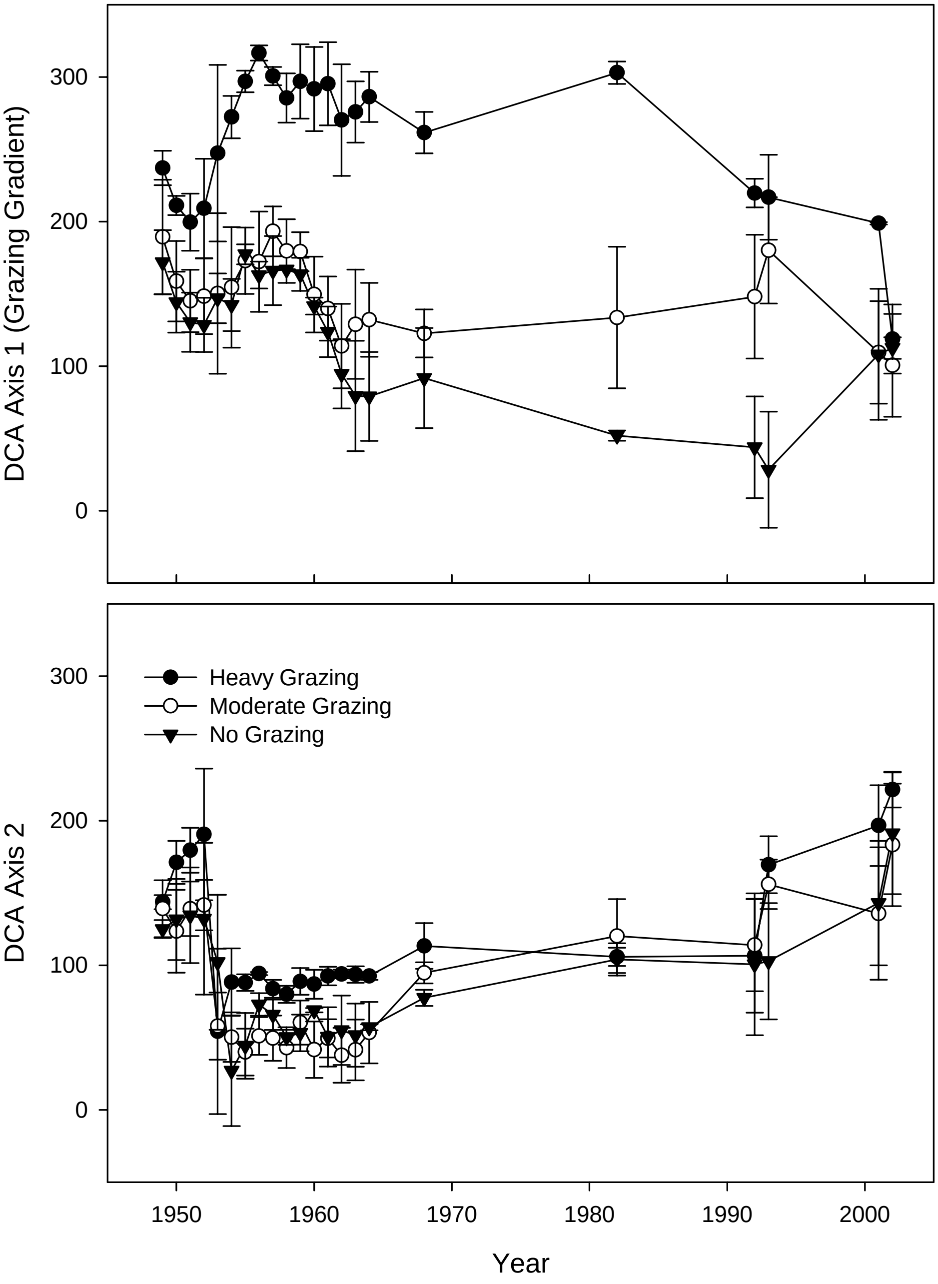


Fig. 6. DCA Axis 1 and Axis 2 scores for heavy (n = 2), moderate (n = 4), and no grazing (n = 2) treatments across 53 years at the Sonora Experiment Station. Error bars represent standard deviations between treatment units.

The no grazing treatment maintained a position similar to the 1983 axis 1 score around 50. All three grazing treatments converged during the drought years of 2001 and 2002 with a complete convergence of all three grazing treatments to a similar position occurring in 2002 (Fig. 6).

Differences in perennial grass species composition between grazing treatments were found with the DCA ordination during the drought of the 1950's (Fig. 6). The composition and community structure of perennial grass species in the heavy grazing treatment were different enough that the heavy grazing treatment separated from the moderate and no grazing treatment and moved to the highest position on the grazing gradient (DCA axis 1 score around 300) during the drought of the 1950's. This pattern occurred again during the drought of 2001 where all three grazing treatments moved to similar positions to that of 1953. All grazing treatments converged to a similar position on the grazing gradient during the year 2002 (DCA aixs 1 score around 100). The pattern for both drought events can be explained with a closer examination of the vegetation data.

During the drought of the 1950's, *Bouteloua trifida* was the dominate species among the 10 perennial grass species used in the DCA ordination for the heavy grazing treatment in 1953, making up over 60% of the total basal area for this group of species. Basal area for *Bouteloua trifida* in the heavy grazing treatment was 2.5 times greater than basal area in the moderate and no grazing treatments. *Bouteloua curtipendula* accounted for approximately 20% of the basal area for the moderate and no grazing treatments, more than five times greater than the basal area in the heavy grazing treatment. The remaining species were fairly ubiquitous across all three grazing treatments with the exception of *Aristida purpurea* which had 15 times greater basal area in the no grazing treatment than in the moderate or heavy grazing treatments (Table 2).

Table 2. Mean basal area (BA) (cm^2 / m^2), basal area per plant (BA/P) (cm^2 / individual), and density (Den) (individuals / m^2) for *Hilaria belangeri* and the 10 perennial grass species utilized in the DCA of the heavy grazing (HC) (n = 2), moderate grazing (Mod) (n = 4), and no grazing (NG) (n = 2) treatments at the Sonora Experiment Station for the years 1949, 1953, 1963, 1993, 2001 and 2002. ARPU = *Aristida purpurea* BOBA = *Bothriochloa barbinodis* BOCU = *Bouteloua curtipendula,* BOHI = *Bouteloua hirsute* BOTR = *Bouteloua trifida* DICO = *Digitaria cognatum* ERPI = *Erioneuron pilosum* ERSE = *Eriochloa sericea* HIBE = *Hilaria belangeri* PAHA = *Panicum hallii* STLE = *Stipa leucotricha*

			ARPU	BOBA	BOCU	BOHI	BOTR	DICO	ERPI	ERSE	HIBE	PAHA	STLE	Total
1949	BA	HC	44.4	0.0	1.0	13.1	60.6	9.0	28.9	0.0	430.6	0.9	2.7	591.2
		Mod	23.4	0.7	4.8	3.3	10.0	7.4	14.2	0.3	285.1	0.0	3.5	352.7
		NG	19.0	5.8	5.0	6.8	3.3	3.7	20.6	0.0	222.1	0.8	1.6	288.7
	BA/P	HC	6.5	0.0	0.8	4.6	2.7	1.9	1.2	0.0	2.0	0.5	1.8	2.1
		Mod	2.7	4.9	0.7	2.1	1.1	1.4	0.9	3.9	1.0	0.1	0.4	1.0
		NG	2.4	7.8	0.6	1.2	0.6	1.2	1.2	0.0	0.9	2.7	0.5	1.0
	Den	HC	6.9	0.0	1.2	2.8	22.3	4.6	23.3	0.0	216.6	1.9	1.5	281.1
		Mod	8.7	0.2	7.6	1.6	9.1	5.4	16.3	0.1	278.9	0.1	8.4	336.4
		NG	7.9	0.8	6.9	5.7	5.4	3.1	16.7	0.0	243.0	0.3	3.0	292.8
1953	BA	HC	0.2	0.0	0.2	0.0	5.8	2.2	0.3	0.0	22.5	0.6	0.3	32.1
		Mod	0.4	0.7	2.8	0.1	2.4	4.8	0.6	0.1	25.5	0.7	1.7	39.8
		NG	6.0	0.2	6.9	1.1	0.2	8.0	2.6	0.0	27.3	1.3	0.1	53.7
	BA/P	HC	0.3	0.0	0.3	0.0	0.3	0.4	0.1	0.0	0.4	0.2	0.2	0.3
		Mod	0.6	1.9	0.8	0.5	0.5	0.7	0.2	0.6	0.4	0.4	0.5	0.5
		NG	4.5	0.5	1.6	0.6	0.1	0.7	0.5	0.0	0.5	0.7	0.1	0.7
	Den	HC	0.8	0.0	0.9	0.0	19.9	6.0	2.5	0.0	63.4	2.8	1.5	97.8
		Mod	0.8	0.4	3.5	0.2	5.2	6.5	3.2	0.2	58.9	1.8	3.7	84.4
		NG	1.3	0.5	4.5	1.8	2.5	11.7	5.2	0.0	52.2	1.9	0.9	82.5
1963	BA	HC	4.0	0.0	0.0	0.5	27.0	2.8	26.4	0.0	87.2	1.2	0.5	149.6
		Mod	4.4	14.9	25.0	0.9	7.6	34.0	19.2	15.3	276.8	5.8	0.6	404.5
		NG	6.7	23.0	25.5	16.0	1.6	43.7	12.0	44.9	86.6	5.6	9.0	274.6
	BA/P	HC	1.1	0.0	0.0	0.5	1.0	0.6	0.9	0.0	1.0	0.6	0.9	1.0
		Mod	2.5	10.0	1.6	0.9	1.3	1.5	0.8	5.3	2.0	0.9	0.6	1.8
		NG	4.1	77.0	3.1	4.1	0.8	2.9	0.9	0.0	3.2	0.8	10.0	3.4
	Den	HC	3.7	0.0	0.0	1.2	27.0	4.5	30.9	0.0	85.9	1.9	0.6	155.7
		Mod	1.9	1.5	15.6	1.1	6.1	22.9	24.3	2.9	139.9	6.4	1.1	223.7
		NG	1.6	0.3	8.2	3.9	2.1	14.9	13.1	2.1	27.2	7.0	0.9	81.3
1993	BA	HC	56.4	0.0	0.7	1.4	23.7	9.6	11.0	0.0	73.3	0.3	0.5	176.9
		Mod	30.6	0.1	13.1	4.4	19.5	2.8	15.2	3.9	141.5	0.1	4.3	235.5
		NG	11.8	0.3	30.7	10.5	0.2	2.0	4.4	75.2	26.2	0.2	5.3	166.8
	BA/P	HC	6.1	0.0	2.3	0.8	0.9	1.8	0.6	0.0	1.0	0.4	0.6	1.3
		Mod	6.7	0.7	1.5	2.8	3.5	1.6	2.4	1.7	2.0	0.3	0.7	2.2
		NG	3.2	2.0	2.4	3.2	0.7	1.4	2.2	7.3	2.5	1.3	1.5	3.5
	Den	HC	9.2	0.0	0.3	2.7	25.7	5.3	17.6	0.0	75.0	0.8	0.8	137.4
		Mod	4.6	0.1	9.0	1.6	5.6	1.7	6.2	2.3	69.3	0.4	6.6	107.4
		NG	3.6	0.2	12.6	3.3	0.3	1.5	2.0	10.3	10.4	0.2	3.5	47.9
2001	BA	HC	12.8	0.0	0.1	0.0	6.7	0.0	0.3	0.0	4.6	3.4	3.2	31.1
		Mod	9.2	0.0	14.5	10.1	0.0	1.6	4.7	0.3	28.2	0.1	2.8	71.5
		NG	14.1	0.0	13.1	0.9	0.0	1.5	1.6	0.0	11.1	1.2	0.5	44.0
	BA/P	HC	3.5	0.0	0.7	0.0	3.5	0.0	0.3	0.0	1.9	0.6	0.8	2.3
		Mod	16.9	0.0	7.2	6.5	0.0	4.4	5.7	2.9	3.7	0.5	1.2	4.6
		NG	4.6	0.0	1.6	0.5	0.0	0.6	1.9	0.0	3.5	1.9	0.4	2.0
	Den	HC	3.7	0.0	0.2	0.0	1.9	0.0	0.9	0.0	2.5	0.5	3.9	13.6
		Mod	0.6	0.0	2.0	1.6	0.0	0.4	0.8	0.1	7.6	0.2	2.4	15.7
		NG	3.2	0.0	8.4	2.0	0.0	2.4	0.8	0.0	3.2	0.7	1.4	22.1
2002	BA	HC	14.6	0.0	0.0	2.6	0.1	0.0	0.0	0.0	18.8	0.6	6.0	42.7
		Mod	22.8	0.0	8.1	0.6	0.0	0.8	2.2	0.9	35.7	0.0	11.0	82.1
		NG	15.8	0.0	9.8	0.0	0.0	0.3	0.0	1.3	14.2	1.1	4.2	46.7
	BA/P	HC	6.9	0.0	0.0	8.1	0.31	0.0	0.0	0.0	5.2	0.4	2.3	4.2
		Mod	27.1	0.0	8.8	2.2	0.00	2.9	0.0	5.4	4.5	0.3	2.5	5.3
		NG	9.1	0.0	2.1	0.0	0.00	2.0	5.2	4.1	5.6	3.6	5.3	4.4
	Den	HC	2.1	0.0	0.0	0.3	0.16	0.0	0.0	0.0	3.6	1.3	2.6	10.1
		Mod	0.8	0.0	0.9	0.3	0.00	0.3	0.4	0.2	7.9	0.1	4.5	15.4
		NG	1.7	0.0	4.7	0.0	0.00	0.2	0.0	0.3	2.5	0.3	0.8	10.5

The relative abundance of *Aristida purpurea* seemed to have had little impact on the DCA ordination given that the moderate and no grazing treatments occupy the same statistical position in Fig. 6 for 1953.

This pattern of the heavy grazing treatment separating from the moderate and no grazing treatment in 1953 based on the distribution of *Bouteloua trifida* and *Bouteloua curtipendula* agrees with the correlation of these species with the grazing gradient (DCA axis 1) (Fig. 6). Correlations for both species were strongly significant ($p<0.01$) with large coefficients: *Bouteloua trifida* $r = 0.73$ and *Bouteloua curtipendula* $r = -0.54$. Only one other species had as large a significant correlation coefficient, *Eriochloa sericea* with $r = -0.55$ (Table 1), but this species accounted for less than 1% of the total basal area in 1953 for the 10 species used in the DCA ordination.

Of the 10 species used for the DCA ordination, the most abundant species across all grazing treatments for the year 2001 was *Aristida purpurea* accounting for 37% of the basal area on average across grazing treatments (Table 1). This number increased to 53% in 2002. *Aristida purpurea*, though accounting for a large percentage of basal area, was evenly distributed across all grazing treatments. The distribution of *Bouteloua trifida* and *Bouteloua curtipendula* in 2001 followed a pattern similar to 1953 with a majority of basal area for *Bouteloua trifida* found in the heavy grazing treatment and a majority of basal area for *Bouteloua curtipendula* found in the moderate and no grazing treatments. This pattern accounted for the separation of the heavy grazing treatment from the moderate and no grazing treatments along the grazing gradient in 2001. The same pattern did not hold true in 2002 where basal area for *Bouteloua trifida* across all grazing treatments was essentially zero. Basal area in 2002 for *Bouteloua curtipendula* followed the same pattern as 2001 but with a 35% reduction in basal area. This pattern, as well as the large amount of *Stipa leucotricha* evenly distributed across grazing treatments, accounts for the collapse of all three grazing treatments to a similar position on the grazing gradient in 2002. It is interesting to note that 2002 had the third largest mean basal area for *Stipa leucotricha* across the 53 year history of this data set while at the same time having the third lowest total basal area for the data set as a whole. Only the years 1982 and 1992 had larger mean basal area values for *Stipa leucotricha* and both years had abundant to normal annual precipitation with over eight times the total basal area of 2002. Abundant cool season precipitation over the last several years could explain this shift in abundance.

The grazing tolerant stoloniferous grass *Hilaria belangeri* was the dominant perennial grass prior to and during the drought of the 1950's (Table 2). The dominance of *H. belangeri* and other grazing tolerant short grasses during this time period was a result of over 60 years of continuous heavy grazing at the Sonora Experiment Station prior to the establishment of the different grazing treatments in 1949. Short grasses composed over 80% of the perennial grass basal area across all grazing treatments at the time of initial sampling (Fuhlendorf et al. 2001) In 1953, *H. belangeri* accounted for over 50% of the total basal area in the no grazing treatment units and over 60% in the grazed treatment units as well as over 60% of the perennial grass density across all grazing treatments. *H. belangeri* was less dominant during the drought year 2002 but still accounted for a majority of the perennial grass basal area and density.

