

Effects of fire, grazing, and the presence of shrubs on Chihuahuan desert grasslands

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Responses of herbaceous and suffrutescent species to fire, grazing, and presence of Prosopis glandulosa were examined in a Chihuahuan desert grassland in south-central New Mexico. Treatments were assigned randomly to eight 12×8 m plots within each of two blocks. Following fires in June 1995, unfenced plots were exposed to livestock grazing over 4 years. Plots were established that either included or excluded P. glandulosa. Perennial grass cover, primarily Bouteloua eriopoda, decreased by 13% in burned plots but increased 5% in unburned areas. Conversely, perennial forb cover was 4% greater after fire. Perennial grass frequency decreased 30% more and perennial forb frequency increased 10% more following burning. Further, increases in evenness after fire resulted in a 225% increase in species diversity. Grazing also resulted in a decrease in perennial grass cover while frequency decreased 22% more in grazed than ungrazed plots. Only frequency and not cover of perennial forbs and annual grasses increased more following grazing. Presence of P. glandulosa had no differential effect on responses of non-shrub species. Fires were conducted during near drought conditions while grazing occurred during years of precipitation equivalent to the long-term average. Precipitation immediately following fire may be critical for recovery of B. eriopoda-dominated desert grasslands; relationships between fire and postfire precipitation patterns require future investigation.

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Introduction

Desert grasslands of the south-western U.S.A. were once characterized by fires occurring mostly during the late spring and early summer (late June–early July) when a high frequency of lightning strikes, just prior to a summer rainy season (July–September), ignited dry vegetation (Gosz *et al.*, 1995; McPherson, 1995; Gosz & Gosz, 1996). Fires topkilled much of the vegetation (especially dominant perennial grasses) and reduced canopy cover and distributions of encroaching shrubs, followed by an increase in perennial forbs and opportunistic annuals (Cable, 1972; 1976; Wright, 1980; Valone & Kelt, 1999). Compared to other North American grassland types, south-western desert grasslands produce the lowest total biomass (Sims & Singh, 1978) and may have burned every 7–10 years (Wright, 1980; McPherson, 1995), coinciding with the time required for rangeland containing primarily perennial grasses to reach pre-fire levels of biomass (Cable, 1967).

Evidence to suggest that fires were once present in the Southwest can be traced back to the early 1500 s in Arizona and Texas grasslands (Humphrey, 1958). In south-eastern Arizona, fires may have periodically burned hundreds of hectares of land (Humphrey, 1949; Bahre, 1991) before the late 1800s when livestock grazing decreased cover and biomass of herbaceous vegetation, thus reducing the size and frequency of fires (McPherson, 1995). Prior to 1880, shrubs were probably not as abundant, and distributions were confined mostly to bottomlands of drainages or to upland areas with shallow soil (Humphrey, 1958). Frequent fires may have been effective in complete-killing newly established, encroaching shrub seedlings and seeds on the soil surface (Cable, 1972). Since then, decreased fire frequencies have coincided with expanded shrub distributions. Fire-free intervals of >10 years have resulted in increased shrub establishment, growth, and production of seeds, many of which are disseminated by livestock (Cox *et al.*, 1993; McPherson, 1995).

Little is known about the size and frequency of fires in southern New Mexico grasslands located in the northern Chihuahuan Desert. Evidence to support the notion that fires were once common in the region is lacking (Buffington & Herbel, 1965). Southern New Mexico has also experienced historical overgrazing that resulted in primarily perennial vegetation that is sparse, not uniformly distributed, and unlikely to support fire (Wooten, 1908; Buffington & Herbel, 1965; Schlesinger *et al.*, 1990). Additionally, prescribed burning has negatively affected cover and biomass of *Bouteloua eriopoda* (black grama), the dominant perennial grass, but only when prescriptions were conducted during periods of drought (Reynolds & Bohning, 1956; Cable, 1967; 1972; Valone & Kelt, 1999). Thus, the use of prescribed burning as a tool for maintenance of desert grasslands in southern New Mexico has been questioned (Buffington & Herbel, 1965; Dick-Peddie, 1993).

