Consequences of shrub expansion in mesic grassland: Resource alterations and graminoid responses

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Abstract. In the mesic grasslands of the central United States, the shrub *Cornus drummondi* has undergone widespread expansion in the absence of recurrent fire. We quantified alterations in light, water and N caused by *C. drummondi* expansion in tall-grass prairie and assessed the hypothesis that these alterations are consistent with models of resource enrichment by woody plants. Responses in graminoid species, particularly the dominant C₄ grass *Andropogon gerardii*, were concurrently evaluated. We also removed established shrub islands to quantify their legacy effect on resource availability and assess the capability of this grassland to recover in sites formerly dominated by woody plants. The primary effect of shrub expansion on resource availability was a 87% reduction in light available to the herbaceous understory. This reduced C uptake and N use efficiency in *A. gerardii* and lowered graminoid cover and ANPP at the grass-shrub ecotone relative to undisturbed grassland. Shrub removal created a pulse in light and N availability, eliciting high C gain in *A. gerardii* in the first year after removal. By year two, light and N availability within shrub removal areas returned to levels typical of grassland, as had graminoid cover and ANPP were similar to those in open grassland. Recovery within central areas of shrub removal sites lagged behind that at the former grass-shrub ecotone. These results indicate that the apparent alternative stable state of *C. drummondi* dominance in tall-grass prairie is biotically maintained and driven by reductions in light, rather than resource enrichment. Within areas of shrub removal, the legacy effect of *C. drummondi* dominance is manifest primarily through the loss of rhizomes of the dominant grasses, rather than any long-term changes in resource availability. *C. drummondi* removal facilitates grassland recovery, but the effort required to initiate this transition is a significant cost of woody plant expansion in mesic grasslands. Prevention of woody plant expansion in remnant tall-grass prairies is, therefore, a preferred management option.

Keywords: *Cornus drummondi*; Grassland recovery; Land cover change; Tall-grass prairie; Woody plant expansion.

Nomenclature: Anon. (1986)

Abbreviations: Ψ = Leaf water potential; ANPP = Above-ground net primary production; N_leaf = Leaf nitrogen concentration; NUE = Nitrogen use efficiency; PFD = Photon flux density; SLM = Specific leaf mass; WUE = Water use efficiency.

Introduction

Land cover change is one of the most widespread global changes occurring in ecosystems today (Vitousek 1994). When this change involves replacement of one dominant growth form by another, impacts on ecosystem structure and function are likely to be particularly large (Hooper & Vitousek 1997). The worldwide increase in density and cover of woody vegetation in grasslands and savannas is one such case, with changes in climate, CO₂ concentration, livestock grazing and fire regimes implicated as causal factors (Archer 1989; Bahre & Shelton 1993; Archer 1994; Soulé & Knapp 1999; Van Auken 2000).

In mesic grasslands (tall-grass prairies) of the central United States, the displacement of grassland by woody vegetation in the last 100 years is primarily related to a reduction in fire frequency (Bragg & Hulbert 1976; Abrams 1986; Briggs & Gibson 1992; Knight et al. 1994; Hoch & Briggs 1999). Historically, frequent fire maintained a landscape almost devoid of woody vegetation (Wells 1970). Exclusion of woody vegetation was achieved through negative effects of fire on the above-ground meristems of woody species and perhaps through indirect effects on resource availability. With fire suppression, however, litter accumulates and graminoid cover and production decrease (Knapp & Seastedt 1986). Concurrently, woody plants expand in cover, especially C₃ shrubs, which are only a minor component of frequently burned grasslands (Gibson & Hulbert 1987; Briggs & Gibson 1992; Briggs et al. 2002b). Grassland fragmentation and loss of biodiversity that result from woody plant expansion are significant threats to tall-grass prairie conservation because only an estimated 4% of the historic extent of this grassland currently remains (Samson & Knopf 1994; Sala et al. 2000).