Perennial Grass Community Structure Between Drought Events

The difference in perennial grass basal area between drought years and non-drought years was significant. The mean perennial grass basal area for the years 1953, 2001, and 2002 (41.9, 48.9 & 57.2 cm^2 / m^2) were the lowest measurements for the 22 years of data across a 53 year time span (Table 2). Mean basal area for non-drought years was on average 6 times greater.

Perennial grass community structure for the drought years 1953 and 2002 showed no differences in perennial grass basal area but there were significant differences in how this basal area was distributed. Scheirer-Ray-Hare non-parametric analysis of variance showed no difference in perennial grass basal area between years and across grazing intensities (Fig. 7, Table 3). Wilcoxon signed rank tests also showed no difference in basal area between the years 1953 and 2002 (Fig. 8, Table 4). Analysis of variance for perennial grass basal area summed by treatment unit also showed no difference between years and across grazing intensities (Fig. 9, Table 5).

Significant differences were found at all levels of analysis for perennial grass density between the years 1953 and 2002 but not across grazing intensities (Tables 3 & 4). Both Scheirer-Ray-Hare non-parametric analysis of variance and Wilcoxon signed rank tests were significant for differences in perennial grass density between the years 1953 and 2002 (Table 3 & 4). Analysis of variance for perennial grass density summed by treatment unit was also significant between years but not across grazing intensities (Fig. 9,Table 5).

Significant differences between years for perennial grass basal area per plant were found with the Wilcoxon signed rank test when basal area per plant was grouped by year (Fig. 8, Table 4). No significant differences were found when basal area per plant was analyzed by combinations of year and grazing intensity with the Scheirer-Ray-Hare non-parametric analysis of variance (Fig. 7, Table 3).

The percentage of quadrats with zero values plotted by grazing intensity illustrates the dramatic differences in perennial grass community structure between the drought years 1953 and 2002 (Fig. 10). Approximately 10% of the quadrats sampled in 1953 had zero values with no live plants. In 2002 this number increased to approximately 55% of the measured quadrats. This pattern was consistent across grazing intensities for both years and reflected the pattern found with the comparisons of perennial grass basal area and density.

The perennial grass community structure in 1953 was one of a high density of small basal area plants compared to a low density of high basal area plants in 2002. The percentage of quadrats with zero values for 2002 illustrate that basal area was concentrated in a relatively small number of quadrats having large basal area plants.

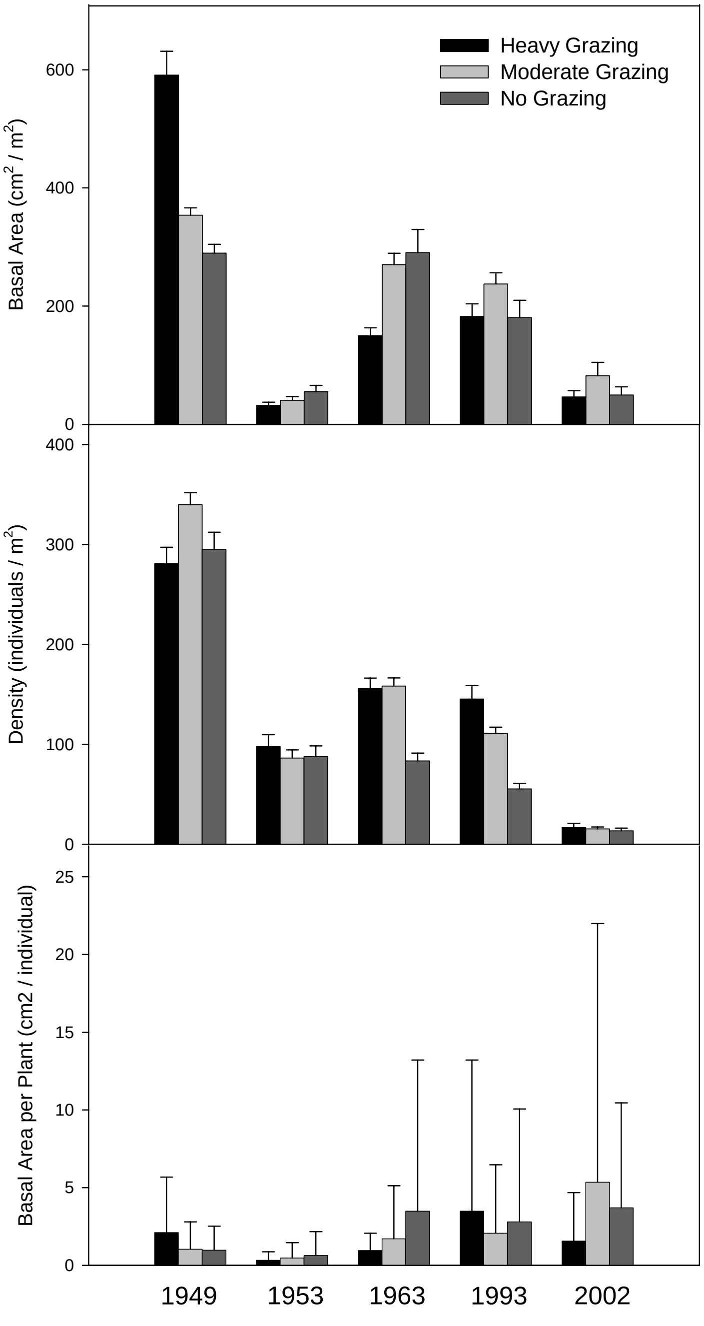


Fig. 7. Mean perennial grass basal area, density, and basal area per plant for heavy grazing (n = 2), moderate grazing (n = 4) and no grazing (n = 2) treatments at the Sonora Experiment Station for the years 1949, 1953, 1963, 1993, and 2002. Error bars = standard error of the mean. Note that this figure includes all perennial grass species while Table 2 includes the 10 perennial grass species utilized in the DCA.

Table 3. Scheirer-Ray-Hare non-parametric analysis of variance for perennial grass basal area, plant density, and basal area per plant across heavy, moderate, and no grazing treatments between the drought years 1953 and 2002.

	SS	SS/MS_{total}	d.f.	P-value
Basal Area				
Year	126.19	0.04	1	0.15
Grazing	2091.79	0.63	2	0.27
Year X Grazing	4538.05	1.37	2	0.50
Density				
Year	5950.45	67.41	1	0.00
Grazing	44.25	0.50	2	0.78
Year X Grazing	27.79	0.32	2	0.85
BA/Plant				
Year	29597.04	12.25	1	1.00
Grazing	2930.46	0.45	2	0.20
Year X Grazing	4486.05	0.43	2	0.20

Table 4. Wilcoxon signed rank tests for perennial grass basal area, plant density, and basal area per plant between the drought years of 1953 and 2002.

	N	Mean Rank	Sum	Z Score	P-value
2002 BA – 1953 BA					
Negative Ranks	158[a]	99.66	15746.5		
Positive Ranks	85[b]	163.52	13899.5		
Ties	19[c]				
Total	262			-0.842	0.400
2002 Den – 1953 Den					
Negative Ranks	200[d]	126.71	25342.5		
Positive Ranks	32[e]	52.67	1685.5		
Ties	30[f]				
Total	262			-11.570	0.000
2002 BA/P – 1953 BA/P					
Negative Ranks	141[g]	82.42	11621.5		
Positive Ranks	103[h]	177.36	18268.5		
Ties	18[i]				
Total	262			-3.012	0.003

a: BA02<BA53, b: BA02>BA53, c: BA02=BA53, d: Den02<Den53, e: Den02>Den53
f: Den02=Den53, g: BA/Pl02<BA/Pl53, h: BA/Pl02>BA/Pl53, i: BA/Pl02=BA/Pl53

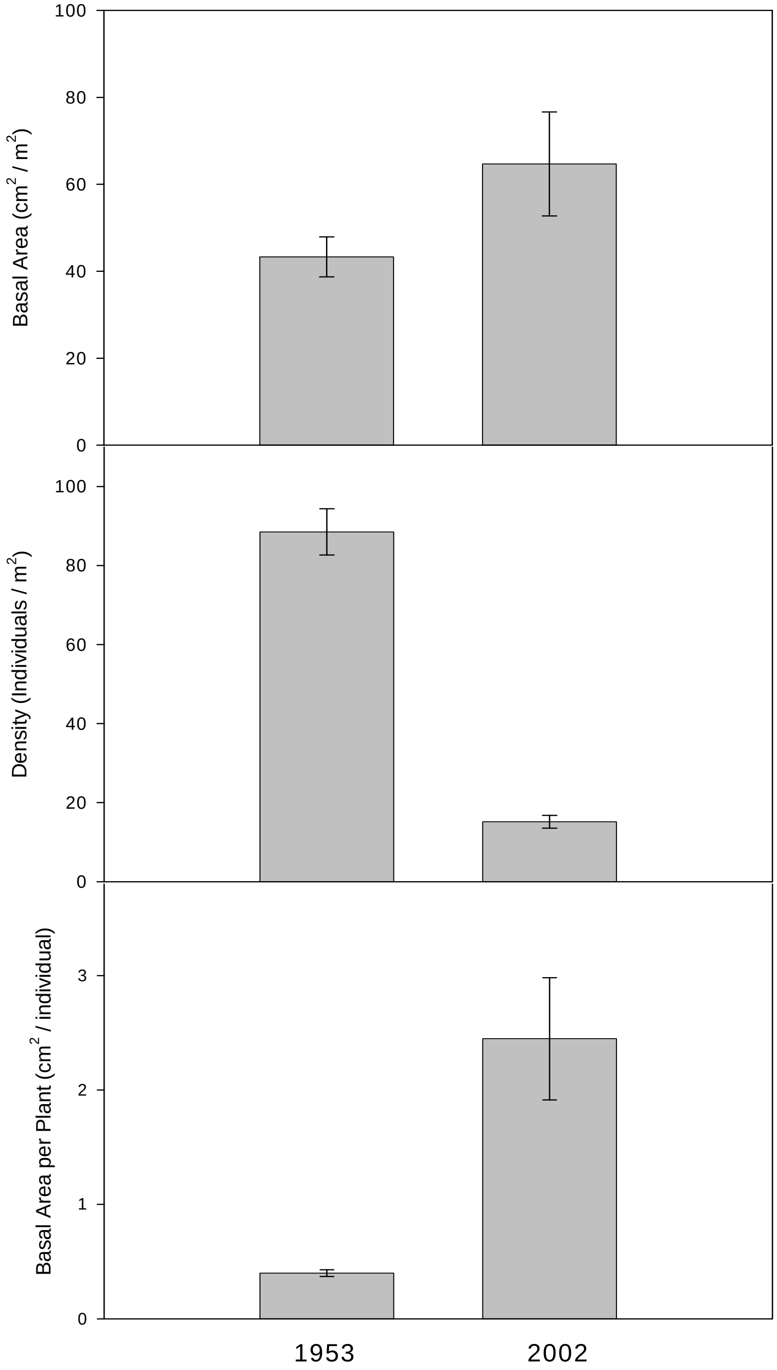


Fig. 8. Mean perennial grass basal area, density and basal area per plant for the two drought years 1953 and 2002 across all grazing treatments at the Sonora Experiment Station. Error bars = standard error of the mean.

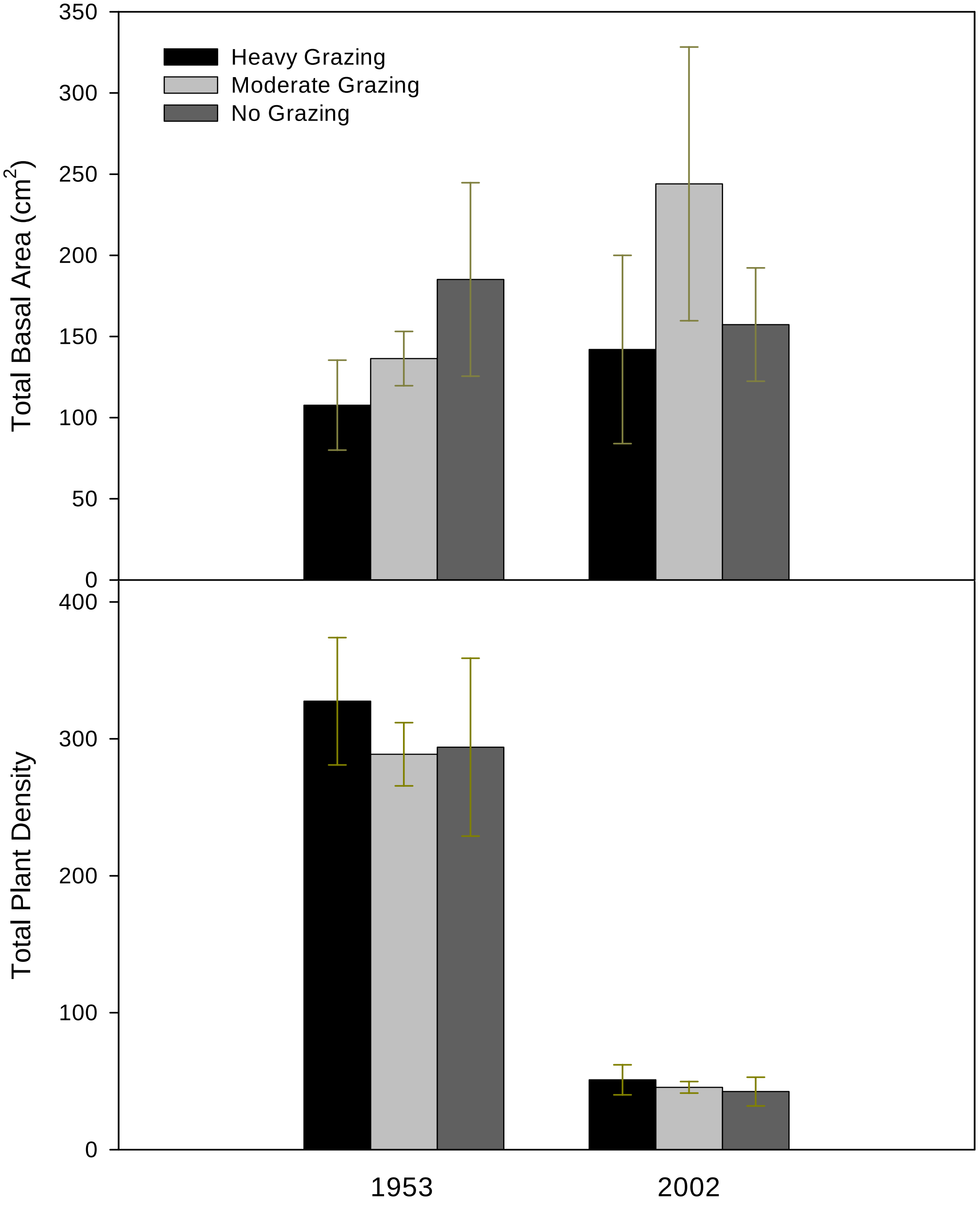


Fig. 9. Mean perennial grass basal area and plant density summations for the heavy grazing (n=2), moderate grazing (n=4), and no grazing (n=2) treatments for the years 1953 and 2002. Error bars = standard error of the mean.

Table 5. Analysis of variance for perennial grass basal area and plant density summed by treatment unit for heavy (n=2), moderate (n=4), and no grazing (n=2) treatments for the drought years 1953 and 2002.