Northern Chihuahuan desert grasslands are driven mostly by seasonal patterns of precipitation, under conditions of conservative livestock grazing (i.e. <40% of biomass consumed) (Paulsen & Ares, 1962). Historically, overgrazing and severe periods of drought in desert grasslands have resulted in rates of recovery that can exceed 50 years (Wright, 1980; Hennessy *et al.*, 1983; Archer, 1991). Further, overgrazing has not only locally expanded shrub distributions and abundances, but has also contributed to soil erosion, making regrowth, reproduction, and establishment of perennial grasses increasingly difficult (Hennessy *et al.*, 1983; Schlesinger *et al.*, 1990). The presence of shrubs within existing desert grasslands may adversely affect the growth of dominant perennial grasses, especially during periods of drought (Scifres & Polk, 1974; Dahl *et al.*, 1978; McDaniel *et al.*, 1982; Herbel *et al.*, 1983; Gibbens *et al.*, 1986). When precipitation is equivalent to or greater than the long-term average, grazing activities, rather than shrub dominance, may have greater impact on recovery of indigenous herbaceous species (Warren *et al.*, 1996).

Fire studies should consider interactions between fire, livestock grazing, and the presence of shrubs in anthropogenically altered desert grasslands (Valone & Kelt, 1999). The interaction of fire with these and possibly other factors may yield vegetation responses that would not have occurred had fire, grazing, or shrub presence been studied individually (Whelan, 1995). In this study, our objective was to examine the effects of fire, livestock grazing, presence of shrubs, and interactions between these three factors on changes in cover and frequency of mostly herbaceous species in Chihuahuan desert grasslands of south-central New Mexico.

Methods

Study sites

Our study was conducted on the Jornada Experimental Range (JER), located 37 km north-east of Las Cruces, Doña Ana Co., New Mexico (32°37'N; 106°40'W). The JER

is situated on the southern end of the Jornada del Muerto Basin between the San Andres Mountains and the Rio Grande River. Located at an elevation of approximately 1260 m (Gibbens *et al.*, 1992), it represents an arid ecotone between grasslands and shrublands of the northern Chihuahuan Desert. Based on data collected from a weather station located 1 km away from our study sites, the JER receives 227 mm annual precipitation (81-year average, 1918–1999), 55% of which occurs from July to September as localized convective thunderstorms (Fig. 1 (a)). Compared to the summer rainy season, winter precipitation occurs at lower intensity and covers larger areas (Gibbens *et al.*, 1992). Mean monthly maximum and minimum temperatures occur in June (36°C) and January (13°C) respectively (Gibbens *et al.*, 1986; 1992; Reynolds *et al.*, 1999). Though the frost-free period averages 200 days, the effective growing season is only 90 days (Gibbens *et al.*, 1992).

Study sites were located in a 1252-ha pasture where gravelly sandy loams (haplargids) occur on gently rolling fans (Bullock & Neher, 1980). These soils are underlain by a layer of calcium bicarbonate (caliche) at soil depths from a few centimeters to >1 m (Gibbens *et al.*, 1986). Desert grasslands of the JER were once dominated by C_4 perennial grasses such as *B. eriopoda*. Following the introduction of domestic livestock in the 1800 s, much of the area has become dominated by shrubs such as *Prosopis glandulosa* (honey mesquite) and *Larrea tridentata* (creosotebush) (Buffington & Herbel, 1965). Our sites bear a known history of livestock grazing over the past 85 years. Prior to applying experimental treatments in this study, annual stocking rates averaged 4.87 ha AUM⁻¹ (1949–1994); 73% of livestock grazing occurred from January through June. Other common species in the study area include other C_4 perennial grasses such as *Gutierrezia sphaerocephala* (annual broomweed) and *G. sarothrae* (broom snakeweed).

