

Population and clonal level responses of a perennial grass following fire in the northern Chihuahuan Desert

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Abstract Relationships involving fire and perennial grasses are controversial in Chihuahuan Desert grasslands of southern New Mexico, USA. Research suggests that fire delays the resprouting of perennial grasses well after two growing seasons. However, such results are confounded by livestock grazing, soil erosion, and drought. Additionally, post-fire grass responses may depend on initial clone size. We evaluated the effects of fire, grazing, and clone size on *Bouteloua eriopoda* (black grama) in southern New Mexico grasslands. Four 2-ha plots were established in each of four sites. Fire and grazing were applied or not applied in 1999 such that four treatment combinations were assigned randomly to plots within each site. Within each plot, small (0–10 cm² basal area), medium (10–30 cm²), and large (> 30 cm²) clones were initially mapped in five 0.91-m² quadrats where grass attributes and litter cover were evaluated before and at the end of two growing seasons following fire. Maximum fire temperature was also measured. At a population level, canopy and litter cover were each approximately 50% less in burned than unburned areas. However, compared to initial levels, canopy height had increased by

10% at the end of the study, regardless of fire. At a clonal level, basal cover reductions were attributed mostly to large clones that survived fire. Smaller clone densities had decreased by as much as 19% in burned compared to unburned areas, and fire reduced the basal cover of medium clones. Basal and canopy cover, recruitment, and clone basal area decreased with increased fire temperatures. Almost all responses were independent of grazing, and interactive effects of grazing and fire were not detected. Fire did not kill all perennial grass clones, regardless of size. However, rapid responses were likely influenced by above-average precipitation after fire. Future studies in desert grasslands should examine how perennial grass dynamics are affected by fire, precipitation patterns, and interactions with grazing.

Keywords *Bouteloua eriopoda* · Fire intensity · Grazing · Precipitation · Resprouting

Introduction

Fire is often invoked as a key environmental driver that fosters the persistence of perennial grasses in pyrogenic ecosystems worldwide. Examples include tallgrass prairies of the American Midwest (Collins 1987; Briggs and Knapp 1995), savannas of the southeastern and southwestern USA (Platt et al. 1991; Sparks et al. 1998; McFarland and Mitchell 2000), South African grasslands (Uys et al. 2004), and mallee shrublands of Australia (Vesk et al. 2004). In grasslands, the resprouting of perennial grasses tends to occur rapidly within one or two growing seasons following fire such that cover, aboveground productivity,

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and tiller density can equal or exceed levels in fire-excluded areas (Knapp and Hulbert 1986; McFarland and Mitchell 2000; De Luis et al. 2004).

Resprouting dynamics of perennial grasses are influenced by variation in fire regime characteristics, including intensity (Engle and Bidwell 2001). In turn, fire intensity is determined by fuel characteristics (Byram 1959; Alexander 1982), such as perennial grass abundance (Rossiter et al. 2003) and the depth and dryness of soil organic matter or litter which influences heat penetration into soil and, thus, the amount of damage to bud banks. Localized variation in such fuels has been shown to influence survivorship, aboveground productivity, and reproductive output of numerous (Schimmel and Granstrom 1996) – but not all – perennial grass species (Pelaez et al. 1997, 2001).

In contrast to numerous fire-prone ecosystems worldwide, relationships involving the resprouting dynamics of perennial grasses and fire regimes in Chihuahuan Desert grasslands of southern New Mexico, USA, are highly controversial. Based on mostly anecdotal evidence, there have been strong suggestions that fire has catastrophic effects on perennial grasses, with reduced coverage followed by the low recruitment of some species (Buffington and Herbel 1965; Dick-Peddie 1993). Additionally, experiments in nearby southeastern Arizona revealed reduced abundances of perennial grasses following prescribed fire that persisted even after two growing seasons (Reynolds and Bohning 1956; Cable 1965, 1967).

However, there are three concerns regarding these findings. First, they are confounded by livestock grazing that continues to characterize southwestern grasslands. In particular, excessive livestock grazing in the late 19th century, subsequent wind erosion of soils, and periodic drought collectively have reduced the abundances of perennial grasses, the effects of which remain visible today (Schlesinger et al. 1990). Second, these findings do not make sense in an evolutionary context. Perennial grasses have likely evolved resistance to chronic fires that continue to characterize Chihuahuan Desert grasslands. These fires predictably occur from June through September when there is a high frequency of lightning strikes that can ignite dry vegetation (Gosz et al. 1995; Drewa et al. 2001). Although speculative, these fires can be large (>2 ha) and occur at approximately 10-year return intervals (Schmid and Rogers 1985; Rogers and Vint 1987; McPherson 1995). Third, past research has evaluated perennial grass responses to fire by measuring general, population level changes in aerial and basal cover. However, perennial grasses are comprised of clones or clumps of different basal area sizes that can be affected differently

by fire (Vesk et al. 2004). It is not understood if such reductions in cover, as reported in past research, were attributed to clones that survived or did not survive fire.