Source	d.f.	MS	F	P-value
Basal Area				
Graze	2	5709.07	0.54	0.60
Year	1	5201.04	0.49	0.50
Graze X Year	2	6413.89	0.60	0.57
Density				
Graze	2	0.03	0.51	0.62
Year	1	12.83	243.06	0.00
Graze X Year	2	0.00	0.05	0.95

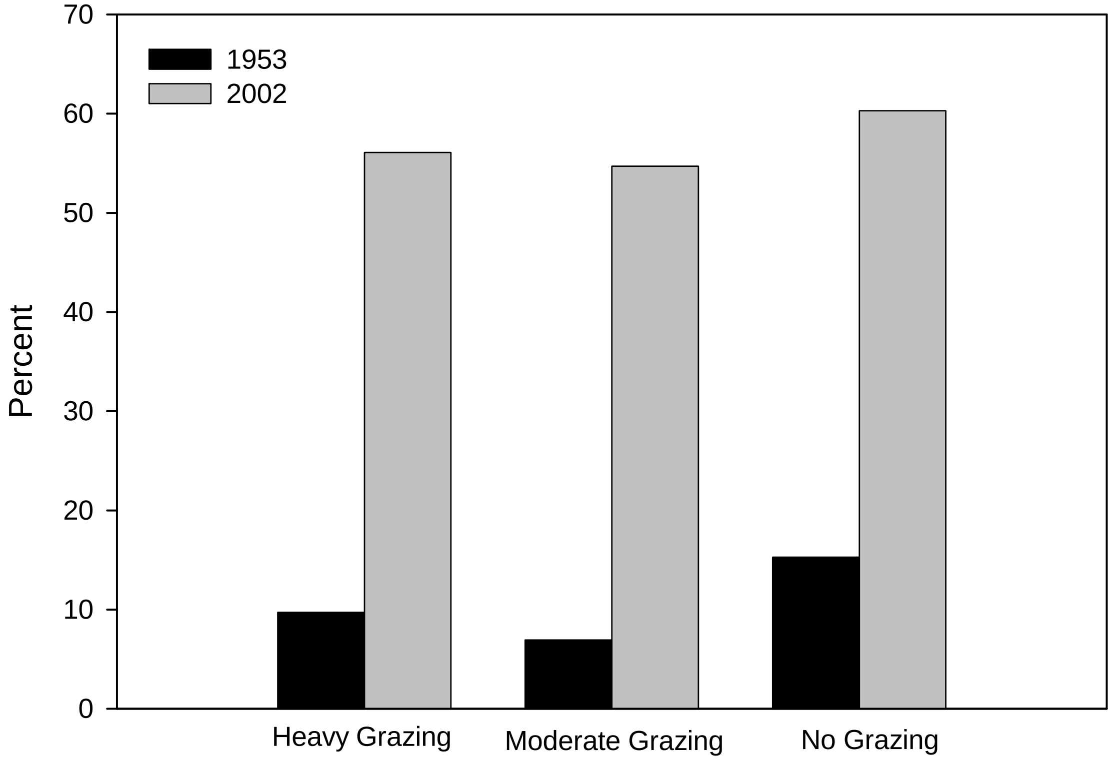


Fig. 10. Percentage of long-term permanent plots with 0 values (no perennial grasses) for the heavy grazing, moderate grazing, and no grazing treatments at the Sonora Experiment Station for the drought years 1953 and 2002.

Discussion

Perennial grass community response to each drought event was unique. The difference in perennial grass mortality between drought events is a function of the unique climatic structure of each drought interacting with the perennial grass community structure and composition at that point in time. The composition and community structure of perennial grasses during each drought event is a function of the long term grazing history of the Sonora Experiment Station.

The drought events of 1951 to 1956 and the more recent drought events centered on the year 2000 are structurally very different. Vegetation mortality associated with the drought of the 1950's was brought about by a roughly six year period of continuous year round extreme to moderate drought. This drought event was noted as the most severe uninterrupted drought sequence in Texas since 1698 (Stahle and Cleaveland 1988). Vegetation mortality during the more recent drought event was brought about by the interaction of discrete periods of alternating drought and abundant cool season precipitation. This repeating pattern of abundant precipitation followed by moderate to extreme drought across the years 1997 to 2001 is a unique event in the 83 years of weather records for the Sonora Experiment Station. The impact on perennial grass mortality by the interaction of these events was perhaps greater than the impact of these events individually. The order in which these events occurred may have amplified their negative impact on perennial grass production.

The long term grazing history of the Sonora Experiment Station is reflected in the temporal shift from a high density community of small basal area plants to a low density community of large basal area plants along a grazing intensity gradient (Fuhlendorf et al. 2001). This is seen in the high density, low basal area per plant perennial grass community structure in the drought of the 1950's and the low density, high basal area per plant community structure for the recent drought of 2001 and 2002 (Fig. 7). Total basal area for both drought events is at least five times less than basal area for non-drought years yet the influence of grazing across time is still a major driver of perennial grass community structure and composition during these events.

Compositional differences between grazing treatments were evident in the 1950’s drought. This was seen primarily in the heavy grazing treatment separation from the moderate and no grazing treatments in the DCA ordination analysis (Fig. 6). Compositional differences were seen in 2001 as well with the heavy graze treatment separating from the moderate and no grazing treatments by roughly the same distance on the grazing gradient, around 100 units (Fig. 6). These compositional differences disappeared in 2002 due to the significant perennial grass mortality across all species and grazing treatments. This high percentage of perennial grass mortality suppressed any compositional differences between grazing treatments.

The drought of the 1950’s was of longer duration and greater intensity than the drought event centered around the year 2000 based on Palmer drought severity index values yet no appreciable differences where found in basal area between these events (Fig. 7). Large differences in perennial grass density and basal area per plant were found between drought events (Fig. 7) suggesting that larger basal area plants had lower rates of mortality during the drought years 2001 and 2002.

Differences in perennial grass mortality by size class during drought events have been documented on deeper soil sites with larger plants appearing to be more drought tolerant (Chamrad and Box 1965, Box 1967, Hodgkinson 1996). Perennial grass populations dominated by high densities of small basal area plants due to grazing induced shifts in community structure showed higher rates of mortality during drought than communities with low densities of high basal area plants under light or no grazing pressure (O'Connor 1995, Hodgkinson 1996).

Perennial grass basal area per plant was higher coming into the current drought of 2001 and 2002 than basal area per plant measurements prior to the drought of the 1950’s (Fig. 7). Large basal area perennial grasses have been shown to alter their environment by producing and incorporating larger amounts of organic matter into the surrounding soil and more effectively capturing redistributed resources (Derner et al. 1997, Tongway and Ludwig 1997a). This larger pool of resources could impact individual plant drought persistence. However, the large basal area per plant measurements recorded during the more recent drought is not indicative of larger plants being more drought resistant. Perennial grass mortality in permanently marked quadrats was more wide spread across grazing treatments and species in the drought of 2001 and 2002 than the drought of the 1950's despite the larger individual plant size prior to drought onset (Fig. 10). Given the heterogeneous soil environment of the Sonora Experiment Station, plant survival is most likely a function of favorable landscape position and micro-site potential (rock fissures or outcrops, runon sites, pockets of deeper soil, etc) than the influence of plant size characteristics.

The grazing induced proportion and community structure of short and mid-grasses within a perennial grass community prior to drought onset may influence vegetation persistence during the drought event. The mid-grass *Bouteloua curtipendula* exhibited higher rates of mortality in the heavy grazing treatment than in the moderate or no grazing treatment during a short-term drought in the early 1990's at the Sonora Experiment Station (Briske and Hendrickson 1998) Heavy grazed, short-grass dominated communities have shown greater fluctuations in response to variable precipitation than communities with mixed populations of short and mid-grasses under moderate or no grazing (Fuhlendorf et al. 2001).

The perennial grass community prior to the drought of the 1950's was dominated by the short-grass *Hilaria belangeri* across all grazing treatments. The perennial grass community in the years prior to the drought of 2001 and 2002 was a mix of short and mid-grasses with the mid-grasses more abundant in the moderate and no grazing treatments and the short-grasses more dominant in the heavy grazing treatment (Fuhlendorf and Smeins 1997, Fuhlendorf et al. 2001). In a study examining the response of short and mid-grasses to small rainfall events, the short grass *H. belangeri* and the mid-grass *B. curtipendula* both showed improved leaf water potential and leaf conductance from 10 mm simulated rainfall events. However, the mid-grass *B. curtipendula* appeared to have greater drought avoidance than *H. belangeri* by maintaining less negative water status in situations with less available soil water than *H. belangeri* and by extracting soil water faster and from greater depths than *H. belangeri* (Norman 1991).

Given that mid-grasses are theoretically more drought resistant than short grasses (Norman 1991) and the long term shift to a mid-grass dominated herbaceous community along a grazing intensity gradient at the Sonora Experiment Station (Fuhlendorf et al. 2001), the differences in the amount of perennial grass mortality between these two drought events based on the percent of permanent quadrats with measured zero values is a function of something other than the differences in grazing intensity at the time of these two drought events.

One major difference in the overall plant community composition between these two time periods is the percent woody cover occurring within each grazing treatment unit. Evaluation of woody cover prior to the establishment of grazing treatments in 1949 showed that woody cover was on average 22% across all grazing treatment units. The woody plants *Juniperus ashei* and *Juniperus pinchotii* were hand cut from the Experiment Station in 1948, reducing woody cover to around 10% across all grazing treatments with *Quercus* species accounting for a majority of the remaining woody cover. By 1983 woody plants had increased significantly and accounted for around 30% of total plant cover with *Juniperus* species accounting for around 37% of the total woody cover (Smeins and Merrill 1988). This represents approximately a 20% increase in woody cover between the drought of the 1950’s and the drought of 2001 and 2002. Changes in woody plant cover between the early 1980’s and 2002 are unknown.

Semi-arid vegetation communities characterized by a patchy distribution of woody vegetation are often organized into a sink-source system of nutrient and resource distribution (Ludwig and Tongway 1995, Tongway and Ludwig 1997a). These changes in woody plant cover at the Sonora Experiment Station may have altered the spatial distribution and flow of resources as well as the competitive environment for soil moisture between woody and herbaceous plants. These changes could have resulted in a shift in the mortality threshold of a drought event. Due to altered flow paths of resources in a patchy, sink-source environment, shorter droughts of less intensity may result in perennial grass mortality equal to that from longer more intense droughts occurring in a less patchy environment with more continuous resource flow pathways.

Rainfall events that did occur during the peak of both droughts were small (under 10 mm) and infrequent. The difference in woody plant cover between drought events may have significantly altered perennial grass response to these small rainfall events. The impact of *Juniperus* species canopy cover on the fate of small rainfall events is significant. Over 60% of the rainfall from an event less than 10 mm is intercepted by *Juniperus* species canopy without reaching the herbaceous vegetation layer (Owens et al. 2001).

Small rainfall events are of ecological significance in semiarid environments (Sala and Lauenroth 1982). Rapid response to small rainfall events in semiarid environments has been documented in the perennial short grass *Bouteloua gracilis*. An effect on both leaf water potential and leaf conductance to water vapor was seen from a 5 mm simulated rainfall event applied to a soil with low water availability (Sala and Lauenroth 1982). Similar responses were recorded from 10 mm simulated rainfall events for both the grazing tolerant short-grass *Hilaria belangeri* and the grazing intolerant mid-grass *Bouteloua curtipendula* at the Sonora Experiment Station (Norman 1991). Small rainfall pulses that occurred in June, July and August of 1953 facilitated vegetative production and seedling establishment of *H. belangeri*. An average of 118 seedlings and 65 clones per m^2 established during these rainfall events at the Sonora Experiment Station (Merrill 1953). The redistribution of small rainfall events due to woody plant canopy interception could exacerbate drought impact on herbaceous vegetation by impacting both the spatial distribution of rainfall as well as the percentage of a given event reaching herbaceous vegetation. It should be noted that quadrats located in the heavy grazing treatment units in an area that had been cleared of *Juniperus* species for a watershed study project in the 1980’s did not show any difference in perennial grass mortality. *Juniperus* species in this area were younger plants of smaller stature without an extensive canopy (Smeins and Merrill 1988).

A second major difference between the overall plant community composition between these two drought events is the abundance of cool season annuals. A shift in dominance to annual cool season forbs was documented in 2001 across all grazing treatments in response to the pattern of abundant cool season precipitation in 1999 and 2001. Surveys of vegetation composition across grazing treatments performed from mid-April to mid-June of 2001 found vegetation cover and density dominated by the cool season annuals *Croton monothogynus, Chaetopappa asteroids, Hedeoma drummondii*, *Ratibida columnifera*, and *Plantago rhodosperma* across all grazing treatments. In addition, *Scutellaria drummondii* was common in the heavy grazing treatment units and *Daucus pusillus* was common in the no grazing treatment units. Perennial grasses were uncommon during this survey period (N. Nicolai, Personal Communication Jan. 2004).

This dominance of cool season annual forbs early in the spring of 2001 combined with the continuous year round drought of 2000 may have set the stage for perennial grass mortality during the growing season of 2001. Studies examining the differential use of soil moisture between cool season forbs and grasses compared to warm season grasses show that cool season plants are able to extract soil water from both deep and shallow soil layers earlier and more rapidly than warm season grasses (Harris 1967, Harris and Wilson 1970, Eissenstat and Caldwell 1988, Yoder et al. 1998). Plants that are able to rapidly extract water from the soil profile have a significant competitive advantage over plants that extract water at a slower rate (Eissenstat and Caldwell 1988). The introduced annual *Bromus tectorum* is able to gain a competitive advantage over the native perennial vegetation of the Great Basin due to its ability to rapidly elongate its roots at cool temperatures and utilize soil moisture. The native perennial grasses are left in dry soil at the onset of the growing season drought due to this inability to extract soil moisture early in the growing season (Harris and Wilson 1970).

A third major difference between these two drought events is grazing pressure. Stocking rates prior to the establishment of the grazing treatments in 1948 were continuous and heavy across all treatment units. This continuous grazing pressure had a significant impact of the perennial grass community composition and structure prior to the onset of the drought of the 1950’s (Fuhlendorf and Smeins 1997). Stocking rates during the 1950’s were much higher than current stocking rates. Stocking rates of the heavy grazing treatment were 3 times greater in the 1950’s than current stocking rates (5.4 ha/auy in the 1950s versus 16.2 ha/auy currently). Stocking rates of the moderate grazing treatment was 2 times greater in the 1950’s than currently (8.1 ha/auy in the 1950’s versus 16.2 ha/auy currently). In 1983, the stocking rates of both the heavy grazing and moderate grazing treatments were reduced. Until that point, the stocking rate of the heavy grazing treatment had always been greater than the moderate grazing treatment. The stocking rates of the heavy and moderate grazing treatments have been the same since 1983. These changes in grazing intensity resulted in a shift in the perennial grass community composition and structure (Fuhlendorf and Smeins 1997). Given that no differences in perennial grass community structure were found only between years and not between grazing treatments, differences in perennial grass mortality between drought events is not a result of these shifts in grazing intensity.

The drought events of 1951 to 1956 and the drought event centered on the year 2000 both resulted in significant perennial grass mortality. The perennial grass community structure and composition during each drought event is a reflection of the long term grazing history of the Sonora Experiment Station. The pattern and intensity of each drought event were both similar and unique. Similar in that both events had a continuous period of moderate to extreme drought for a full year based on Palmer drought severity index values and unique based on the differences in duration, intensity, temperature and distribution of cool season precipitation. What is clear is that a perennial grass mortality threshold was crossed sometime during both drought events. Where this threshold lies is unclear. The response of a perennial grass community to grazing induced shifts in community structure and composition as well as the sequence and interaction of unique climatic events in a heterogeneous topo-edaphic environment may be chaotic in nature and largely unpredictable (Hastings et al. 1993).

Thus, while not conclusively documented in this study, a possible scenario for the differential perennial grass mortality response between the drought of the 1950’s and the drought event centered on the year 2000 was the interaction of discrete climatic events combined with shifts in vegetation community composition. Though the drought event centered on the year 2000 was of shorter duration and less intensity than the drought of the 1950’s based on Palmer drought severity index comparisons, temperatures were much higher for a continuous 12 month period in the year 2000 than any time during the drought of the 1950’s. This combined with an overlapping 12 month lack of precipitation may have set the stage for perennial grass mortality. Abundant winter precipitation following the drought of 2000 resulted in an abundance of cool season forbs. This abundance of forbs may have created a competitive soil moisture environment for perennial grasses already impacted by the previous year’s drought. The combination and temporal sequence of these two events may have sent the perennial grass community beyond a recoverable mortality threshold that exceeded the drought of the 1950’s.

CHAPTER IV

PATCH SPECIFIC RESPSONSE TO DROUGHT AND HERBIVORY ON THE EDWARDS PLATEAU: TOPO-EDAPHIC VARIATION AND PERENNIAL GRASS SURVIVAL

Introduction

The topo-edaphic environments of many semi-arid rangeland ecosystems are inherently spatially heterogeneous. The climatic landscape of semi-arid ecosystems is characterized by infrequent, discrete, and largely unpredictable precipitation patterns. This heterogeneous topo-edaphic climatic environment often results in patch specific vegetation community response to the interaction of herbivory and climatic variation.

A recent major drought event beginning in the late-1990's offered an opportunity to examine patch specific response to both grazing and extreme drought at the Sonora Experiment Station. Initial observations of plant community dynamics in response to this drought event showed that some patch types experienced greater perennial grass mortality than others. This differential mortality provides an ideal opportunity to characterize patch features that facilitate the survival of perennial grass in extreme drought events.

