

Fire season and simulated grazing differentially affect the stability and drought resilience of a C₄ bunchgrass, C₃ bunchgrass and C₄ lawngrass

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Abstract

We used a fully factorial experimental design to examine the effects of fire season, simulated grazing and their interaction on the temporal stability (year-to-year variation in production) of the C₄ bunchgrass, *Bouteloua curtipendula*, the C₃ bunchgrass, *Nassella leucotricha*, and the C₄ lawngrass, *Buchloe dactyloides*. Treatments included three levels of fire (winter fire, summer fire, and no fire) and two levels of grazing (simulated grazing and no grazing). Additionally, a severe drought during the fourth year of the five year study allowed us to examine each species' post-drought resilience. In the southern Great Plains, USA, these three perennial grass species are economically and ecologically important; each species is a dominant member of their functional group and important as livestock forage. Temporal stability and drought resilience of the C₄ bunchgrass, *Bouteloua*, were significantly greatest in the summer fire treatments. In contrast, temporal stability of the C₃ bunchgrass, *Nassella*, was significantly greatest in the no-fire treatments and its drought resilience was significantly greatest in the no-graze treatments. Temporal stability and drought resilience of the C₄ lawngrass, *Buchloe*, were not affected by any of the treatments. The contrasting effect of fire on the C₄ and C₃ bunchgrasses is consistent with the hypothesis that fire favors C₄ over C₃ grasses due to differences in post-fire soil conditions such as increased temperature, reduced moisture and reduced mineralizable nitrogen.

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1. Introduction

Fire, grazing and their interaction have been the subjects of much basic and applied grassland ecology work (e.g., Valone and Kelt, 1999; van Langevelde et al., 2003; Fuhlendorf and Engle, 2004; Archibald et al., 2005). In the North American Great Plains, a majority of this work has focused on winter or early spring fires rather than summer fires (Engle and Bidwell, 2001). However, fire intensity and vegetation physiologies vary with season (Govender et al., 2006); thus, vegetation can respond differently to season of fire (e.g., Howe, 1994; Sparks et al., 1998; Copeland et al., 2002; Ruthven et al., 2003). Nonetheless, vegetation responses to season of fire are unclear. Moreover, most fire ecology research only measures vegetation responses 1–2 years post-fire and does not include different seasons of fire and their interaction with grazing in a factorial design (Engle and Bidwell, 2001). Accordingly, the effects of fire season and grazing on vegetation population dynamics such as temporal stability (defined as the year-to-year variation in production relative to its mean; Tilman, 1996; Tilman et al., 2006) and drought resilience are not well understood.

In arid and semiarid grasslands, such as the southern Great Plains, variability in precipitation has a large effect on grass production. Indeed, in these systems, year-to-year variability in precipitation can have a greater effect on annual herbaceous production than grazing or fire (Ansley et al., 2006). Thus, grassland management strategies that increase the temporal stability of annual grass production without negatively affecting mean annual grass production will benefit livestock fodder management (Tilman et al., 2006).

Here, we use 5 years of post-fire annual production data to examine the effects of summer fire, winter fire and no-fire as well as their interaction with simulated grazing and no-grazing on the temporal stability and mean annual production of one C₄ bunchgrass (*Bouteloua curtipendula*), one C₄ lawngrass (*Buchloe dactyloides*) and one C₃ bunchgrass (*Nassella leucotricha*). Additionally, a severe drought during the fourth year of the study allowed us to examine each species' post-drought resilience in the fifth and final year of the study. The three grass species included in the study are abundant, and important livestock forages in the southern Great Plains. To control for confounding effects of diversity and interspecific competition on temporal stability and drought resilience (e.g., Tilman, 1996), we sampled within large (10–20 m²), replicate, monospecific patches of each species.

2. Methods

2.1. Site description

Research was conducted in the Rolling Plains ecological area of north Texas (33°51'N, 99°26'W; elev. 381 m). Mean annual rainfall is 665 mm and bimodally distributed with mean monthly maxima in May (119 mm) and September (77 mm). Mean monthly air temperatures range from an average daily maximum of 36 °C in July to an average daily minimum of –2.5 °C in January. C₄ grasses' growing season is from April to October and C₃ grasses' growing season is from February to June and September to November.