Given these three concerns, the main objective of the investigation reported here was to experimentally examine the effects of fire and livestock grazing on the resprouting dynamics of *Bouteloua eriopoda* (Torr.) Torr. (black grama) at population and clonal levels in Chihuahuan Desert grasslands of southern New Mexico. This stoloniferous, perennial C₄ grass is abundant in Chihuahuan and Sonoran Desert grasslands of Texas, New Mexico, Arizona, and northern Mexico and is a key forage species for livestock (Gould 1979; USDA-NRCS 2004). Resprouting responses were compared between burned and unburned areas, both exposed to and excluded from cattle grazing. Maximum fire temperatures were also measured as an indicator of fire intensity and related to *B. eriopoda* characteristics before and after fire. Since fuels comprised both *B. eriopoda* and litter, we also evaluated fire effects on litter cover. Three questions were posed:

- (1) At the population level, how are attributes of *B. eriopoda* (cover, canopy height, and stoloniferous recruitment) and litter cover affected by fire and livestock grazing?
- (2) At the clonal level, how are survivorship, basal cover, and the basal area of *B. eriopoda* clones of different size classes affected by fire and livestock grazing?
- (3) Is there a feedback mechanism where fuel attributes of *B. eriopoda* and litter influence localized variation in fire intensity, and are these attributes, in turn, influenced by fire intensity?

Materials and methods

Study area

Our study was conducted on the Jornada Experimental Range, located 37 km northeast of Las Cruces, Dona Ana County, New Mexico, USA (32°37'N, 106°40'W; 1260 m a.s.l.). The average temperature is 15°C, and mean monthly maximum and minimum temperatures occur in June (26°C) and January (4°C), respectively (1915–1997). The area receives 245 mm annual precipitation on average (1915–2000), of which approximately 54% occurs as localized convective thunderstorms from July through September (Fig. 1).

The study area was a 410-ha pasture located on a level upland with deep loamy fine sands and sandy

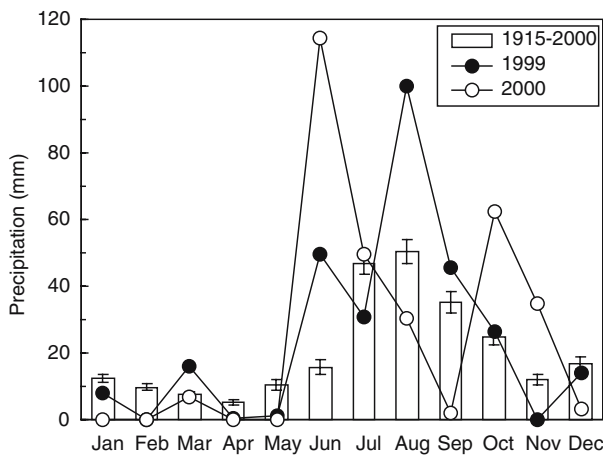


Fig. 1 Mean (\pm SE) monthly precipitation (1915–2000; bars) and monthly precipitation for 1999 (closed circles) and 2000 (open circles) on the Jornada Experimental Range, New Mexico

loam soils, underlain by a layer of calcium bicarbonate at depths of 24 cm to >1 m (Gibbens et al. 1986). Annual stocking rates averaged 2.5 ha/Animal Unit Month from 1953 to 1998. Animal Unit Month is the amount of vegetation required to sustain a 454-kg cow aged >6 months for 1 month (Scarnecchia 1985). In our study area, *B. eriopoda* comprises 75% of the plant cover (Buffington and Herbel 1965), but other perennial grasses are common, including *Aristida* spp. (three-awns), *Sporobolus cryptandrus*, and *Sporobolus flexuosus* (sand and mesa dropseed, respectively). There are also numerous forbs (e.g., *Dimorphocarpa wislizenii*, *Solanum elaeagnifolium*), annuals (*Aristida adscensionis*, *Bouteloua aristidoides*), and shrubs (*Yucca elata*, *Prosopis glandulosa*) (Drewa et al. 2001; Natural Resources Conservation Service 2005).

Experimental design and field data collection

We examined the effects of fire and cattle grazing on *B. eriopoda* using a randomized block design with subsampling. Four 200 \times 200-m² plots were established in each of four locations (blocks) that were approximately 100 m from one another. In each location, plots were arranged in a square and separated by a 25-m buffer. Four combinations of fire and cattle grazing were assigned randomly to one of four plots within each block: (1) fire and grazing, (2) fire and no grazing, (3) no fire and grazing, and (4) no fire and no grazing.

Prior to subjecting the plots to fire, cattle were excluded from the pasture from July 1998 through September 1999 to ensure that perennial grass fuels were available for burning. Head fires, driven by 12- to 32-km/h winds and <10% relative humidity, were prescribed to plots individually in June 1999. We were able to contain

each of these fires within the plots because we had established a 1-m wide fire line around the perimeter of each plot using a drip torch prior to administering fire treatments. Flame lengths were 50 cm–1 m based on visual estimates. We also used a drip torch to burn remaining patches of vegetation. Following the fires, non-grazed plots were fenced, and year-round grazing was applied in October 1999. During our study, perennial grass utilization was 33%, determined using methods explained by Bonham (1989).

