

DIRECT AND INDIRECT EFFECTS OF FIRE ON SHRUB DENSITY AND ABOVEGROUND PRODUCTIVITY IN A MESIC GRASSLAND

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Abstract. Determinants of the balance between grass and woody vegetation in grasslands and savannas have received considerable attention because of the potential for dramatic shifts in ecosystem structure and function as one growth form replaces the other. We studied a mesic grassland where recently established “shrub islands” are increasing in abundance due to fire suppression. Our objective was to assess the role of the direct effects of fire vs. indirect alterations in resource availability (N and light), as mechanisms that may constrain/facilitate shrub (*Cornus drummondii*) encroachment.

The direct effects of fire in 2001 and 2002 were 100% aboveground mortality of *C. drummondii* shoots and removal of the detrital layer. Post-fire resprouting resulted in ~600% increase in stem density compared to a 200% increase in shrub islands protected from fire. In burned shrub islands with an added detrital layer, temperature and light penetration to the soil surface were reduced (by 6.5°C and to <3% of full sunlight), but stem density still increased by ~400%. Thus, both the direct effects of fire and the indirect effect on the energy environment increased *C. drummondii* stem densities. In contrast, N additions did not influence new stem production or aboveground net primary productivity (ANPP; grams per square meter per year), suggesting that N availability did not constrain shrub growth during this study. While fire did not impact total ANPP, it did shift the relative abundance of growth forms. Grass productivity (360.7 ± 20.1 g/m² [mean ± 1 SE]) was stimulated (an increase of ~30%) by the high light conditions of the post-fire environment, while *C. drummondii* ANPP (34.2 ± 2.4 g/m²) was reduced by ~30%. In shrub islands protected from fire, *C. drummondii* ANPP was greatest (50.4 ± 2.2 g/m²), whereas lower graminoid ANPP (282.5 ± 19.9 g/m²) was observed. The persistence of woody vegetation, despite two successive fires, along with a significant reduction in grass ANPP (~30%) suggests that once established, *C. drummondii* can persist and exclude C₄ grasses. Thus, restoring fire to mesic grasslands may prevent further conversion to shrub/woodland, but the abundance of shrubs is likely to remain unchanged with community structure co-dominated by multiple growth forms.

Key words: *Cornus drummondii*; ecosystem transition; fire; Konza Prairie, Kansas (USA); mesic grassland; nitrogen; resource availability; woody plant encroachment.

INTRODUCTION

An increase in woody plant abundance in grasslands and savannas has been observed worldwide (Brown and Carter 1998, Van Auken 2000, Roques et al. 2001, Briggs et al. 2002). This directional change in plant functional type has been attributed to a number of factors including climate change (Idso 1992, Archer et al. 1995), elevated atmospheric CO₂ (Polley et al. 1997, Bond and Midgely 2001), reductions in fire frequency (Bragg and Hulbert 1976), and intense grazing pressures (Scholes and Archer 1997, McPherson and Wright 1990). Given the significant implications for carbon cycling and storage (Gill and Burke 1999, Jackson et al. 2002), plant community structure/biodiversity

(Hobbs and Mooney 1986, Leach and Givnish 1996, Hoch et al. 2002), and resource availability (Schlesinger et al. 1990), experimental studies are needed that characterize the mechanism(s) driving this conversion of grassland to shrubland.

Periodic fire is considered essential for the maintenance and function of mesic grasslands within central North America (tallgrass prairies; Axelrod 1985, Collins and Wallace 1990) as it directly impacts the existing plant community and indirectly alters resource availability and the abiotic conditions of the post-fire environment. High productivity leads to the accumulation of a dense detrital layer in the absence of frequent fire and grazing (Knapp and Seastedt 1986). As time since fire increases, grass productivity declines and woody species increase in both frequency and cover (Bragg and Hulbert 1976, Knight et al. 1994, Hoch and Briggs 1999). This suggests that frequent fire strongly influences the balance between grass and woody plant abundance in this ecosystem, and that fire suppression

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is the primary cause of shrub expansion. While no mechanistic basis for this shift in growth forms has been experimentally elucidated, a reasonable explanation is that, when released from the direct negative constraints imposed by fire, shrubs outcompete and replace C_4 grasses. The competitive effects of shrubs increase with the accumulation of biomass (a process facilitated by fire suppression), primarily due to their ability to grow above the grass canopy and preempt light. Lett and Knapp (2003) measured extreme reductions in light beneath large established shrub islands suggesting that shrubs reduce light below that required for grasses (Li and Wilson 1998). However, shrubs suffer considerable losses when exposed to fire due to the location of shrub meristems (both above- and below-ground) and the investment in aboveground support tissues. Many woody species in fire-prone biomes resprout after episodic fire events, suggesting that their interaction with fire is complex (Hodgkinson 1998, Hoffman 1998, Brown and Archer 1999). Productivity of grasses with belowground meristems is stimulated directly by fire through the removal of senescent shoots and standing biomass and indirectly by enhancing the energy environment (both light availability and soil temperature; Knapp and Seastedt 1986). In this grassland ecosystem, the association between frequent fire, high grass aboveground net primary productivity (ANPP), and minimal shrub cover is well supported (Towne and Owensby 1984, Briggs and Knapp 1995, Abrams et al. 1986).

The microclimate that results from fire suppression may favor recruitment of shrubs and subsequently a rapid increase in shrub cover. Indeed, a recent analysis of fire frequency and associated long-term patterns of shrub expansion documented that periods without fire (≥ 4 years) are necessary for recruitment of new shrub species and individuals (Heisler et al. 2003). Once established, however, most shrubs respond somewhat positively to periodic fire and increase in cover at rates faster than those in long-term unburned grassland (Briggs et al. 2002, Heisler et al. 2003). During fire-free intervals, Blair (1997) determined that an accumulation of inorganic and mineralizable nitrogen (N) occurs, likely as a consequence of reduced demand and uptake by energy-limited grasses (Knapp 1984, Knapp and Seastedt 1986). Given that N is the nutrient most likely to limit productivity within mesic grasslands (Owensby et al. 1970, Risser and Parton 1982, Seastedt et al. 1991), C_3 shrubs (with greater N demands per gram C produced) may respond to increases in available N that accompany a reduction in productivity by C_4 grasses.