Experimental design and data collection

We used a randomized complete block, $2 \times 2 \times 2$ factorial experimental design. Fire, livestock grazing and shrub treatments were allocated to eight 12×8 m plots in each of two study sites (blocks) at two levels: applied and not applied. Each of the eight treatment combinations of fire, grazing, and shrubs was assigned randomly to one of the eight plots within each block: (1) burned, grazed, and shrubs present; (2) burned, grazed, and shrubs absent; (3) burned, ungrazed, shrubs present; (4) burned, ungrazed, shrubs absent; (7) unburned, grazed, shrubs present; and (8) unburned, ungrazed, shrubs absent. Study sites were located approximately 1 km from each other. All plots within a site were oriented in a random direction and were located at least 10 m from one another. Shrubs were not removed from shrub-excluded plots. Instead, these plots were selected to avoid inclusion of *P. glandulosa*. In plots where shrubs were present, each shrub was <1 m diameter and <1 m in height. Overall *P. glandulosa* canopy cover within each of the assigned plots was $\leq 20\%$, and all plots contained >70% cover of the dominant perennial grass, *B. eriopoda*.

Prescribed fires were applied to assigned plots on 23 June 1995 to simulate natural, lightning season fires. Head fires, driven by south-westerly winds, were initiated separately for each plot. Remaining patches of vegetation within assigned plots were burned using a drip torch. Our prescribed fires likely burned at highly variable temperatures because of unevenly distributed fuels of varying biomass (McPherson, 1995). Fires probably burned at comparable temperatures to those in south-eastern Arizona desert grasslands and southern mixed prairies of Texas that ranged from 83°C to 682°C (Stinson & Wright, 1969; Britton & Wright, 1971; Ruyle *et al.*, 1988). Ungrazed plots were then fenced after burning, and unfenced plots

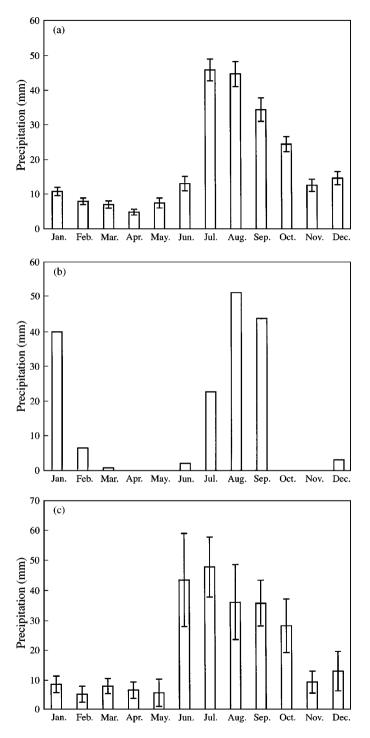


Figure 1. Precipitation data for the Jornada Experimental Range: (a) mean (\pm S.E.) monthly precipitation (1918–1999); (b) monthly precipitation for 1995; and (c) mean (\pm S.E.) monthly precipitation (1996–1999).

| Time | | | |
|----------|-----------|-----------|-----------------------|
| Month(s) | Year | Treatment | Data collection |
| May–Jun | 1995 | | Pre-treatment sample |
| Jun | 1995 | Fire | 1 |
| Dec-Jun | 1995-1996 | Grazing | |
| Aug–Sep | 1996 | Grazing | |
| Jan–Mar | 1997 | Grazing | |
| Aug | 1997 | Grazing | |
| Jan | 1998 | Grazing | |
| Aug | 1998 | Grazing | |
| Jan | 1999 | Grazing | |
| Öct | 1999 | C | Post-treatment sample |

Table 1. Timeline of vegetation measurements and fire and livestock

 grazing treatment applications

were subsequently exposed to mostly dormant season grazing over the next 4 years. Specifically, grazing occurred during the months of December 1995–January 1996 after which cattle were removed from the study areas. Livestock grazing resumed during August–September 1996 and then occurred from January–March 1997. Grazing also occurred only during August 1997, January 1998, August 1998, and January 1999. On average, this pasture was exposed to a stocking rate of 12.73 ha AUM⁻¹ (Table 1).

Cover and frequency data of 45 encountered herbaceous and suffrutescent species were collected in June 1995 and 4 years later in October 1999 (Table 1). We used a vertical line point intercept method (Pieper, 1973) every 10 cm along five parallel, 8 m transects randomly positioned along the long axis of each plot (400 sampling points per plot). Nomenclature follows Allred (1997).

