

FIRE AND RESOURCE AVAILABILITY INFLUENCE CARBON AND WATER RELATIONS OF THE C₃ SHRUB ROUGHLEAF DOGWOOD IN A MESIC GRASSLAND

Jana L. Heisler¹ and Alan K. Knapp

Colorado State University, Department of Biology, Fort Collins, CO 80523, USA

J.M. Briggs

Arizona State University, School of Life Sciences, Tempe, AZ 85287, USA

ABSTRACT

A dramatic increase in cover by woody vegetation has been observed in grasslands worldwide, due to independent and interacting global changes. In the C₄-dominated mesic tallgrass prairie of North America, the most proximate factor driving this shift in growth-form dominance is fire exclusion. In 2001, we reintroduced annual fire into a C₄-dominated mesic grassland where it had been excluded for >10 y, and evaluated changes in stem density and ecophysiology of an increasingly abundant C₃ woody plant, roughleaf dogwood (*Cornus drummondii*). Our primary objective was to quantify the impacts of fire-induced aboveground mortality and resource constraints on the persistence of roughleaf dogwood in this ecosystem.

In both years of the study (2001–2002), burned shrubs suffered a complete loss of aboveground biomass due to top-kill from spring fire but persisted via resprouting. A considerable reduction in total growing-season precipitation in 2002, as compared to 2001, revealed that resprouts had lower mortality with reduced soil moisture, were less vulnerable to reductions in soil moisture availability, and maintained higher predawn xylem pressure potentials and rates of photosynthesis than did unburned shrubs. Additionally, enrichment of $\delta^{13}\text{C}_{\text{leaf}}$ in burned shrubs in 2002 was indicative of greater water use efficiency of resprouting stems. During the drought that occurred in the second growing season, mortality of stems within unburned shrub islands increased and was nearly 9 times more than in burned shrub islands. Thus, resprouting shrubs—with their characteristics of reduced leaf tissue, taller stems, and greater stem densities—are efficient in rapidly reoccupying post-fire environments, even with the added stress of below-average precipitation during the growing season. The results of this study suggest that within this grassland, reintroduction of fire will not eliminate roughleaf dogwood in the short term because of its ability to resprout vigorously and persist, even under stressful moisture conditions. Given that North American grasslands are important both economically and ecologically, fire management plans should therefore emphasize frequent fire to prevent shrub establishment.

keywords: C₃ shrubs, carbon isotope ratios, *Cornus drummondii*, fire, Kansas, mesic grasslands, roughleaf dogwood, woody plant encroachment.

Citation: Heisler, J.L., A.K. Knapp, and J.M. Briggs. 2007. Fire and resource availability influence carbon and water relations of the C₃ shrub roughleaf dogwood in a mesic grassland. Pages 86–93 in R.E. Masters and K.E.M. Galley (eds.). Proceedings of the 23rd Tall Timbers Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems. Tall Timbers Research Station, Tallahassee, Florida, USA.

INTRODUCTION

Worldwide, dramatic shifts have occurred in the relative abundances of grass versus woody vegetation, where a growth-form transition to woody dominance has been ascribed to both independent and interacting global changes (Schlesinger et al. 1990, Scholes and Archer 1997, Van Auken 2000, Archer et al. 2001). C₃ woody plant species are native to mesic grasslands of central North America but historically have been maintained as minor components of this ecosystem (Hulbert 1986) dominated by warm-season C₄ grasses that respond positively to frequent fire (Knapp and Seastedt 1998). When the time interval between subsequent fire events is extended (≥ 4 y), shrub cover and abundance may increase rapidly (Briggs et al. 2002, Heisler et al. 2003) while grass productivity declines (Knapp and Seastedt 1986). In extreme cases of fire suppression,

grasslands have become completely dominated by trees and shrubs (Hoch et al. 2002), demonstrating the integral nature of fire in influencing grass–shrub interactions.

The replacement of C₄ grasses by C₃ shrubs requires a transition phase during which small shrubs compete directly with grasses for resources. While many shrub species resprout in response to topkill from fire (Knapp 1986, Hodgkinson 1998, Hoffmann 1998, Brown and Archer 1999), new shoots produced following fire events confront a suite of biotic and abiotic conditions that may constrain their ability to gain carbon. Given their morphology, fire may negatively impact established shrubs 1) directly through loss of woody support tissues and destruction of aboveground meristems, or 2) indirectly via increased competition for soil resources (nutrients and water) from fire-stimulated grasses. Nitrogen (N) is the nutrient most likely to limit productivity in this system (Risser and Parton 1982); thus, competition between grasses and shrubs

¹ Corresponding author (jheisler@lamar.colostate.edu).

in mesic grasslands is considered strongest for this resource (Kochy and Wilson 2000). Additionally, annual fire reduces available N in the soil due to consistently high levels of plant production (Blair et al. 1998). Because fires in this region occur most often in spring (March–May), the combined effect of removing accumulated plant litter and low albedo of blackened soils contributes to rapid warming and subsequent drying of the soil (Knapp and Seastedt 1986). Such conditions may negatively impact plant–water relations, further constrain carbon gain, and reduce the ability of resprouting shrubs to recover and reoccupy sites. We expected that shrubs in this transition stage (young and recently established) would show clearest evidence of the adverse effects of fire and reduced resource availability, given a less developed root system and smaller carbohydrate stores.

