

Responses of a remnant California native bunchgrass population to grazing, burning and climatic variation

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Received 1 February 2003; accepted in revised form 11 March 2005

Key words: Burning, California, Climatic variation, Grasslands, Grazing, *Nassella pulchra*, Purple needlegrass

Abstract

This study examined the interactive effects of grazing intensity and burning on a remnant population of the California native bunchgrass *Nassella pulchra*. We measured growth, reproduction and mortality of permanently marked bunchgrasses and measured bunchgrass seedling recruitment and density in permanent quadrats. We burned half of the treatment plots in late spring 1998. Grazing treatments were implemented in 1998, 1999 and 2000 at four different intensities: ungrazed, light rotational grazing (31% average biomass removal), heavy rotational grazing (42% average biomass removal), and continuously grazed. Both burning and grazing affected the bunchgrass population. Bunchgrass mortality was 10% higher in burned vs. unburned plots but was not significantly different among grazing treatments. Seedling density was 100% higher in burned vs. unburned plots 2 years after the burn, however seedling densities never attained pre-burn levels. Seedling densities did not differ significantly among grazing treatments, but grazing reduced the height and reproduction of the mature bunchgrasses. Adult bunchgrass density did not differ significantly in any of the treatments but experienced a five-fold decrease over the 4 years of the experiment. Although the continuous grazing treatment reduced the number of culms produced per plant by 75% from the baseline year, the effect on culm production in the continuous grazing treatment was not consistently greater than the rotational grazing treatments. The interaction of grazing and burning had no significant impacts on the *N. pulchra* populations except on the diameter of adult bunchgrasses which was highest in the lightly grazed, unburned treatments 2 years following the burn. All response variables except bunchgrass height followed a similar pattern in time over the 4 years of the experiment regardless of treatment, peaking in 1998 and then declining in 1999 and 2000. We believe the above average rainfall and below average temperatures experienced late in the growing season in 1998 provided conditions that favored the native bunchgrasses. Overall, we found few interactive effects of grazing and burning but the separate treatments did affect bunchgrass growth, reproduction and mortality, and these effects were modulated by the ubiquitous effects of climatic fluctuations.

Introduction

Fire and grazing are disturbances commonly associated with grasslands occurring throughout the world (Noy-Meier et al. 1989; Milchunas and Lauenroth 1993; Noss 1994; Whelan 1995). Increased human use and alteration of these grasslands has shifted the frequency, seasonality, intensity and extent of these disturbances relative to historic regimes (Heady 1988; Fleischner 1994; Perevolotsky and Seligman 1998) and has in many cases dramatically altered the grassland species composition (Westoby et al. 1989; Barbour et al. 1993; Grace et al. 2001). The extent of these changes is determined in part by the intensity and duration of the disturbance as well as the interaction with climatic patterns (Mack 1989). The need to understand how multiple disturbance agents may act together to affect both community structure as well as the demography of component species has been emphasized as an important goal for field experimentation in grassland ecology (Collins 1987; Silletti and Knapp 2002). Not only is aboveground composition and productivity affected by the disturbance regime, but belowground processes such as root growth, soil respiration, and nutrient cycling also respond differentially to the effects of fire and grazing (McNaughton 1985; Johnson and Matchett 2001). In general, a better understanding of the relative importance of separate and interactive effects of multiple disturbance factors is required if we hope to manage disturbance to promote the diversity and persistence of native grassland systems (Harrison et al. 2003).

Despite a growing number of studies that have examined the effects of fire and grazing on grassland structure and population dynamics (Noy-Meir 1995; Harrison et al. 2003), there are still relatively few studies that have focused specifically on the potential interactive effects of these important disturbance agents especially in an experimental context (Engle and Bidwell 2001). Some of the strongest support for the importance of the interactive effects of grazing and fire comes from research on the tallgrass prairie in midwestern North America (Collins 1987; Knapp et al. 1999). In this mesic grassland system, C4 grasses tend to dominate following repeated fires and bison (*Bison bison*) grazing serves to modulate this dominance and promote greater plant diversity.

Although the evidence is strong that the interaction of fire and grazing is critical for the maintenance of species diversity in tallgrass prairie, it is not so clear that this result is generally true for other grassland systems. In particular, there have been studies in more arid grasslands where there is little or no indication of interactive effects of fire and grazing on grassland composition and species diversity (Valone and Kelt 1999; Drewa and Havstad 2001; Harrison et al. 2003). It has been suggested that more xeric conditions may reduce the capacity of canopy dominants to respond to fire and thus the potential modulation by grazing is less likely to be apparent or important (Drewa and Havstad 2001).