Statistical analyses

Effects of fire, grazing, and *P. glandulosa* shrubs on collective compositional changes of all species were analysed using pre- and post-treatment data. ANOVA was used to examine the effects of experimental treatments on percentage change in species diversity. Simpson's diversity index was selected among other diversity indices because it is most sensitive to changes in more abundant rather than rare species (Peet, 1974; Krebs, 1989). Percentage change in species richness and evenness (overall abundance) were analysed separately in the same way.

Effects of experimental treatments on responses of different functional groups of species were analysed in a similar fashion. ANOVA was used to analyse changes in frequency and cover of the following species groups: perennial grasses, perennial forbs, annual grasses, and annual forbs. It was not possible to analyse responses of many individual species because of their low occurrence. Changes in frequency and cover of only five species, encountered in all 16 plots, were examined separately. Of these, *B. eriopoda* and *S. flexuosus* were the two most dominant perennial grasses in our study area. *Gutierrezia sarothrae*, a perennial suffrutescent, and *Dimorphocarpa wislizenii* (spectacle-pod), a perennial forb, were also common floral components of desert grasslands on the JER. *Aphanostephus ramosissimus* (faintcrown)

was the most common annual forb. All statistical analyses were conducted using PROC GLM in SAS (SAS Institute, 1994). Our data compiled with ANOVA assumptions; thus, transformations of data were not required.

Results

Fire

In fire treated plots, species diversity increased 303% compared to 78% in unburned areas (p = 0.017; Fig. 2(a)). While species richness increased regardless of fire (p = 0.572), species evenness increased 38% following fires but decreased 27% in unburned plots (p = 0.038).

Perennials were affected by fire. Following prescribed fires, cover of perennial grasses decreased 13% but increased 5% in unburned areas (p = 0.017; Fig. 3 (a)). Also, frequency of perennial grasses decreased 30% more in burned than fire-excluded plots (p = 0.004; Fig. 3 (b)). Compared to unburned areas, perennial forb cover increased 4% more (Fig. 3a) and frequency increased almost 10% more (Fig. 3 (b)) following fires (p < 0.001 and p < 0.001).

Cover and frequency of annuals increased regardless of fire. Burning had no effect on cover (p = 0.569) or frequency (p = 0.235) of annual grasses (Fig. 3). Similarly, increases in cover and frequency of annual forbs were not attributed to fire (p = 0.256 and p = 0.115 respectively).

Individual species were affected differently by fire. Cover of *B. eriopoda*, the dominant perennial grass, decreased 14.5% in burned plots and increased 5% in unburned plots (p = 0.012; Fig. 3(a)). Frequency of *B. eriopoda* decreased 32% more (p = 0.007) in burned compared to unburned areas (Fig. 3(b)). In contrast, fire did not affect cover (p = 0.434) or frequency (p = 0.412) of another perennial grass, *S. flexuosus*. Also, cover of the perennial forb, *D. wislizenii*, was not affected by fire (p = 0.139). However, its frequency increased by 5% in burned plots compared to < 3% in unburned plots (p = 0.028). Fire had no effect on cover (p = 0.913) and frequency (p = 0.389) of *G. sarothrae*, a perennial suffrutescent. Cover and frequency of *A. ramosissimus*, an annual forb, were not affected by fire (p = 0.716 and p = 0.587 respectively).

Grazing

Increases in species diversity were not significantly greater in grazed than ungrazed plots (p = 0.250; Fig. 2(b)). Species richness increased regardless of grazing (p = 0.482). Similar to responses in burned and unburned plots, changes in evenness occurred in grazed and ungrazed areas but were not significantly different (p = 0.227). Additionally, interactions involving grazing and fire were not detected for species diversity, richness, and evenness (p > 0.260).