From a management perspective, understanding the mechanisms that constrain or facilitate growth of shrubs during this transition stage is essential. We refer to this as a “transition stage” because, from a plant community perspective, young shrubs in this stage exist as 40–60 clumped stems (>0.8 m in height) within a matrix of C₄ grasses and C₃ forbs (circa 5–8 m² in area). While many shrub islands may be spread across the landscape, herbaceous vegetation biomass remains high and represents fuels effective at carrying fire. In contrast, advanced stages of shrub growth and expansion in this ecosystem exhibit limited herbaceous biomass (fuels) in and around shrub islands that fail to support fire. Thus, introduction of annual fire during the transition phase may reduce or eliminate shrubs. However, when the fire return interval is extended to >4 y, shrubs rapidly establish and increase in cover (Heisler et al. 2003).

While Lett and Knapp (2003) demonstrated that physical removal of large shrub islands promotes a return to a more grass-dominated ecosystem, the time required for complete restoration is uncertain and the process is labor intensive. Such a landscape in which C₄ grasses and mature C₃ shrubs are codominant has been characterized as an alternative stable state that is biotically maintained by shrub-induced low light levels that eliminate understory grasses (Briggs et al. 2005). This evidence suggests that research focusing on the initial years post-establishment, when shrubs coexist with grasses, may be the most effective time to intervene.

The primary goal of this research was to reintroduce annual fire into a landscape in which it had been excluded for >10 y to assess whether successive fire events would reduce or eliminate recently established shrubs in this ecosystem. We selected roughleaf dogwood (*Cornus drummondii*) as a focal species because it is one of the most abundant shrubs in this grassland and tends to form monospecific stands (or “islands”) as it matures in the absence of frequent fire. Given the difference in total growing-season precipitation between the two years of this study, we were able to quantify the response of both burned and unburned shrubs to “average” (2001) and stressful (2002) below-average moisture conditions.

We tested the following hypotheses: 1) leaf-level photosynthetic rates of resprouts, as compared to unburned shrubs, would be reduced; 2) water limitations in burned shrubs would be greater, with resprouts having lower predawn xylem pressure potentials (XPPs) and greater water use efficiency (WUE) than preexisting stems; and 3) N additions would result in elevated rates of photosynthesis in both burned and unburned shrubs as compared to their respective unfertilized counterparts, suggesting competition with grasses for plant-available N in the soil. To test these hypotheses, we utilized both instantaneous and integrative measurements of plant carbon and water relations (leaf-level photosynthetic rates, predawn XPPs, and carbon isotope ratios) and estimated stem densities of burned and unburned shrubs in a factorial experiment that included fire and N addition during the 2001–2002 growing seasons.

STUDY AREA

This study was conducted during the 2001 and 2002 growing seasons at the Konza Prairie Biological Station (KPBS), a 3,487-ha tract of unplowed native tallgrass prairie located approximately 15 km south of Manhattan, Kansas (39°05′N, 96°35′W). KPBS is located within the Flint Hills and exists as the largest continuous tract (1.6 million ha) of unplowed tallgrass prairie in North America. KPBS is characterized by a stream-dissected landscape and rolling hills eroded from chert-bearing limestone and shale of Permian age. Elevation ranges from 320 m in the lowlands to 440 m in uplands and soil (Oviatt 1998). Soil depth varies with topographic position, with shallow, rocky upland soils and considerably deeper lowland soils that may extend to >1 m. In 1981, KPBS was incorporated into the National Science Foundation’s Long-Term Ecological Research network. The location of this study was an experimental unit that has been designated as unburned and ungrazed since 1981; however, a wildfire occurred in 1991, resulting in a 10-y post-fire recovery.

The plant community of KPBS was dominated by C₄ perennial grasses, such as big bluestem (*Andropogon gerardii*) and Indiangrass (*Sorghastrum nutans*), but the presence of several hundred native forb species (non-graminoid herbs) greatly increased plant community diversity (Freeman 1998). C₃ shrubs such as roughleaf dogwood and smooth sumac (*Rhus glabra*) were native to this ecosystem and became increasingly abundant in areas in which fire occurred less frequently (Bragg and Hulbert 1976, Heisler et al. 2003).

The climate of KPBS was characterized by a high degree of interannual variability in precipitation. Mean annual precipitation (100-y average) was 835 mm, 75% of which fell during the growing season (April–September; approximately 630 mm). Precipitation during the 2001 growing season was 720 mm and above average; however, only 510 mm of rain fell during the 2002 growing season.

METHODS

Experimental Treatments

In the spring of 2001, 32 shrub islands of rough-leaf dogwood were selected from an experimental unit within KPBS (approximately 37 ha in area) in which fire had been excluded for >10 y. Because we were interested in the transition phase that precedes dominance by this species, we selected individuals that were 3–5 y old (as determined by counting annual growth rings) and currently nested within a matrix of native grasses and forbs. All islands were located in upland areas with similar topography and soil type. The experimental design was based on a factorial manipulation of fire and nitrogen and therefore included four treatments described below. All fire treatments are described in reference to the entire study site, which was burned on 24 April 2001 and 29 April 2002. Each shrub island was randomly assigned to one of the following four treatments ($n = 8$ shrub islands/treatment type):

1) *Unburned 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. Islands were then surrounded with large strips of sheet metal to protect them from potential scorch damage. In this way, we were able to burn the area immediately adjacent to each island without affecting the interior.