In this study, we focused on the transition period during which grasses and shrubs coexist to determine the mechanism driving this shift in growth forms. We explored how fire mediates the grass–shrub tension zone in mesic grasslands by focusing on the shrub *Cornus drummondii*, one of the most aggressive species in

this system with cover $>11\%$ in infrequently burned sites (Briggs et al. 2002). With fire suppression, *C. drummondii* tends to form discrete monospecific “islands” within the landscape, which can be as large as 60 m^2 . Closure of the canopy results in the rapid exclusion of herbaceous vegetation (Lett and Knapp 2003). This reduction in fine fuel discourages fire from burning through these shrub islands; consequently, the potential for fire to topkill shrubs and initiate recovery by grasses is limited. Where graminoid and shrub growth forms still co-occur, fire can still cause significant aboveground mortality in shrubs and influence resource availability in the post-fire environment. In this stage, quantifying the individual responses of grasses and shrubs to fire, along with potential interactions between growth forms, will provide insight into biotic and abiotic components of observed shifts in shrub abundance that have occurred during the past two decades (Heisler et al. 2003).

The objectives of this study were to uncouple the direct effects of fire from the indirect effects, or changes in resource availability (primarily light and N), that are characteristic of the post-fire environment. In separating the indirect and direct effects of fire on both grasses and shrubs, our goal was to quantify the relative importance of resource limitation and aboveground mortality/survivorship as consequences of fire that may affect the balance between grass and shrub dominance in this grassland. We manipulated fire, light (via the addition of a litter layer), and N availability, and measured changes in stem density, aboveground mortality/persistence, and ANPP. We tested the following specific hypotheses: (1) The direct effects of fire will reduce stem density and ANPP of shrub islands in which grasses are codominant. (2) Shrub growth, particularly following fire when competition from grasses is intensified, is N-limited. Consequently, increasing N availability will result in greater stem density and shrub ANPP. (3) The post-fire energy environment is essential in driving the graminoid ANPP response; therefore, islands with litter (regardless of fire regime) will have reduced grass ANPP and increased shrub ANPP in contrast to those in which litter is absent.

METHODS

Study site

This study was conducted during the 2001 and 2002 growing seasons at Konza Prairie Biological Station (KPBS), a 3487-ha native C_4 grassland located in north-eastern Kansas, USA ($39^{\circ}05' \text{ N}$, $96^{\circ}35' \text{ W}$). KPBS is located within the Flint Hills, an area that remains the largest continuous expanse of unplowed tallgrass prairie in North America (Knapp et al. 1998) due to its steep-sided hills and rocky, shallow soils. The climate of KPBS is characterized by a high degree of inter-annual variability in both precipitation and temperature. Mean annual precipitation is 835 mm, 75% of

TABLE 1. Summary of treatments by main effect (fire, nitrogen, and litter) and according to the combination of direct and indirect effects of fire to which a shrub island was exposed ($n = 8$ shrub islands per treatment type) in 2001 and 2002 at the Konza Prairie Biological Station, Kansas, USA.

Treatment	Main effect			Fire effects	
	Fire	Nitrogen	Litter	Direct effects	Indirect effects
Protected	unburned	control	present	no	no
Protected + nitrogen	unburned	N addition	present	no	no
Burned	burned	control	absent	yes	yes
Burned + nitrogen	burned	N addition	absent	yes	yes
Burned + litter	burned	control	present	yes	no

which falls during the growing season (April–September; Hayden 1998). The plant community is dominated by native perennial C_4 grasses, specifically *Andropogon gerardii* Vitman (big bluestem) and *Sorghastrum nutans* (L.) Nash (Indian grass). Forbs (primarily C_3 dicots) account for the majority of plant species diversity (greater than 600 species of higher plants) despite being much less abundant than grasses (Freeman 1998). Cool-season shrubs, such as *Cornus drummondii* C. A. Mey and *Rhus glabra* L., form islands of woody vegetation along ridges and slopes and have become increasingly abundant across the landscape in areas with reduced fire frequency (Bragg and Hulbert 1976, Heisler et al. 2003).

Experimental design

In 2001, 40 shrub islands (*C. drummondii*) were selected from an experimental unit within KPBS (~37 ha in size) in which fire had been excluded for 10 years and grazing by cattle had been excluded for >30 years. Islands were randomly assigned to one of the five treatments described below ($n = 8$ islands/treatment type; Table 1). Herein we refer to individuals as “islands,” due to the tendency of this clonal species to form discrete, closed-canopy stands. Shrub islands were 3–8 m² in area and included a mixed plant community in which grasses, forbs, and *C. drummondii* coexisted. By counting annual growth rings, we determined that shrub islands were likely 3–6 years in age and had therefore established since the last fire within this site (1991). All islands were located in upland plateaus, with similar topography and soil type.

The following experimental design was based on the main effects of fire, nitrogen, and litter:

1) *Protected islands*. Shrub islands were protected from spring burning (24 April 2001, 29 April 2002) of the entire watershed by burning a mowed 1-m buffer around the perimeter of each island and surrounding islands with large strips of sheet metal as protection from potential scorch damage. In this way, we were able to burn the area immediately adjacent to each island without affecting the interior.

2) *Protected + nitrogen islands*. Shrub islands were protected as described in the previous paragraph, and

nitrogen (10 g N/m²), in the form of NH_4NO_3 , was applied to each island on 15 June 2001 and 2002. This amount has been shown to stimulate ANPP in annually burned tallgrass prairie (Seastedt et al. 1991, Knapp et al. 1998).

3) *Burned islands*. Shrub islands were burned when the entire watershed was burned.

4) *Burned + nitrogen islands*. Shrub islands were burned and nitrogen (10 g N/m²), in the form of NH_4NO_3 , was applied to each island on 15 June 2001 and 2002.

5) *Burned + litter islands*. Shrub islands were burned and grassland litter was returned to each island within 24 h of the fire. Litter amount was determined according to initial island area and collected onsite prior to the fire event. After each fire, litter was spread evenly throughout the island and held in place with mesh netting and aluminum stakes until new growth was sufficient to anchor it (approximately one month post-fire).

Grassland plots were established within adjacent areas of the uplands that were generally devoid of woody vegetation. Plots were ~4 m² in area (based on average initial size of shrub islands) and represented typical upland prairie in plant community structure. Grassland plots were burned in 2001 and 2002 and designated as control plots or N addition plots ($n = 8$ per treatment type), the latter of which received 10 g N/m² (NH_4NO_3) on 15 June 2001 and 2002.

Resource availability and microclimate

The post-fire energy environment in all shrub islands was characterized by measuring light availability (photon flux density; PFD) and soil temperature. Both were measured at ~10-d intervals between 1100 and 1300 h central daylight time (CDT) from May through August within a subset of islands ($n = 5$ islands per treatment). Within a given island, three locations were randomly selected and PFD was measured: (1) within the shrub canopy, (2) above the litter layer, and (3) at the soil surface using a 1.0-m ceptometer (Decagon Devices, Incorporated, Pullman, Washington, USA). Flux densities were standardized to above canopy values (maximum PFD). Soil temperature was measured at the

soil surface and at 10 cm below the soil surface in two locations within a given shrub island. All measurements were made on days of full sun.