Methods

Vegetation and Plot Sampling

Fifteen 2 m x 1 m paired quadrats (30 quadrats total) were randomly established in eight grazing treatment units: 2 heavy grazing, 4 moderate grazing and 2 no grazing. Quadrat pairing was based on the presence or absence of large or abundant surface rock features. For the purpose of discussion, quadrats with a high density of large surface rock fragments will be referred to as the rock quadrats while quadrats with a low density of large surface rock fragments will be referred to as the non-rock quadrats. The rock quadrat of a quadrat pair had a high percentage of surface stone and cobble rock area (Table 6) and a non-continuous soil surface, while the non-rock quadrat of a pair had a low percentage of surface stone and cobble rock area with a more uniform soil surface. Efforts were made to keep quadrat pairs in close proximity (within 10 m) in order to maintain similarity of features such as the structure and composition of surrounding vegetation and landscape position. The vegetation community and physical environment of each quadrat was characterized with a total of 12 parameters (Table 6).

Soil depth measurements were obtained by driving a 0.5 cm diameter steel probe into the soil at five locations within each quadrat. The mean of the five soil depth measurements was used as the soil depth for the quadrat. The standard deviation of these measurements was used to express soil depth variation within each quadrat. Soil volume was measured in cm^3/m^2 of plant available area by taking the mean soil depth and multiplying by the soil surface area corrected for surface rock cover (the plant available area, discussed later in the data analysis section).

Visual estimates of the percentage of surface rock cover were recorded for three classes of surface rock: gravel (< 8 cm diameter), cobble (8 – 25 cm diameter), and stone (>25 cm diameter) (Wiedenfeld and McAndrew 1968). Cover estimates of each surface rock class were made with a 0.25 m^2 gird overlay of each quadrat in conjunction with a percent cover visual estimation guide.

Measures of landscape features and position include percent slope as measured with a clinometer, slope position based on quadrat position at the top, middle or bottom of a slope, and the dominant slope aspect.

Distance of the closest woody plant was measured for each of the four cardinal directions in m from the quadrat center. Height of the woody vegetation was visually estimated in m. A shade index was developed as a measure of the degree of shading from woody vegetation in each quadrat. Index values were a function of woody vegetation height, distance from quadrat center, and aspect relative to the quadrat. The shade index had a range of 1 – 4 with 1 = no shade, 2 = light shade for much of the day, 3 = moderate shade for much of the day, 4 = full shade.

Table 6. Paired quadrat vegetation and physical environment and vegetation characterization parameters.

Parameter	Description
1. Soil Depth	Mean of five individual depth probes (cm) per quadrat
2. Soil Depth Variation	Standard deviation of soil depth
3. Soil Volume	In cm^3/m^2, calculated from the average soil depth and the soil surface area corrected for surface rock cover.
4. Percent Surface Rock Cover	By rock type as defined by Wiedenfelf and McAndrew (1968) • Gravel (< 8 cm in diameter) • Cobble (8 – 25 cm in diameter) • Stone (> 25 cm in diameter)
5. Percent Slope	Percent slope of quadrat as measured with a clinomter
6. Slope Position	Position of plot relative to location along a slope • Top, Middle, or Bottom
7. Slope Aspect	Predominant aspect of a slope (N, S, E, W)
8. Shade Index	Measure by class (1 – 4) of the shading influence of the nearest woody plants in the four cardinal directions 1 = no shade, 2 = light shade for much of the day 3 = moderate shade for much of the day, 4 = full shade
9. Woody Plant Distance	Distance of nearest woody plant from plot center (m) in the four cardinal directions
10. Woody Plant Height	Height of nearest woody plant from plot center (m) in the four cardinal directions
11. Species Composition	Basal area measurements of all perennial grass species within a quadrat
12. Rock Site Type	Characterization of the quadrat by the dominant surface rock features • Limestone Blockfield = site dominated by large stone fragments >25 cm in diameter partially integrated into the soil surface, usually associated with fractured, blocky outcrops of Edwards limestone on the upper third of a slope • Debris Slope = site dominated by rock fragments 8 – 25 cm in diameter predominately found on the soil surface, usually found in the middle third of a slope • Slab Limestone Bench = site dominated by large slabs of exposed limestone with long linear fractures and pocket of shallow soils, usually associated with resistant layers of limestone at either the top or bottom of a slope

Species composition was obtained by basal diameter measures of all perennial grasses within each quadrat. Individual plant basal diameter measurements were converted into circular basal area measurements for each individual plant. Measurements of individual plants were converted into plant density. All perennial grasses rooted within the quadrat were measured.

Basal area and plant density measurements were summarized for each quadrat as cm^2 of basal area and number of plants per m^2 of area. Measurements on a per m^2 basis do not reflect the spatial heterogeneity of soil surface features and are not the best measurement for the comparison of plant basal area and density in a heterogeneous environment. In order to better account for soil surface features, measurements in m^2 of area were converted into m^2 of plant available area. Plant available area (PAA) is a measure of the surface area available for plant rooting within an individual quadrat. PAA was derived for each quadrat by summing the percent cover measurements of each surface rock class (gravel, cobble, stone) into a single percentage measure of total rock cover. This percentage measure was then converted into area and subtracted from the total area of each quadrat yielding the total surface area available for plant rooting in each quadrat – the plant available area. For example, the total basal area for a single 2-m^2 quadrat is 250 cm^2 of basal area, or 125 cm^2 / m^2. If surface rock accounts for 25% of the total area of the quadrat then 1.5 m^2 of the quadrat surface area is available for plant rooting. When corrected for rock cover, basal area per unit area is 166 cm^2 / m^2 of plant available area, a 32% increase in basal area per unit of surface area when compared to the standard measure.

Initial measurements from the rock quadrats showed a differential response of the plant community based on the type of surface rock features found within a quadrat. As a result of this observation the rock quadrat pairings of 5 grazing treatment units, 1 heavy graze, 2 no grazing, and 2 moderate grazing treatment units were assigned categorical values as limestone blockfield, debris slope, or slab limestone bench sites based on the dominant surface rock features of the quadrat. Limestone blockfield sites are dominated by large stone fragments >25 cm in diameter. These fragments are blocky in shape, are integrated into the soil surface, and can have heights >30 cm above the soil surface. These rock fragments are tightly arranged creating a network of crevices with relatively deep soils. They are usually associated with fractured, blocky outcrops of exposed Edwards's limestone on the upper third of a slope.

Debris slope sites are dominated by smaller rock fragments 8 – 25 cm in diameter. These fragments of decomposed or fractured limestone sit on the soil surface and can form a continuous layer of small rock fragments several centimeters deep. Debris slopes are primarily found in the middle third of a slope.

Slab limestone benches are dominated by large, flat slabs of near surface or exposed limestone with pockets of deeper soil found in long linear fractures in the rock surface. The exposed limestone slabs not protruding more than a few centimeters from the soil surface. They are usually associated with resistant layers of Edward's limestone at either the top or bottom of a slope.

Data Analysis

Perennial Grass Community Structure

A two factorial, split-plot design was utilized to test for the effects of grazing intensity and surface rocks on perennial grass basal area and density (Zar 1999). Analysis of variance was conducted with the general linear model univariate analysis option of SPSS (SPSS 2001). The ANOVA model was built with the three grazing intensities (heavy, moderate and no grazing) as the whole plot treatment and rock site or non-rock site as the within plot treatment. Assumptions of normality and equality of variance were met with a natural log transformation of both the perennial grass basal area and density data sets. Zero values (12 data points out of a total of 210) were removed from the density data set in order to meet the assumptions of normality and equality of variance. Significance levels for the tests were set at $\alpha = 0.05$. Bonferroni multiple comparisons were utilized for separating means of the three grazing treatments (Zar 1999).

A comparison of perennial grass basal area per plant was performed by pooling individual plant basal areas for each species across all quadrats across all replications into one of three grazing intensity categories. These pooled measurements were split into rock and non-rock quadrats within each grazing treatment. Since assumptions of normality and equality of variance were not met for this data set, the non-parametric Kruskal-Wallis analysis of variance by rank tests was utilized to examine differences in perennial grass basal area per plant between rock and non-rock quadrats within the three grazing intensities (Zar 1999). Multiple comparisons of grazing intensities were conducted with the Kruskal-Wallis test utilizing the Bonferroni approach for preserving alpha level and minimizing experiment-wise error. Alpha levels for individual comparisons of grazing intensities were set at $\alpha = 0.05/3.0=0.017$ following the protocol of the Bonferroni inequality (Ott and Longnecker 2001).

Driving Parameters

A correlation matrix was generated relating perennial grass basal area and density to all measured variables for the paired rock and non-rock quadrats (Table 6) utilizing both Pearson’s linear and Spearman’s rank correlations. Strong correlations with statistically significant relationships to basal area were examined with exploratory statistics. Promising relationships were analyzed with general linear model parametric statistics, non-parametric Kruskal-Wallis tests, regression analysis, or multivariate statistics.

Simple linear regression was used to examine the relationship of surface rock area and perennial grass basal area. In order to meet the assumptions of normality and equality of variance, a natural log transformation was performed on the perennial grass basal area data. Alpha levels were set at 0.05.

Analysis of the distribution of perennial grass basal area between limestone blockfield, debris slope, and slab limestone bench sites was performed with the non-parametric Kruskal-Wallis analysis of variance by rank test. The basal area data set for the limestone blockfield, debris slope, and slab limestone bench sites was non-normal with unequal variance. Each data set had a similar distribution and met the criteria for use of the Kruskal-Wallis test. Alpha levels were set at 0.05.

Multiple comparisons of the limestone blockfield, debris slope, and slab limestone bench sites were conducted with the Kruskal-Wallis test utilizing the Bonferroni approach for preserving alpha level and minimizing experiment-wise error. Alpha levels for individual comparisons of grazing intensities were set at $\alpha = 0.05/3.0=0.017$ following the protocol of the Bonferroni inequality (Ott and Longnecker 2001).

Species Relationships

Detrended Correspondence Analysis (DCA) was conducted with the default settings in PC-Ord using the 13 most abundant perennial grass species to ordinate all combinations of rock and non-rock quadrats for each grazing treatment replication (n=14) (Hill 1979, Hill and Gauch 1980, Gauch 1982, McCune and Mefford 1999). Species included in the analysis were *Aristida purpurea*, *Bouteloua curtipendula*, *Bouteloua hirsuta*, *Bouteloua trifida*,*Carex planostrachys*, *Digitaria cognatum*, *Erioneuron pilosum*, *Eriochloa sericea*, *Hilaria belangeri*, *Panicum hallii*, *Schedonnardus paniculatus*, *Stipa leucotricha*, and *Tridens muticus*. The basal area in cm^2/m^2 of plant available area for each species was summed for all rock and non-rock quadrats within each grazing treatment replication. The absolute values of these summations were utilized in the ordination.

Species were selected for the ordination if they occurred in greater than 3 of the 14 combinations. The elimination or down rating of rare species is a common practice in DCA and other ordination techniques in order to minimize the stochastic influence of these species on the analysis (Hill and Gauch 1980, Gauch 1982, Jongman et al. 1995).

An additional DCA ordination was conducted of perennial grass grazing response groups. Thirteen perennial grass species were divided into 3 grazing response groups based on the fit of a second order polynomial for individual species basal area along a grazing intensity gradient (Fuhlendorf and Smeins 1997). A fourth response group was created based on individual species shade tolerance. The species groupings were as follows:

- Grazing Tolerant Species - *Bouteloua trifida*, *Erioneuron pillosum*, *Hilaria belangeri*.
- Intermediate Species - *Aristida purpurea*, *Digitaria cognatum*, *Panicum hallii*.
- Grazing Intolerant Species - *Bouteloua curtipendula*, *Bothriochloa barbinodis*, *Bouteloua hirsute*, *Eriochloa sericea*, *Tridens muticus*.
- Shade Tolerant Species – *Carex planostrachys*, *Stipa leucotricha*.

The total basal area for each grazing response group was summed by grazing treatment replication for all rock and non-rock quadrats within heavy grazing (n = 1), moderate grazing (n = 4) and no grazing (n = 2) treatment replications. The response group summations were relativized by grazing treatment replication utilizing the General Relativization procedure in PC-Ord (McCune and Mefford 1999).

Non-linear regression curves were fit to the DCA axis 1 score and summed basal area of each of the four response groups for each treatment unit. In order to meet the assumptions of normality and equality of variance, a natural log transformation was performed on the summed basal area data from the grazing intolerant response group. Parametric assumptions were met for all other perennial grass response groups.

One replication of the heavy grazing treatment was excluded from all analysis due to the influence of a large rainfall event occurring between sampling periods. Basal area measurements for quadrats in this replication were over 2.5 times the basal area measurements for other grazing treatment units. The influence of this rainfall event confounded meaningful analysis of drought conditions by masking main effect differences for the influence of grazing intensity.

Results

Perennial Grass Community Structure

Three historical grazing intensity treatments and the rock and non-rock sites within each grazing treatment were evaluated for their effect on perennial grass basal area, density, and basal area per plant during an extreme drought event at the Sonora Experiment Station (Table 7).

No significant differences were found between grazing intensities for perennial grass basal area ($p = 0.72$) but differences between rock and non-rock quadrats were highly significant ($p < 0.001$) (Table 8, Fig. 11). There was nearly a 10 fold difference between the basal area of the non-rock and rock quadrats (23.9 cm^2 of basal area vs. 225.6 cm^2 of basal area, respectively, Table 7).

The differences between basal area measurements in cm^2 / m^2 of plant available area and cm^2 / m^2 of absolute area illustrate the significance of accounting for available soil surface plant rooting space in a heterogeneous environment. There is nearly a two fold difference in basal area for rock quadrats across all grazing treatments when measured in m^2 of plant available area compared to m^2 of absolute area and no real difference in basal area for non-rock quadrats (Fig. 11).

Significant differences were found between grazing treatments for perennial grass density ($p < 0.01$, Table 8) as well as between rock and non-rock quadrats ($p < 0.01$, Table 8). Mean separation with Bonferonni multiple comparisons found significant differences in the perennial grass density between the moderate grazing and the no grazing treatments ($p < 0.01$, Table 8). No differences were found between the remaining grazing intensity comparisons. Rock quadrats had from 3 to 7 times more plants per m^2 of plant available area than non-rock quadrats (Fig. 12).