Vegetation and litter data were collected before and at the end of two growing seasons following treatments. At the onset of the study, five 0.9 \times 0.9-m² quadrats were randomly located in *B. eriopoda*-dominated areas of each plot. Aerial cover of other species was <5%. In each quadrat, we visually estimated the percentage of ground covered by the canopy of *B. eriopoda* plants and litter. Five measures of canopy height of *B. eriopoda* were obtained: one from the center, while the other four were taken from the corners, but 10 cm from any quadrat edge. Average height per quadrat was used in the analyses. We also mapped all individual clones of *B. eriopoda* in each quadrat. Each clone was estimated for basal area, using two perpendicular measurements of basal diameter and assuming an ellipsoid shape. Clones were distinctive grass clumps that were >3 cm apart from one another.

Quadrats were relocated after the treatments in October 2000 and measured for canopy cover and height of *B. eriopoda* and litter cover. Mapped clones were evaluated for survivorship, and live clones were each re-measured for basal area. Clones that were new in appearance were also mapped and measured. These clones were a result of stoloniferous regeneration since each was attached to an older clone; seedlings were not observed. Other species responses were not measured because their total cover was <5%.

The maximum temperatures of our fires were measured in quadrats. Before burning, a set of heat-sensitive tablets (Tempil, South Plainfield, N.J.), each wrapped in heavy-duty aluminum foil, was strung on aluminum wire and placed in the center of each quadrat under the grass canopy at ground level. Each set consisted of a series of consecutive tablets designed to melt at 48, 132, 212, 302, 371, 454, 538, 621, 732, 816, 954, 1038, 1149, and 1232°C. Sets were collected immediately after the fire, and maximum temperatures were determined based on which tablets had melted. Because aluminum foil raises the ambient temperature at which the tablets melt, we estimated the actual melting temperatures of wrapped tablets using the equation, $Y=1.24X + 25.63$ where Y = actual melting temperature (°C) and X = Tempil temperature rating

(°C) ($P < 0.001$, $r^2 = 0.999$; Drewa et al. 2002). Actual melting temperatures were 85, 189, 289, 400, 486, 589, 693, 796, 933, 1037, 1209, 1313, 1450, and 1553°C.

Our use of heat-sensitive tablets provided coarse estimates of maximum fire temperatures. The difference in melting temperature between any two consecutive tablets in a series was approximately 100°C. At this coarse resolution, we were unable to measure maximum temperatures of fires that may have burned at some temperature between (1) the tablet with the highest temperature that actually melted and (2) the next consecutive temperature of a tablet in a series that did not melt. Thus, our estimates were likely immediately below the actual maximum fire temperatures.

Statistical analyses

Population level responses to fire and grazing

We examined fire and grazing effects on total basal cover of *B. eriopoda* using ANCOVA and pre-treatment basal cover data as a covariate. For each quadrat, total basal cover was the collective basal area of all clones, expressed as a percentage of the quadrat area. Post-treatment basal cover data included clones that survived our treatments plus recruits. Two ANCOVAs were performed on post-treatment canopy cover and canopy height data using initial canopy cover and canopy height data as a covariate, respectively. We examined fire and grazing effects on stoloniferous recruitment with ANOVA. Treatment effects on litter cover were examined using ANCOVA and pre-treatment litter cover data as a covariate. The latter two analyses were performed on natural log-transformed data to meet model assumptions.

Clonal level responses to fire and grazing

Using initial clone density data as a covariate, we used ANCOVA to examine if *B. eriopoda* survivorship was

affected by fire, grazing, as well as clone size, a split-plot factor. At the onset of the study, we mapped 2483 clones of *B. eriopoda* (Fig. 2). Each of these clones was designated as small, medium, or large corresponding to three broad basal area size classes: 0–10, 10–30, and >30 cm², respectively. In this way, we ensured that different size classes were well represented such that an average of 20.4 small clones/m² (± 1.3 SE), 9.7 medium clones/m² (± 0.6 SE), and 6.6 large clones/m² (± 0.3 SE) occurred in each quadrat.

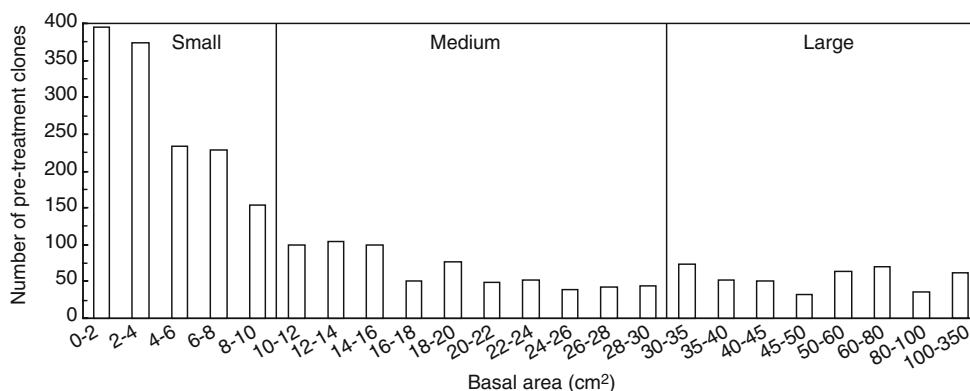
We also examined fire and grazing effects on basal cover of *B. eriopoda* comprising small, medium, and large clones using pre-treatment basal cover data as a covariate. A third ANCOVA was used to examine treatment effects on the basal area of individual small, medium, and large clones using pre-treatment basal area as a covariate. Unlike the former two analyses, a clone rather than a quadrat served as our experimental unit.