The Mediterranean grassland systems of California represent a relatively arid grassland type where both grazing and fire have been important natural disturbance agents though their frequency, season and intensity have changed dramatically since pre-European settlement (Heady 1988). More specifically, the season and intensity of grazing on grassland species has changed since the introduction of livestock grazing to California. Native grazers such as pronghorn antelope (*Antilocarpa americana*), tule elk (*Cervus elaphus nannodes*) and deer (*Odocoileus hemionus*) were abundant and probably grazed the Central Valley grasslands seasonally (Heady 1988; Edwards 1992). After the Spanish introduced livestock to California grasslands in the late 18th century, year-round, high-intensity grazing was common throughout the Valley. Peak livestock densities coupled with a severe, prolonged drought in the late 1800s have been suggested as reasons for the shift in species composition from dominance by perennial bunchgrasses to non-native annual grasses and forbs (Burcham 1957; Heady 1988; Mack 1989). Although extreme grazing pressure may have contributed to a decline in native bunchgrasses in California grasslands, removal of grazing has not increased native bunchgrass populations (Bartolome and Gemmill 1981).

Historically, lightning strikes and intentional burning by Native Americans periodically ignited the litter in California grasslands (Hervey 1949; Daubenmire 1968; Biswell 1989; Barbour et al. 1993). Fires likely occurred every 1–15 years in these grasslands (Greenlee and Langenheim 1990) and helped maintain plant diversity. Native bunchgrass species such as *Nassella pulchra*

(Hitchc.) Barkworth (purple needlegrass) are believed to be fire tolerant and may experience increased recruitment and growth following fire (Ahmed 1983; Menke 1992; Dyer et al. 1996). Fire is thought to be important for promoting native bunchgrass growth and reproduction by creating a nutrient rich ash, removing thatch from between bunches, and keeping woody plants from becoming established in the grasslands (Biswell 1989; Barbour et al. 1993). Experiments in California grasslands have shown that periodic fire reduces the competitive ability of exotic annual grasses without adversely affecting established populations of native bunchgrasses (Ahmed 1983; Pollak and Kan 1998; Dyer 2003).

Using experimental manipulations of grazing and fire we studied: (1) the effects of four different grazing intensities, (2) early-summer burning, and (3) the interaction of grazing and burning on the growth, density, reproduction and mortality of a remnant population of *N. pulchra* in the foothills of California. Based on our literature review, we generally expected grazing to negatively impact the growth, survival and reproduction of *N. pulchra* and fire to increase growth, recruitment and reproduction of the bunchgrass population.

Methods

Study site

We conducted this study on Beale Air Force Base (BAFB), located 16 km east of Marysville in Yuba County, California, USA (39°10' N, 121°40' W). At BAFB, much of the grassland has been used as open rangeland for the last 200 years (Reinhardt pers. comm.). Currently, cattle seasonally graze ca. 5000 ha. of grassland on the site. As is true for most California grasslands, perennial bunchgrasses are rare in the grasslands on BAFB. Less than ten small (<1 ha.) remnant patches of the native bunchgrass *N. pulchra* remain on BAFB (Marty pers. obs.).

N. pulchra is a densely tufted, perennial bunchgrass that grows from 30 to 100 cm tall. It is found growing in small patches throughout the Central Valley in oak woodland, chaparral and grassland habitats up to 1300 m (Crampton 1974; Hickman 1993). *N. pulchra* grows throughout the winter, generally produces culms (reproductive tillers)

beginning in late April, and sets seed in May. The extensive root system of this bunchgrass reaches depths of up to 3 m (Hull and Muller 1975; Dyer and Rice 1997), which allows it to remain green throughout the dry summer in California's Mediterranean climate (Sampson and McCarty 1930). In the fall, *N. pulchra* requires less than 1 cm of rainfall to begin growing and can initiate tiller extension without any rainfall at all (Biswell 1989).

Experimental plots were located within a 10 ha. pasture that has been used by BAFB for exercising and grazing horses for at least the past 30 years but has not been grazed by cattle for at least 50 years. The site is on a south-facing slope in rolling upland hills adjacent to the Sierra Nevada foothills. The vegetation is dominated by various non-native annual grasses and forbs. These include *Brachypodium distachyon*, *Bromus* spp. (brome), *Erodium* spp. (filaree), *Avena barbata* (slender wild oats), *Centaurea solstitialis* (yellow starthistle) and *Taenatherum caput-medusae* (medusahead). Of the native species present at the site, *Quercus douglasii* (blue oak) and *Nassella pulchra* are the most abundant. A very small number of mule deer (*Odocoileus hemionus*) represent the only large, native grazing animal remaining on the site.

Precipitation and temperature patterns for the years of the experiment are shown in Figure 1. The winter of 1998, an El Niño year, had over 200% higher than average rainfall. 1998 also had late spring (April–May) rainfall and lower temperatures in May and June compared to those months in the other three years of the experiment. The effects of these weather patterns on the vegetation were evident while we were attempting to burn the pasture in 1998. We were unable to burn the pasture until early July because there was too much moisture in the vegetation to carry a fire. In all other years the vegetation senesced and dried by late May or early June.

Experimental design

We used a split-plot design arranged in blocks with two levels of burning (main plot factor) and four levels of grazing intensity (within plot factor). Each block was replicated five times at the site. Each block consisted of eight, 20 m × 20 m treatment plots (4 levels of grazing × 2 levels of burning × 5 blocks = 40 treatment plots).