Table 7. Sample size (n), mean and standard error (SE) for perennial grass basal area, density, and basal area per plant for rock and non-rock quadrats across heavy grazing, moderate grazing and no grazing treatments. Values were derived from the non-normal, untransformed data of unequal variance. Basal area is in cm^2 / m^2 of plant available area, density is in individuals / m^2 of plant available area, basal area per plant is in cm^2 / individual.

	n	Mean	SE
Perennial Grass Basal Area			
Rock Quadrats			
Heavy Grazing	15	232.6	60.7
Moderate Grazing	60	209.1	30.1
No Grazing	30	255.0	55.5
All Grazing Treatments	105	225.6	24.8
Non-Rock Quadrats			
Heavy Continuous	15	15.2	4.9
Moderate Rotational	60	20.8	3.7
No Grazing	30	34.3	13.1
All Grazing Treatments	105	23.9	4.4
Perennial Grass Density			
Rock Quadrats			
Heavy Grazing	15	40.1	12.6
Moderate Grazing	60	41.0	8.1
No Grazing	30	19.9	2.7
All Grazing Treatments	105	34.8	5.1
Non-Rock Quadrats			
Heavy Grazing	15	6.4	2.3
Moderate Grazing	60	9.8	1.9
No Grazing	30	6.0	1.6
All Grazing Treatments	105	8.2	1.2
Perennial Grass Basal Area per Plant			
Rock Quadrats			
Heavy Grazing	313	4.6	0.3
Moderate Grazing	1272	4.5	0.2
No Grazing	299	10.8	1.1
All Grazing Treatments	1884	5.5	0.2
Non-Rock Quadrats			
Heavy Grazing	144	2.3	0.2
Moderate Grazing	805	2.3	0.1
No Grazing	245	6.5	0.5
All Grazing Treatments	1194	3.1	0.1

Table 8. Split plot analysis of variance for perennial grass basal area and density between rock and non-rock quadrats across heavy, moderate, and no grazing treatments. Bonferroni multiple comparisons of perennial grass density are given across 3 grazing treatments. One replication of the heavy continuous grazing treatment was not included in the analysis. $\alpha = 0.05$

	d.f.	MS	F	P-value
Basal Area				
Whole Plot				
Treatment (Graze)	2	1.14	0.36	0.72
Error (Graze X Treatment Unit)	4	3.13		
Split Plot				
Treatment (Rock vs. Non-Rock)	1	262.27	107.42	0.00
Interaction (Graze X Rock)	2	0.48	0.20	0.82
Error	200	2.44		
Density				
Whole Plot				
Treatment (Graze)	2	7.37	33.54	0.00
Error (Graze X Treatment Unit)	4	0.19		
Split Plot				
Treatment (Rock vs. Non-Rock)	1	91.02	66.35	0.00
Interaction (Graze X Rock)	2	1.12	0.82	0.44
Error	188	1.37		

Bonferroni Multiple Comparisons For Density	Mean Difference	Std. Error	P-value
No Grazing			
Vs. Moderate Grazing	-0.62	0.19	0.00
Vs. Heavy Grazing	-0.43	0.27	0.35
Moderate Grazing			
Vs. Heavy Grazing	0.19	0.25	1.00

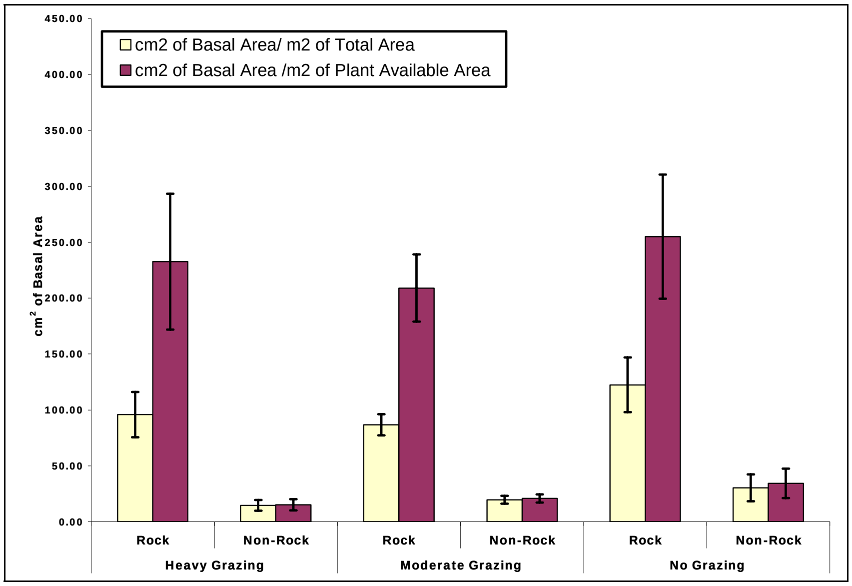


Fig. 11. Mean perennial grass basal area per m^2 of sampled area and per m^2 of plant available area for rock and non-rock quadrats across heavy grazing, moderate grazing, and no grazing treatments. Error bars = standard error of the mean. Values were derived from the non-normal, untransformed data.

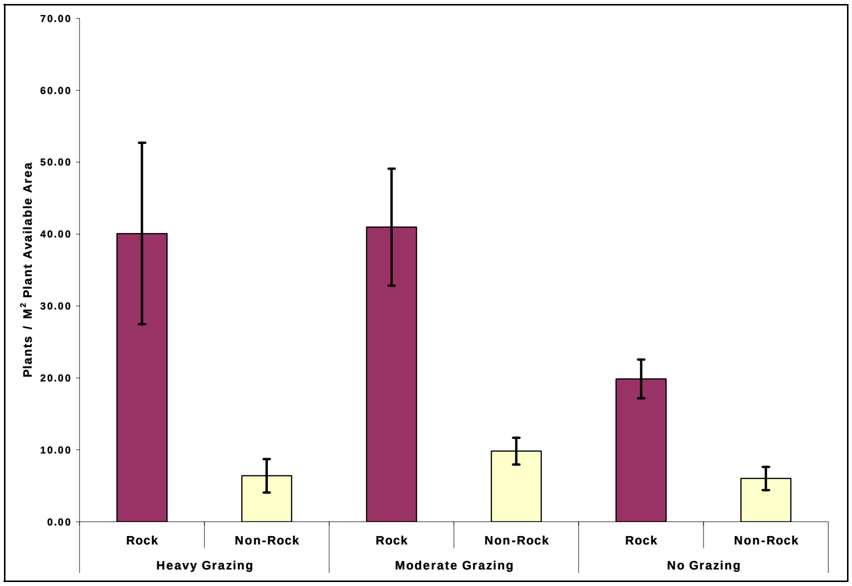


Fig. 12. Mean perennial grass density for rock and non-rock quadrats for heavy grazing, moderate grazing and no grazing treatments. Error bars = standard error of the mean. Values were derived from the non-normal, untransformed data.

Kruskal-Wallis analysis of variance by rank tests were significant for differences in perennial grass basal area per plant between the rock and non-rock quadrats (Table 9, Fig. 13). Comparisons between the grazing treatments when rock and non-rock measurements were combined were also significant for differences in perennial grass basal area per plant across all three grazing treatments. Multiple comparisons for rock quadrats between grazing treatments using the Kruskal-Wallis test were significant for comparisons between the no grazing treatment and both the moderate grazing and heavy grazing treatments for perennial grass basal area per plant. No differences were found for the moderate grazing and heavy grazing comparison. Significant differences for perennial grass basal area per plant for non-rock sites were found for the no grazing and moderate grazing comparison as well as the no grazing and heavy grazing comparison with no difference shown for the moderate and heavy grazing comparison (Table 9, Fig. 13).

The general pattern for basal area per plant was:

- Differences between all three grazing treatments when examined by grazing treatment alone without separation by rock or non-rock site
- Differences between rock and non-rock sites when examined by rock and non-rock sites alone without separation by grazing treatment
- Differences between the rock sites of the no graze treatment and the two grazed treatments but no difference between the two grazed treatments
- Differences between the non-rock sites of the no graze treatment and the two grazed treatments but no difference between the two grazed treatments

Values of basal area per plant were generally 2 times greater on rock quadrats than non-rock quadrats for all grazing treatments. Values for both rock and non-rock quadrats were generally 3 times greater for the no graze treatment than the two grazed treatments (Fig. 13).

The lack of significant difference for perennial grass density between the moderate grazing and heavy grazing treatments was puzzling upon initial observation given that there was a significant difference between the no grazing and the moderate grazing treatments yet no significant difference between the no grazing and heavy grazing treatments. A more detailed examination of the 95% confidence intervals for each grazing treatment presented an explanation for this apparent inconsistency. The confidence interval for the heavy grazing treatment unit had a very wide range compared to the other two treatments. There was a distinct overlap of the confidence intervals for the heavy grazing and no grazing treatments and no overlap for the narrower confidence intervals of the moderate grazing and no grazing treatments. This large variation in basal area per plant within the heavy graze treatment is perhaps a function of the smaller sample size from only one treatment unit being utilized in the analysis and the application of the central limit theorem (Zar 1999).

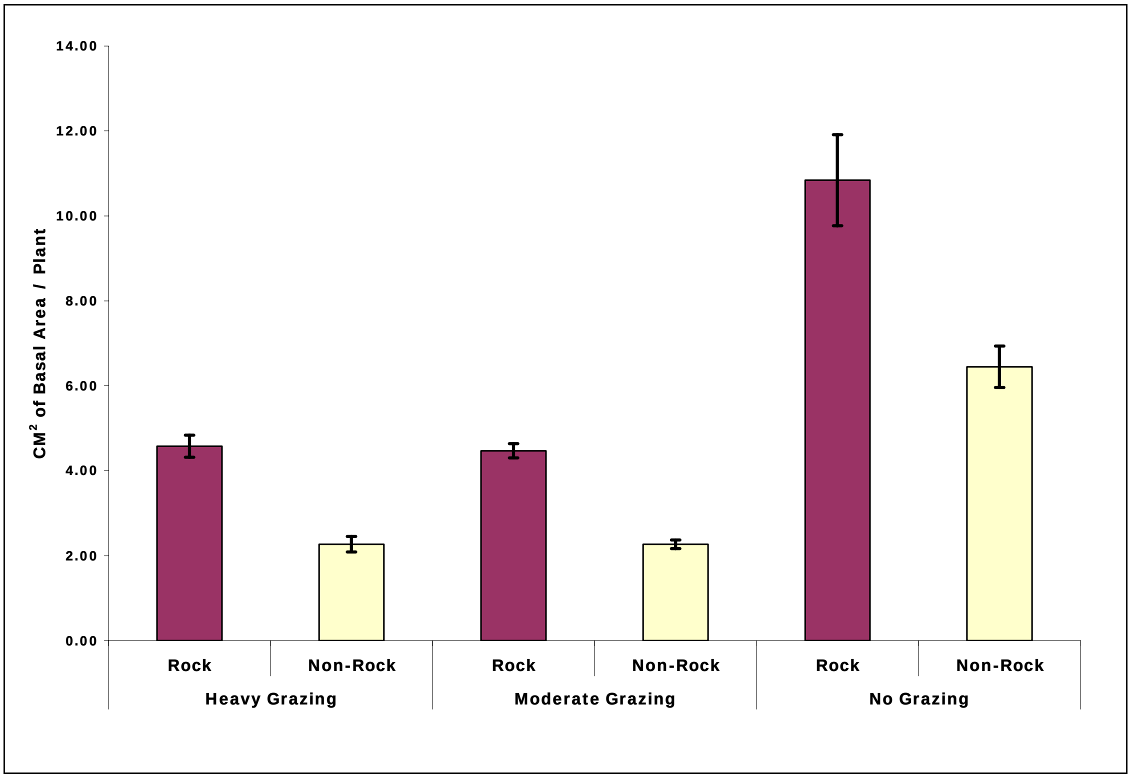


Fig. 13. Mean basal area per plant for rock and non-rock quadrats across heavy grazing, moderate grazing, and no grazing treatments. Error bars = standard error of the mean. Values were derived from the non-normal, untransformed data.

Table 9. Kruskal-Wallis analysis of variance by rank for perennial grass basal area per plant between rock and non-rock quadrats across 3 grazing treatments. α = 0.05 for each test. Kruskal-Wallis multiple comparison of perennial grass basal area per plant between rock and non-rock quadrats across 3 grazing treatments. α = 0.017 for each comparison.

Comparison	**n**	**Mean Rank**	**Chi-Square H**	**Asymptotic P Value**
Rock & Non-Rock Quadrats				
No Grazing	544	1968.36		
Moderate Grazing	2077	1421.99		
Heavy Grazing	457	1563.05		
			183.20	0.00
All Grazing Treatments				
Rock Quadrats	1884	1695.74		
Non-Rock Quadrats	1194	1292.97		
			168.39	0.00
Rock Quadrats				
No Grazing	299	1172.12		
Moderate Grazing	1272	884.20		
Heavy Grazing	313	960.09		
			74.61	0.00
Non-Rock Quadrats				
No Grazing	245	814.07		
Moderate Grazing	805	537.22		
Heavy Grazing	144	566.04		
			151.91	0.00

Multiple Comparisons	**n**	**Mean Rank**	**Chi-Square H**	**Asymptotic P Value**
Rock & Non-Rock Quadrats				
No Grazing	544	1676.68		
Vs. Moderate Grazing	2077	1215.22	179.98	0.000
No Grazing	544	564.18		
Vs. Heavy Grazing	457	425.79	61.49	0.000
Moderate Grazing	2077	1245.77		
Vs. Heavy Grazing	457	1366.26	11.70	0.001
Rock Quadrats				
No Grazing	299	978.56		
Vs. Moderate Grazing	1272	740.74	72.72	0.000
No Grazing	299	271.10		
Vs. Heavy Grazing	313	343.56	27.67	0.000
Moderate Grazing	1272	779.96		
Vs. Heavy Grazing	313	846.00	5.78	0.017
Non-Rock Quadrats				
No Grazing	245	711.08		
Vs. Moderate Grazing	805	469.02	147.73	0.000
No Grazing	245	225.98		
Vs. Heavy Grazing	144	142.29	55.38	0.000
Moderate Grazing	805	471.20		
Vs. Heavy Grazing	144	496.25	1.40	0.236

Driving Variables

Correlation analysis was used to examine the relationship of perennial grass basal area to all physical and vegetation characterization parameters measured for the rock and non-rock quadrats (Table 6). Pearson linear correlation was utilized for all analysis with the exception of the rock quadrat site type and shade index correlations where Spearman's rho was utilized due to the non-parametric, categorical nature of the data (Zar 1999).

Field measurements of the variables percent slope, slope position, and slope aspect where confounded due to the topographic complexity of the Sonora Experiment Station and were excluded from the analysis. Categorization of the rock site type as limestone blockfield, debris slope, or slab limestone bench was believed to be a better method for describing landscape features that could influence perennial grass production. Correlation of perennial grass basal area with a gradient of increasing rock cover was done by assigning rock site types a value of 1 to 3 based on the mean rock cover of the three different site types: 1 = debris slope, 2 = slab limestone bench, 3 = limestone blockfield. Spearman's correlation analysis was then performed on the basal area data set with the rock site type categorical values.

Several soil structure parameters had strong significant correlations with perennial grass basal area. The strongest significant correlations with basal area were with surface rock area ($r = 0.65$), gradient of rock cover (see Table 10) ($r = 0.60$), and soil depth standard deviation ($r = 0.24$) (Table 10).

Significant correlations of perennial grass basal area to the parameters of woody plant distance from quadrat center and height of nearest woody plant were generally weak. The strongest significant correlations to perennial grass basal area in the woody plant height and distance group were with woody plant distance to the east ($r = -0.20$) (Table 11).

Table 10. Correlation matrix of perennial grass basal area, percent surface rock cover, gradient of site type, and the soil parameters of mean depth, standard deviation of depth, and volume.

#p<0.10 *p<0.05 **p<0.01		Rock Cover	Soil Depth	Soil SD	Soil Vol	Basal Area	Site Type
Rock Cover	Correlation	////	-0.20	0.16	-0.20	0.65	0.26
	Significance	////	0.00**	0.02*	0.00**	0.00**	0.02**
Soil Depth	Correlation	-0.20	////	0.55	1.00	0.00	0.21
	Significance	0.00**	////	0.00**	0.00**	0.95	0.07#
Soil SD	Correlation	0.16	0.55	////	0.55	0.24	0.30
	Significance	0.02*	0.00**	////	0.00**	0.00**	0.01**
Soil Vol	Correlation	-0.20	1.00	0.55	////	0.00	0.20
	Significance	0.00**	0.00**	0.00**	////	0.97	0.08#
Basal Area	Correlation	0.65	0.00	0.24	0.00	////	0.60
	Significance	0.00**	0.95	0.00**	0.97	////	0.00**
Site Type	Correlation	0.26	0.21	0.31	0.20	0.60	////
	Significance	0.02*	0.07#	0.01**	0.08#	0.00**	////

Table 11. Correlation matrix of perennial grass basal area to woody plant distance from the quadrat center, woody plant height, and shading from woody plants in the four cardinal directions.

#p<0.10 *p<0.05 **p<0.01		Distance N	Distance E	Distance S	Distance W
Basal Area	Correlation	-0.12	-0.20	-0.12	-0.12
	Significance	0.08#	0.03*	0.08#	0.08#

#p<0.10 *p<0.05 **p<0.01		Height N	Height E	Height S	Height W
Basal Area	Correlation	0.01	0.10	0.08	0.14
	Significance	0.85	0.17	0.23	0.05*

#p<0.10 *p<0.05 **p<0.01		Shade N	Shade E	Shade S	Shade W	Shade Sum
Basal Area	Correlation	0.14	0.20	0.19	0.28	0.35
	Significance	0.04*	0.00**	0.01**	0.00**	0.00**

Stronger significant relationships were found with the Spearman's rho shade index correlations. Perennial grass basal area was most strongly correlated with a summation of all shade index values for a given quadrat (r = 0.35), followed by shading from the west (r = 0.28), shading from the east (r = 0.20), and shading from the south (r = 0.19) (Table 11).

All correlations of basal area to the distance of woody vegetation from the quadrat center were negative (basal area was smaller the further woody vegetation was from the quadrat center). Three of the four correlations were marginally significant ($p < 0.10$) with relatively weak r values. Only one of the four woody plant height parameters was significant, woody height to the west, but this had a small r value of 0.14 ($p < 0.05$).

Given that the shade index for a given quadrat is a function of woody plant proximity and height, the correlations of basal area to the shade index parameters may be of more utility than the correlations of woody vegetation distance and height when discussing perennial grass basal area response.