2) *Unburned + nitrogen islands*.—Shrub islands were protected as described above, and nitrogen (10 g N/m²), in the form of NH₄NO₃, was applied to each island on 15 June, 2001 and 2002. This amount has been shown to stimulate aboveground net primary productivity (ANPP) in annually burned tallgrass prairie (Seastedt et al. 1991, Knapp and Seastedt 1998).

3) *Burned islands*.—Shrub islands were burned along with surrounding vegetation when the entire watershed was burned.

4) *Burned + nitrogen islands*.—Shrub islands were burned as above treatment 3 and nitrogen was applied as above treatment 2.

Population Parameters

Prior to the first fire in April 2001, stem density was estimated within each shrub island by counting the total number of stems (stems/m²). In May 2001, all stems in unburned islands were tagged and given a unique identification number. In order to document additional stem production (“new stems”) or mortality from May to September, shrub islands were revisited at approximately 2-week intervals for a total of six tagging events. A similar protocol was followed in 2002; however, only stems produced in that year required a tag, as tags from the 2001 growing season remained attached to stems. In burned shrub islands, the first visit immediately following the April 2001 fire revealed that 100% aboveground mortality had occurred and no live stems were present to be tagged. Similar to the protocol followed in the unburned shrub islands, burned shrub islands were revisited at approx-

imately 2-week intervals throughout the growing season. During each visit, tags bearing unique identification numbers were applied to all resprouts and new stems. We characterized “resprouts” as shoots produced at the base of charred stems (basal resprouts) and “new stems” as shoots produced from underground rhizomes.

The height and basal diameter of individual stems were measured in a subset ($n = 5$ per treatment) of all shrub islands at the end of the growing season in both 2001 and 2002. Given the variability in stem heights within islands, especially those with multiple stem cohorts, we characterized stem height according to the tallest 10 preexisting stems (stems initiated prior to 2001) as well as the tallest new stems produced in a given year (2001 or 2002, respectively).

Field Measurements of Carbon and Water Relations

Gas exchange (net photosynthesis, A_{net}) of rough-leaf dogwood was measured between 1100 and 1300 hours CST under high light conditions with an LI-6200 portable photosynthesis system (Li-Cor, Lincoln, NE) equipped with a 0.25-L chamber. Measurements were taken at approximately 15-d intervals from June to August and were conducted on individual leaves within five randomly selected shrub islands among the eight replicates per treatment. For each shrub island, two single attached upper canopy leaves were measured and then collected to determine leaf area, using an LI-3100 leaf area meter (Li-Cor, Lincoln, NE). On the same days, water availability was estimated by measuring predawn XPP in the field on either resprouts from burned shrubs or preexisting stems in unburned shrubs between 0530 and 0630 hours CDT using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR).

Nitrogen and Isotopic ($\delta^{13}\text{C}$) Analyses of Leaf Tissue

Leaf tissue from roughleaf dogwood and big bluestem (the dominant C₄ grass on KPBS) was collected on 14 June (early season, pre-N addition) and 15 July (mid-season, post-N addition) in both 2001 and 2002 in order to quantify leaf N. Tissue was sampled from all shrub islands. Leaves were dried at 60°C for approximately 1 week, ground and analyzed for total N content (% dry weight) by combustion and gas chromatography on a Carlo Erba NA 1500 analyzer (Carlo Erba, Milan, Italy). It is important to note that the response of big bluestem was not a focus of this experiment; however, we were interested in determining whether N was a limiting resource for which grasses and shrubs were competing. Elevated levels of N in tissue of big bluestem and/or roughleaf dogwood in response to N additions would suggest N limitation and subsequently competition for this soil resource.

To quantify WUE, a 6.5- to 7.0-mg subsample of roughleaf dogwood leaf tissue was used for carbon isotope analyses. $\delta^{13}\text{C}_{\text{leaf}}$ was measured via combustion using a ThermoFinnigan Delta Plus mass spectrometer (ThermoFinnigan, Bremen, Germany) equipped with an elemental analyzer and continuous flow interface.

Table 1. Population characteristics of burned and unburned roughleaf dogwood shrub islands, Konza Prairie Biological Station, Kansas, in 2001–2002. Values presented are treatment means \pm 1 SE. Significant differences between treatments for a given year are indicated by different lowercase letters.

Characteristic	Pre-fire	2001		2002	
		Unburned	Burned	Unburned	Burned
Stem density (no./m ²)	4.16 \pm 0.31	9.14 \pm 0.78a	16.22 \pm 1.00b	13.85 \pm 1.35a	23.13 \pm 1.85b
Stem height (m)					
Preexisting		0.72 \pm 0.05a	NA ^a	0.77 \pm 0.05a	NA
Resprouts–new stems		0.32 \pm 0.02b	0.45 \pm 0.02c	0.33 \pm 0.03b	0.38 \pm 0.01b

^a In 2001–2002, 100% mortality occurred to preexisting stems in burned shrub islands; consequently, there are no data available (NA) for this stem class.