All research plots were on a portion of a private ranch that was grazed by cattle at a moderate level (8–12 ha animal unit⁻¹) for > 50 years until 1988 when cattle were excluded. Throughout the site, soils are fine, mixed, thermic Typic Paleustolls of the Tillman series that are 3–4 m deep alluvial clay loams underlain by sandstone and shale parent material

(Koos et al., 1962). All monospecific patches of each grass species were located in interstitial spaces within a mesquite (*Prosopis glandulosa*) savanna.

2.2. Treatments

Twenty-seven 10–20 m² monospecific patches (nine each of *Bouteloua*, *Buchloe* and *Nassella*) were randomly located. For each species three patches were not burned, three patches were subjected to winter fires in 1993 and 1995, and three patches were subjected to summer fires in 1992 and 1994. All winter fires were applied from late-February to mid-March, and all summer fires were applied in September. Summer fires were burned before winter fires so that in a given year post-fire both winter and summer fire treatments had an equal number of post-fire growing seasons. Fires were applied as headfires using drip torches. Vegetation around plots was removed to contain fires. Although an ideal experimental design would have included only nine burned patches, with each burned patch containing one monospecific patch of each of the three species, this was not possible due to the lack of availability. Thus, we only compare response direction across the three species.

The fire treatments were imposed as a prescription to suppress encroaching woody vegetation in the southern Great Plains where woody species such as *Prosopis glandulosa* (mesquite) inhibit herbaceous production. With this prescription, the two repeated burns (with rest during 1 year) are used to maximize woody vegetation suppression and increase herbaceous production; afterwards, livestock are typically grazed for 5–7 years until post-fire re-growth of woody vegetation once again begins to inhibit herbaceous production (Ansley and Jacoby, 1998).

The following procedure was used to quantify spring annual aboveground production for each species: within each monospecific patch, two 0.6 × 0.9 m (0.54 m²) subplots were permanently marked. In one subplot, all herbaceous material was clipped to a 5-cm stubble height once each spring (end of May) for 7 years (1993–1999) to simulate a high intensity, low-frequency grazing pattern (simulated grazed). The other plot remained unclipped (no-graze). Thus, both clipped and unclipped plots occurred within each fire treatment and served as statistical replicates ($n = 3$). Once each year, within a week after each spring clipping event, a 0.5 m border area was mowed around each of the clipped plots to reduce the competitive impact of surrounding vegetation.

In the clipped treatment, spring production was measured by saving the clipped material. In the unclipped treatment, spring production was estimated by harvesting all of the species' aboveground tissue within a 0.25 m² quadrat that was within 5 m of the marked 0.6 × 0.9 m unclipped plot and resembled it in terms of percent foliar cover. A 0.25 m² quadrat was harvested from a different location each year. Sampling was conducted from 1993 to 1999 excluding 1998 due to a severe drought that resulted in no observed production.

All samples were oven dried at 60 °C to a constant weight and weighed. A subsample of each sample was used to separate live from dead tissue and estimate spring aboveground production. From here on this measurement is termed “production”. At study termination in May 1999, all 0.6 × 0.9 m plots (both simulated grazed and ungrazed) were clipped to quantify 1999 production. Only post-fire data (1995–1999) were analyzed.

Temporal stability of production was measured by obtaining the coefficient of variation ($CV_{(1995-1999)} = 100 * 1SD / \text{mean}_{(1995-1999)}$) of production for each replicate (e.g., Tilman,

1996). This measure provides an index of year-to-year variation in each population's production relative to the mean. An increase in CV indicates a decrease in temporal stability. Drought resilience was measured by calculating the difference between each replicate's post-drought production and its predrought average (Drought resilience = First Year Post-drought Production₍₁₉₉₉₎ – Mean Pre-drought Production_(1995–1997)) (Tilman, 1996). A value of zero indicates that first year post-drought production was equal to pre-drought mean annual production; a positive value indicates first-year post drought production surpassed pre-drought mean annual production and a negative value indicates the opposite.