Soil samples (2 cm in diameter from the top 10 cm) were taken on 25 May 2001 and 25 April 2002. Four cores were taken and composited into a single sample in all shrub islands (in 2002, soil cores were also sampled from grassland plots). Samples of field-moist soil were sieved through a 4-mm screen, extracted with 2 mol/L KCl solution, and concentrations of inorganic N ($\text{NH}_4\text{-N}$ and $[\text{NO}_2 + \text{NO}_3]\text{-N}$) were determined colorimetrically using an Alpkem FlowSolution analyzer (Perstop Analytical Environmental, Wilsonville, Oregon, USA). Additional subsamples were dried at 60°C to determine gravimetric soil water content and to calculate extractable soil N concentrations as N mass per unit mass of dry soil. Bray-extractable P, exchangeable Mg, K, and Ca concentrations, and cation exchange capacity (CEC) were determined on subsamples of soil collected in 2001.

Available N in soils was measured June–September 2002 using mixed cation–anion exchange resin bags. Resin bags were made from sheer nylon stockings filled with equal mixtures (10 g each) of strong anion and cation exchangers. Intact bags were soaked in 0.6 N HCl to clean them and preload the resins with H^+ and Cl^- ions. Four resin bags were placed 5 cm deep in a subsample of plots ($n = 5$) in early June and removed in September. In the lab, resin bags were rinsed with deionized water, extracted with 2 mol/L KCl solution, and concentrations of inorganic N ($\text{NH}_4\text{-N}$ and $[\text{NO}_2 + \text{NO}_3]\text{-N}$) were determined colorimetrically.

Green leaf tissue from *C. drummondii* and *A. gerardii* (the dominant C_4 grass on KPBS; Freeman and Hulbert 1985) was collected on 15 June and 15 July in 2001 and 2002 to quantify total leaf N pre- and post-N addition. Tissue was sampled from all shrub islands as well as grassland plots. Leaves were dried at 60°C for ~1 wk, ground, and analyzed for total N content (percentage dry mass) by combustion and gas chromatography (Carlo Erba NA 1500 analyzer; Carlo Erba, Milano, Italy).

Stem density

In March 2001, the total number of stems within each island was quantified so that all subsequent changes in stem density could be compared to this initial census. After fire, islands were resurveyed to quantify stem mortality. At this time, all surviving stems (present only in protected islands) were tagged, assigned a unique number, and their height and basal diameter were measured. At ~15-d intervals thereafter, all islands were resurveyed to tag new stems, record mortality, and measure the height and basal diameter of all previously tagged stems.

A similar protocol was followed in burned islands, whereby all new shoots were tagged upon reaching a height of ~10 cm. The rationale for tagging each stem

in all islands was to (1) monitor growth throughout the growing season (to estimate productivity); (2) estimate the total number of stems in a particular island; and (3) track the dynamics of stem production, growth, and mortality across the growing season. In total, >12 000 stems were tagged and monitored.

Annual aboveground net primary production

Peak aboveground biomass (excluding *C. drummondii*) was harvested in shrub islands and grassland plots in September 2001 and 2002 to estimate aboveground net primary productivity (ANPP). Replicate 0.10-m² quadrats ($n = 2$) were randomly placed within each shrub island/grassland plot and the current year's live and dead plant material was clipped at ground level and separated into graminoid, forb, and woody components. Biomass was dried at 60°C for ~1 wk and then weighed to the nearest 0.1 g. The identification number of any *C. drummondii* stems that were contained within a given quadrat was recorded so that ANPP could be calculated allometrically.

To estimate shrub biomass without sampling destructively, ~150 *C. drummondii* stems were harvested from adjacent plots in 2001 and an allometric relationship between biomass and stem height and basal diameter was determined. Equations were derived individually for both stem and leaf tissue as indicated below:

Leaf tissue:

$$\log(\text{leaf biomass}) = -5.313 + 1.610 \times \log(\text{diameter}) + 0.826 \times \log(\text{height})$$

Stem tissue:

$$\log(\text{stem biomass}) = -7.344 + 0.672 \times \log(\text{diameter}) + 2.130 \times \log(\text{height}).$$

For leaf tissue, $R^2 = 0.92$, $P < 0.01$, and for stem tissue, $R^2 = 0.94$, $P < 0.01$.

Statistical methods

We used a two-factor analysis of variance (ANOVA) model with fire and N as main effects to test for significant differences in abiotic and biotic responses. Due to the unbalanced experimental design and potential for confounding effects of fire and litter, a single-factor ANOVA with litter as the main effect was used to address differences among litter-absent (burned treatments), litter-added (burned + litter treatment), and litter-present (protected treatments) shrub islands. Duncan's Test was used to contrast group means after significant ANOVA results.

For both soil temperature and light availability, a repeated-measures ANOVA was used to evaluate time and treatment effects and interactions. For stem density, a mixed-model ANOVA (Proc Mixed, SAS 2000) was used to evaluate time and treatment effects due to

subsampling during several census periods. The LSMEANS (SAS 2000) procedure was used to test for significant differences among means, according to pre-planned hypotheses.

To compare shrub islands and grassland plots (primarily soils and ANPP data), we used a two-factor ANOVA with community type and N as main effects. Because shrub islands and grassland plots used in this analysis were burned in both years of the study, it was not necessary to incorporate fire as a main effect.

All proportional data (i.e., percentage leaf tissue N) were arcsine square-root transformed prior to analyses (Sokal and Rohlf 1995). Values presented are means \pm 1 SE, with back-transformed means where appropriate. All analyses were conducted using SAS version 8.1 (SAS 2000), and the level of significance for all tests was $P \leq 0.05$ unless otherwise indicated. In cases in which there was no significant effect of N, we combined treatment groups according to the main effect of fire (burned or protected) and have reported mean responses in the text and figures.

RESULTS

Impacts of fire on microclimate

In 2001 and 2002, the primary direct effect of fire was the removal of the detrital layer and 100% above-ground mortality of *C. drummondii* stems in burned islands. Fire was a significant main effect in increasing the availability of light to emerging shoots at the soil surface ($P < 0.01$). During the first 20 days post-fire, PFD at the soil surface (Fig. 1a) was significantly greater in burned compared to protected islands ($74.9 \pm 2.6\%$ vs. $4.6 \pm 0.8\%$; $P < 0.01$) and remained $\sim 50\%$ greater through day 45 post-burn. Due to herbaceous production in the post-fire environment, light availability at the soil surface in burned islands gradually diminished during the growing season (fire \times time interaction significant, $P < 0.01$; Fig. 1a). Light availability at the end of the growing season (~ 125 days post-fire; September) was $9.4 \pm 1.5\%$ and $3.3 \pm 0.7\%$ in the burned and protected islands, respectively. N addition as a main effect was not significant ($P = 0.95$), nor was the fire \times nitrogen interaction ($P = 0.55$).