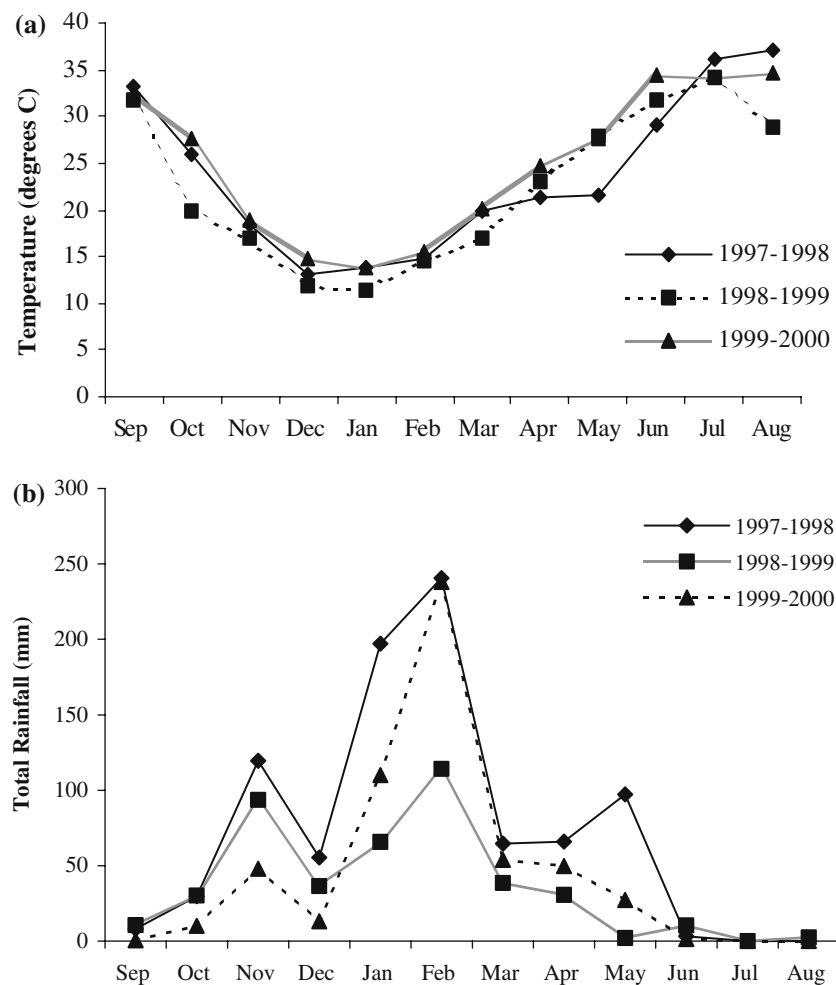


Figure 1. Maximum monthly (a) temperature and (b) total monthly precipitation recorded in Marysville, CA.

All blocks were randomly split into burned and unburned treatments. A split-plot design was chosen for fire safety and ease of logistics. The BAFB Fire Department burned half of the plots in each block in July 1998 using a combination of backing and heading fires. No measures of fire intensity were recorded. The burn was conducted in early summer to minimize mortality of mature *N. pulchra* plants while maximizing the removal of thatch and post-dispersal weed seed in the plots (Biswell 1989).

Four levels of cattle grazing intensity were used in this experiment: light, heavy, continuous and ungrazed treatments. The different grazing regimes were designed to compare the effects of rotational, controlled grazing at two intensity levels vs. the standard continuous, uncontrolled grazing

practiced on most rangeland in California. Because it was beyond the scope of this project to calculate the amount of time the cattle spent in the continuous grazing treatment, we do not directly compare stocking densities between the controlled and continuous grazing treatments. The light and heavy cattle grazing treatments utilized controlled grazing cycles (2 cycles per season) differentiated by percentage of biomass removed. These treatments involved short-term, intense grazing of a fixed number of cattle followed by a vegetation rest period (Table 1). The cattle required anywhere from 2 to 20 h to remove the requisite amount of biomass from the plots. The vegetation rest period averaged 35 days between grazing cycles. Cattle were introduced into the controlled (light and heavy) grazing treatment plots once the total

Table 1. Grazing data for the heavy and light grazed treatments.