The three ANCOVAs were complemented with more tests. When the effect of clone size on survivorship, basal cover, or clone basal area was significant, treatment differences were examined using Tukey-Kramer pair-wise comparisons. We also used contrasts to explore the interactive effects of fire, grazing, and clone size, in particular to determine if responses to fire or grazing differed between small, medium, and large clones. Analyses involving clonal level responses to fire and grazing were performed on square root-transformed data. Recruitment data were not used in any analyses at the clonal level because we were interested in evaluating responses of only those clones that received our treatments.

Feedbacks involving maximum fire temperature, *Bouteloua eriopoda*, and litter cover

Multiple regression was used to examine if maximum fire temperatures depended on initial litter cover, initial fuel load, and initial basal cover of *B. eriopoda*.

Fig. 2 Size-class distribution of 2483 clones of *Bouteloua eriopoda* that were individually mapped and measured for basal area at the onset of the study. Clonal level responses to fire and livestock grazing were examined using three sizes of clones corresponding to three broad basal area size classes: small (0–10 cm²), medium (10–30 cm²), and large (>30 cm²)



Initial fuel load in each quadrat was the product of quadrat area, initial canopy cover, and initial canopy height of *B. eriopoda*. Temperature data were natural log-transformed, and the three independent variables were not correlated with one another (Pearson correlation coefficients ranged from -0.20 to 0.08 ; $P > 0.215$). A significant relationship involving temperature and any one of the three independent variables was more succinctly summarized as a simple linear regression.

Using a simple linear regression, we also examined if post-fire canopy cover of *B. eriopoda*, relative to initial levels [and expressed as percentage (%) change], depended on maximum fire temperatures. Another regression was performed using recruitment as a dependent variable. Similarly, two additional regressions were performed using % change in canopy height and litter cover data as response variables. Recruitment data were natural log-transformed.

We determined if survivorship of *B. eriopoda* was influenced by maximum fire temperatures and if this relationship depended on clone size, using ANCOVA and pre-fire clone densities as a covariate. We repeated this analysis using basal cover and then clone basal area, which were both square-root transformed. In these analyses, initial basal cover and initial clone basal area served as a covariate, respectively. Any significant relationships involving survivorship, basal cover, and clone basal area as a function of maximum fire temperature were each summarized as a simple linear regression. For each regression, the response variable was standardized in relation to initial levels and expressed as % change.

ANCOVAs, ANOVAs, Tukey-Kramer pair-wise comparisons, and contrasts were performed in PROC MIXED of SAS (SAS Institute 2001). Regressions were performed in PROC REG. For all analyses, $\alpha = 0.05$.

Results

Precipitation patterns

Following the fires prescribed in the investigation during the first half of June 1999, precipitation occurred within a day. Precipitation in June 1999 was threefold higher than the long-term (1915–2000) average amount for that month (Fig. 1). In addition, the amount of precipitation that fell during the 1999 growing season (July–September) was 133% of the long-term average. Similarly, in June 2000, the amount of precipitation was sevenfold higher than the long-term average for the month. In the same year, the amount of

precipitation was equivalent to the average for July, but was 60% of the average for August.

Population level responses to fire and grazing

Following fire, basal cover (Fig. 3a) and canopy cover (Fig. 3b) of *B. eriopoda* were 42% less in the areas subjected to fire than in the unburned areas ($P = 0.002$ and $P < 0.001$, respectively; Table 1). However, over the course of the study, canopy height increased 10%, regardless of fire (Fig. 3c). Recruitment was also similar in burned (4.9 clones/m² ± 1.2 SE) and unburned areas (2.2 clones/m² ± 0.5 SE). Following fire, litter cover was 50% less on the burned plots than on the unburned plots (Fig. 3d; $P = 0.002$). Following grazing, canopy height was 28.6 cm (± 1.3 SE); in the non-grazed areas it was 35.9 cm (± 1.1 SE) ($P = 0.007$). However, grazing and its interaction with fire had no detectable effects on other response variables of *B. eriopoda* or litter cover.

Clonal level responses to fire and grazing

Survivorship

Fire influenced clone survivorship; densities of clones that were censused prior to treatments were subsequently 24% greater in unburned than in burned areas at the end of the study ($P = 0.002$; Table 2). In contrast, the densities of these clones were not affected by grazing and its interaction with the other treatments. The densities of clones that were censused at the onset of the study differed among the three size classes after the treatments ($P = 0.006$). Specifically, the densities of small clones were twice that of the medium- and large-sized clones (Tukey-Kramer $P = 0.017$ and $P = 0.006$, respectively); the densities of the medium- and large-sized clones were equivalent.

Fire-induced mortality of *B. eriopoda* decreased with increased size of clones ($P < 0.001$; Table 2). The densities of small clones that were censused at the start of our experiment were 19% less in burned than fire-excluded areas at the end of the study ($P < 0.001$; Fig. 4a). Similarly, densities of medium clones were 9% less in burned than unburned grasslands ($P = 0.017$). Fire, however, had no detectable effects on the densities of the large clones.