Perennials were generally affected by grazing. Cover of perennial grasses decreased 11% in grazed but increased 3% in ungrazed areas (p = 0.042; Fig. 4(a)). Further, perennial grass frequency decreased 22% more in grazed than ungrazed plots (p = 0.016; Fig. 4(b)). In Fig. 4(a), cover of perennial forbs was not significantly greater in grazed than ungrazed plots (p = 0.068). However, perennial forb frequency increased by 10% in grazed plots but <7% in ungrazed plots (p = 0.028; Fig. 4(b)).

Increases in cover and frequency of annuals were only rarely attributed to grazing. Collectively, annual grass cover increased 11% in grazed plots and 3% in ungrazed plots (Fig. 4(a)), but these values tended to differ (p = 0.062). However, annual grasses were >14% more frequent in grazed than ungrazed areas (p = 0.040; Fig. 4(b)).

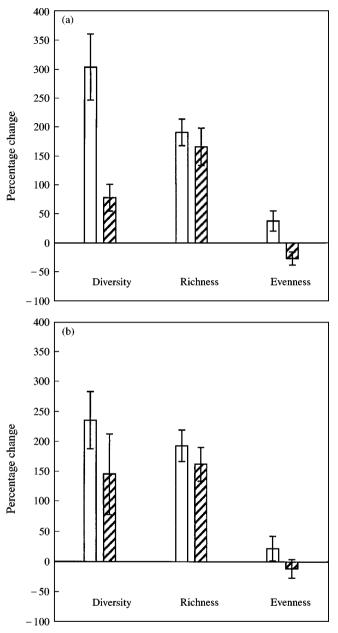


Figure 2. Mean $(\pm S.E.)$ percentage change in species diversity, richness, and evenness in experimental plots following (a) prescribed June burning (fire \Box ; no fire Ξ) and (b) mostly dormant season grazing over 4 years (grazing \Box ; no grazing Ξ).

Changes in cover of annual forbs were not increased after grazing (p = 0.626), and its frequency was also unaffected (p = 0.538).

Grazing affected individual species differently. Cover of *B. eriopoda* decreased 11.5% following grazing and increased approximately 2% in ungrazed areas but only approached significance (p = 0.055) (Fig. 4(a)). Its frequency decreased 21% more in grazed areas compared to ungrazed plots (p = 0.046; Fig. 4(b)). In contrast,

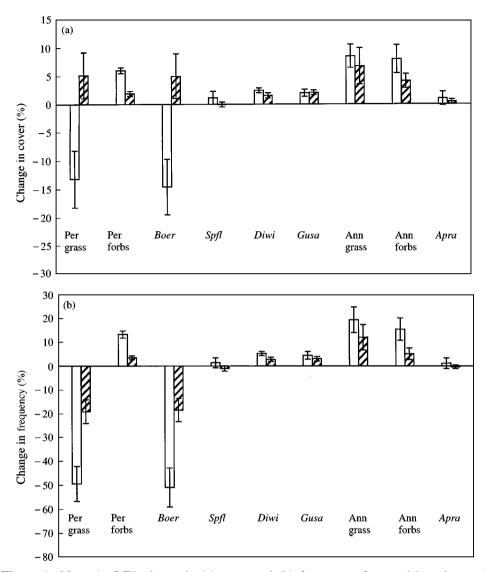


Figure 3. Mean (\pm S.E.) change in (a) cover and (b) frequency of perennials and annuals, 4 years following prescribed June burning. Fire (\Box); no fire (\blacksquare). Per grass; perennial grasses; Per forbs: perennial forbs; *Boer. Bouteloua eriopoda* (perennial grass); *Spfl: Sporobolus flexuosus*, (perennial grass); *Diwi: Dimorphocarpa wislizenii* (perennial forb); *Gusa: Gutierrezia sarothrae* (perennial suffrutescent); Ann grass: annual grasses; Ann forbs: annual forbs; *Apra: Aphanostephus ramosissimus* (annual forb).

grazing did not affect cover (p = 0.354) or frequency (p = 0.549) of *S. flexuosus* (Fig. 4). Respectively, cover and frequency of *D. wislizenii* were 1.3% (p = 0.050) and 3% (p = 0.012) greater in grazed than ungrazed areas (Fig. 4). Neither cover (p = 0.516) nor frequency (p = 0.307) of *G. sarothrae* was affected by grazing. Similarly, marginal decreases in the cover and frequency of *A. ramosissimus* were not attributed to grazing (p = 0.207 and p = 0.174 respectively). Interactions involving grazing and fire were not detected for these species individually, perennial grasses and forbs, or annual grasses and forbs (p > 0.130).