Litter was identified as a significant main effect ($P < 0.01$) with the addition or presence of litter similarly effective in reducing light at the soil surface (seasonal means = $4.7 \pm 0.6\%$ and $2.7 \pm 0.2\%$, respectively). Thus, in the litter addition treatment, we imposed the direct effect of fire (shrub stem mortality) but not the indirect effect with regard to light availability (Fig. 1a). While light was significantly different in the first 30 days of the growing season between these two treatments ($P < 0.01$), this can be attributed to the additional effect of the shrub canopy reducing light in protected islands, or in the case of the burned + litter islands, the absence of the shrub canopy.

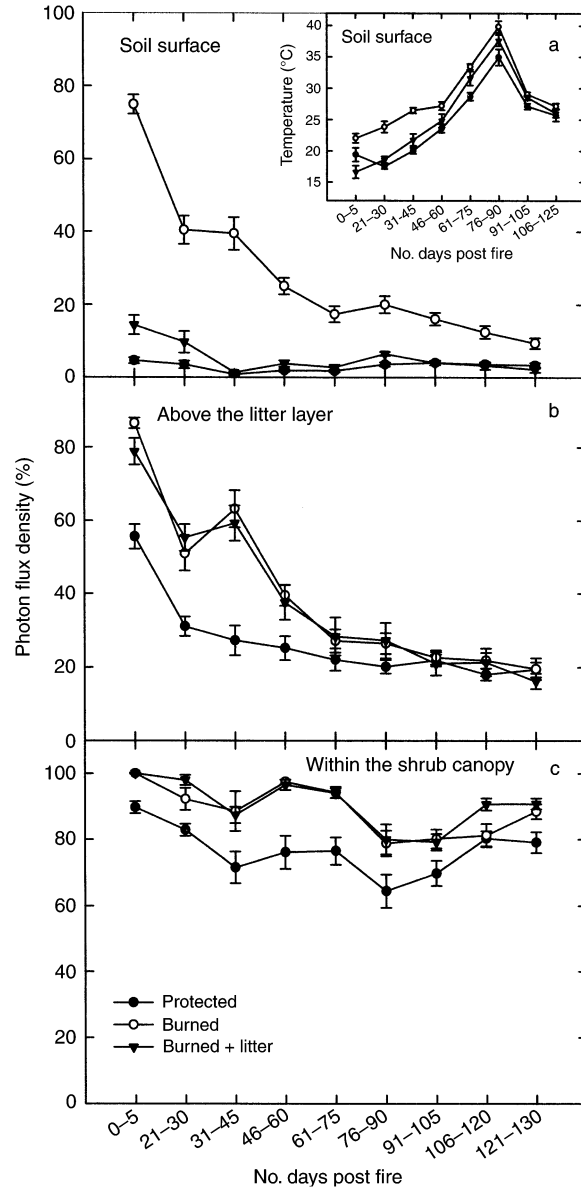


FIG. 1. Light availability (photon flux density [PFD]) at (a) the soil surface, (b) above the litter layer, and (c) within the shrub canopy following spring fire in 2001 and 2002. The inset shows temperature ($^{\circ}\text{C}$) at the soil surface. Fire and litter were the significant main effects ($P < 0.01$, $P < 0.01$, respectively); therefore only protected, burned, and burned + litter shrub islands are shown. Values for a given time interval are pooled means from 2001 to 2002 and represent means \pm 1 SE.

Stratified measurements allowed us to quantify the relative contribution of the litter layer vs. the shrub canopy in reducing incident light at the soil surface. Light above the litter layer was equivalent in burned and burned + litter islands (seasonal mean = $35.7 \pm 2.0\%$; $P = 0.44$), and as vegetation emerged above the litter, it was subjected to high light (Fig. 1b). Comparison of PFD in “the canopy” of burned vs. protected

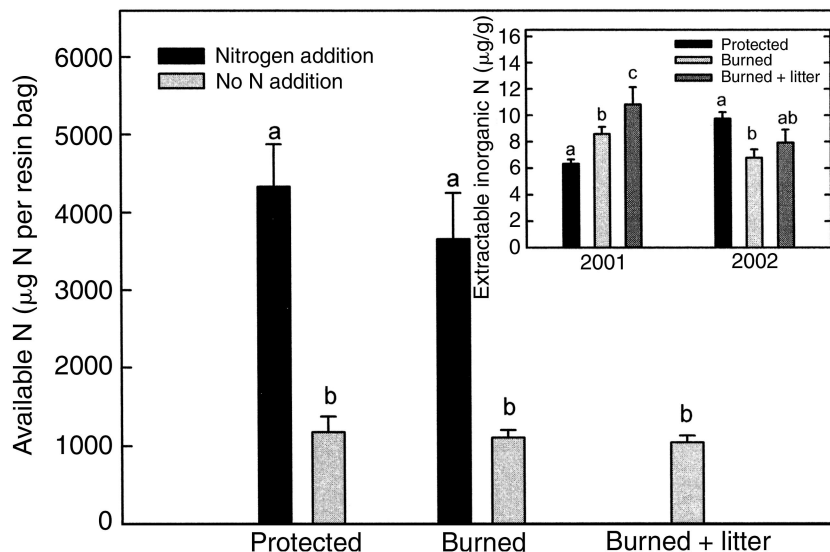


FIG. 2. Relative availability of inorganic soil nitrogen from June to September 2002 in all treatments. Significant differences among treatments ($P < 0.05$) are indicated by different letters, and values represent means \pm 1 SE. The inset shows total available inorganic nitrogen in 2001 (post-fire) and 2002 (pre-fire) in protected, burned, and burned + litter shrub islands. Values are treatment means \pm 1 SE and significant differences ($P < 0.05$) for a given sampling period are indicated with different letters. Soil cores were taken prior to N addition and therefore only the main effects of fire and litter are emphasized.

islands suggests that the canopy of these diffuse islands reduced light by $\sim 10\%$ ($P < 0.01$), and that in this transition stage, the shrub canopy is not the primary cause of the reduction in light. Shrub leaves in the canopy of protected islands were provided with high light throughout the entire growing season ($75.4 \pm 1.1\%$; Fig. 1c).

Temperature at the soil surface was also significantly affected by fire ($P < 0.01$). Removal of the litter layer resulted in a significant increase in soil temperature during the first 45 days after fire ($26.5^\circ \pm 0.5^\circ\text{C}$ vs. $20.0^\circ \pm 0.5^\circ\text{C}$, $P = 0.02$; Fig. 1 inset). The shrub island microclimate remained significantly warmer in burned islands through 90 days post-fire in which seasonal maximum temperatures of $39.9^\circ \pm 1.0^\circ\text{C}$ and $34.9^\circ \pm 1.3^\circ\text{C}$ were recorded in the burned and protected islands, respectively ($P < 0.01$). The added litter appeared to be generally as effective an insulator as the intact litter layer in the protected islands. Nitrogen as a main effect did not significantly affect soil temperature ($P = 0.11$). Measurements of soil temperature 10 cm beneath the ground surface revealed similar trends despite being $\sim 5^\circ\text{--}7^\circ\text{C}$ cooler.