Parameters with the strongest significant correlations to perennial grass basal area were:

1. Percent rock cover (r = 0.65, $p < 0.01$)
2. Gradient of rock cover (rock site type) (r = 0.60, $p < 0.01$)
3. Summation of the shade index for a given quadrat (r = 0.35, $p < 0.01$)
4. Shading from the west (r = 0.28, $p < 0.01$)
5. Soil depth standard deviation (r = 0.24, $p < 0.01$)

Linear regression analysis of rock surface area and perennial grass basal area was strongly significant showing a curvilinear relationship between basal area and rock cover (Table 12, Fig. 14). As seen in Fig. 14, a majority of basal area measurements are below 200 cm^2 with rock cover below 10%. Basal area becomes more variable as rock cover increases.

Table 12. ANOVA table for the regression of perennial grass basal area and rock surface area across all grazing treatments at the Sonora Experiment Station. $n = 210$, $\alpha = 0.05$

	d.f.	SS	MS	F	P-value
Regression	2	350.35	175.18	93.78	<0.0001
Residual	196	336.10	1.87		
Total	198	716.46	3.62		
Equation $y = 1.94 + 6.17x - 0.84$					

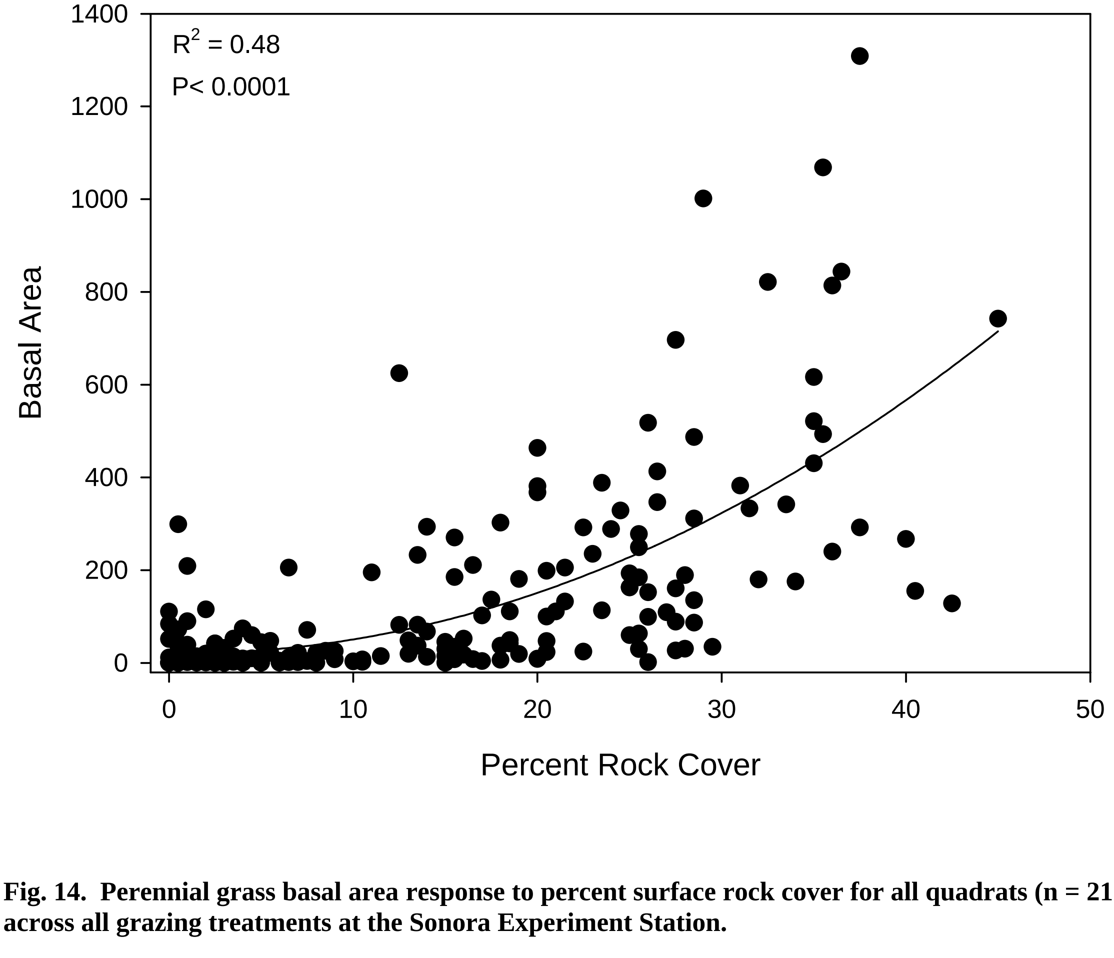


Fig. 14. Perennial grass basal area response to percent surface rock cover for all quadrats (n = 210) across all grazing treatments at the Sonora Experiment Station.

The Kruskal-Wallis analysis of variance by rank test was significant for comparisons of perennial grass basal area between the slab limestone bench, debris slope, and limestone blockfield site types ($p < 0.001$) (Table 13, Fig. 15). Mean basal area of the limestone blockfield sites was 340 cm^2 / m^2 of plant available area while the debris slope and slab limestone bench sites were both less than 150 cm^2 / m^2 of plant available area, a difference of at least 44% in plant production between site types. There was essentially a doubling of mean basal area moving from debris slopes to slab limestone benches to limestone blockfields (Table 13, Fig. 15).

Table 13. Mean, standard error of the mean (SE), Kruskal-Wallis analysis of variance by rank, and multiple comparisons for perennial grass basal area between slab limestone bench, debris slope, and limestone blockfield sites across 3 grazing treatments. $\alpha = 0.05$ for the full comparison, $\alpha = 0.017$ for each multiple comparison test.

Descriptive Statistics				
Rock Site Type	n	Mean Basal Area	SE	
Slab Limestone Bench	15	149.1	53.8	
Debris Slope	16	80.4	46.3	
Limestone Blockfield	44	346.6	44.3	
Kruskal-Wallis Tests				
Site Type Comparison	N	Mean Rank	Chi-Square H	Asymptotic P-value
Slab Limestone Bench	15	30.00		
Debris Slope	16	17.13		
Limestone Blockfield	44	48.32		
			26.56	0.000
Multiple Comparisons				
Slab Limestone Bench	15	20.20		
Vs. Debris Slope	16	12.06	6.20	0.013
Slab Limestone Bench	15	17.80		
Vs. Limestone Blockfield	44	34.16	10.15	0.001
Debris Slope	16	13.56		
Vs. Limestone Blockfield	44	26.66	20.52	0.000

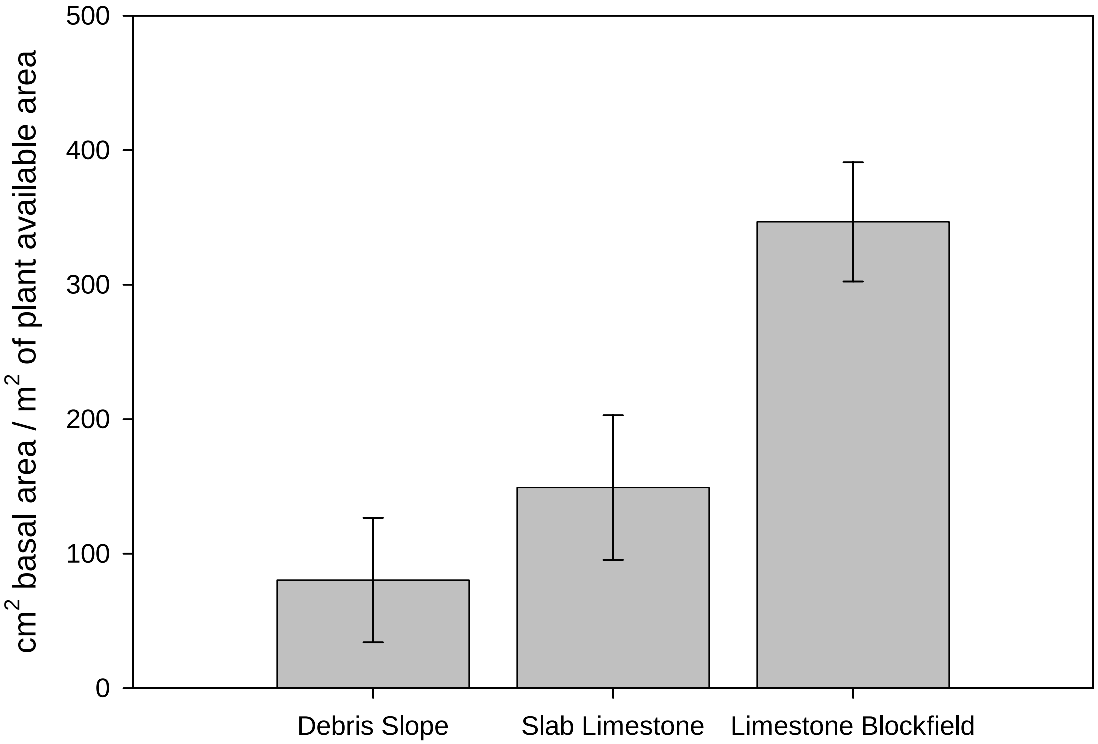


Fig. 15. Mean perennial grass basal area for the limestone blockfield, debris slope, and slab limestone bench sites. Site types are in order by increasing mean rock cover. Error bars = standard error of the mean.

Species Relationships

Detrended correspondence analysis of the basal area summations of the most abundant perennial grass species for the rock and non-rock sites within the heavy, moderate and no grazing treatment replications reduced the variation from 13 species to three DCA axes. The ordination accounted for 48.5% of the total species variation with 42.6% of this variation accounted for in the first two ordination axes (Table 14).

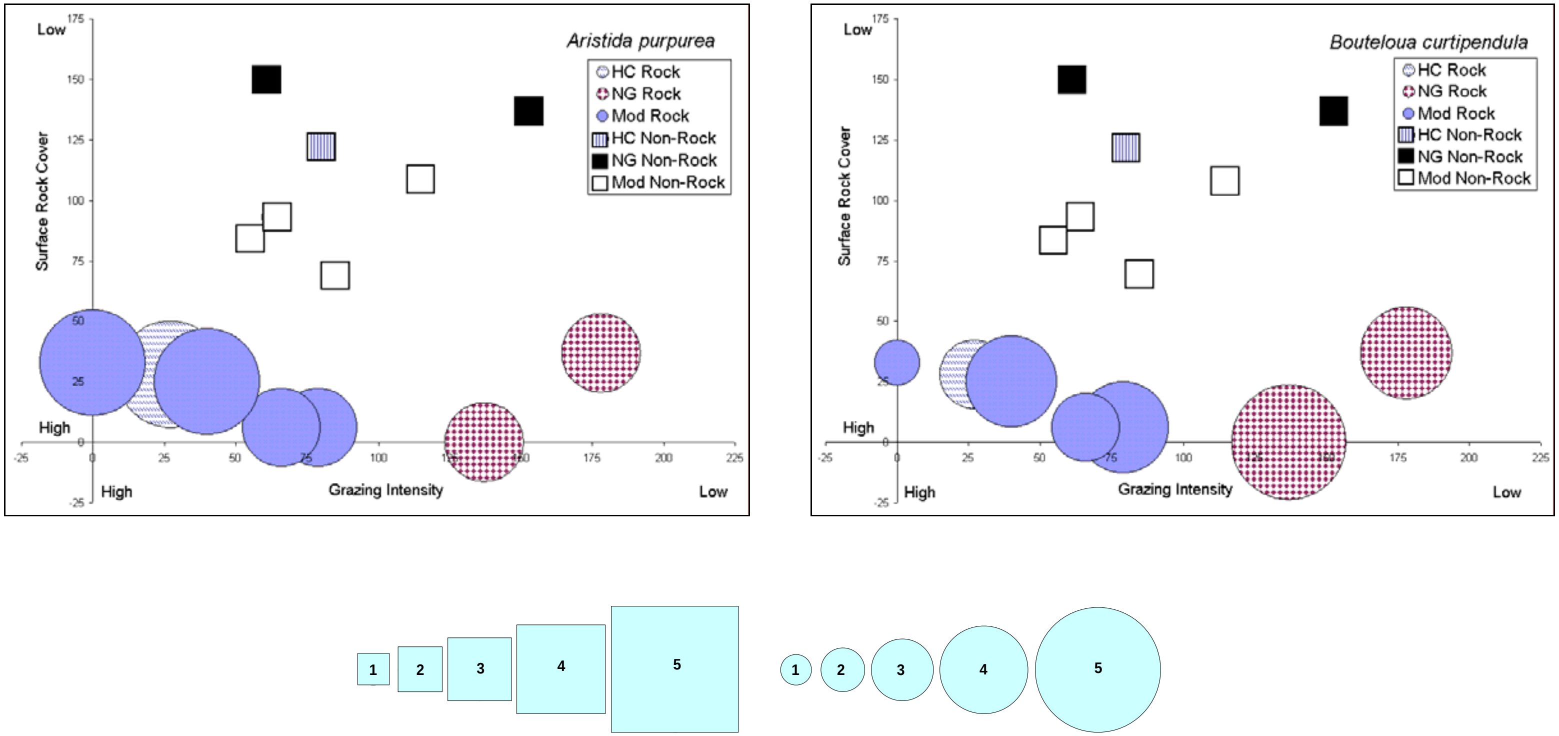
Correlation analysis of DCA axes scores to external variables showed a moderately significant relationship ($p = 0.06$, $r = -0.51$) of axis 1 scores to grazing intensity and a strongly significant relationship ($p < 0.001$, $r = -0.86$) of axis 2 scores to surface rock cover (Table 14). Axis 1 accounted for the largest amount of variance from the species data (31.8%) followed by axis 2 (10.8%) and axis 3 (2.6%) (Table 14). This would indicate that grazing intensity was the primary variable driving species composition with surface rock cover playing a secondary role.

The correlation of axis 1 scores to grazing intensity is not as strong or as significant as the relationship of axis 2 scores to surface rock cover but it is the primary driver of perennial grass species composition none-the-less. The strength of the correlation of axis 2 scores and surface rock cover makes sense in light of the dramatic10 fold difference in perennial grass basal area between rock and non-rock sites. The relationship between axis 2 scores and surface rock cover is more a function of basal area than perennial grass species composition. This is evident in the graphs of species basal area along DCA axis 1 and axis 2 (Fig. 16).

The weaker correlation of axis 1 scores and grazing intensity is logical due to the large pool of species that can be found across all grazing treatments. Of the 13 species included in the ordination, 2 species - *Eriochloa sericea* and *Tridens muticus* – can be thought of as indicators of little or no grazing pressure. The remaining 11 species can be found in all grazing treatments but their relative abundance within a treatment unit is primarily driven by grazing pressure (Fuhlendorf and Smeins 1997, Fuhlendorf et al. 2001).

Table 14. Results of the detrended correspondence analysis of the 13 most abundant perennial grass species within the heavy grazing (n = 1), moderate grazing (n = 4), and no grazing (n = 2) treatments at the Sonora Experiment Station.

Variable	DCA Axis		
	1	2	3
Total species variance (inertia) in the species data: 1.130			
Eigenvalue	0.359	0.122	0.029
Cumulative percentage of variance from the species data	31.8	42.6	45.2
Pearson's Correlation of species with ordination axes			
Aristida purpurea	-0.60 *	-0.51 #	0.05
Bouteloua curtipendula	0.34	-0.66 **	0.34
Bouteloua hirsuta	-0.47 #	-0.20	-0.01
Bouteloua trifida	-0.37	-0.28	0.06
Carex species	-0.35	-0.01	-0.14
Digitaria cognatum	-0.14	-0.58 *	-0.02
Erioneuron pilosum	-0.47 #	-0.09	0.50 #
Eriochloa sericea	0.58 *	-0.31	0.08
Hilaria belangeri	-0.63 *	-0.64 *	0.02
Panicum hallii	0.04	-0.60 *	0.09
Schedonnardus paniculatus	-0.04	-0.36	0.12
Stipa leucotricha	0.69 **	-0.02	-0.37
Tridens muticus	0.66 *	-0.39	0.27
Correlation of DCA axes with			
Grazing intensity (Spearman's)	-0.51 #	-0.10	-0.22
Surface rock cover (Pearson's)	-0.15	-0.86 **	0.22
#p<0.10 *p<0.05 **p<0.01			



Non-rock sites are represented by squares, rock sites by bubbles. Square or bubble sizes are in 5 classes based on the summed basal area per treatment unit:1 = 0 - 3 cm^2, 2 = 4 - 9 cm^2, 3 = 10 – 27 cm^2, 4 = 28 – 81 cm^2, 5 = >81cm^2.