2.3. Analyses

One 3 × 2 two-way analysis of variance (ANOVA) was used to analyze each species' CV. One 3 × 2 two-way ANOVA was used to analyze each species' drought resilience. Mean annual post-fire production was calculated by averaging the annual production of each replicate from 1995 to 1999. One 3 × 2 two-way ANOVA was used to analyze mean annual post-fire production for each species. For all analyses, significant main effects were analyzed with Tukey's HSD post hoc analysis. All data met the assumptions of ANOVA.

3. Results

3.1. Temporal stability of production

There was a significant main effect of fire season on the temporal stability of *Bouteloua* production ($P < 0.01$) (Fig. 1A). The summer fire treatment had a significantly lower CV than winter fire or no-fire treatments, which indicated that *Bouteloua* temporal stability was greater in the summer fire treatment relative to the winter fire or no-fire treatments. There were no significant effects of fire, clipping or their interaction on *Buchloe* temporal stability ($P = 0.408$) (Fig. 1B). Similar to *Bouteloua*, there was a significant main effect of fire season on *Nassella* temporal stability ($P = 0.08$) (Fig. 1C). However, in contrast to *Bouteloua* CV, *Nassella* CV was lowest in the no-fire treatment, which indicated that *Nassella* temporal stability was greater in the no-fire treatment relative to the summer fire or winter fire treatments ($P = 0.08$). Treatment means are displayed in Table 1.

3.2. Drought resilience

There was a significant main effect of fire on *Bouteloua* drought resilience ($P < 0.01$) (Fig. 2A). After a major drought in 1998, *Bouteloua* annual production was more resilient in the summer fire treatment than in the winter fire or no-fire treatments ($P < 0.01$). There were no fire, clipping or interaction effects on *Buchloe* drought resilience (Table 1). There was a significant main effect of clipping treatment on *Nassella* drought resilience; simulated grazed *Nassella* was less resilient than ungrazed *Nassella* ($P < 0.01$) (Fig. 2B).

3.3. Mean production

There was a significant fire × grazing interaction on mean production (1995–1999) of *Bouteloua* ($P = 0.056$). Within the simulated grazed treatments, fire had no effect.