Basal cover and clone basal area

The basal cover of *B. eriopoda* in plots that had been subjected to fire was 55% of that in fire-excluded plots ($P = 0.005$; Table 2), but the effects of fire on basal cover

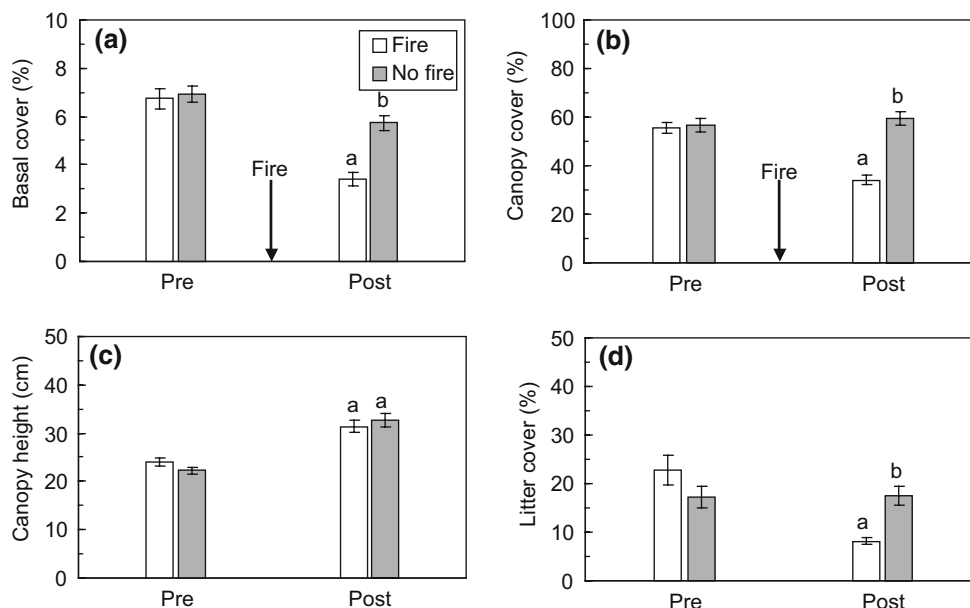


Fig. 3 Mean (\pm SE) basal cover (a), canopy cover (b), and canopy height (c) of *B. eriopoda* as well as litter cover (d) before fire (Pre) and at the end of two growing seasons following fire (Post)

in Chihuahuan Desert grasslands. Bars with different letters indicate statistical significance

Table 1 Sources of variation and *P* values for fixed effects following ANCOVA and ANOVA that were used to examine fire and livestock grazing effects on basal cover, canopy cover, canopy

height, and stoloniferous recruitment of *Bouteloua eriopoda* as well as litter cover (n/a not applicable)

Source	Basal cover	Canopy cover	Canopy height	Recruitment	Litter cover
Covariate	<0.001	<0.001	<0.001	n/a	0.012
Blocks					
Fire	0.002	<0.001	0.333	0.056	0.002
Grazing	0.095	0.181	0.007	0.312	0.729
Fire \times grazing	0.726	0.246	0.406	0.289	0.943
Blocks \times fire \times grazing					
Quadrats(blocks \times fire \times grazing)					

also depended on clone size ($P < 0.001$). The collective basal cover of small clones was similar between fire treatments (Fig. 4b). In contrast, the basal cover of medium clones was almost 1.5-fold greater and that of large clones was roughly threefold greater in unburned than burned areas ($P = 0.034$ and $P < 0.001$, respectively). Neither livestock grazing nor clone size influenced basal cover, and interactions involving grazing and fire, grazing and size, as well as all treatments were not significant.

In general, clone basal area in burned plots was 48% of that in unburned plots ($P = 0.002$; Table 2). Clone basal area was also affected by an interaction involving fire and clone size at the onset of the study ($P < 0.001$). The basal area of small clones was similar between burned and unburned areas (Fig. 4c); however, after fire, the basal area of medium-sized clones was 72% and that of large-sized clones was 45% of that in

unburned areas ($P = 0.009$ and $P < 0.001$, respectively). Basal area was not affected by grazing, initial clone size, or interactions involving grazing and the other treatments.

Feedbacks involving maximum fire temperature, *B. eriopoda*, and litter cover

During the fires, the maximum temperature registered by our heat-sensitive tablets averaged 362°C (± 28 SE) and ranged from 85 to 796°C . Localized variation in these temperatures depended on initial litter cover ($P = 0.026$), but not initial fuel load of *B. eriopoda* or basal cover of *B. eriopoda* at the onset of the study. Temperatures increased linearly with increased litter cover based on the simple linear regression equation (maximum fire temperature) $^{1/2} = 0.068$ (pre-treatment litter cover) + 16.823 ($P = 0.044$, $r^2 = 0.102$).