All carbon isotopes are expressed in delta notation (δ) and calculated according to a within-laboratory standard. Precision of measurements is 0.1–0.2‰.

Statistical Analyses

Data were analyzed using a 2-factor analysis of variance (ANOVA; Proc GLM) with fire (burned or unburned) and nitrogen (control or addition) as main effects (for a total of four treatments). To calculate seasonal means, measurements of net photosynthesis and XPP were analyzed collectively from all days within a growing season. For leaf tissue N analyses, a repeated-measures ANOVA, using initial conditions as covariates, was used to evaluate time and treatment effects as well as interactions. In order to improve normality, an arcsine square-root transformation was conducted on all proportional data. Values presented are means \pm 1 SE, with back-transformed means where appropriate. Duncan's Test was used to contrast group means after significant ANOVA results. All analyses were conducted in SAS 8.1 (SAS Institute, Cary, NC) and the level of significance for all tests was $P < 0.05$, unless otherwise indicated.

RESULTS

Population Parameters

Prior to the first fire in 2001, stem density in shrub islands was 4.16 ± 0.31 stems/m² and similar among all roughleaf dogwood shrub islands. By the end of the first growing season, the density of stems within burned islands increased approximately 4-fold (16.22 ± 1.00 stems/m²) and was significantly greater ($P < 0.05$) than in unburned islands, where a 2-fold increase was observed (9.14 ± 0.78 stems/m²; Table 1). Following fire in 2002, stem density in burned shrub islands further increased to 23.13 ± 1.85 stems/m², which again exceeded new stem production in unburned shrub islands where stem density had risen to 13.85 ± 1.35 stems/m² by the end of the growing season. In burned shrub islands, new stems allocated greater resources to stem rather than to leaf tissue (see Heisler et al. 2004 for details) and reached an average height of 0.45 ± 0.02 m by the end of the growing season in 2001 (Table 1). Compared to new stems in unburned islands, new stems in burned islands were significantly ($P = 0.01$) taller, but remained shorter in stature than preexisting stems (0.72 ± 0.05 m). In

2002, preexisting stems in unburned islands did not increase significantly in height across the growing season, likely due to their relatively large investment to leaf tissue as compared to new stems (Table 1). Height of new stems in burned and unburned shrub islands did not differ significantly in 2002 ($P = 0.38$; Table 1).

Carbon and Water Relations

Seasonal averages of net photosynthesis for resprouts and unburned stems in shrub islands differed dramatically during the two growing seasons of this study. In 2001, fire was significant as a main effect ($P < 0.01$) and reduced photosynthetic rates of resprouts within burned shrub islands (11.11 ± 0.57 $\mu\text{mol m}^{-2} \text{s}^{-1}$) relative to preexisting stems of unburned shrubs (12.79 ± 0.67 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Figure 1). The addition of N did not significantly affect either treatment group ($P = 0.14$). In 2002, fire was again significant as a main effect ($P < 0.01$) and resulted in higher average photosynthetic rates in resprouts of burned shrubs as compared to unburned shrubs (5.34 ± 0.54 $\mu\text{mol m}^{-2} \text{s}^{-1}$ versus 6.81 ± 0.56 $\mu\text{mol m}^{-2} \text{s}^{-1}$; Figure 1). Similar to results for 2001, no effect of N was observed ($P > 0.05$).

Seasonal averages of XPP demonstrated a consistent pattern in both 2001 and 2002, with resprouts having significantly higher values than unburned shrubs (Figure 1). Fire was significant as a main effect ($P < 0.05$), with resprouts of burned shrubs having higher XPP (-0.86 ± 0.08 MPa) than preexisting stems in unburned shrub islands (-1.21 ± 0.12 MPa). The addition of N did not influence XPP in either year of the study ($P > 0.05$).

N content was elevated in leaf tissue from resprouts in burned shrub islands, indicating that the main effect of fire was significant ($P < 0.05$). In June 2001, leaf tissue N was $2.84 \pm 0.06\%$ in burned shrub islands and was reduced across the duration of the growing season to $1.87 \pm 0.05\%$, as measured in July (Table 2). While a similar reduction was observed in unburned shrub islands, leaf tissue N was significantly less ($P < 0.05$) during both sampling periods ($2.19 \pm 0.09\%$ and $1.72 \pm 0.04\%$, respectively; Table 2). A similar trend was observed for roughleaf dogwood in 2002 and consistent in both years was no effect of N addition on leaf tissue N content ($P > 0.05$).