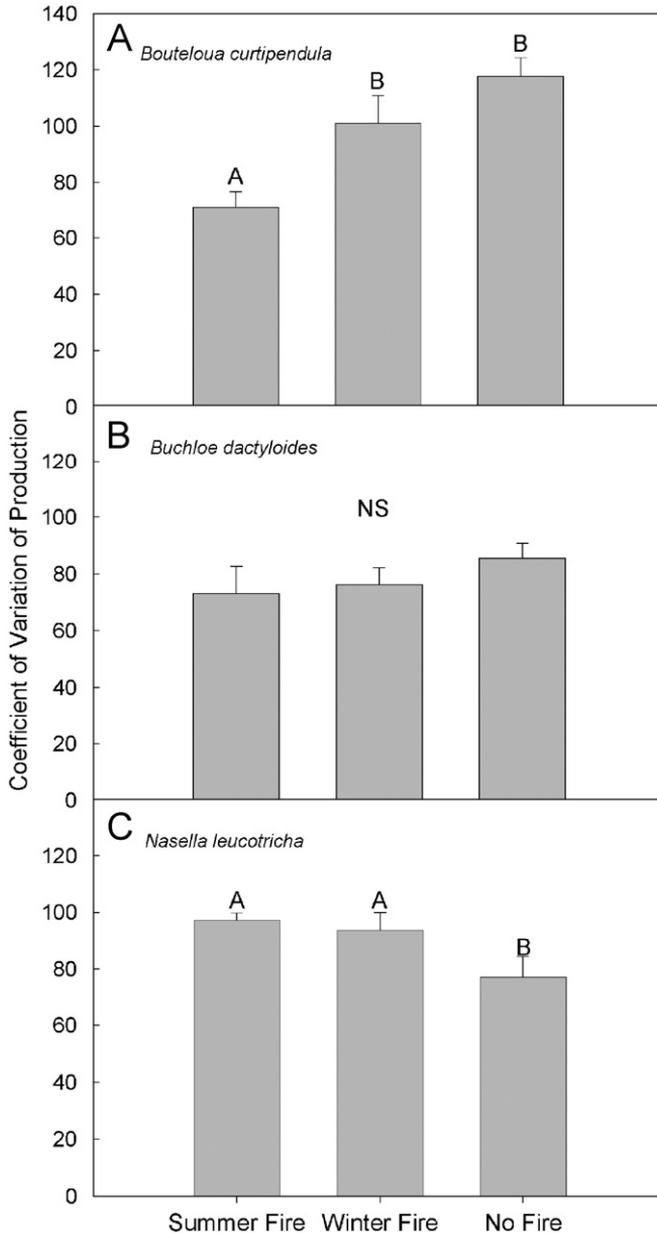


Fig. 1. Main effect of fire on the coefficient of variation of mean annual production 1995–1999 (mean \pm SE). Lower values indicate greater temporal stability. Different letters indicate significantly different means; (NS) indicates effect not significant.

However, within the ungrazed treatments, one-way ANOVA post hoc indicated production in the winter fire treatments was greater than in the summer fire treatments ($P = 0.058$) (Fig. 3A). There was no effect of fire, grazing or their interaction on *Buchloe* mean production (Table 1). There was only a grazing main effect on *Nassella* mean

Table 1

Mean production (g m^{-2}), coefficient of variation (CV), and resilience (g m^{-2}) for each treatment within each species (standard error bars in parentheses)

Treatment	Production (se)	CV (se)	Resilience (se)
<i>Bouteloua curtipendula</i>			
No Fire, No Grazing	88.25 (6.87)	127.54 (10.99)	-115.43 (14.85)
No Fire, Clipping	60.12 (8.36)	107.79 (1.19)	-76.68 (11.23)
Winter Fire, No Grazing	112.78 (10.09)	102.77 (23.01)	-57.34 (51.35)
Winter Fire, Clipping	57.31 (4.08)	99.30 (9.77)	-83.74 (7.66)
Summer Fire, No Grazing	58.53 (8.38)	59.13 (7.04)	14.33 (7.63)
Summer Fire, Clipping	62.72 (20.65)	82.48 (6.58)	38.77 (14.65)
<i>Nasella leucotricha</i>			
No Fire, No Grazing	59.97 (0.88)	70.67 (6.44)	-58.13 (8.14)
No Fire, Clipping	34.80 (7.20)	83.82 (13.39)	-45.60 (13.75)
Winter Fire, No Grazing	57.58 (15.60)	102.32 (2.78)	-81.21 (10.91)
Winter Fire, Clipping	32.81 (18.24)	85.42 (12.50)	-37.10 (25.64)
Summer Fire, No Grazing	53.09 (1.09)	97.66 (5.17)	-79.96 (3.25)
Summer Fire, Clipping	35.42 (3.77)	96.91 (3.63)	-54.03 (6.58)
<i>Buchloe dactyloides</i>			
No Fire, No Grazing	36.39 (8.73)	106.65 (5.59)	-55.82 (9.81)
No Fire, Clipping	34.64 (7.77)	110.08 (10.31)	-53.44 (11.48)
Winter Fire, No Grazing	45.05 (13.54)	92.77 (3.09)	-38.20 (5.34)
Winter Fire, Clipping	43.55 (7.47)	107.29 (10.04)	-50.59 (7.40)
Summer Fire, No Grazing	45.45 (8.78)	87.243 (2.12)	-56.97 (10.67)
Summer Fire, Clipping	38.14 (6.82)	108.023 (18.61)	-29.59 (14.4)

production; ungrazed treatments were more productive than simulated grazed treatments ($P < 0.01$) (Fig. 3B).

4. Discussion

Bouteloua (C_4 bunchgrass) temporal stability and drought resilience were significantly highest in the summer fire treatments. Relative to the winter fire and no-fire treatments, *Bouteloua*'s first year post-drought resilience in the summer fire treatment increased its temporal stability; first year post-drought production in the summer fire treatment was closer to mean annual pre-drought production than in the winter fire and no-fire treatments (Fig. 2A). The closer any single year's production is to mean annual production, the greater the temporal stability (lower CV). Thus, *Bouteloua* summer fire treatment's high drought resilience helps to explain its high temporal stability relative to the winter fire and no-fire treatments.