Table 2 Sources of variation and *P* values for fixed effects following ANCOVA, Tukey-Kramer comparisons, and contrasts (*n/a* not applicable). These tests were used to examine fire and livestock grazing effects on survivorship, collective basal cover, and clone basal area for three size classes of *B. eriopoda* clones: small (0–10 cm² basal area), medium (10–30 cm²), and large (>30 cm²)

Source	Survivorship	Collective basal cover	Clone basal area
Covariate	<0.001	<0.001	<0.001
Blocks			
Fire	0.002	0.005	0.002
Grazing	0.851	0.153	0.158
Fire × grazing	0.935	0.961	0.875
Blocks × fire × grazing			
Quadrats(blocks × fire × grazing)			
Size	0.006	0.372	0.848
Size × fire	<0.001	<0.001	<0.001
Size × grazing	0.860	0.373	0.302
Size × fire × grazing	0.614	0.303	0.160
Size × blocks × fire × grazing			
Size × quadrats(blocks × fire × grazing)			
Clone (size × quadrats × blocks × fire × grazing)	<i>n/a</i>	<i>n/a</i>	
Tukey-Kramer			
Small versus medium	0.017	<i>n/a</i>	<i>n/a</i>
Small versus large	0.006	<i>n/a</i>	<i>n/a</i>
Medium versus large	0.740	<i>n/a</i>	<i>n/a</i>
Contrasts ^a			
FS versus NS	<0.001	0.302	0.140
FM versus NM	0.017	0.034	0.009
FL versus NL	0.091	<0.001	<0.001

^a F, Fire; N, no fire; S, small clones; M, medium clones; L, large clones

Moreover, litter cover was initially 5–25% in 33 quadrats that burned at 342°C (±33 SE), but 40–86% in seven quadrats that yielded temperatures of 458°C (±28 SE).

At the end of the study, canopy cover of *B. eriopoda* had decreased with increased fire temperatures ($P=0.033$, $r^2=0.163$; Fig. 5a). Relative to initial levels, the change in the canopy cover following fire averaged –21% (±8 SE) in areas <400°C. In contrast, where fire had burned at >400°C, the canopy cover had changed by –57% (±4 SE) by the end of the study. Stoloniferous recruitment also decreased with increased temperatures ($P=0.002$, $r^2=0.236$; Fig. 5b). Recruit densities averaged seven clones/m² (±2 SE) in areas <400°C. Hotter temperatures resulted in only two recruits/m² (±1 SE). Neither canopy height nor litter cover at the end of the study shared linear relationships with maximum fire temperature.

Clone survivorship was not contingent on maximum fire temperature (Table 3). Additionally, an interaction involving maximum fire temperature and clone size

was not significant, suggesting that survivorship of small, medium, or large clones was not related to our temperature data.

The basal cover of *B. eriopoda* was affected by maximum fire temperatures ($P<0.001$; Table 3), but an interaction involving temperature and clone size was not significant. Basal cover decreased with increased fire temperatures ($P=0.016$, $r^2=0.263$; Fig. 5c), with the change relative to initial levels being –34% (±5 SE) in areas <400°C but –65% (±4 SE) in areas where temperatures were >400°C.

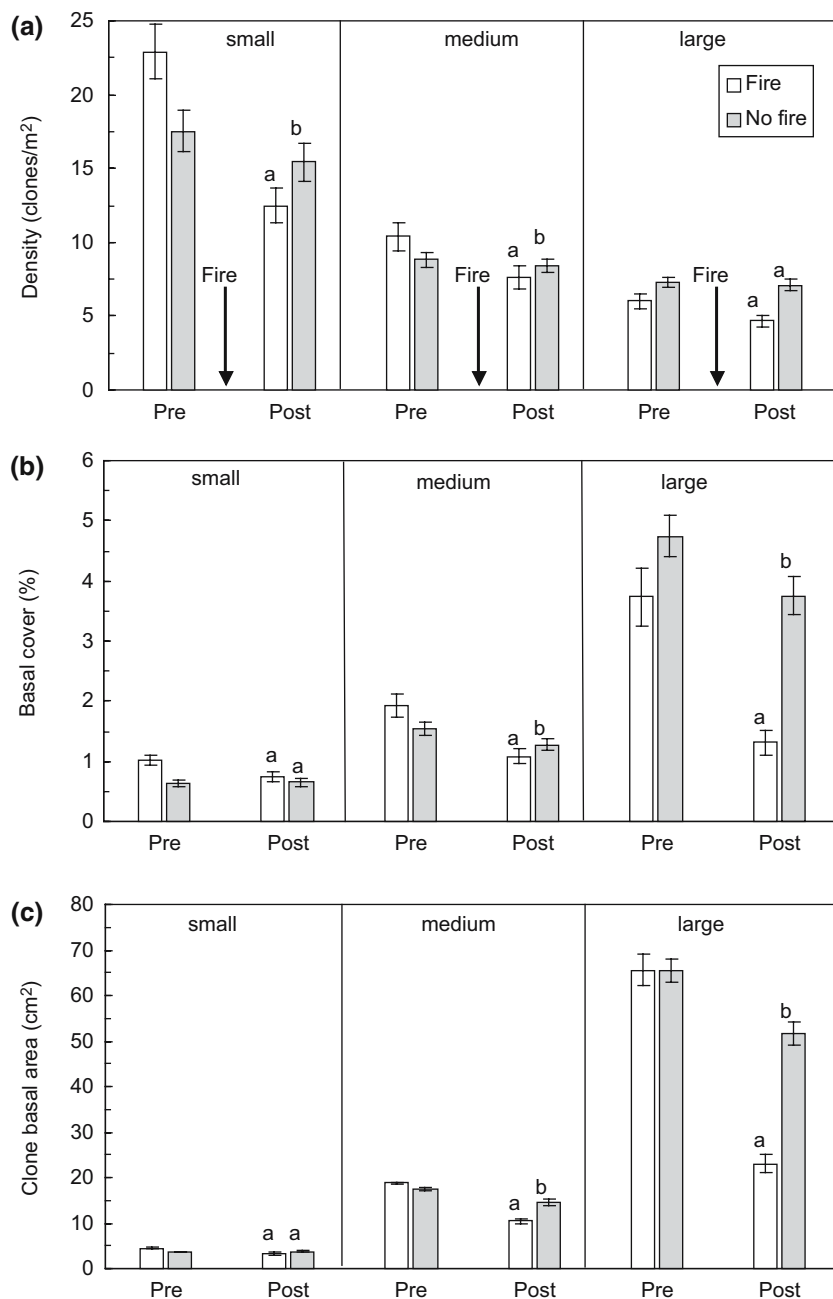
Clone basal area was also affected by fire temperatures ($P=0.006$; Table 3). However, small-, medium-, and large-sized clones were similarly influenced by these temperatures. Thus, the change in clone basal area in relation to initial levels decreased in exactly the same way as the % change in collective basal cover of clones with increased maximum fire temperatures (see Fig. 5c).