	Grazing data for heavy and light grazing treatments					
	1998		1999		2000	
Grazing measure	Heavy	Light	Heavy	Light	Heavy	Light
Cowhours	104.3 ± 18.8	73.7 ± 22.8	20.9 ± 1.9	14.8 ± 1.4	10.8 ± 0.9	8.1 ± 0.8
Percent utilization	48.0 ± 4.0	31.8 ± 3.0	42.3 ± 2.0	30.3 ± 3.1	37.4 ± 2.3	30.1 ± 2.6
Stocking rate (AU/ha)	150.0	150.0	126.1 ± 1.4	124.8 ± 1.8	109.4 ± 3.5	109.4 ± 3.2
Fecal pats	31.3 ± 6.0	22.8 ± 5.4	13.9 ± 1.3	9.3 ± 1.8	6.4 ± 0.7	4.7 ± 0.5

Data shown are mean values (\pm SE) for the one or two grazing periods used during the grazing season. In 1998, three of the five blocks were grazed one time at the end of the grazing season. In 1999 and 2000, all five blocks were grazed twice during the grazing season. The cowhour variable was calculated as the number of animal units (AUs) multiplied by the number of total hours the cattle spent in the plot. The formula for percent utilization is presented in the methods section. Stocking rates were extrapolated from number of AUs per 400 m² plot to AUs per hectare.

biomass reached 1200 kg/ha. The target standing biomass utilization rate in the heavy grazing treatment was an average of 50% (600 kg/ha) and the target for light grazing treatment was an average of 25% (300 kg/ha) (actual utilization rates are given in Table 1). These rates were chosen after conducting grazing trials in 1998 to determine the maximum biomass the cattle would consume in a 24-h period (50% utilization rate). That figure was halved to obtain the target utilization rate for the light grazing treatment. Average standing biomass was measured in the field by randomly placing eight to ten, 0.10 m² circular quadrats within a treatment plot, clipping all the plant material inside the quadrat, and weighing total plant biomass using a field scale. Calibrated visual estimation of the grazed vegetation was used to determine when to remove cattle from plots. Average standing biomass was again measured immediately after cattle removal in order to calculate percent utilization for the treatment plot. Grazing treatments were applied twice during the grazing season (January–May) once biomass growth in the plots reached 1200 kg/ha. Percent utilization was calculated as:

$$\% \text{Utilization} = (B_{\text{pre}} - B_{\text{post}}/B_{\text{pre}}) \times 100$$

where B_{pre} is the average above-ground biomass before grazing and B_{post} is the average biomass after grazing. Total grazing time and number of fecal pats deposited were recorded once cattle were removed from each controlled grazing treatment plot (Table 1).

Continuously grazed treatments were unfenced and subject to grazing by cattle during the entire grazing season (January–May). In 1998, the entire

10-ha pasture was stocked with six cow-calf pairs at an average stocking rate of 0.75 animal units (AU) per hectare. The grazing season was reduced that year to 1.5 months (1 May–15 June) because the construction of the pasture's perimeter fence was delayed. Due to the shortened grazing period, we were only able to implement one grazing cycle in three of the five blocks using all six cow-calf pairs in each plot (12 total treatment plots). Consequently, the shortened grazing season left the continuously grazed plots underutilized for that year. In 1999 and 2000, the pasture was stocked for six months (December–May) with six heifers equating to a stocking rate of 0.64 AU per hectare. Two of the plots in each block were left as ungrazed controls.

Vegetation sampling

All of the experimental plots were established in June 1997, and baseline data were collected on *N. pulchra* plants in these plots from June to September 1997. In each plot, we mapped and individually tagged up to 50 naturally occurring *N. pulchra* plants (1943 total). We counted the number of reproductive culms and measured average blade height and basal diameter (using calipers) of each plant. Average blade height was calculated as the average of the shortest and the tallest blade of each individual plant. Approximately 1200 (30 per treatment plot) of these marked plants were located and measured in spring 1998, 1999 and 2000. We used a metal detector (Radio Shack, Ft. Worth, TX) to locate the tags. We did not locate all 50 tags each year in

each plot because several tags in each plot were lost to gopher activity, and it was inefficient to locate more than 30 tags. Percent mortality was computed annually as the number of tagged dead individual plants in each plot divided by the total number of tags located in each plot.

Three to five, 1 m × 1 m quadrats were randomly placed and permanently marked in each plot in spring 1997 for future location (197 total). Within these quadrats, each *N. pulchra* adult (basal diameter ≥ 1 cm) and seedling (basal diameter < 1 cm) was mapped and measured for basal diameter, the number of culms and average blade height (except seedlings for which only the blade height and the number of blades were measured). These quadrats were located in spring 1998, 1999 and 2000 and the number of *N. pulchra* seedlings and adults were recorded.

Data analysis

Plant response data (diameter, height, number of culms, mortality, seedling and adult density) were analyzed as a split-plot design with block, burning (whole plot factor) and grazing (within plot factor) as main effects. We included burning by grazing and block by burning interaction terms in the model. Plot means for all variables were analyzed

first with MANOVA, then separately with “protected” ANOVAs (Scheiner 1993). All multiple pairwise tests were analyzed with linear contrasts and evaluated for significance ($p < 0.05$) using Tukey’s HSD test. Data were tested for the ANOVA assumptions of homogeneity of variances, independence and normality. In the cases where data were either non-normal or heteroscedastic, ANOVA tests were run on rank-average-transformed data (Conover and Iman 1981). Correlation analysis was performed for the 1999 data (one year post-burn) on bunchgrass diameter and mortality grouped by burn treatment. All analyses were performed with JMP version 5.1 (SAS Institute 2004).