The transition from a grass to a woody plant-dominated system has important consequences at both the community and ecosystem levels. As woody species increase in cover and abundance, total above-ground biomass increases (Harcombe et al. 1993; Norris et al. 2001;
Peltzer & Köchy 2001); decomposition rates, nutrient availability and soil C dynamics are altered (Schlesinger et al. 1990; Wilson 1993; Gill & Burke 1999; Seastedt & Adams 2001; Jackson et al. 2002); herbaceous cover and production are reduced, which often results in significant decreases in grassland species richness and diversity (Hobbs & Mooney 1986; Briggs et al. 2002a). Moreover, established woody plants can facilitate growth of conspecifics and other woody species, creating positive feedback that may render woody plant encroachment irreversible (Archer et al. 1988; Callaway & Davis 1998; Barnes & Archer 1999; Rouset & Lepart 1999).

The clonal shrub *Cornus drummondii* (rough-leaved dogwood) is a primary contributor to woody plant expansion in tall-grass prairies of the central USA. *C. drummondii* comprises less than 0.01% of the total area of annually burned sites (Briggs unpubl.). With fire suppression, however, it forms dense thickets through production of stems from rhizomes, creating discrete ‘islands’ of woody vegetation within the grassland matrix and eliminating the dominant graminoid vegetation from its understory in as few as seven years. In landscapes where fire has been excluded, *C. drummondii* can exceed 11% of the total area (Briggs unpubl.), and individual shrub islands can reach 15-20 m in diameter and may coalesce to form a closed canopy shrubland.

Given that shrub expansion in tall-grass prairie is a consequence of fire suppression, it may seem intuitive that the return of fire would reduce woody plant abundance and allow for graminoid recovery. However, after shrubs are established, frequent fire may not be sufficient to initiate such a transition (Archer 1989), primarily because *C. drummondii* resprouts rapidly following fire. Indeed, Briggs et al. (2002b) reported that the area occupied by *C. drummondii* increased at an intermediate fire frequency (once every four years). Thus, fire does not initiate grassland recovery once there is substantial shrub cover. This suggests that an alternative stable state has been reached (Archer 1989; Laycock 1991) and that more labour intensive means of shrub removal are required to promote grassland recovery.

Three key resources control above-ground net primary production (ANPP) in tall-grass prairie: light, water and nitrogen. Alterations in these resources via climate, fire and grazing drive most community and ecosystem dynamics (Seastedt & Knapp 1993; Blair 1997; Knapp et al. 1998). With loss of the direct negative effects of fire on woody species, increased shrub abundance may further alter availability of these resources (Petranka & McPherson 1979; Belsky et al. 1989; Köchy & Wilson 2000; Archer et al. 2001; Forseth et al. 2001; Peltzer & Köchy 2001), reinforcing shrub dominance. The goals of our research were to quantify alterations in light, water and nitrogen caused by *C. drummondii* expansion in tall-grass prairie to (1) determine if models of resource enrichment by woody plants (Schlesinger et al. 1990) are appropriate for this grassland and (2) assess the hypothesis that these resource alterations are consistent with the displacement of grasses, particularly the dominant C₄ grass *Andropogon gerardii* (big bluestem). Given that fire is ineffective at removing established shrubs, we mechanically eliminated established *C. drummondii* islands from the grassland. This allowed us to quantify the short-term legacy effect of this shrub on resource availability, as well as the capability of this grassland ecosystem to recover from shrub dominance. Although the legacy impact and recovery from woody plant dominance may encompass many years (Seastedt & Adams 2001), we focus on the first two growing seasons of recovery to capture initial ecosystem responses. We hypothesized that shrub dominance would reduce light availability and increase both water and N available to the grasses, while shrub removal would increase availability of all three resources relative to that in intact grassland.