Discussion

In our study, fire had non-catastrophic effects on responses of *B. eriopoda*. Although fire reduced the basal cover and average basal area of primarily large clones, survivorship was similar between burned and unburned areas. Other studies have reported similar reductions in basal cover of *B. eriopoda* and other perennial grasses after at least two growing seasons following fire in Sonoran (Reynolds and Bohning 1956; Cable 1967) and Chihuahuan Desert grasslands (Valone and Kelt 1999; Drewa and Havstad 2001). However, almost all of these studies employed a line point intercept sampling protocol (see Bonham 1989) to measure only population-level changes in basal cover of perennial grasses before and after fire. Thus, there is no way of knowing if these reductions were attributable to (1) clones that survived fire, but decreased in basal area or (2) clones that were completely killed by fire. By contrast, we have demonstrated the importance of evaluating perennial grass responses to fire at the clonal level since it enabled us to account for the fate of individual clones and thus reveal the potential for regrowth and reproduction in the post-fire environment.

Our results also suggest that, in contrast to large clones, greater numbers of medium- and small-sized clones of *B. eriopoda* are completely killed by fire. Similarly, in ecosystems characterized by fire that occurs more than once a decade, fire appreciably reduces the survivorship of the smaller size classes of vegetation, including perennial grass clones. Examples include

Fig. 4 Mean (\pm SE) density (a), collective basal cover (b), and clone basal area (c) of small (0–10 cm²), medium (10–30 cm²), and large (>30 cm²) clones of *B. eriopoda* that were sampled before fire (*Pre*) and then re-measured at the end of two growing seasons following fire (*Post*) in Chihuahuan Desert grasslands. Bars with different letters indicate statistical significance



southeastern longleaf pine savannas (Grace and Platt 1995; Mulligan and Kirkman 2002) and savannas and shrublands of Belize (Miyaniishi and Kellman 1986) and Australia (Radford et al. 2001; Vesk et al. 2004). Perennial grass clones of smaller size classes may be more susceptible to complete kill after fire because their root systems are less developed than larger clones and thus they lack the necessary resources for resprouting (Grace and Platt 1995). In all of these fire-prone ecosystems, including Chihuahuan Desert grasslands, fire at these temperatures and followed by rain does not kill all clones, regardless of size, thus further

emphasizing the non-catastrophic nature of such fires on perennial grass responses.

Large amounts of precipitation in the immediate post-fire environment were likely responsible for the rapid resprouting of *B. eriopoda* clones, such that grass canopy height was similar between burned and unburned areas within approximately 1 year. A similar result was reported by Cable (1967) who found that the basal cover of perennial grasses in the Sonoran Desert was equivalent to preburn levels within a year following a June fire when there was average precipitation during the growing season. By contrast, when fire was