Impacts of fire on soil resource availability

Concentrations of exchangeable Ca, K, and Mg, and cation exchange capacity (CEC) in soils did not differ among the five treatments in 2001. However, Bray P concentration (data not shown) was significantly greater ($P = 0.03$) in islands that were burned and received the litter addition (19.6 ± 7.1 ppm) than in either

burned shrub islands (10.6 ± 0.4 ppm) or protected shrub islands (10.1 ± 0.4 ppm).

In 2001, extractable soil inorganic N was significantly different among treatments ~ 1 mo following the first fire. Fire had a significant main effect ($P < 0.01$) as did litter (absent, added, or present; $P = 0.03$). The effect of fire was to increase extractable N, and this was observed in both the burned (8.6 ± 0.5 $\mu\text{g/g}$) and burned + litter shrub islands (10.8 ± 1.3 $\mu\text{g/g}$; Fig. 2 inset), relative to 6.3 ± 0.3 $\mu\text{g/g}$ in protected islands. The presence of litter in burned shrub islands served to further enhance extractable N ($P = 0.03$), at least in the short term. Because cores were taken prior to N addition, N as a main effect was not evaluated in these analyses.

Extractable inorganic N from cores taken prior to the fire in 2002 demonstrated a different pattern, and likely reflected the net results of the previous growing season. Extractable N in protected islands (9.7 ± 0.5 $\mu\text{g/g}$) was significantly greater than in shrub islands that had been burned the previous year (6.8 ± 0.6 $\mu\text{g/g}$, $P < 0.01$), suggesting that N had been depleted as a consequence of resprouting and new shoot production (Fig. 2 inset). Litter addition islands were intermediate to and not significantly different from either treatment (7.9 ± 1.0 $\mu\text{g/g}$; Fig. 2 inset). The main effect of N addition from the previous year was not significant ($P = 0.07$).

Relative availability of inorganic soil N measured with resin bags during June–September 2002 was not significantly different among burned, protected, and burned + litter treatments, suggesting that the main

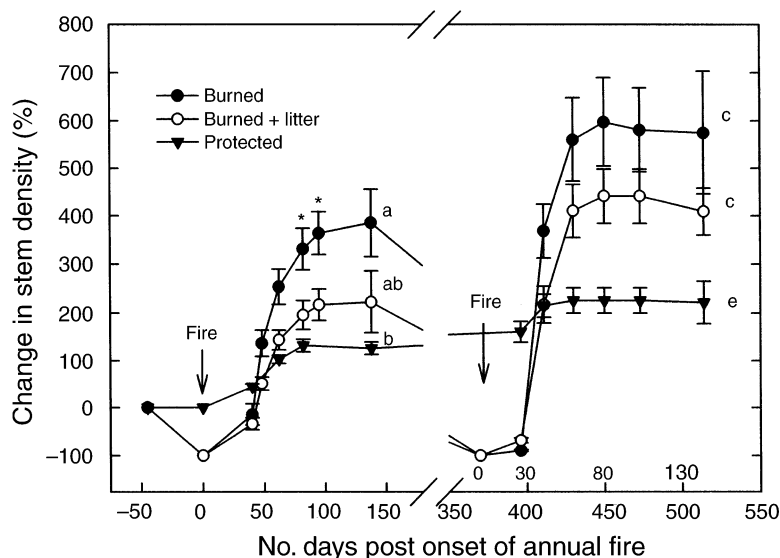


FIG. 3. Percentage change in stem density (mean \pm 1 SE) in 2001 and 2002 within *Cornus drummondii* islands in response to fire. Fire and litter were identified as significant main effects ($P < 0.05$), and therefore only the treatments of protected, burned, and burned + litter are shown. Individual fire events are indicated by arrows and occurred on 24 April 2001 and 29 April 2002, respectively. All values are treatment means for a given census period (± 4 days) and are calculated with respect to pre-experimental stem densities (measured on 15 March 2001). Means with different letters are significantly different ($P < 0.05$). Asterisks indicate census periods in which burned and burned + litter shrub islands differed significantly in their stem densities.

effects of fire and litter were not significant ($P = 0.57$, $P = 0.78$, respectively) in influencing N availability across the growing season. As expected, N addition was significant as a main effect ($P < 0.01$) with islands receiving supplemental N (either burned or protected) having the greatest available soil N (mean value = $3993.6 \pm 568.0 \mu\text{g N}$ per resin bag vs. $1144.0 \pm 147.8 \mu\text{g N}$ per resin bag; Fig. 2). The fire \times nitrogen interaction was not significant ($P = 0.46$).

We compared the community effect of N addition in shrub and grass communities in 2002, by comparing extractable soil N from cores taken in burned grassland and burned shrub islands. There was no significant effect of community type ($P = 0.16$) or N addition ($P = 0.06$).

Changes in C. drummondii stem density

Based on monitoring over 12000 individual *C. drummondii* stems, fire significantly increased stem density ($P = 0.02$), while N addition had no effect ($P = 0.83$). Similarly, the fire \times time interaction was significant ($P < 0.01$), while the N \times time interaction was not ($P = 0.97$). In 2001 and 2002, 100% aboveground mortality was observed in shrub islands exposed to fire (Fig. 3). Basal resprouting and new stem production followed this immediate response to fire. At 40 days post-fire (2001), burned islands had replaced stems lost in the fire with new stems, resulting in similar stem densities in both burned and protected islands ($P = 0.10$). By ~ 60 days post-fire, stem density in burned islands had increased by $253 \pm 36\%$ (Fig. 3) compared

to an increase of $95 \pm 9\%$ in the protected islands ($P < 0.01$). In the final census period in August, burned islands had increased by $\sim 385\%$, while protected islands had only increased by $\sim 125\%$ (Fig. 3).

Adding litter to burned shrub islands revealed that the post-fire energy environment influences the initiation of new stems following a fire ($P < 0.01$; Fig. 3). Stem density in burned + litter shrub islands lagged behind burned shrub islands at 50 days post-fire ($\sim 50\%$ vs. 135%). By 82 days post-fire, it was evident that reducing light and soil temperature in these islands constrained new stem production ($331 \pm 43\%$ in burned vs. $196 \pm 30\%$ in burned + litter; Fig. 3). While burned and burned + litter shrub islands did not differ significantly during the final census period, this can be attributed to substantial variability in these data.