Results

Plant size

The *N. pulchra* plants in the unburned plots were larger than those in the burned plots prior to burning in both 1997 and 1998 (Table 2). So, we tested whether the change in diameter (e.g. diameter 98–diameter 97) was significantly different for any treatments in any combination of years and found no significant results. Plant diameter did not

Table 2. Analysis of variance of (a) basal diameter, (b) height, (c) culms, (d) mortality, (e) seedling density and (f) adult density of the bunchgrass *Nassella pulchra* at Beale Air Force Base in a study of grazing and burning effects.

Year	Effect	Diameter (cm)	Height (cm)	Culms (#/plant)	Mortality (%)	Seedling density (#/m ²)	Adult grass density (#/m ²)
1997	Burn	10.97*	0.09	3.01	–	0.10	5.26
	Graze	1.79	0.78	0.59	–	0.21	0.39
	B × G	2.29	1.15	0.13	–	1.03	1.23
1998	Burn	14.92*	0.83	2.10	1.84	4.14	0.02
	Graze	0.64	4.61**	4.30*	1.49	4.46*	0.35
	B × G	0.80	1.16	0.97	0.48	3.47*	1.06
1999	Burn	9.76*	1.42	1.97	1.36 ($F = 6.93^{***}$, Block × burn)	0.49	0.03
	Graze	0.73	26.00***	21.44***	1.78	1.69	0.61
	B × G	2.54	2.72	1.74	0.96	2.02	0.26
2000	Burn	7.51†	4.94	1.94	2.49	1.75	0.20
	Graze	1.57	12.42***	12.66***	0.62	0.72	1.77
	B × G	4.78**	0.93	1.09	1.47	0.77	0.26
MANOVA	Burn	2.07	2.40	1.88	2.49	3.56*	1.56
	Graze	1.10	3.17***	7.49***	0.80	1.48	1.13
	B × G	0.90	0.42	0.97	1.68	1.10	0.94
	Time	62.96***	176.51***	121.28***	70.42***	55.57***	42.44***

Main effects are block (df Numerator, denominator = 4, 4), burning (df = 1, 4) and grazing (df = 3, 24). We also included a grazing by burning (df = 3, 24) and burning by block interaction (df = 4, 24) but do not report the F values in this table. F values are for the univariate tests. Repeated measures (MANOVA) values are Wilk’s lambda. † $p = 0.052$; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

Table 3. Mean and standard error for *N. pulchra* basal diameter, height, number of culms, mortality (1997, $n = 1946$; 1998, $n = 1058$; 1999, $n = 809$; 2000, $n = 529$), adult and seedling density per quadrat ($n = 197$) by year for the 4 years of the experiment.

	1997	1998	1999	2000
Diameter (cm)	2.86 (± 0.11)	3.6 (± 0.13)	2.66 (± 0.13)	2.62 (± 0.12)
Height (cm)	25.27 (± 0.75)	21.7 (± 1.29)	11.79 (± 0.67)	14.46 (± 0.99)
Number of culms	3.09 (± 0.23)	3.9 (± 0.39)	1.5 (± 0.20)	1.26 (± 0.17)
Mortality (%)	**	14.72 (± 1.00)	25.06 (± 2.0)	27.82 (± 2.0)
Adult density	4.88 (± 0.55)	5.78 (± 0.44)	5.26 (± 0.46)	1.07 (± 0.08)
Seedling density	2.77 (± 0.33)	4.10 (± 0.41)	1.81 (± 0.35)	1.57 (± 0.27)

differ significantly among treatments in 1999. In 2000, plants in the light grazed unburned treatment were significantly larger than those in any other grazing by burning treatment combination ($p < 0.01$). Diameter differed significantly over the 4 years of the experiment ($p < 0.001$, Table 2) peaking in 1998 with an increase of nearly 30% from the 1997 baseline year. In 1999, the average diameter decreased by 30% and then remained constant in 2000 (Table 3). These changes were independent of grazing and burning treatments.

We found significant effects of grazing on the average height of the *N. pulchra* plants throughout the experiment ($p < 0.001$, Table 2). In 1998, plants in the heavy grazed plots were shorter than those in any other grazing treatment ($p < 0.05$). In 1999, the continuously grazed plants were significantly shorter than those in all other grazing treatments while in 2000 the continuously grazed plants were shorter than the ungrazed and light grazed plants only ($p < 0.05$, $p < 0.05$ respectively).

Reproduction

Grazing significantly reduced the average number of culms produced by the adult *N. pulchra* plants in all years ($p < 0.001$, Figure 2). In 1998, plants in the heavy grazed treatments had the fewest culms per plant while those in the ungrazed plots had the most culms ($p < 0.05$). In 1999 ungrazed plants produced more culms than those in any of the other grazing treatments ($p < 0.05$). In 2000 plants in continuously grazed plots produced significantly fewer culms than those in the light grazed treatment plots only ($p < 0.05$).