In order to determine whether the dominant grasses within shrub islands had responded to fertilization, we measured leaf tissue N in big bluestem. While the

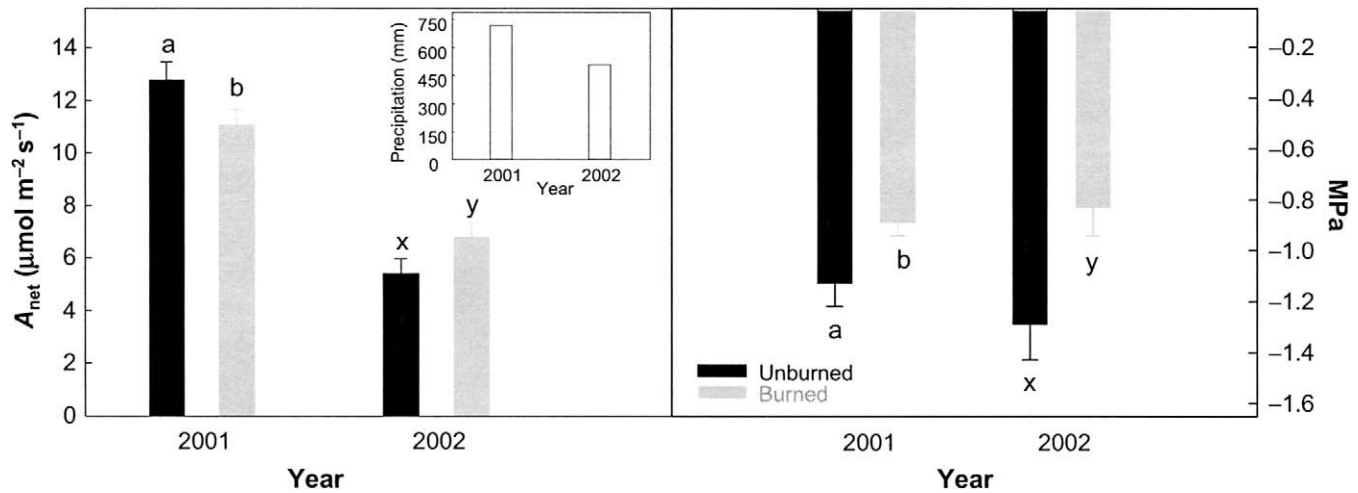


Fig. 1. Seasonal means for net photosynthetic rates (A_{net} ; left), predawn xylem pressure potentials (right), and precipitation (inset) during the 2001–2002 growing seasons for burned and unburned shrub islands of roughleaf dogwood, Konza Prairie Biological Station, Kansas. Vertical bars represent ± 1 SE. Within years and according to measurement type, significant differences ($P < 0.05$) are indicated by different letters.

main effect of fire did not significantly influence leaf tissue N content in big bluestem ($P > 0.05$), in 2001 the addition of N resulted in an increase in leaf tissue N content in fertilized islands as compared to controls ($1.44 \pm 0.06\%$ versus $1.26 \pm 0.03\%$; Table 2). There was no effect of fire or N observed in 2002.

In 2001, burned and unburned shrubs had similar carbon isotope ratios and thus WUE over the course of the growing season (Figure 2). In contrast, growing-season precipitation was reduced by approximately 200 mm in the 2002 growing season, and resprouts of burned shrubs were enriched in $\delta^{13}\text{C}$ ($-25.8 \pm 33\%$) as compared to unburned shrubs ($-26.90 \pm 0.25\%$). This enrichment of ^{13}C in the leaf tissue of burned shrubs indicates greater WUE (Figure 2).

Stem Mortality

An assessment of growing-season stem mortality revealed that in 2001, rates were significantly greater

within unburned shrub islands ($8.45 \pm 1.51\%$) than within burned shrub islands ($2.50 \pm 0.06\%$; $P < 0.01$; Figure 3). While similar rates were observed in 2002 for burned shrub islands ($2.72 \pm 0.67\%$), mortality rates in protected islands increased to $17.58 \pm 2.76\%$.

DISCUSSION

Grasslands are structured by the interaction of fire, climate variability, and herbivory (Cowles 1928), and tallgrass prairie is no exception. Historically, this combination of factors has mediated a tension zone between C_4 grass and C_3 woody species, resulting in an ecosystem that is dominated by herbaceous plants. During the last century, however, reductions in the intensity and frequency of fire have been associated with an increase in woody vegetation abundance. Roughleaf dogwood has proven to be a particularly aggressive species, as mature shrub islands completely exclude

Table 2. Leaf tissue nitrogen (N; %) for roughleaf dogwood and big bluestem within shrub islands, Konza Prairie Biological Station, Kansas, in 2001 and 2002. Samples were taken in June (pre-N addition) and July (approximately 1 mo post-N addition). Values shown are means ± 1 SE. Lowercase letters indicate significant differences ($P < 0.05$) for main effects both within and between time periods.