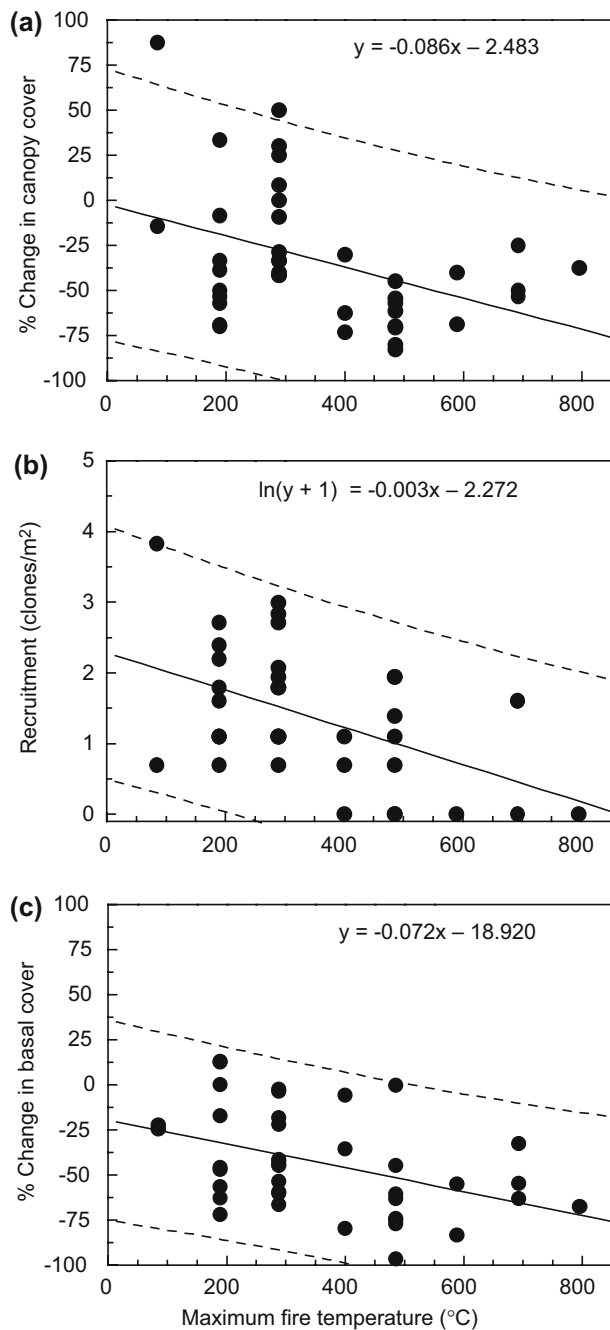


Fig. 5 Linear relationships between % change in canopy cover (a), recruitment (b), and % change in basal cover (c) of *B. eriopoda* versus maximum fire temperatures. Recruitment data were natural log-transformed. y = dependent variable on the y -axis; x = maximum fire temperature

prescribed during drought conditions that extended into the immediate post-fire environment, regeneration of *B. eriopoda* and other perennial grasses, was delayed for many years (Reynolds and Bohning 1956; Cable 1967; Valone and Kelt 1999; Drewa and Havstad 2001).

Localized variation in fire intensity was influenced by litter cover, but not live fuels in the form of *B. eriopoda*.

Table 3 Sources of variation and P values for fixed effects following ANCOVA that was used to examine the influence of clone size, maximum fire temperatures, and their interaction on three attributes of *B. eriopoda*: clone survivorship, basal cover, and clone basal area

Source	Survivorship	Basal cover	Clone basal area
Covariate	<0.001	<0.001	<0.071
Size	0.285	0.691	0.044
Maximum fire temperature	0.092	<0.001	0.006
Maximum fire temperature \times size	0.469	0.323	0.214

This finding is not surprising because fire temperatures vary vertically in space (Hobbs et al. 1984). Our fire temperatures were measured at ground level where there is mostly litter, but most live fuels were several centimeters above the soil surface. There have been suggestions that the organic content of desert grasslands soils is too low to influence fire effects on vegetation pattern (York and Dick-Peddie 1969). However, our maximum fire temperatures averaged $362 \pm 360^\circ\text{C}$ (95% confidence limits), emphasizing also that localized variation in these temperatures affected most attributes of *B. eriopoda*, including canopy cover, basal cover, and clone basal area, but not clone survivorship. At the same time, we acknowledge that the effects of fire intensity on such attributes require more direct attention and should be studied by evaluating post-fire grass responses following experimental fuel manipulations prior to burning (see Drewa 2003).

We were unable to detect any effects of livestock grazing on all attributes of *B. eriopoda* with one exception: canopy height was 20% less in grazed than ungrazed grasslands at the end of the study. Cattle grazing can have negligible effects on basal cover and biomass of *B. eriopoda* when aboveground biomass utilization is <40% (Paulsen and Ares 1962), similar to our study. Also, we were unable to detect any interactive effects of grazing and fire on *B. eriopoda* responses, a result which is in agreement with those of past studies in which livestock utilization was also <40% (Valone and Kelt 1999; Drewa and Havstad 2001). On a cautionary note, since our general inability to detect grass responses to either grazing or interactions involving grazing and fire is likely the result of low stocking rates, our grazing-related findings should not be extrapolated to other rangelands, particularly in the American Southwest, where stocking rates are likely to be different. Instead, we hope that our study will provide impetus for future experiments involving fire and grazing intensity through direct manipulation of cattle stocking rates.

Our study underscores two main reasons why there has been a prevailing belief that fire delays recovery and has catastrophic effects on perennial grasses in Chihuahuan Desert grasslands of southern New Mexico. First, past research has not considered responses at the clonal level. Second, past findings have not accounted for post-fire weather, especially as it pertains to patterns of precipitation. We advocate further study to examine how resprouting dynamics of perennial grasses are influenced by such patterns in the immediate post-fire environment. Experiments involving the effects of fire and precipitation pattern manipulations (e.g., timing in relation to fire occurrence, amount) will help address this issue.

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