Nassella pulchra reproductive culm production was greater in 1997 and 1998 than in 1999 and 2000 independent of grazing or burning treatments ($p < 0.001$, Table 2). Culm production peaked in

1998 at nearly four culms per plant then decreased by 61% in 1999 and another 15% in 2000 (Table 3).

Mortality

Nassella pulchra mortality was higher in burned plots than unburned plots in four of the five blocks in 1999 ($p < 0.001$, Table 2) but not in 2000. Mortality in the burned plots nearly doubled one year after the burn and then remained constant at 30% in 2000. In the unburned plots, *N. pulchra* mortality steadily increased on average 3–6% from 1998 to 2000. Plant mortality was negatively correlated with *N. pulchra* diameter in 1999 (Figure 3), but only for the burned treatment plots ($r = -0.47$, $p < 0.05$). Grazing did not have a statistically significant effect on mortality (Table 2). Mortality nearly doubled between 1998 and 1999 and then remained nearly constant between 1999 and 2000 ($p < 0.001$, Table 3).

Plant density

Adult *N. pulchra* (diameter > 1 cm) density in $1 \text{ m} \times 1 \text{ m}$ permanent quadrats did not differ significantly between treatments. In 1998 the number of seedlings (diameter < 1.0 cm) was two times higher in continuous grazed, unburned plots than any other treatment combination. We found a significant effect of burning on *N. pulchra* over time where the number of seedlings found in the burned plots was not significantly different than the unburned plots until 2000 where two times more seedlings were found in burned vs. unburned plots (Figure 4).

Nassella pulchra density (seedlings and adults) increased by 23% from 1997 to 1998 then

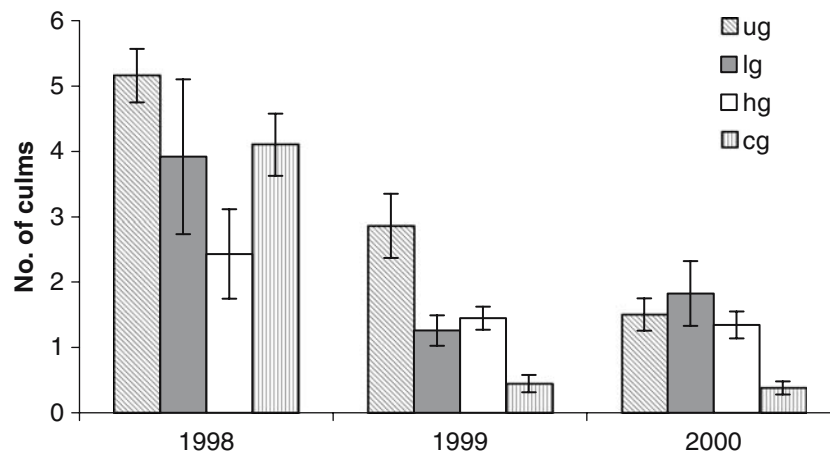


Figure 2. Number of culms per plant (mean \pm SE) for each grazing treatment in 1998, 1999 and 2000. Grazing treatments are: ug = ungrazed, lg = light grazed, hg = heavy grazed, and cg = continuous grazed.

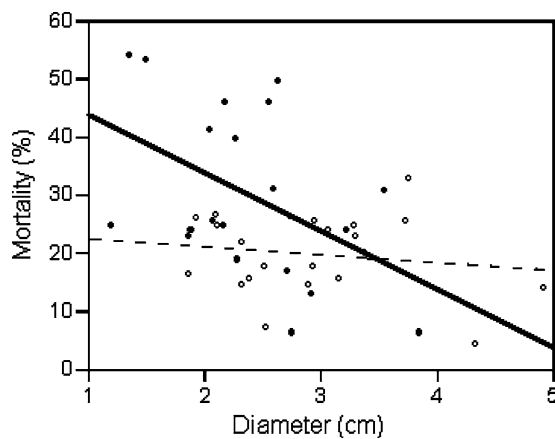


Figure 3. Relationship between *N. pulchra* mortality and diameter in 1999 by burn treatment (solid circles = burned treatment; open circles = unburned treatment). Only the burned treatment was significant ($r = -0.47$, $p < 0.05$).

decreased by 30% between 1998 and 1999 and decreased an additional 60% between 1999 and 2000 ($p < 0.001$, Table 2). This decline in density in 2000 was mainly due to a five-fold decrease in the number of adult plants found in the plots. The number of seedlings decreased by only 13% during the same period (Table 3).