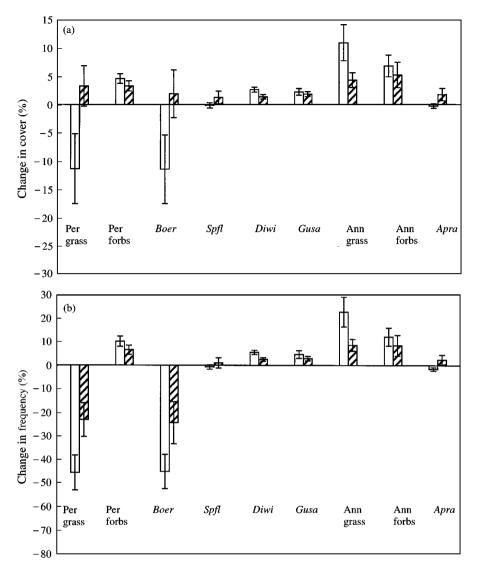


Figure 4. Mean $(\pm S.E.)$ change in (a) cover and (b) frequency of perennials and annuals, following 4 years of mostly dormant season grazing. Species abbreviations follow Fig. 3. Grazing (\Box); no grazing (Ξ).

Shrubs

Changes in diversity were not related to the presence of *P. glandulosa* (data not shown). Species diversity increased 196% in shrub-absent plots but increased 185% in areas where *P. glandulosa* was present (p = 0.891). Species richness increased only 18% less in *P. glandulosa* plots than in plots without shrubs (p = 0.678). Evenness was also unaffected by the presence of *P. glandulosa* (p = 0.775). Interactions involving shrubs, fire, and grazing did not affect overall diversity, richness, or evenness (p > 0.689).

Responses of perennials and annuals were not different between areas where *P. glandulosa* was either present or absent. Respectively, changes in cover and frequency

of perennial grasses were not affected by the presence of *P. glandulosa* (p = 0.408 and p = 0.543). Further, cover (p = 0.188) and frequency (p = 0.188) of perennial forbs increased > 3.5% in plots where *P. glandulosa* was either present or absent. Though annual grass cover increased 5% more and its frequency increased 11% more in *P. glandulosa*-absent plots than areas containing shrubs, these differences only approached significance (p = 0.099 and p = 0.105 respectively). Additionally, cover and frequency of annual forbs increased only numerically more in plots containing *P. glandulosa* (8% and 15% respectively) than untreated areas (4% and 5%) (p = 0.192 and p = 0.134 respectively). Finally, interactions involving fire, grazing, and *P. glandulosa* had no effect on cover and frequency of either perennials (p > 0.297) or annuals (p > 0.460).

Cover and frequency of *B. eriopoda*, *S. flexuosus*, *G. sarothrae*, and *A. ramosissimus* were not affected by the presence of *P. glandulosa* (p > 0.090). However, *D. wislizenii* increased 2% more in plots where *P. glandulosa* was present than shrub-absent areas (p = 0.041). Interactions between fire, grazing, and the presence of shrubs did not affect these species individually (p > 0.320).

Precipitation

Experimental fires were prescribed during near drought conditions. In contrast to the long-term average (1918–1999) (Fig. 1(a)), our study areas did not receive any precipitation for April and May, just prior to prescribed fires in 1995 (Fig. 1(b)). Further, only 16% of expected precipitation occurred in June. Following fires, study sites received only 50% of precipitation expected in July, although August and September were above average.

During years in which grazing treatments were applied (1996–1999), patterns of precipitation were generally similar to the long-term average (Fig. 1 (c)). During the months in which livestock grazing was conducted over those 4 years, precipitation was 85% and 96% of the long-term average for January–March and August–October respectively. In contrast, study areas received 233% more precipitation expected for June, while precipitation during July was slightly greater than the long-term average (*cf.* Fig. 1 (a)).