Additionally, the effect of summer fire on *Bouteloua* drought resilience was completely consistent; 1 year after a major drought in 1998 that resulted in less than one-third of mean annual precipitation, all summer-fire-treatment *Bouteloua* patches (clipped and unclipped, $n = 6$) produced above pre-drought mean production while all other patches (winter fire and no-fire, clipped and unclipped $n = 12$) produced below the pre-drought mean. The positive effect of summer fire on *Bouteloua* temporal stability and drought resilience is consistent with two studies that have found positive effects of summer fire on *Bouteloua* production (Taylor, 2001; Ansley et al., 2006). It is important to note that the increased

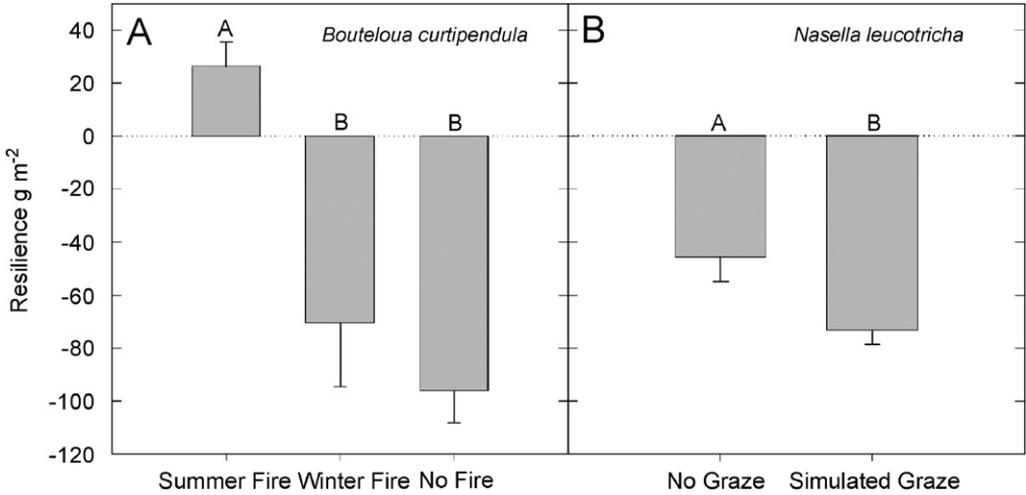


Fig. 2. (A) Main effect of fire season on post drought resilience of *Bouteloua curtipendula* (B) Main effect of clipping on post-drought resilience of *Nassella leucotricha* production (mean \pm SE). Different letters indicate significantly different means. The y-axis indicates first year post-drought production (1999) relative to the pre-drought mean (1995–1997) indicated by zero (see methods).