Discussion

Burning and grazing as separate disturbances significantly affected the population of *N. pulchra* at this site. Grazing tended to negatively impact the height and reproductive output of the plants and burning significantly increased the mortality and

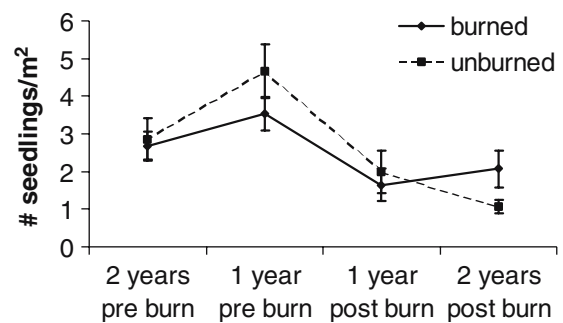


Figure 4. *N. pulchra* seedling density (mean \pm SE) by burn treatment measured in 1 m \times 1 m quadrats over the 4 years of the experiment.

density of seedlings in the population. We found only one true interactive effect of these two disturbances on the population which was a tendency for the light-grazed unburned plants to be larger than all others.

We did not find significantly higher mortality in our grazed treatments, however grazing does have the potential to negatively impact the population of *N. pulchra* at this site by reducing the reproductive output of the plants. Rotational grazing has been proposed as a way to reduce thatch and non-native species in these systems while still allowing the native bunchgrasses to maximize reproduction (Barry 2003). Our results only partially support this hypothesis. While continuous grazing clearly reduced the reproductive output of the plants, the plants in the rotational grazing treatments did not consistently produce more culms than those in the

continuous grazing treatment. We also did not see evidence that a decrease in culm production resulted in decreased recruitment in the population during the study. In fact we saw some evidence that continuous grazing might improve survival of seedlings in some years likely due to reduced competition from exotic annual grasses (Dyer 2003). Although culm production remained high in the ungrazed treatments, seedling production remained low. The short duration of this study and the long-lived nature of this species make it difficult to predict the long-term effects of grazing on *N. pulchra*.

Burning significantly increased the mortality of *N. pulchra* in this experiment. One year following the burn, approximately 30% of the plants had been lost in the burned plots compared to 20% in the unburned plots. This result appears to contradict those of other studies showing positive effects of burning on *N. pulchra* populations (Ahmed 1983; Dyer et al. 1996; Pollak and Kan 1998; Barry 2003). This may be a result of the sampling methods and measures used in these other studies. In the current study, we utilized both demographic methods (tagging and tracking individuals) and density measurements within permanent plots. We were unable to detect a significant burn effect on bunchgrass density measured in our permanent plots even though there was a significant increase in bunchgrass mortality revealed by monitoring individuals over time. This result highlights the importance of using appropriate demographic methods to understand population dynamics. For example, it is possible to detect an increase in *N. pulchra* density within a population following a disturbance while also finding an increase in mortality. An individual *N. pulchra* bunchgrass can become fragmented aboveground after disturbance and appear to be separate individual plants. Each fragment would likely be counted as an individual, thus artificially inflating density measures. By tagging and tracking individuals over time, this problem is reduced.

It is possible that site conditions prior to burning may have also played a role in the increased *N. pulchra* mortality. In this case, the pasture where this study was conducted had not been burned in at least two but probably three or four decades. Additionally, the past grazing intensity (horse grazing) was light and restricted to certain areas of the pasture (Reinhardt pers. comm.). The

result was an extensive build up of thatch around and in the crown of the plants which resulted in high fire intensity (Noy-Meir 1995). The backing fires used in this study are commonly used for grassland burns for fire safety and control reasons. Backing fires as opposed to heading fires have a longer residence time and burn the fuel more completely (Biswell 1989). The effect of the combination of excessive thatch and a backing fire is to essentially “cook” the mature plants. Our results showed a tendency for larger plants to die in the fire than smaller plants potentially as a result of years of excessive thatch build up surrounding the older plant’s live vegetative tillers. Another important point to note is that, although 10% more of the plants in the burned plots died than the unburned plots, the mortality leveled off 2 years after the burn in the burned plots but continued to increase in the unburned plots. So the fire may have eliminated the plants in the population that would have died in the next year.

Seedling recruitment was higher 2 years after the burn in the burned plots vs. the unburned plots which may partially offset the loss of adult plants in the burned plots. However, the total seedling density in the burned plots in 2000 was still lower than the pre-burn seedling density measured in 1997 and 1998. It is unlikely that this increase in seedling recruitment 2 years after burning would compensate for the loss of adult plants especially given the potential for high seedling mortality as was witnessed between 1998 and 1999. However, other studies have shown that seedling recruitment in perennial grasses is naturally low (Lauenroth and Aguilera 1998). Lauenroth et al. (1994) used a modeling approach to estimate the frequency of appropriate microenvironmental conditions for recruitment of the bunchgrass *Bouteloua gracilis*. The appropriate soil texture and precipitation conditions were predicted to be met only once every 50 years for silty soils and only up to once every 5000 years for very sandy soils. In a study of restored *N. pulchra* at Beale AFB, we intensively monitored a 1 m² radius around each of 100 reproductive bunchgrasses and found only two seedlings after 2 years of growth and viable seed production (Marty 2002).