Discussion

In this study, cover of perennial grasses, comprised almost exclusively of *B. eriopoda* decreased 13% following prescribed fire, but increased 5% in unburned plots. Delaved recovery may have been a result of fires being applied during near-drought conditions that persisted into the immediate post-fire environment. In contrast, annual precipitation for the 4 years after fire treatments was equivalent to the long-term average. These responses to fire were similar to those following 4 years of continuous, mostly dormant season grazing. Similarly, delayed recovery of perennials in burned and grazed areas was reported for desert grasslands of south-eastern Arizona when drought conditions occurred immediately following prescribed fires (Valone & Kelt, 1999). In the same region, however, frequency of dominant perennial grasses was unaffected by June fires but only when rainfall immediately occurred during the summer and was equivalent to the long term average (Cable, 1967, 1972). In southern New Mexico and south-western Texas desert grasslands, a combination of drought and grazing resulted in delayed recovery of perennial grasses (Nelson, 1934; Canfield, 1939; Wright, 1980. In central New Mexico, cover and biomass of B. eriopoda were very sensitive to high inter-annual amounts of precipitation following fire and simulated grazing (Gosz & Gosz, 1996). Near our study sites, mortality of B. eriopoda was attributed to prolonged drought conditions (1951–1956) (Herbel et al., 1972). All these

studies suggest that *B. eriopoda* may be sensitive to drought conditions when they co-occur with other disturbances such as fire and grazing.

Decreased abundances of perennial grasses are often associated with increased perennial forbs and annuals after burning or grazing in south-western desert grasslands (Wright, 1980). Decreased cover of *B. eriopoda* following fire coincided with a 4% greater cover of perennial forbs in burned than unburned areas in our study. A similar but nonsignificant cover pattern was observed after grazing. Annual grasses and forbs both increased in cover regardless of fire and grazing treatments. Decreased abundances of perennial grasses and increased abundances of annual plants occurred following fires and grazing in similar desert grasslands of south-eastern Arizona (Cable, 1972; Valone & Kelt, 1999) and following summer grazing in Oklahoma tallgrass prairies (Collins, 1987). In Colorado shortgrass steppe, increased abundances of annuals and then perennial forbs were associated with reductions of perennial grasses following grazing (Coffin *et al.*, 1998).

Effects of fire and grazing on diversity can not be generalized for south-western grasslands; species responses are contingent on other important factors such as weather conditions and land-use history (Kelt & Valone, 1995). We observed a 225% increase in overall diversity in burned vs. unburned areas. This increase was attributed to changes in species evenness, a result of decreases in dominant perennial grass frequency (mostly B. eriopoda) and increases in perennial forbs. Similar response patterns occurred between grazed and ungrazed areas but were not significant. In south-eastern Arizona desert grasslands, richness and evenness of annuals increased following burning but were similar between grazed and ungrazed areas (Kelt & Valone, 1995; Valone & Kelt, 1999). Conversely, annual plant diversity increased following release from cattle grazing in Sonoran desert grasslands (Waser & Price, 1981). In other North American grasslands, fire and grazing sometimes increase diversity (Adams et al., 1982; Anderson, 1982; Collins & Steinauer, 1998). For example, in tallgrass prairies, diversity and cover of dominant C₄ grasses are contingent on whether burns are conducted during or outside the lightning season (Collins, 1987; Howe, 1994; 2000). Summer grazed areas of mixed- and tallgrass-prairies exhibited greater species diversity than ungrazed areas (Collins & Barber, 1985; Collins 1987). In general, effects of these disturbances on species diversity depend not only on such factors as moisture availability before and after disturbances (McPherson, 1995; Engle et al., 2000) but also on the degree to which prescribed fires and grazing simulate natural disturbance regimes (Denslow, 1980).