Fig. 16. The distribution of basal area by species along DCA axis 1 (grazing intensity) and axis 2 (surface rock cover) for rock and non-rock sites within the no-grazing (NG) (n = 2), moderate grazing (Mod) (n = 4), and heavy grazing (HC) (n = 1) treatments.

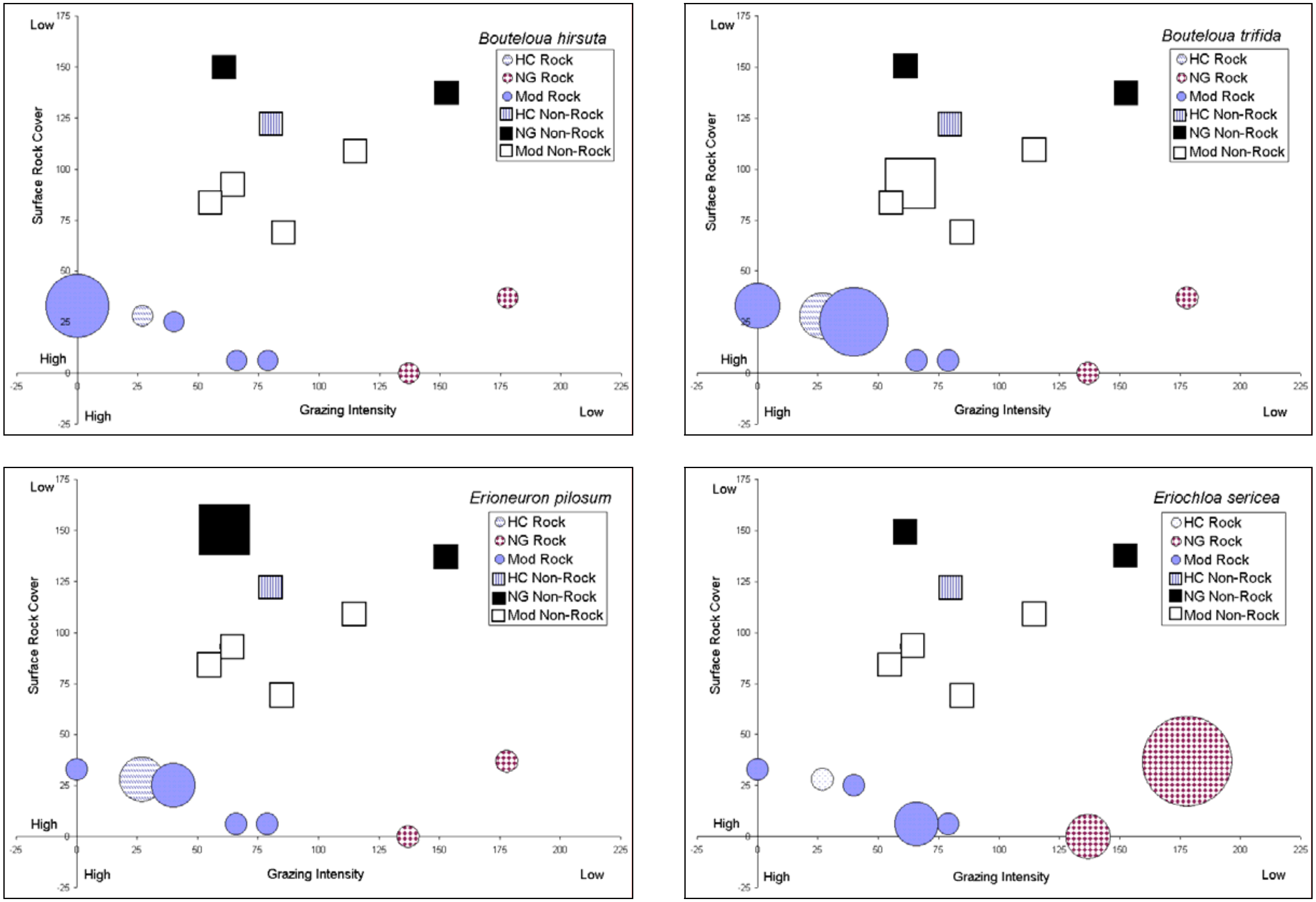


Fig. 16 Continued.

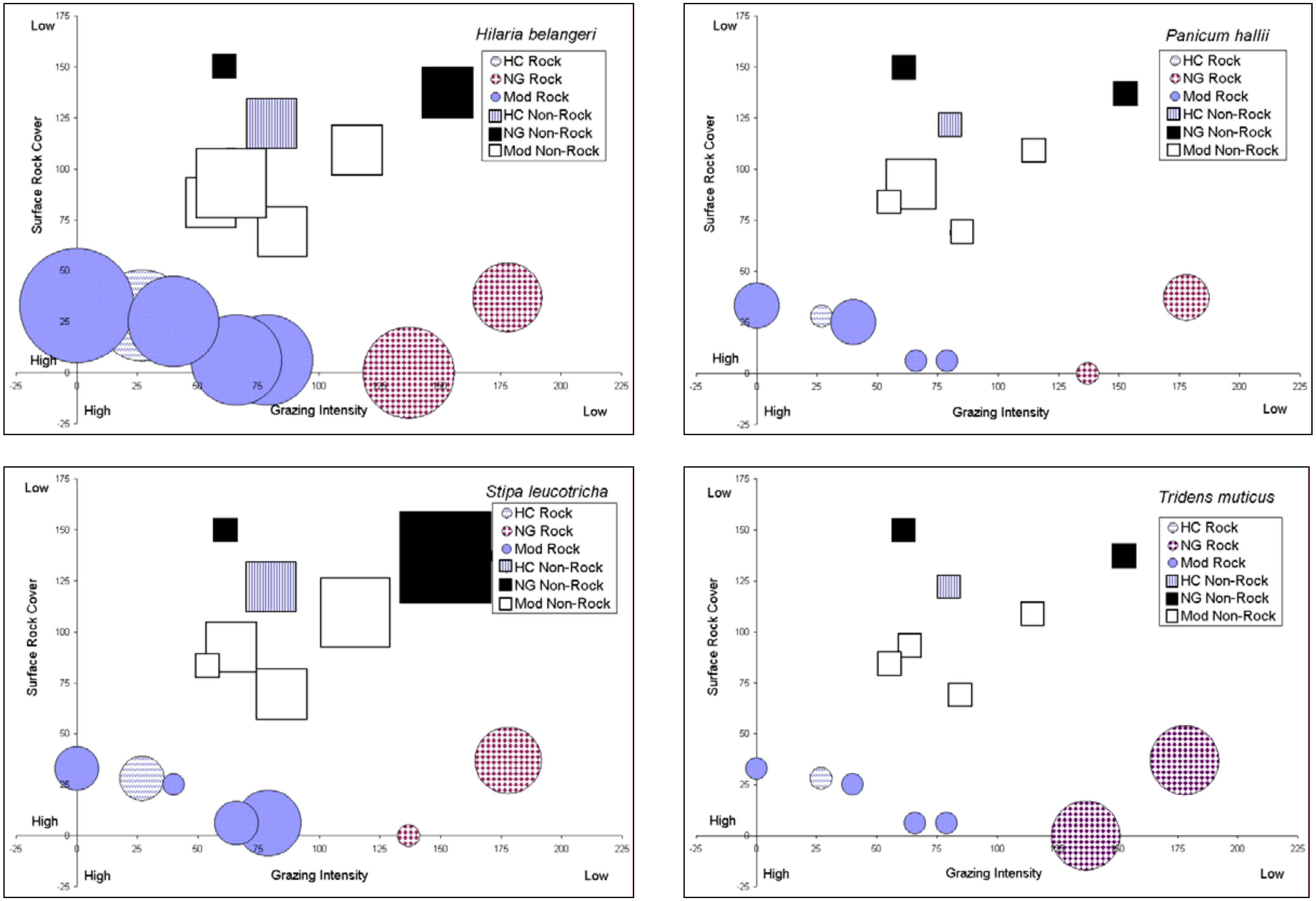


Fig. 16 Continued

The individual species relationship to grazing intensity and surface rock cover can be clearly seen when the basal area of individual species is plotted by treatment unit along the axis 1 grazing gradient and the axis 2 surface rock gradient (Fig. 16). The species *Carex planostrachys, Digitaria cognatum,* and *Schedonnardus paniculatus* were not included in these figures due to the small contribution of these species to the total basal area and their lack of influence on the results of the DCA ordination.

The distribution of basal area for the species *Aristida purpurea*, *Eriochloa sericea*, *Hilaria belangeri*, *Stipa leucotricha*, and *Tridens muticus* (Fig. 16) reflects the strength and significance of their basal area correlations with the DCA axis 1 scores (grazing gradient) found in Table 14. *Aristida purpurea* and *Hilaria belangeri* have strong negative correlations reflecting a decrease in abundance with a decrease in grazing intensity. *Eriochloa sericea* and *Tridens muticus* have strong positive correlations reflecting an increase in abundance with a decrease in grazing intensity. The strong negative correlation of *Stipa leucotricha* may not necessarily reflect a grazing intensity response but may be more of an indicator of woody vegetation edge density within the treatment units. *Stipa leucotricha* is a species that thrives in the dappled shade along the edges of woody vegetation patches and during periods of abundant cool season precipitation. The distribution of *S. leucotricha* basal area in Fig. 16 shows that a majority of basal area is found in the non-rock sites in a gradient moving from the grazed treatments to the no graze treatment. Edge density due to woody plant cover is highest in the no graze treatments. This combined with a pattern of abundant cool season precipitation may explain the abundance of *S. leucotricha* in this sampling period. Past analysis of the response of *Stipa leucotricha* to grazing intensity showed a slightly negative correlation of basal area to grazing intensity (Fuhlendorf 1996).

The lack of a significant correlation between *Bouteloua curtipendula* basal area and the DCA axis 1 scores (grazing gradient) is surprising given the strength of the negative correlation of basal area to grazing intensity from past grazing response analysis (Fuhlendorf 1996, Fuhlendorf and Smeins 1997). Past analysis of the suite of species utilized in this analysis showed that response to grazing intensity was individualistic but that species could be broken into three distinct grazing response groups: grazing intolerant, intermediate, and grazing tolerant (Fuhlendorf and Smeins 1997, 1998). In order to more clearly examine the relationship of grazing intensity to perennial grass species distribution during an extreme drought event these grazing response groups were used for a second detrended correspondence analysis of this data set. A fourth response group of shade tolerant perennial grass species was created for this analysis (Table 15).

Detrended correspondence analysis reduced the variation from the four perennial grass response groups to three axes and accounted for 63.8% of the total data variation. The first DCA axis accounted for a majority of the variance explained by the ordination (58.6%) while the second and third axes collectively accounted for around 5% of the total variation (Table 16).

The first DCA axis is both a grazing and surface rock cover gradient. The rock sites for each grazing treatment have positions on the lower half of the DCA axis 1 with scores below 100 while the non-rock sites position is on the upper half of the axis with values greater than 100 (Fig. 17). A grazing gradient is apparent within each of the rock and non-rock groupings with the no grazing replications holding positions at opposite ends of the first DCA axis with the grazed replications holding mid-axis positions. The exception to this pattern is the first replication of the no grazing rock site (NG1 NR in Table 16). This non-rock site has a similar position on DCA axis 1 as several of the moderate grazing rock sites. This is due to the similarity of the relative values of the response group summations used in the ordination. The absolute values for the four response groups for NG1 NR found in Table 16 are similar to the other non-rock response group values, but due to the very small value of the shade tolerant response group, the relative values of each response group used in the analysis were very similar to several of the moderate grazing rock sites.

Table 15. Basal area summation by treatment unit for the DCA ordination of the grazing intolerant, intermediate, grazing tolerant, and shade tolerant perennial grass species response groups for rock (R) and non-rock (NR) sites within the heavy grazing (HG) (n=1), moderate grazing (Mod) (n=4) and no grazing (NG) (n=2) treatment units at the Sonora Experiment Station.

	Grazing Response Group Basal Area (cm^2 / m^2)			
Treatment Unit	Grazing Intolerant	Intermediate	Grazing Tolerant	Shade Tolerant
HG1 R	25.4	62.1	85.2	5.6
HG1 NR	0.8	2.1	6.5	5.7
Mod1 R	52.0	18.5	72.1	10.7
Mod1 NR	2.5	2.5	7.0	14.6
Mod2 R	30.7	22.5	61.2	5.7
Mod2 NR	0.4	2.1	7.4	4.4
Mod3 R	19.4	79.6	111.5	6.0
Mod3 NR	1.9	4.8	14.6	8.3
Mod4 R	35.2	19.9	65.5	1.5
Mod4 NR	0.2	3.0	7.5	2.3
NG1 R	148.4	21.8	34.7	1.5
NG1 NR	4.1	1.9	9.9	0.3
NG2 R	182.4	18.3	13.4	23.6
NG2 NR	3.4	1.0	9.7	35.0

Table 16. Results of the detrended correspondence analysis of the 4 perennial grass grazing responses groups within the heavy grazing (n = 1), moderate grazing (n = 4), and no grazing (n = 2) treatments at the Sonora Experiment Station.

Variable	DCA Axis		
	1	2	3
Total species variance (inertia) in the species data: 0.609			
Eigenvalue	0.357	0.027	0.005
Cumulative percentage of variance from the species data	58.6	63.0	63.8

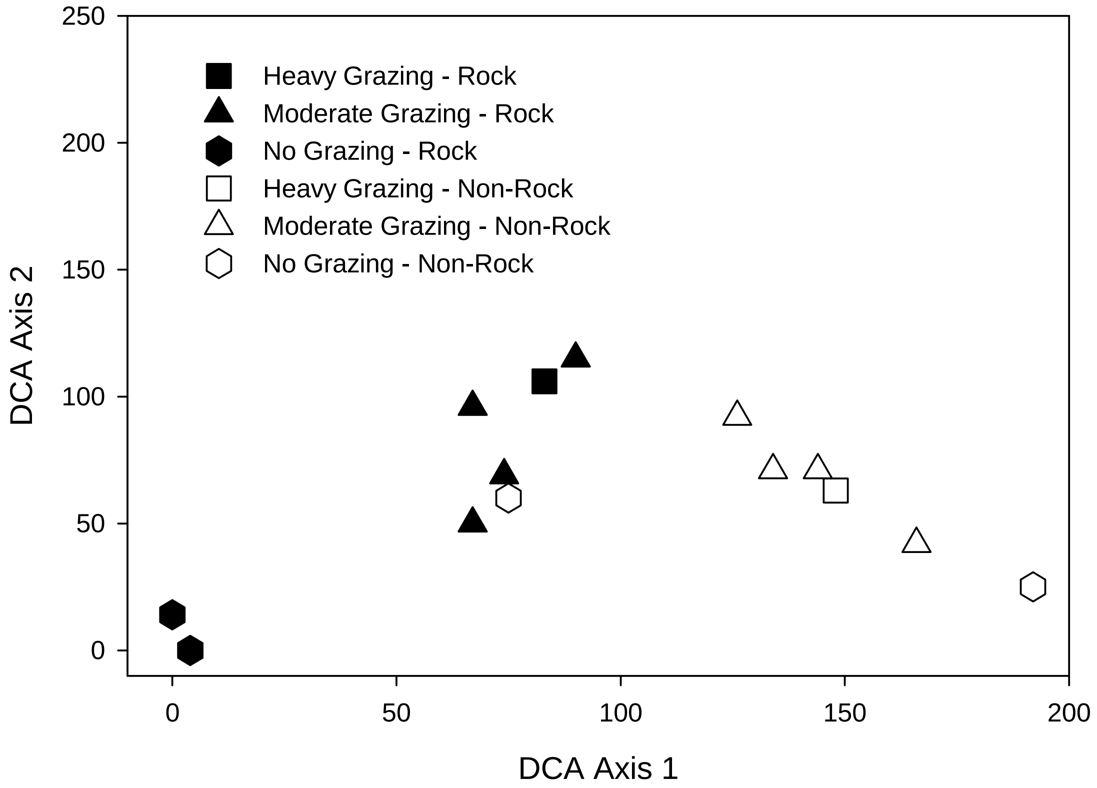


Fig. 17. DCA ordination of the grazing intolerant, intermediate, grazing intolerant, and shade tolerant perennial grass species response groups for rock and non-rock sites within the heavy grazing (n=1), moderate grazing (n=4) and no grazing (n=2) treatment units at the Sonora Experiment Station.