**Methods and Material**

**Site description**

This research was conducted during the 2000 and 2001 growing seasons at Konza Prairie Biological Station, a 3487-ha native tall-grass prairie in the Flint Hills of NE Kansas, USA (39°05' N, 96°35' W). Konza Prairie is characterized by highly dissected terrain, with steep-sided lowlands and flat, upland ridges. Soil depth varies greatly with topographic position, with shallow, rocky upland soils and lowland soils that may extend to a depth of greater than 1 m. Konza Prairie has a typical midwestern continental climate with warm, wet summers and cold, dry winters. Mean annual air temperature is 12.8 °C, with a mean monthly low of −3°C in January and a mean monthly high of 29.3°C in July. Mean annual precipitation is 835 mm, with 75% falling during the April to September growing season. The flora of Konza Prairie is dominated by the C₄ (warm-season) grasses *Andropogon gerardii*, *A. scoparius*, *Sorghastrum nutans* and *Panicum virgatum*. Forbs (primarily C₃ dicots) are much less abundant, but account for the majority of plant species diversity on Konza Prairie. In infrequently burned areas, C₃ shrubs, primarily *C. drummondii* and *Rhus glabra*, occur as islands of woody vegetation along ridges and slopes within the grassland matrix.
In spring of 2000, we selected 28 shrub islands composed primarily of C. drummondii. Half of these islands had been burned in the spring (a common management practice in the region) at 4-yr intervals since 1992 (including April of 2000); the rest had been burned only twice since 1980 (1980 and 1991) and were considered unburned, as the effects of fire on resource availability are no longer apparent after one year (Seastedt & Knapp 1993). Shrub islands were selected based on their similarities in size, topographic position, isolation from other shrub islands and sparse understory cover. Seven of the 14 burned and unburned C. drummondii islands were then randomly selected for removal, while the remaining shrub islands were left undisturbed. Finally, 14 shrub-free grassland plots similar in size to the shrub islands and shrub removal plots were randomly located within open grassland for comparative purposes. Seven of these were burned in 2000 and seven were left unburned. The same plots were used in 2001, but no plots of any treatment were burned in that year. Thus, six treatments were assessed in 2000: burned and unburned grassland, burned and unburned shrub islands, and burned and unburned shrub removal plots (n = 7 plots per treatment), and only unburned treatments were available in 2001 (n = 14 plots per treatment). The area of the shrub islands and shrub removal plots did not differ significantly, at ca. 37 m². Stem density of C. drummondii (measured in four 0.1 m² quadrats in both the grass-shrub ecotone and the center of each island) over 2000 and 2001 was greater in the historically frequently burned shrub islands (43 stems.m⁻²) than in the unburned shrub islands (22 stems.m⁻²; P = 0.0014), probably due to the fact that this species vigorously resprouts following fire.

Shrub removal was accomplished by cutting all C. drummondii stems at their base and then applying the herbicide 'Crossbow' (Dow AgroSciences LLC, Indianapolis, USA; active ingredients: triclopyr and 2,4-dichlorophenoxyacetic acid) to the cut surface of each stem, with care taken to avoid contamination of adjacent plants and the soil. All stems were removed in each island, including stems in the grass-shrub ecotone and edge of each island. Other woody species, primarily R. glabra and Symphoricarpos orbicularus, growing in the understory of the C. drummondii canopy were also removed. Removal occurred between 2 April and 15 May of 2000. In the second year of study, only minor retreatment of stems was necessary to maintain these plots.