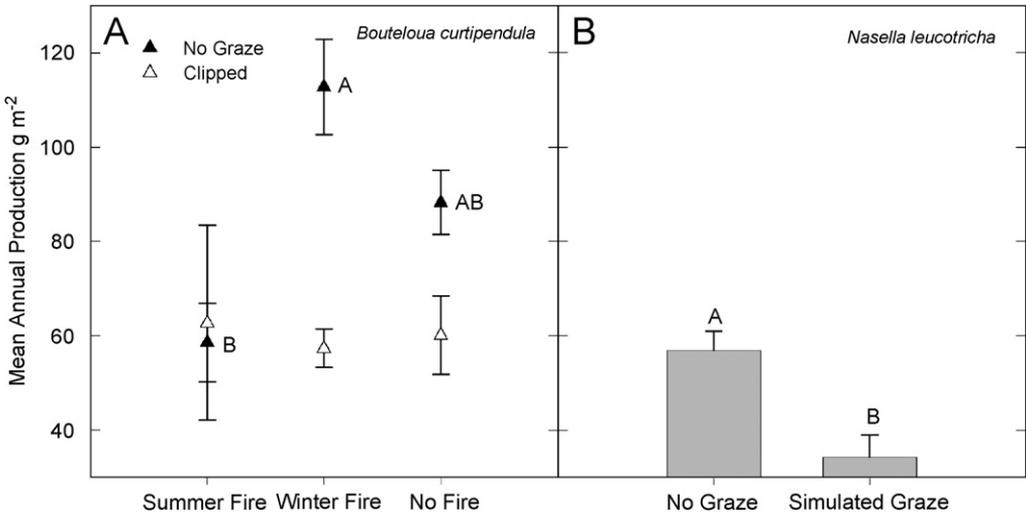


Fig. 3. Mean (\pm SE) annual production. (A) Significant interaction between fire and clipping on *Bouteloua curtipendula* production. One-way ANOVA post hoc analysis within the no-graze treatment indicated a significant effect of fire season. (B) Main effect of clipping on spring *Nassella leucotricha* production ($P < 0.01$). Different letters indicate significantly different means.

temporal stability of summer fire treated *Bouteloua* (Fig. 1A) was not realized at the expense of production within clipped treatments; mean annual production was similar across all clipped fire treatments (Fig. 3A).

In contrast to *Bouteloua*, *Nassella* (C_3 bunchgrass) temporal stability was significantly lowest in the summer fire treatment relative to the winter fire and no-fire treatment.

Furthermore, there was no effect of fire season on drought resilience. However, *Nassella* drought resilience was significantly lower in the clipped treatments, which was consistent with the negative effect of grazing on mean production.

The lack of any treatment effect on *Buchloe* may be consistent with its ability to establish and persist in overgrazed, degraded systems (Ford, 1999; Ansley and Taylor, 2004). It is predicted that bunchgrasses will usurp lawngrasses if fire is frequent and grazers are removed (Archibald et al., 2005). Although the time scale of this process is not clear, in the long-term, frequent fire and no grazing might destabilize lawngrasses.

Although our data examine only one species from each functional group, our results are consistent with the hypothesis that fire may favor C_4 over C_3 grasses. *Bouteloua* and *Nassella* use the C_4 and C_3 photosynthetic pathways, respectively. The contrasting effects of fire on these species' temporal stability may be due to differences in the two functional groups' performance in post-fire soil conditions. Fire reduces soil moisture while increasing soil temperature (Briggs and Knapp, 1995; Collins and Steinauer, 1998). Additionally, repeated fires reduce soil N availability (Ojima et al., 1994; Seastedt et al., 1991). Summer fire may exacerbate these conditions because the greater intensity of summer fires results in more complete fuel combustion (Ansley and Jacoby, 1998). These conditions favor the C_4 over the C_3 photosynthetic pathway because C_4 grasses perform better under warm, dry conditions and have greater nitrogen use efficiency (NUE) than C_3 grasses (Seastedt et al., 1991; Wedin and Tilman, 1996; Blair et al., 1998). Furthermore, C_4 grasses store a larger proportion of their total N in belowground structures while C_3 grasses store a greater proportion of their total N in aboveground structures (Epstein et al., 1998; Reich et al., 2001). Thus, removal of aboveground biomass may be expected to negatively affect C_3 grasses more than C_4 grasses. In this study, the lack of a clipping effect on the stability and resilience of C_4 grasses and the negative clipping effect on the C_3 bunchgrass *Nassella* resilience, is consistent with this idea. Further work is required to determine if these species' contrasting responses to fire and grazing are characteristic of their functional groups and a direct result of differences in N limitation and storage.

Our results have implications for the use of seasonal fires to manage southern Great Plains grasslands where these three grass species are abundant and important livestock forages. Summer fires did not negatively impact either C_4 grass species' temporal stability or drought resilience. Moreover, when combined with simulated grazing, none of the fire treatments negatively impacted the grasses' mean annual production. Thus, summer fires appear to enhance (*Bouteloua*) or have no effect (*Buchloe*) on these C_4 grasses' stability and resilience. In contrast, fire (regardless of season) appears to decrease the C_3 grass, *Nassella*, stability while clipping lowers resilience.

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