Interactions between fire and grazing can affect plant community composition. Relative to spring fires and summer grazing alone, a combination of these disturbances maximized species diversity in tallgrass prairies; grazers were effective in reducing postfire growth of dominant perennial grasses and increasing the abundances of mostly C_3 species (Collins & Barber, 1985; Collins, 1987, 1992). In Mediterranean grasslands, burned areas exhibited less diversity in ungrazed areas in which greater fire intensities may have imposed additional stress on plant species as opposed to grazed areas where fuel loads were less (Noy-Meir, 1995). Post-fire seedling herbivory in California chaparral may have determined the relative abundances of species (Mills, 1986). In our study areas, drought conditions may have negated any potential interaction involving fire and grazing. Because of the extremely slow recovery of *B. eriopoda* following fire and drought conditions, grazing activity may have been considerably less in burned plots since cattle primarily target perennial grasses as a feed source.

Gutierrezia sarothrae is negatively affected by both moisture stress and fire. In Arizona desert grasslands, prescribed June fires achieved 100% mortality of *G. sarothrae*. However, appreciable mortality was achieved also in unburned areas because of drought (Valone & Kelt, 1999). Germination of this subshrub is inversely related to moisture stress (Kruse, 1970) which affects both root growth and photosynthesis (Wan *et al.*, 1993*a*, *b*). However, complete kill of *G. sarothrae* occurred following June fires despite

unusually high moisture conditions on similar grassland sites in Arizona (Humphrey & Everson, 1951). June–July summer burns, rather than early spring fires, were more effective for killing *G. sarothrae* in central New Mexico because most of its carbohydrates, needed for resprouting, are located in above ground stems during this time (McDaniel *et al.*, 1997). Our results indicated little difference in cover or frequency of *G. sarothrae* between burned and unburned areas. Despite reductions in cover and frequency of perennial grasses and thus increased area for colonization, drought conditions may have been responsible for very slow recruitment of *G. sarothrae* (Valone & Kelt, 1999).

Presence of shrubs may affect cover and frequency of perennials and annuals. Biomass of primarily perennial grasses was less in areas where shrubs were present compared to areas where they had been complete-killed with herbicide (Gibbens *et al.*, 1986). Shrubs such as *P. glandulosa* may outcompete forbs and grasses for moisture during excessively dry conditions because they possess expansive underground root systems that can proliferate rapidly and spread over longer distances than herbs (Heitschmidt *et al.*, 1988; Gile *et al.*, 1997). Additionally, once established, fire is rarely effective in root-killing and reducing local distributions of *P. glandulosa* (Ansley & Jacoby, 1998). Reductions in frequency and cover of perennial grasses were not attributed to shrubs in our study. Drought conditions may not have been of sufficient duration to observe any negative effects of shrubs on non-woody species.

Our burns were prescribed during environmental conditions that may not have been conducive to regrowth following fires. Though highly speculative, if excessively dry conditions had not occurred immediately before and especially after burning, responses of dominant perennials may have been different. From an evolutionary perspective, species adapted to predictable fire regimes should possess traits that confer resistance to fire as well as the post-fire environment (Platt, 1994). Further, precipitation immediately following lightning-season fires may be a necessary component of such a post-fire environment in south-western desert grasslands. When precipitation is below the long term average, prescribed burned areas may provide adverse conditions for survival and regrowth of perennial grasses. From a management perspective, Gosz and Gosz (1996) suggested that June fires might be prescribed before El Niño events in desert grasslands, ensuring ample moisture during fall and winter seasons just after burning. In desert grasslands of south-central New Mexico, precipitation influenced by El Niño may not be soon enough if precipitation is well below the average during the summer following fires. Prior to European settlement, fires may have reduced abundance of perennial grasses, creating 'gaps' in the resource space. These openings may have enabled perennial forbs, annuals, and even perennial grasses to colonize and complete life histories (Coffin & Lauenroth, 1990). Duration of these gaps, a function of the rate and degree of perennial grass recovery, remains in question. The contribution of our study is that gap duration may have been a function of precipitation patterns immediately following fires during the summer. Thus, the influence of fire on south-central New Mexico grasslands warrants further investigation with an emphasis on examining relationships between prescribed lightning season fires and post-fire precipitation patterns.

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