Year	Species	Main effect	Treatment	Month	
				Jun	Jul
2001	Roughleaf dogwood	Fire	Burned	$2.84 \pm 0.06\text{a}$	$1.87 \pm 0.05\text{c}$
		Unburned	$2.19 \pm 0.09\text{b}$	$1.72 \pm 0.04\text{d}$	
	Nitrogen	Control	$2.57 \pm 0.02\text{a}$	$1.82 \pm 0.05\text{b}$	
		Addition	$2.48 \pm 0.11\text{a}$	$1.78 \pm 0.06\text{b}$	
Big bluestem	Fire	Burned	$1.57 \pm 0.04\text{a}$	$1.37 \pm 0.06\text{b}$	
		Unburned	$1.55 \pm 0.05\text{a}$	$1.33 \pm 0.03\text{b}$	
	Nitrogen	Control	$1.53 \pm 0.05\text{a}$	$1.26 \pm 0.03\text{b}$	
		Addition	$1.59 \pm 0.04\text{a}$	$1.44 \pm 0.06\text{c}$	
2002	Roughleaf dogwood	Fire	Burned	$2.60 \pm 0.06\text{a}$	$1.60 \pm 0.04\text{c}$
			Unburned	$2.31 \pm 0.05\text{b}$	$1.47 \pm 0.03\text{d}$
		Nitrogen	Control	$2.50 \pm 0.06\text{a}$	$1.51 \pm 0.04\text{b}$
			Addition	$2.38 \pm 0.06\text{a}$	$1.55 \pm 0.03\text{b}$
	Big bluestem	Fire	Burned	$2.18 \pm 0.04\text{a}$	$1.09 \pm 0.03\text{b}$
			Unburned	$2.04 \pm 0.05\text{a}$	$1.14 \pm 0.03\text{b}$
		Nitrogen	Control	$2.11 \pm 0.04\text{a}$	$1.13 \pm 0.03\text{b}$
			Addition	$2.09 \pm 0.06\text{a}$	$1.11 \pm 0.03\text{b}$

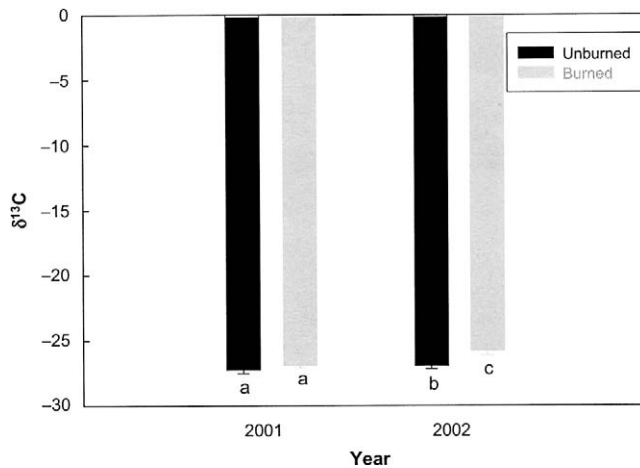


Fig. 2. Carbon isotope signatures for burned and unburned shrubs (roughleaf dogwood) from the 2001 and 2002 growing seasons, Konza Prairie Biological Station, Kansas. $\delta^{13}\text{C}$ values reflect carbon isotope signatures from leaf tissue collected on 15 July, 2001 and 2002. Treatment means ± 1 SE are reported. Means with different letters are significantly different at $P < 0.05$.

understory vegetation by reducing light levels (Lett and Knapp 2003). Mature shrub islands are characterized by >400 dense stems (circa 35 m^2 area), which are in many cases several meters tall, and fire is no longer an effective management tool for reducing shrub cover. Our objective, therefore, was to reintroduce fire into a transitional landscape and document the influence of fire and resource availability on stem densities, leaf-level gas exchange, and water relations.

During this 2-y study, recurrent fire, and its interaction with moisture availability, had significant effects on population characteristics and the ecophysiology of roughleaf dogwood. A high degree of inter-annual variability in precipitation is characteristic of tallgrass prairie (Knapp and Seastedt 1998). In the time frame of this study, considerable differences in growing-season precipitation from 2001 (above average; 720 mm) to 2002 (below average; 510 mm) allowed us to evaluate the response of unburned shrub islands to changes in moisture availability as well as the interaction of fire and short-term drought in resprouts of burned shrub islands. As hypothesized, photosynthetic rates of resprouts from burned shrub islands were lower, on average, than those from unburned shrubs; however, this response was constrained to the 2001 growing season, which was characterized by greater moisture availability. In 2002, improved water relations and greater WUE of resprouts enabled them to better withstand drought conditions, and contributed to greater carbon gain over the long term, via higher rates of photosynthesis. Soil moisture is generally lower in burned as compared to unburned prairie (Hulbert 1969, Rice and Parenti 1978), primarily due to the absence of the litter layer. In unburned shrub islands, the litter layer reduces the amount of light incident to the soil surface and subsequently evaporative demand. This suggests that resprouts in burned shrub islands potentially confront greater moisture constraints. However, morphological characteristics of resprouts versus

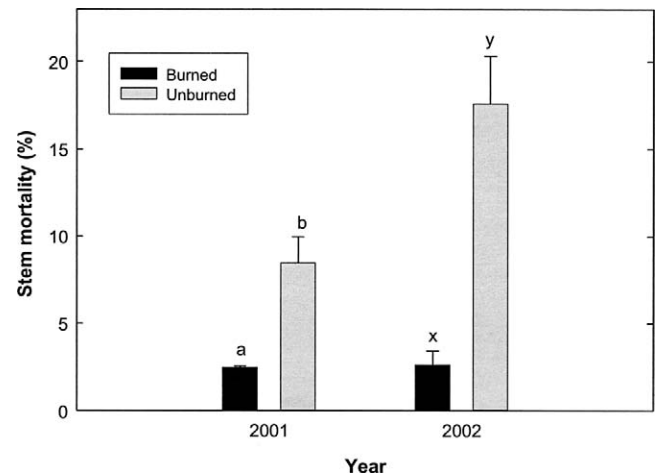


Fig. 3. Mortality (%) of stems in burned and unburned shrub islands of roughleaf dogwood during the 2001 and 2002 growing seasons, Konza Prairie Biological Station, Kansas. Values represent treatment means ± 1 SE and quantify observed stem mortality post-fire and throughout a growing season. Within each year, means with different letters are significantly different at $P < 0.05$.