In 2002, burned shrub islands had replaced all stems by 41 days post-fire, and stem density did not differ significantly from the end of the growing season in 2001 ($368 \pm 56\%$, $P > 0.05$). In protected islands, the small increase in new stems in 2002 was not significantly different ($P > 0.05$) from the end of the growing season in 2001 (Fig. 3). In contrast, stem densities in burned and burned + litter islands increased by $575 \pm 129\%$ and $409 \pm 49\%$, respectively, by the final census in 2002 with significantly increased density this second growing season (Fig. 3).

Primary productivity within shrub islands

While fire did not significantly impact total productivity within shrub islands ($P = 0.26$), it did affect the

TABLE 2. Shrub island annual aboveground net primary productivity (ANPP; all values are g/m²) according to growth form and the main effects of fire, nitrogen, and litter.

Main effect	Grass	Forb	<i>C. drummondii</i>	Total
Fire				
Burned	360.7 ^a ± 20.2	59.8 ^a ± 7.2	34.3 ^a ± 2.5	454.8 ^a ± 20.7
Protected	282.5 ^b ± 19.9	87.8 ^a ± 12.2	50.4 ^b ± 2.2	420.7 ^a ± 20.5
Nitrogen				
Control	341.1 ^a ± 23.4	76.1 ^a ± 10.9	45.4 ^a ± 3.6	462.5 ^a ± 18.0
Addition	300.0 ^a ± 17.8	73.0 ^a ± 9.9	39.2 ^a ± 5.2	412.2 ^a ± 23.2
Litter				
Absent	360.7 ^a ± 20.2	59.8 ^a ± 7.2	34.3 ^a ± 2.2	454.8 ^a ± 20.7
Added	304.3 ^{ab} ± 19.7	80.9 ^a ± 18.6	45.2 ^{ab} ± 4.7	430.4 ^a ± 25.2
Present	282.5 ^b ± 19.9	87.8 ^a ± 12.2	50.4 ^b ± 2.2	420.7 ^a ± 20.5

Notes: Mean values (± 1 SE) are from the 2001 and 2002 growing seasons. Means within a column and for a given main effect (fire, nitrogen addition, litter) followed by different letters were statistically different ($P < 0.05$).

relative abundance of different growth forms. Similarly, neither litter or N addition, nor their respective interactions influenced total shrub island ANPP (Tables 2 and 3). The main effect of fire was to increase graminoid production ($P < 0.01$) and reduce productivity of *C. drummondii* ($P = 0.02$). Thus, grass productivity was ~20% greater in burned compared to protected shrub islands (360.7 ± 20.2 g/m² vs. 282.5 ± 19.9 g/m²; Tables 2 and 3). Despite the increase in stem density, fire reduced *C. drummondii* ANPP in burned shrub islands by ~30% (34.3 ± 2.5 g/m² vs. 50.4 ± 2.2 g/m² in protected islands; Tables 2 and 3). Litter was significant as a main effect ($P = 0.01$), indicating the key role of fire in removing the litter layer. Burned + litter shrub islands remained intermediate to burned and protected islands in both grass and *C. drummondii* ANPP. This suggests an interaction between the fire event itself and the post-fire energy environment in influencing productivity of these different growth forms. The addition of N did not significantly affect ANPP of individual growth forms (Tables 2 and 3).

Allocation to stem vs. leaf tissue in *C. drummondii* differed between pre-existing and new stems (Tables 4 and 5). Pre-existing stems, contained exclusively with-

in protected islands, allocated a much greater percentage of their resources to leaf tissue (stem : leaf ratio = 1.1 ± 0.1) compared to new stems, which allocated a greater portion to stem tissue (3.7 ± 0.1 ; Tables 4 and 5). The main effect of litter, at least for burned islands, was significant, and suggests that stems produced via basal resprouting grow rapidly in order to emerge from the light constraints of the litter layer.

Productivity in grassland as compared to shrub islands

Patterns of aboveground ANPP differed between burned grassland plots and burned shrub islands (Tables 6 and 7). After fire, total productivity in the adjacent grassland (523.3 ± 22.8 g/m²) was greater than within shrub islands (449.5 ± 20.7 g/m², $P = 0.02$). This response was largely driven by graminoid productivity, which was reduced by nearly 30% in the shrub islands compared to the prairie (360.7 ± 20.2 g/m² vs. 494.3 ± 24.4 g/m²; Tables 6 and 7). Forbs accounted for a significantly greater proportion of total productivity within shrub islands (59.8 ± 7.2 g/m² compared to 29.0 ± 5.0 g/m² in the prairie). The main effect of N was significant ($P = 0.02$) with plots re-

TABLE 3. Results of ANOVA on shrub island annual aboveground net primary productivity according to growth form and the effects of fire, nitrogen, and litter.

Main effect	df	Grass		Forb		<i>C. drummondii</i>		Total	
		F	P	F	P	F	P	F	P
Fire									
Burned	1,64	7.54	0.007	3.61	0.060	7.67	0.010	1.26	0.263
Protected	1,64	7.54	0.007	3.61	0.060	7.67	0.010	1.26	0.263
Nitrogen									
Control	1,64	1.67	0.200	0.01	0.920	0.80	0.378	2.18	0.142
Addition	1,64	1.67	0.200	0.01	0.920	0.80	0.378	2.18	0.142
Litter									
Absent	2,81	4.33	0.015	1.73	0.180	4.35	0.020	0.82	0.444
Added	2,81	4.33	0.015	1.73	0.180	4.35	0.020	0.82	0.444
Present	2,81	4.33	0.015	1.73	0.180	4.35	0.020	0.82	0.444

TABLE 4. *C. drummondii* ANPP (g/m²) within protected, burned, and burned + litter shrub islands.

Main effect (island)	ANPP			Stem : leaf ratio	
	Pre-existing	New stems	Total	Pre-existing	New stems
Protected (litter present)	41.3 ± 4.6	9.0 ^a ± 1.3	50.3 ^a ± 5.2	1.1 ± 0.1	3.5 ^a ± 0.1
Burned (litter absent)	0	34.3 ^b ± 2.5	34.3 ^b ± 2.5	0	3.7 ^a ± 0.1
Burned + litter (litter added)	0	45.2 ^c ± 4.7	45.2 ^{ab} ± 4.7	0	4.2 ^b ± 0.2

Notes: ANPP is divided into pre-existing stems (stems that were present before the study began in April 2001) and new stems (stems produced in either 2001 or 2002). Stem : leaf ratio is the relative contribution to stem versus leaf tissue in islands of a given treatment for both pre-existing and new stems. Seasonal means (± 1 SE) for 2001 and 2002 within a column followed by different letters were statistically different ($P < 0.05$). The main effects of fire (protected vs. burned) and litter (all three treatments in table; litter present, litter absent, litter added) are emphasized because N did not significantly affect ANPP within any treatment group.

ceiving N having greater graminoid, but not forb, production.