Collins (1987) found strong interactive effects of grazing and fire in the mesic grasslands of the tallgrass prairie of the United States. He found that the matrix dominant species *Andropogon*

gerardii responds rapidly and vigorously to fire and can dominate stands that are repeatedly burned with a resulting reduction in species diversity. This dominance response by *A. gerardii* can be modulated if grazing is also present because *A. gerardii* is highly palatable and grazing reduces its rate of canopy development. As a result, the initial increase in species richness following a fire in tallgrass prairie is maintained by grazing the canopy dominant. These results have been used to support the idea that the highest levels of species diversity in grasslands should occur under the interactive effects of multiple disturbance agents (Collins 1987; Collins et al. 1998).

In contrast to these studies on burning and grazing, we found few interactive effects of these disturbance agents. Strong grazing and burning interactions can be expected when grazing alters the fuel loads in pastures prior to burning and/or grazers preferentially graze certain species in burned or unburned areas after a burn (Collins 1987; Noy-Meir 1995). In a study of grazing and fire effects in the Mediterranean grasslands of Israel, Noy-Meir (1995) found strong interactive effects of burning and grazing and concluded that this was due in large part to the difference in initial conditions (thatch levels) between the grazed and ungrazed sites prior to the fire. In our study, we reduced confounding of treatments by burning first, followed by controlled cattle grazing in the rotational plots. In some sense our approach is a conservative test of the interactive effects of fire and grazing; we did not allow the burn treatment to alter the intensity of grazing treatments nor did our controlled grazing systematically influence burn intensity. Although generally not recognized, the control, sequence, and timing of burning and grazing treatments might be expected to have a strong influence on the likelihood that interactive effects are important.

Although burning and grazing affected the growth, reproduction and survival of *N. pulchra* adults and seedlings, it appears that year-to-year variation in other factors also had strong effects on these populations during the 4 years of the experiment. All variables measured for both stages showed similar trends over time regardless of treatment. *N. pulchra* growth (basal diameter), reproduction and plant density all peaked in 1998 and then declined sharply in 1999 and either remained low or declined further in 2000.

Differences in weather patterns among years offer a possible explanation for the growth boom in 1998 and possibly the subsequent decline in 1999 and 2000 that we recorded in this study. Coppedge et al. (1998) found that phytomass variation in tallgrass prairie was strongly influenced by climatic variation as well as burn type and bison grazing. In a study of fire effects on vegetation of Santa Cruz Island, California, Klinger and Messer (2001) found that rainfall was an important factor determining species composition in unburned grassland areas. They found that annual grasses had a strong positive response to increased rainfall and suspected that this in turn suppressed the growth of native herbaceous species. Another California grassland study found that annual herbage production was more strongly affected by variation in annual precipitation patterns than varied grazing intensities (Rosiere 1987). Other studies in California have shown that native bunchgrasses are strongly affected by the length of the summer drought while annual grasses are less sensitive (Jackson and Roy 1986).

There are several reasons why the combination of late spring rainfall and cooler temperatures may have favored the *N. pulchra* population. Perennial species with their well-developed rooting systems are better able to take advantage of cool, moist conditions during a period when the annual vegetation is senescing (Jackson and Roy 1986). Non-native annuals negatively affect *N. pulchra* growth and seed production by reducing water availability through competition (Dyer and Rice 1997; Hamilton et al. 1999). By adding water late in the growing season (April–May), Hamilton et al. (1999) significantly increased growth and reproduction of *N. pulchra* adults and seedlings. Dyer et al. (1996) found very low emergence and survival (less than 0.01%) of *N. pulchra* seedlings at Jepson Prairie Preserve, California regardless of grazing or burning treatments. They attributed this effect to below average rainfall. In our study, the fact that the cover of exotic annual grasses in the study area did not change significantly or even follow the same trend as the native bunchgrasses over the 4 years (Marty 2002) supports the hypothesis that additional late-spring rainfall benefited the native bunchgrasses but did not affect the exotic grasses.

Our results indicate that both grazing and burning influence the growth, mortality and recruitment of the native bunchgrass, *N. pulchra*. However, we

did not find evidence of strong interactive effects of these disturbances. We believe that the effects of grazing and burning may interact with and be superseded by climatic variation. Thus long-term monitoring under varying climatic conditions is essential to predict a population response to these treatments. Certain climatic events such as El Niño rainfall conditions in Northern California may have positive effects on the growth of *N. pulchra* adults and seedling recruitment. Clearly with the long-lived nature of these bunchgrasses (Hamilton et al. 1999), annual recruitment is not necessary, but more research into the requirements of these bunchgrasses for successful recruitment and population persistence is sorely needed to predict the long-term viability of both remnant and restored populations.

Acknowledgements

This research was funded by the United States Air Force. The authors wish to thank the Roberti family and their cows, the Beale Air Force Base Fire Department, Ed Broskey, Bruce Reinhardt, Kirsten Christopherson, Joni Gerry, Rob Nordahl, Ben Egert, Rik Smith, Mary Pakenham-Walsh, Rob Klinger, Gerritt Plattenkamp, Paul Cylinder, Truman Young and Christopher Rose for their support and assistance and two anonymous reviewers for their helpful comments on earlier drafts of this manuscript.

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