preexisting stems appear to be more important than soil moisture conditions in determining plant-water relations. While fire results in 100% aboveground mortality, the extensive preexisting root systems of resprouting vegetation together with reduced shoot mass results in greater water availability to growing resprouts (Oechel and Hastings 1983). Furthermore, allocation of biomass to stem tissue rather than to leaf tissue (Heisler et al. 2004) likely reduces whole-plant transpiration, resulting in reduced water stress. Resprouts were less sensitive to significant reductions in growing-season precipitation, as compared to unburned shrubs, which experienced a higher rate of stem mortality (approximately 20%) in 2002. Clearly, short-term drought did not intensify the effects of fire on roughleaf dogwood, in terms of the ability of this species to persist in this grassland.

Following fire, the response of this shrub is to resprout and initiate a new cohort of rapidly growing stems. By the end of the first growing season, resprouts had reached an average height of 0.45 ± 0.02 m and were significantly greater in stature than new stems in unburned islands (0.32 ± 0.02 m). Additionally, stem density had increased nearly 4-fold, with rates of mortality of new stems being approximately 3%. While total ANPP in burned shrub islands is reduced relative to islands that remain unburned (Heisler et al. 2004), persistence of roughleaf dogwood is facilitated by the increase in stem density and height of post-fire resprouts, which enables them to display their leaves in abundant light.

Contrary to our hypothesis that the addition of nitrogen would result in elevated rates of photosynthesis, we could detect no evidence of N limitation in this study. Prior to the initiation of this experiment, fire had been excluded from this site since 1991. Blair (1997) observed that in the absence of fire, a reduction in plant productivity and uptake of soil N results in

the accumulation of this resource. Thus, when N additions accompany fire in long-unburned areas, the production response, if any, is limited. This explains the absence of a response to N addition in 2001. In 2002, a reduction in growing-season precipitation may have resulted in water being a much greater limiting resource rather than soil N. Although resprouts had greater tissue N levels, it was not associated with an increase in photosynthetic rate, suggesting that N was not limiting photosynthesis in roughleaf dogwood.

In summary, short-term reductions in growing-season precipitation, and therefore moisture availability, had a strong impact on seasonal photosynthetic rates and carbon gain of roughleaf dogwood. During a year of above-average precipitation, unburned shrubs had higher rates of photosynthesis as compared to resprouts of burned vegetation. Conversely, when growing-season precipitation was reduced to below average, unburned shrubs experienced greater moisture stress and a reduction in photosynthetic rate as well as elevated rates of stem mortality. While resprouts in burned shrub islands were also impacted by drought, they were able to sustain higher rates of photosynthesis and experienced no increase in stem mortality during the growing season. During dry periods, a well-developed root system and reduced leaf area ameliorate conditions of moisture limitation in resprouts, thereby facilitating persistence of roughleaf dogwood. We present these data with the caveat that responses of roughleaf dogwood are limited to the early stages of restoring annual fire to this ecosystem. We could find no other published studies describing responses of shrubs to an annual fire regime in the long term. While annually burned mesic grasslands are generally devoid of woody vegetation, few data exist to suggest that this is due to the gradual elimination of shrubs. Rather, annual fire instead appears to have prevented shrubs from establishing in C₄-dominated grasslands. Indeed, further studies are needed of how the functional responses of this shrub are affected by repeated cycles of fire and drought, particularly given that climate models predict extreme weather in the future.

MANAGEMENT IMPLICATIONS

The expansion of woody vegetation in grass-dominated ecosystems is a global phenomenon. Fire suppression is the most cited cause of shrub expansion in mesic grasslands, and the long-term effect of eliminating fire from this ecosystem can be the complete conversion of grassland to shrubland. While long-term data suggest that fire remains effective in preventing shrub establishment, it is currently unclear as to whether management strategies that prescribe frequent fire will be effective in reducing or eliminating shrubs from mesic grassland. Our study results suggest that in the short term, fire does not reduce stem densities within shrub islands and that resprouting shrubs possess morphological attributes that enable them to confront moisture constraints that are typical of grasslands. It is our goal to continue monitoring the re-

sponse of roughleaf dogwood to annual fire in order to determine the long-term efficacy of restoring frequent fire to shrub-invaded mesic grasslands. Given the existing data, management plans should emphasize frequent (<4-y fire return intervals) fire in an effort to prevent shrub establishment.

ACKNOWLEDGMENTS

We thank Amy Seery, Barry Broeckleman, and Mark Lundgren for field assistance and sample processing. For their assistance and cooperation in executing the experimental fire treatment regime of this research study, we also thank the Konza Prairie Biological Station. The comments and suggestions of two anonymous reviewers greatly improved this manuscript. This study was funded by National Science Foundation grant 0075350.