DISCUSSION

The interaction of grass and woody plant species, and the balance between these growth forms, should be affected by factors that alter resource availability (Scholes and Archer 1997) or reduce/increase biomass of one growth form more than the other (Kochy and Wilson 2000). In this study, fire influenced *C*₄ grass–*C. drummondii* interactions through aboveground mortality (reductions in biomass), but also via its effect on light availability (and subsequently temperature) at the soil surface. Given that *C. drummondii* resprouted vigorously in response to fire, the negative effects of fire on this species appear to be constrained, over the short term, to resetting its growth trajectory rather than reducing its abundance within this grassland. Fire frequency, therefore, is closely linked with the competitive effects of shrubs as extended periods without fire favor an increase in shrub biomass and a shift from symmetrical to asymmetrical competition between these two growth forms (Kochy and Wilson 2000). This change in the nature of grass–shrub interactions suggests that understanding grass–woody plant interactions requires a temporal perspective that includes past

and present interactions of biotic and abiotic factors as they influence plant community structure.

The key role of light in driving productivity and shrub island dynamics is unique to mesic grasslands and derives from relatively high annual precipitation (and subsequently high herbaceous production and leaf area index [LAI]) compared to more arid grass-dominated systems (Scholes and Archer 1997) in which water tends to be a primary limiting resource. While fire suppression relieves shrubs from physical constraints associated with the direct effects of fire, it also allows for the accumulation of a detrital layer, which restricts the availability of light to grasses emerging from the soil surface (Fig. 1a). Thus, significant reductions in grass ANPP occur as a consequence of both fire exclusion and shrub establishment (Tables 2 and 6), a condition that is not reversed when fire is restored to this system. Grass ANPP in shrub islands that were protected from fire was reduced by nearly 50% compared to adjacent grassland that was burned in both years of this study (282.5 g/m² vs. 494.3 g/m²). Despite complete aboveground mortality of *C. drummondii* as a direct effect of fire, burned shrub islands were characterized by a 30% reduction in grass ANPP (360.7 g/m²), suggesting that, while grasses remain responsive to fire events, the process of grass exclusion has already

TABLE 5. Results of ANOVA on *C. drummondii* ANPP within protected, burned, and burned + litter shrub islands.

Main effect	df	ANPP				Stem : leaf ratio for new stems	
		New stems		Total		<i>F</i>	<i>P</i>
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Fire							
Burned	1,30	87.32	<0.001	7.67	0.010	1.02	0.320
Protected	1,30	87.32	<0.001	7.67	0.010	1.02	0.320
Litter							
Absent	2,39	52.48	<0.001	4.35	0.020	3.98	0.027
Added	2,39	52.48	<0.001	4.35	0.020	3.98	0.027
Present	2,39	52.48	<0.001	4.35	0.020	3.98	0.027

Notes: The main effects of fire (protected vs. burned) and litter (litter present, litter absent, litter added) are emphasized because N did not significantly affect ANPP within any treatment group. Values for pre-existing stems have been excluded from this table, as they occurred only in protected islands, and thus statistical tests for the main effects of fire and litter on this treatment group were not possible.

TABLE 6. Main effects of plant community type (grassland vs. shrub island) and nitrogen on ANPP (all values are g/m²) within burned plots.

Main effect	Grass	Forb	<i>C. drummondii</i>	Total
Community				
Grassland	494.3 ^a ± 24.4	29.0 ^a ± 5.0	0	523.3 ^a ± 22.8
Shrub island	360.7 ^b ± 20.2	59.8 ^b ± 7.2	34.3 ± 2.5	454.8 ^b ± 20.7
Nitrogen				
Control	390.0 ^a ± 19.4	47.7 ^a ± 7.0		437.6 ^a ± 19.1
Addition	465.1 ^b ± 27.0	41.2 ^a ± 5.9		506.3 ^b ± 24.2

Notes: Seasonal means (± 1 SE) for 2001 and 2002 are presented. ANPP is divided into respective growth forms; however, since *C. drummondii* was not present in grassland plots, no statistical tests could be performed on it individually. Statistical tests for total ANPP include all growth forms.

been initiated within these transition zones. Although fire remains effective in reducing both cover and ANPP of *C. drummondii* in the growing season immediately following fire, the six-fold increase in stem density represents an increase in photosynthetic potential (and thus ANPP) for the future. This process of shrub persistence/grass exclusion is likely to continue in subsequent fire-free years in which the litter layer remains intact and light availability at the soil surface is reduced. Given that *C. drummondii* invests considerable resources into stem vs. leaf tissue of post-fire resprouts (4:1 ratio; most stems exceed 30 cm in height by the end of the growing season), light limitations are generally not an important constraint to growth.

Ultimately, light appears to drive the increase in abundance of *C. drummondii* according to the following series of events: (1) The absence of fire provides “windows of opportunity” for shrub establishment. These periods are characterized by a constrained energy environment for grasses (as a consequence of standing litter), reduced grass ANPP, and shrub recruitment. (2) Periodic fire events result in the removal of the detrital layer and aboveground biomass of *C. drummondii*. The direct effects of fire combined with an enhanced energy environment temporarily stimulates grass ANPP (which lags behind adjacent areas of the grassland) and shrub resprouting/new stem production (resulting in a 400–600% increase in stem density despite a reduction in ANPP). (3) During subsequent fire-free years, light

limitations constrain grass productivity but do not limit shrubs, which display their leaves above the detrital layer. Increases in stem density that accompany fire events likely expedite the process of canopy closure and shift the source of light limitation from the accumulation of standing litter to the competitive effect of the shrub canopy. Thus, periodic fire, rather than complete fire suppression, appears to drive the increase in shrub abundance and subsequent grass displacement in this grassland (Heisler et al. 2003).

Interaction of Cornus drummondii and the direct effects of fire

Prior to European settlement, the estimated return interval of fire in mesic grasslands was ~3–5 years (Abrams 1985) with records implying high levels of grass ANPP and limited cover by woody vegetation (Bragg and Hulbert 1976, Risser et al. 1981, Axelrod 1985). Results from this study indicate that shrubs as few as 3–6 years post-establishment can not only survive repeated fires, but resprout vigorously to increase in stem density. Such a response to topkill associated with fire has been documented in species in other regions (Matlack et al. 1993, Hoffmann 1998, Cirne and Scarano 2001) and suggests that either fire frequency was greater or that other factors likely interacted with fire to constrain woody expansion in the past. Fire appears to be less effective in eliminating extant woody plants than it is in preventing the establishment of

TABLE 7. Results of ANOVA for the main effects of plant community type (grassland vs. shrub island) and nitrogen on ANPP within burned plots.