The grazing-surface rock cover gradient is made more apparent when curves are fit to the basal area of each grazing response group plotted against DCA axis 1 position (Fig. 18). Each of the grazing response groups had strong response patterns to the grazing-surface rock cover gradient within the rock sites compared to the flat response of the non-rock sites (Fig. 18). The strongest significant response to the grazing-surface rock cover gradient was with the grazing intolerant group ($r^2 = 0.97$, $p < 0.001$). Basal area was over three times greater for this response group within the no grazing treatment units compared to the grazed treatment units for the rock sites. Basal area was near zero for all grazing treatments for the non-rock sites.

The grazing tolerant group response to the grazing-surface rock cover gradient was strongly significant ($r^2 = 0.91$, $p < 0.01$). Basal area for the rock sites was over three times greater in the grazed treatment units than in the no grazing treatments. Grazing tolerant response group basal area for the non-rock sites was near zero across all grazing treatments.

The intermediate response group response was weaker than the grazing intolerant or grazing tolerant response groups but was moderately significant non-the-less ($r^2 = 0.76$, $p = 0.06$). The distribution of basal area for this response group was ubiquitous across all grazing treatments within the rock quadrats but with a greater amount of basal area distributed in some, but not all, of the grazed treatments.

The behavior of each grazing response group validates the interpretation of DCA axis 1 as a grazing - surface rock cover gradient.

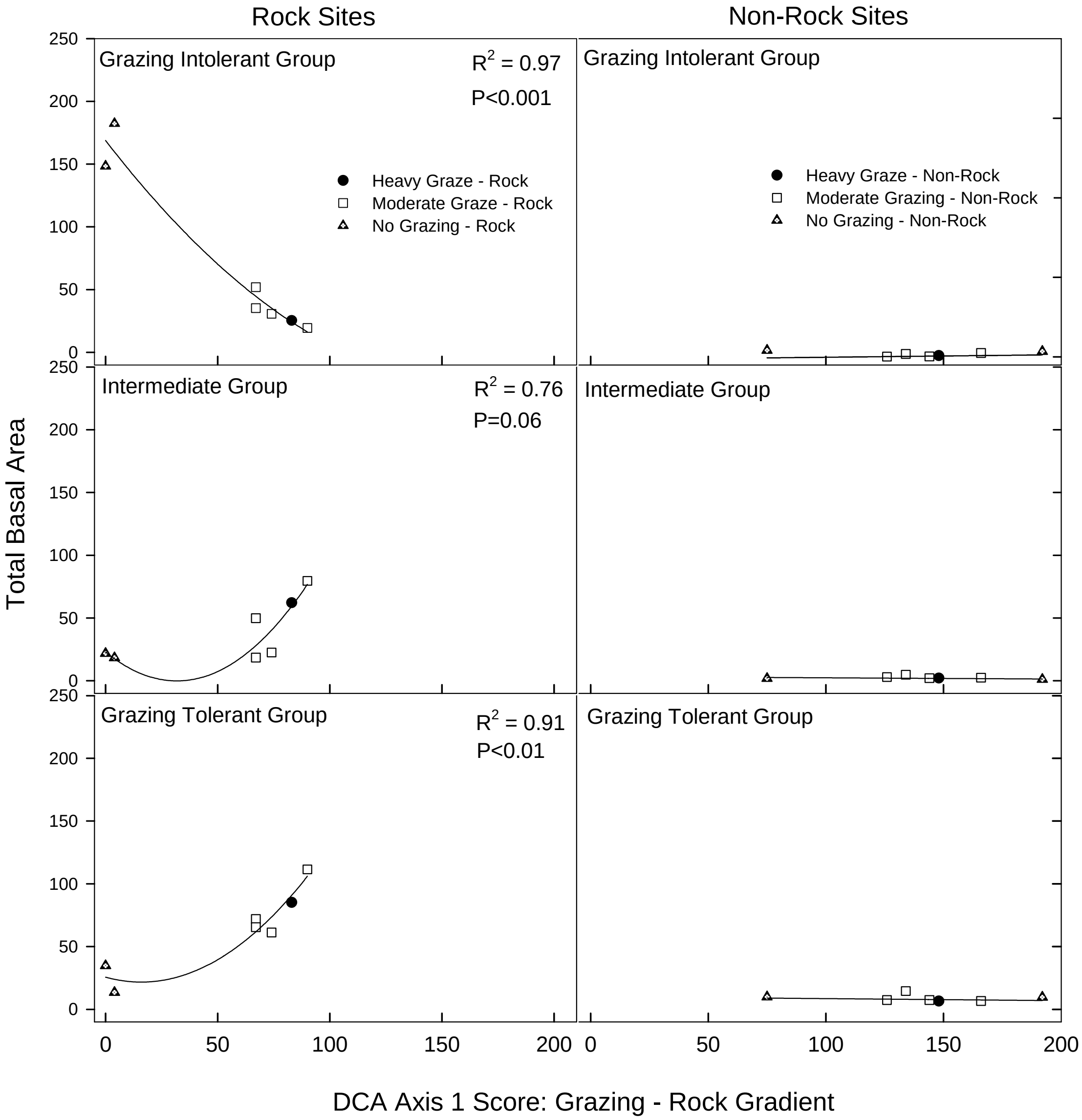


Fig. 18. Basal area (cm^2) of the grazing intolerant, intermediate, and grazing tolerant response groups for the rock and non-rock quadrats within the heavy grazing (n=1), moderate grazing (n=4) and no grazing (n=2) treatment along a grazing-surface rock cover gradient at the Sonora Experiment Station.

Discussion

Perennial Grass Population Structure

Herbivory primarily modifies perennial grass population structure through a reduction in the basal area of individual plants over time (Butler and Briske 1988). This influence can be seen in the perennial grass population structure across grazing treatments at the Sonora Experiment Station. Total perennial grass basal area was no different between the three grazing treatments but was significantly different between the rock and non-rock sites within the grazing treatments. This would indicate that patch features or structure that facilitate the survival of perennial grasses are the primary driving parameter behind the production and persistence of perennial grass basal area during periods of extreme drought on the Edwards Plateau.

The differences found in the density and basal area per plant of perennial grasses both between grazing treatments and between the rock and non-rock sites within the grazing treatments indicate that both grazing and drought influenced how this basal area was distributed across the landscape. Drought was the driving variable behind where perennial grass basal area could persist across the landscape while grazing drove how this basal area was distributed.

Grazed treatments generally had a high density of small basal area plants while the no grazing treatment had a low density of large basal area plants. No differences in total basal area were detected between grazing treatments. These results are consistent with other research documenting the influence of grazing on mean individual plant basal area and density (Sala et al. 1986, Butler and Briske 1988, Briske and Richards 1995, Fuhlendorf et al. 2001). This dynamic of differences in individual plant basal area and density fits the law of constant yield, where basal area is comparable across a range of plant densities (Briske and Richards 1995, Barbour et al. 1999).

This pattern of high densities of smaller plants for grazed treatments and low densities of larger plants for the no grazing treatments holds true across the rock sites but does not appear to be true for the non-rock sites. No real significant differences appear for perennial grass basal area or density between grazing treatments for the non-rock sites. However, significant differences do appear for perennial grass basal area per plant between the non-rock sites of the two grazed treatments and the no grazing treatment. There is a clear pattern of roughly twice as much basal area per plant in the no grazing treatment when compared to the moderate and heavy grazing treatments that are consistent across both the rock and non-rock sites (Fig. 13). This would indicate that the effects of grazing intensity on individual plant basal area still carried over into a community severely impacted by drought mortality in non-refugia sites.

Drought impact on plant basal area can clearly be seen in the differences between the rock and non-rock sites. The effect of both grazing intensity and drought mortality can be seen in the differences in plant density between both grazing treatments and the rock and non-rock sites. The effect of grazing intensity on individual plant basal area can be seen in the differences in basal area per plant between the grazed and no grazing treatments across both rock and non-rock sites.

Species Relationships

Grazing intensity is the primary driver of perennial grass species composition at this scale and complexity of analysis. Even with perennial grass production limited to more favorable sites in response to severe drought (drought refugia), the composition of perennial grass species within these favorable sites is driven by grazing intensity.

Species response to grazing intensity was individualistic along a grazing gradient with perennial grass production limited to favorable rock sites across the larger landscape. The distribution of grazing response groups by rock and non-rock sites provides clarity to the role of grazing intensity on perennial grass species composition (Fig. 18).

Species within each response group were morphologically and functionally similar (Fuhlendorf and Smeins 1997). Taller, more productive, grazing sensitive mid-grasses were dominant in the no grazing treatment rock sites while less productive, grazing resistant short grasses were dominant in the two grazed treatments rock sites. The intermediate response group is more ubiquitous across the rock sites of all grazing treatments. These species are opportunistic in their ability to respond to disturbance or unoccupied sites and tend not to dominate a perennial grass community (Fuhlendorf and Smeins 1997).

The use of grazing defined response groups has utility for the management of rangeland resources. However, these response group relationships have been found to be less appropriate when multiple variables are examined across multiple temporal and spatial scales (Fuhlendorf and Smeins 1998). In this case, the use of grazing response groups is appropriate by providing greater resolution on the impact of grazing intensity on perennial grass species composition between rock and non-rock sites across multiple grazing intensities than when examined by individual species alone.

Driving Variables

Parameters that had the highest significant correlations to perennial grass basal area were site features that maintained a favorable soil physical environment in such a way to facilitate the persistence of vegetation during extreme drought. The two variables with the strongest correlations to perennial grass basal area were rock cover and the gradient of rock quadrat site types based on increasing mean rock cover. Linear correlation analysis showed that basal area increases as rock cover increases (Table 10). The regression analysis gives a more detailed view of the curvilinear relationship between basal area and increasing rock cover (Fig. 14). These analyses together demonstrate the importance of the quantity of rock cover needed for perennial grasses during periods of extreme drought. As seen in Fig. 14, basal area becomes more variable with increasing rock cover. This may be a reflection of variation in soil resources, the effectiveness of a site to act as grazing or drought refugia, as well as the micro-climate features of a site. It is apparent from these analyses that areas of high rock cover act as geologic refugia

(Milchunas and Noy-Meir 2002) for perennial grasses during periods of extreme drought.

Features of geologic refugia such as the arrangement and size of rock fragments may provide positive microenvironment conditions in addition to protection from herbivory (Milchunas and Noy-Meir 2002). These site structural characteristics can enhance soil moisture as well as modify grazing pressure and competition (Noy-Meir et al. 1991b). Surface rock fragments have been shown to create a positive microenvironment by a) protecting soil structure from rainfall impact (Wilcox et al. 1988, Poesen and Ingelmo-Sanchez 1992, Brakensiek and Rawls 1994, Poesen and Lavee 1994, Moustakas et al. 1995), b) concentrating runoff by slowing overland flow (Poesen and Ingelmo-Sanchez 1992), c) increasing infiltration (Wilcox et al. 1988, Poesen et al. 1990, Poesen and Ingelmo-Sanchez 1992, Brakensiek and Rawls 1994, Moustakas et al. 1995), and d) decreasing soil moisture evaporation (Kosmas et al. 1993, Poesen and Lavee 1994, Moustakas et al. 1995).

Temperatures beneath surface rock fragments have been found to be cooler than surrounding soil (Mehuys et al. 1975). This effect can be moderated by rock size and color with cooler temperatures recorded for larger and more lightly colored rocks (Poesen and Lavee 1994). Soil water moves primarily in a vapor phase within a sufficiently dry soil. Because of horizontal temperature gradients, water vapor and heat move towards the cooler profile of soil found under surface rocks during the heating period of the day (Jury and Bellantuoni 1976b, a). Moisture condensation can occur under surface rock fragments as a result of this movement of moisture and heat (Poesen and Lavee 1994). The lower temperatures and accumulation of moisture associated with rock fragments can contribute to a positive microenvironment under drought conditions.

The analysis of basal area and rock site type illustrates the importance of rock size and configuration for the persistence of perennial grasses during extreme drought. Increasing perennial grass basal area was found along a gradient of increasing rock cover, rock size, and available soil resources moving from debris slopes to slab limestone benches to limestone blockfields.

The dynamics of rangeland ecosystems are driven in part by the inherent spatial heterogeneity of rangeland resources and the resulting vegetation communities (Ludwig and Tongway 1997). Differential vegetation response to drought is based in part on this spatial heterogeneity of communities and landscape features. As seen in the results of this research, landscape features that concentrate resources act as refugia for plants during severe drought events.

Refugia are conserving systems holding nutrients, maintaining soil structure and conserving soil moisture. The structure and function of these refugia conserve scarce resources and allow vegetation to persist in times of severe drought. Vegetation is better able to exploit limited resources within refugia than in non-refugia, which may be leaky systems (Ludwig and Tongway 1995, Tongway and Ludwig 1997a, b). Perennial grasses within refugia have been shown to better respond to pulses of moisture input and to conserve this moisture than non-refugia (Hodgkinson and Freudenberger 1997). The conserving system of refugia sites allows vegetation to respond to smaller pulses of water input due to the receptive nature of the physical structures present and their ability to capture resources from resource losing sites.

Vegetation can persist longer with fewer resource inputs due to the conserving system in place. Plant communities outside of the refugia sites once below a threshold are unable to conserve resources from small pulse events. It takes more resources over a longer temporal time frame for losing systems to respond in a similar fashion to conserving systems.

What is clearly evident from this analysis is that rock cover plays a vital role in the survival and persistence of perennial grass communities in the Edward’s Plateau during episodic periods of severe drought and that grazing pressure is the primary driver of perennial grass composition and community structure even during periods of drought.

CHAPTER V

CONCLUSION

Grazing and variable precipitation are seen as two primary forces driving temporal shifts in herbaceous species composition and community structure in semi-arid grasslands (O'Connor 1995). Grazing intensity was the primary driver of perennial grass species composition and community structure both during and between the extreme drought events of 1951 to 1956 and the drought event centered around the year 2000 on the Edwards Plateau. Total basal area during both events was driven primarily by variation in precipitation pattern. Basal area per plant dynamics were significantly influenced by grazing intensity while plant density was driven by both precipitation and grazing intensity.

Perennial grass population recovery from drought may be influenced by grazing intensity. The ability to recover from a severe drought event may be species specific. The recovery of perennial grass populations from severe drought may be influenced by grazing induced shifts in perennial grass community composition and community structure. Initial observations of the Sonora Experiment Station in the fall of 2003 indicate that drought recovery to pre-drought conditions was more extensive in the no grazing treatment. Whether this is a function of the life history of grazing intolerant perennial grasses, tiller demographics and individual plant size, or some other variable is unknown.

Perennial grass community recovery from drought under grazing pressure from unconfined native herbivores may differ significantly than recovery under confined livestock grazing. Native herbivore populations were most likely self-regulating with large decreases in herbivore populations due to decreases in available forage under drought conditions. The return of native herbivore populations would be mediated by the recovery of forage and the reproductive rates of individual animal populations (Ludwig et al. 1997) Grazing pressure from confined domestic livestock is controlled by land managers. Grazing pressure from domestic livestock is often supported beyond the carrying capacity of the natural system during drought by the input of resources by land managers.

Past analysis has shown an interaction of grazing intensity and drought in shifting perennial grass composition, primarily by accentuating grazing intensity in the heavy grazing treatment at the Sonora Experiment Station (Fuhlendorf and Smeins 1997). The resulting shift in species composition due to this interaction of drought and grazing intensity shows the importance of understanding the grazing management hazards and opportunities presented by stochastic climatic events and their role in a dynamic rangeland environment (Westoby et al. 1989).

The spatial heterogeneity of drought refugia significantly influenced the persistence of perennial grasses during an extreme drought event. Grazing intensity was the primary driver of species composition and community structure within both refugia and non-refugia sites on the Edwards Plateau. Drought intensity was the significant driver of differences in perennial grass basal area and density between refugia and non-refugia sites. The influence of grazing intensity on basal area per plant could be seen in both refugia and non-refugia sites between grazing treatments.

Perennial grasses are better able to persist in drought refugia due to the positive microenvironment provided by the refugia physical environment. The structural characteristics of refugia allow them to better hold nutrients, maintain soil structure and conserve soil moisture than non-refugia sites. The effectiveness of refugia sites in maintaining perennial grass basal area during an extreme drought event increased along a gradient of increasing rock cover, rock size, and available soil resources.

Vegetation response within refugia sites may be variable with random climatic events but what makes these sites important for the long-term maintenance of landscape scale vegetation communities is the continued persistence of refugia communities compared to non-refugia communities through all types, frequencies and intensities of disturbance events. These drought refugia store the needed resources and maintain the seed source for community reestablishment in areas of drought induced plant mortality.

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