LITERATURE CITED

- Archer, S., T.W. Boutton, and K.A. Hibbard. 2001. Trees in grasslands: biogeochemical consequences of woody plant expansion. Pages 115–130 in E.-D. Schulze, M. Heimann, S. Harrison, E. Holland, J. Lloyd, I.C. Prentice, and D. Schimel (eds.). *Global biogeochemical cycles in the climate systems*. Academic Press, San Diego, CA.
- Blair, J.M. 1997. Fire, N availability, and plant responses in grasslands: a test of the transient maxima hypothesis. *Ecology* 78:2359–2368.
- Blair, J.M., T.R. Seastedt, C.W. Rice, and R.A. Ramundo. 1998. Terrestrial nutrient cycling in tallgrass prairie. Pages 222–243 in A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins (eds.). *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York.
- Bragg, T.B., and L.C. Hulbert. 1976. Woody plant invasions of unburned Kansas bluestem prairie. *Journal of Range Management* 29:19–23.
- Briggs, J.M., A.K. Knapp, J.M. Blair, J.L. Heisler, G.A. Hoch, M.S. Lett, and K. McCarron. 2005. An ecosystem in transition: woody plant expansion into mesic grassland. *BioScience* 55:243–254.
- Briggs, J.M., A.K. Knapp, and B.L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a 15-year study of fire and fire-grazing interactions. *American Midland Naturalist* 147: 287–294.
- Brown, J.R., and S. Archer. 1999. Shrub invasion of grassland: recruitment is continuous and not regulated by herbaceous biomass or density. *Ecology* 80:2385–2396.
- Cowles, H.C. 1928. Persistence of prairies. *Ecology* 9:380–382.
- Freeman, C.C. 1998. The flora of Konza Prairie: a historical review and contemporary patterns. Pages 69–80 in A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins (eds.). *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York.
- Heisler, J.L., J.M. Briggs, and A.K. Knapp. 2003. Long-term patterns of shrub expansion in a C₄-dominated grassland: fire frequency and the dynamics of shrub cover and abundance. *American Journal of Botany* 90:423–428.
- Heisler, J.L., J.M. Briggs, A.K. Knapp, J.M. Blair, and A. Seery. 2004. Direct and indirect effects of fire on shrub density and aboveground productivity in a mesic grassland. *Ecology* 85:2245–2257.
- Hoch, G.A., J.M. Briggs, and L.C. Johnson. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5:578–586.

- Hodgkinson, K.C. 1998. Sprouting success of shrubs after fire: height-dependent relationships for different strategies. *Oecologia* 115:64–72.
- Hoffmann, W.A. 1998. Post-burn reproduction of woody plants in a Neotropical savanna: the relative importance of sexual and vegetative reproduction. *Journal of Applied Ecology* 35:422–433.
- Hulbert, L.C. 1969. Fire and litter effects in undisturbed blue-stem prairie in Kansas. *Ecology* 50:874–877.
- Hulbert, L.C. 1986. Fire effects on tallgrass prairie. Pages 138–142 in G.K. Clambey and R.H. Pemble (eds.). *Proceedings of the Ninth North American Prairie Conference*, 29 Jul–1 Aug 1984, Moorhead, MN. North Dakota State University, Fargo.
- Knapp, A.K. 1986. Postfire water relations, production, and biomass allocation in the shrub, *Rhus glabra*, in tallgrass prairie. *Botanical Gazette* 147:90–97.
- Knapp, A.K., and T.R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. *BioScience* 36:662–668.
- Knapp, A.K., and T.R. Seastedt. 1998. Introduction: grasslands, Konza Prairie, and long-term ecological research. Pages 3–18 in A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins (eds.). *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York.
- Kochy, M., and S.D. Wilson. 2000. Competitive effects of shrubs and grasses in prairie. *Oikos* 91:385–395.
- Lett, M., and A.K. Knapp. 2003. Consequences of shrub expansion in mesic grassland: resource alterations and graminoid responses. *Journal of Vegetation Science* 14:487–496.
- Oechel, W.C., and S.J. Hastings. 1983. The effects of periodic fire on photosynthesis of chaparral resprouts. Pages 274–285 in F.J. Kruger, D.T. Mitchell, and J.U.M. Jarvis (eds.). *Structure and function of Mediterranean-type ecosystems*. Springer-Verlag, New York.
- Oviatt, C.G. 1998. Geomorphology of Konza Prairie. Pages 35–47 in A.K. Knapp, J.M. Briggs, D.C. Hartnett, and S.L. Collins (eds.). *Grassland dynamics: long-term ecological research in tallgrass prairie*. Oxford University Press, New York.
- Rice, E.L., and R.L. Parenti. 1978. Causes of decreases in productivity in undisturbed tallgrass prairie. *American Journal of Botany* 65:1091–1097.
- Risser, P., and W.J. Parton. 1982. Ecological analysis of a tallgrass prairie: nitrogen cycle. *Ecology* 63:1342–1351.
- Schlesinger, W.H., J.F. Reynolds, G.L. Cunningham, L.R. Huenneke, W.H. Jarrell, R.A. Virginia, and W.G. Whitford. 1990. Biological feedbacks in global desertification. *Science* 247:1043–1048.
- Scholes, R.J., and S.R. Archer. 1997. Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517–544.
- Seastedt, T.R., J.M. Briggs, and D.J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. *Oecologia* 87:72–79.
- Van Auken, O.W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197–215.