Main effect	df	Grass		Forb		Total	
		F	P	F	P	F	P
Community							
Grassland	1,60	18.54	<0.001	12.15	0.001	5.99	0.016
Shrub island	1,60	18.54	<0.001	12.15	0.001	5.99	0.016
Nitrogen							
Control	1,60	5.87	0.017	0.55	0.459	5.72	0.018
Addition	1,60	5.87	0.017	0.55	0.459	5.72	0.018

Notes: Because *C. drummondii* was not present in grassland plots no statistical tests could be performed on it individually. For this reason, no F or P values are reported.

woody plants (Wright et al. 1976, Roques et al. 2001, Heisler et al. 2003), and we suspect that mesic grasslands today reflect a legacy effect of fire suppression and landscape fragmentation that occurred during the last century (Knapp and Seastedt 1998, Hoch et al. 2002). A consequence of this combination of anthropogenic impacts may be increased seed rain from areas of the landscape that have been previously converted to shrubland or are currently being encroached upon by woody species. Changes in the structural complexity of grasslands that have accompanied the establishment of shrubs provide perching sites for birds and internal sources of seed, both of which may act to increase the abundance of *C. drummondii* and other shrub species (McDonnell and Stiles 1983). Given that *C. drummondii* produces bird-dispersed seeds (Willson and Whelan 1993), it is likely that increased seed availability has played an auxiliary role to fire suppression in driving shrub expansion in this system. An increase in vectors of seed dispersal has been suggested as a key driver in the encroachment of mesquite in Texas savannas (Archer et al. 1988, Archer 1989). As seedling establishment is facilitated by woody cover in many environments (Petranka and McPherson 1979, Archer et al. 1988, Callaway 1992), these shrub islands may serve as nuclei in the rapid conversion of grassland to shrubland.

Resource availability and shrub island community structure

Contrary to our hypothesis that N limitations constrain shrub abundance in this grassland, there was no evidence that the availability of N limited the resprouting response to fire or shrub ANPP. Despite an increase in productivity in the grasses, the lack of increased shrub production in response to N additions suggests that N availability in this system was currently adequate to support high levels of plant productivity. While availability of soil N from June through September was significantly greater in shrub islands in which N additions occurred (Fig. 2), leaf tissue N (percentage) was not significantly greater in *C. drummondii* leaves from fertilized islands relative to controls (data not shown). Conversely, leaf tissue N for *A. gerardii* was elevated in 2001 but not in 2002, suggesting grasses responded to fertilization. Shrub islands, in general, lagged considerably behind the prairie in ANPP, so one explanation is that the availability of N exceeded demand for *C. drummondii*. We also speculate that burned shrubs are capable of obtaining sufficient quantities of N through their well-developed root systems, which were not directly affected by fire. Shrubs are thought to be inferior competitors for soil N because of their relatively low root : shoot mass (Caldwell and Richards 1986, Wilson 1993, Jackson et al. 1996), however, top-kill following fire results in a high root : shoot mass for resprouting shrubs.

Shrub islands as transition zones between grassland and shrubland

Despite annual fire, transition zones within mesic grasslands, where graminoids and *C. drummondii* co-exist, remain significantly less productive (by ~15%) than areas within the prairie where shrubs have not yet established. This difference is accounted for by a reduction in graminoid ANPP (~130 g/m²), which is not compensated for by the slight increases in both forb and woody ANPP within these islands. While grasses still account for 80% of the ANPP in burned shrub islands and remain the dominant growth form in these transition areas, *C. drummondii* maintains a significant presence through its stem density. In larger, older (>7 years) shrub islands, aboveground ANPP of *C. drummondii* can greatly exceed undisturbed grassland (Lett and Knapp 2003), indicating that the reduction in ANPP in newly established shrub islands is transient.

Establishment of *C. drummondii* may therefore mark a critical stage in this grassland ecosystem in which new successional processes begin to drive the system. Fire, by increasing stem density, enables this species to potentially expand in cover during fire-free intervals. Further facilitating this process is the reduction in graminoid ANPP that occurs in the absence of fire as light availability at the soil surface is reduced. Jurena and Archer (2003) demonstrated that survival and growth of woody seedlings was enhanced in the absence of belowground competition from grasses. If ANPP is positively correlated with belowground biomass, reduced competition for resources and space may favor successful shrub establishment in fire-free years. While the presence of the detrital layer guarantees that a sufficient fuel load exists to carry fire in these grasslands, fire by itself will not reduce the abundance of *C. drummondii*. For this reason, temporary increases in grass ANPP that accompany fire (and subsequently reductions in shrub ANPP) may be short-lived, rather than representing a directional change towards a more grass-dominated system.

Within this transition stage, our data do not support the presence of "islands of fertility" (Garcia-Moya and McKell 1970) in this grassland; however, changes in N availability that accompany fire in *C. drummondii* islands suggest that the presence of shrubs impacts nutrient dynamics in this system. Approximately one month post-fire (2001), extractable inorganic soil N was significantly greater in burned than protected shrub islands. This increase in extractable inorganic N in response to fire differs from that observed in grass-dominated areas of this ecosystem that lack woody vegetation (Blair 1997). In a Mediterranean shrubland, Romanya et al. (2001) observed that the type of biomass present (grass vs. shrub) could similarly affect N availability. Soil cores taken prior to the second fire support the findings of Blair (1997) that extractable soil N in these grasslands will decline with successive annual

fires, presumably a result of increased plant demand and uptake.

In summary, two annual fires do not appear to be effective in reducing the abundance of the shrub *Cornus drummondii* in an ecosystem in which shrubs and grasses coexist. While the immediate effects of fire are to reduce productivity of this shrub and concurrently stimulate grass production, a dramatic post-fire increase in stem density allows this species to persist and take advantage of fire-free intervals in the future to potentially increase in cover. Additionally, the 30% reduction in grass ANPP in these transition zones suggests that persisting shrubs face reduced competition for space and/or resources. The age at which shrubs can successfully resprout represents a state in which shrub abundance is stable and is not reduced by fire. Contrary to our hypothesis that competition for soil N might constrain shrub growth and/or the ability of burned shrubs to persist following fire, the addition of N to both burned and protected shrub islands failed to affect stem density or productivity of *C. drummondii*. While grasses still account for nearly 80% of the ANPP in burned shrub islands, areas of the landscape in which *C. drummondii* has recently established remain less productive than adjacent areas of prairie. These data indicate that in as little as four years, *C. drummondii* can establish and become a persistent component of the plant community within mesic grasslands in central North America and that periodic fire acts to facilitate increases in shrub stem density and the displacement of C₄ grasses in this system.

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