Patterns of water, light, and nitrogen availability were assessed to determine the mechanism by which shrub expansion and removal might affect suppression and recovery, respectively, of graminoid vegetation. All measures of resource availability (except inorganic N availability, see below) within the shrub island and shrub removal communities were made in the ecotone of each plot, defined in this context specifically as that area within the plot where grasses and C. drummondii co-existed (formerly so in the shrub removal plots). Water availability was estimated by measuring leaf water potential (Ψ) in A. gerardii. Measurements were made at ca. two to three week intervals throughout May to September of 2000 and 2001 on a subset of randomly chosen plots within each treatment (n = 4 plots per treatment). Predawn and midday Ψ were measured on four fully expanded leaves per plot at ca. 0530 hr and 1230 hr CDT, respectively, using a Scholander type pressure chamber (PMS Instrument Co., Corvallis, OR, USA). Light availability (measured as photon flux density, PFD) was measured between 1000 and 1500 hr CDT at two locations in each treatment within a subset of plots (n = 4 plots per treatment) on three dates each in 2000 and 2001. PFD was measured ca. 15 cm above the soil surface (above the litter layer in unburned sites) with a 1.0 m ceptometer (Decagon Devices Inc., Pullman, WA, USA). Flux densities were standardized to above canopy values (maximum PFD). Nitrogen availability was assessed via A. gerardii leaf N concentration (N_leaf) and soil inorganic N (NO₃⁻ and NH₄⁺). Leaves collected for specific leaf mass (SLM) determination (every two to three weeks throughout the growing season, see below) were ground and analyzed for total N content (% dry weight) by dry combustion and gas chromatography on a Carlo Erba NA 1500 analyzer (Carlo Erba, Milano, Italy). Soil samples for nutrient analyses were collected in June and August of 2000 and June, July and August of 2001. Five 2-cm diameter cores per plot (n = 7 plots per treatment) were removed to a depth of 10 cm within the center of each plot (the area nearly devoid of herbaceous vegetation within shrub islands and shrub removal plots) and composited. Subsamples of field moist soil, sieved through a 4 mm screen, were extracted with 2 N KCl solution and analyzed for inorganic N colourimetrically using an Alpkem FlowSolution analyzer (Perstorp Analytical Environmental, Wilsonville, OR, USA). Additional subsamples of soil were dried at 60°C to calculate inorganic N concentrations as N mass per unit mass of dry soil. Bray extractable P (Bray & Kurtz 1945), Mg, Ca and K concentrations and cation exchange capacity (CEC) were determined on subsamples of soil collected from the
center of each plot in June 2000 (and June 2001 for Bray P). For all measures of resource availability in which only a subset of four plots per treatment was sampled (Ψ, PFD and N_leaf), the plots were randomly selected on each measurement date, such that the same four plots were not sampled each time.

**Graminoid responses**

The response of graminoid vegetation (primarily C_4 grasses and sedges) to the presence and removal of C. drummondii was assessed through measurements of A. gerardii gas exchange (net photosynthesis [A_{net}] and transpiration). A. gerardii is the clear dominant on Konza Prairie, comprising 37.6% of total cover (Silletti & Knapp 2002), and C_4 grasses, in general, comprise over 50% of total cover (McAllister et al. 1998). Gas exchange and SLM were measured at ca. two to three week intervals throughout May to September of 2000 and 2001 on a subset of randomly chosen plots within each treatment (n = 4 plots per treatment). As with resource availability, the four plots per treatment were randomly selected on each measurement date to preclude sampling the same four plots each time. Given the lack of A. gerardii tillers within the center of both shrub islands and shrub removal plots, measurements of gas exchange and SLM were made on existing tillers within the ecotone of those plots. Gas exchange was measured between 1030 and 1500 hr CDT on relatively cloudless days (PFD > 1500 µmol m^{-2} s^{-1}) using a closed flow gas exchange system (LI-6200 Portable Photosynthetic System, LI-COR Inc., Lincoln, NE, USA) equipped with a 0.25-L chamber. Measurements were made at two locations per plot on two A. gerardii leaves from different tillers. For measurements made in the shrub islands, A. gerardii leaves were first allowed to equilibrate to full sun conditions for approximately five minutes by holding back the C. drummondii stems. SLM (leaf dry mass / leaf area) was calculated for each of five leaves per plot collected on four dates in 2000 and five dates in 2001. Turgid leaf area was determined to the nearest 0.001 cm² with a LI-3100 Area Meter (LI-COR Inc.), and leaves were dried at 60°C for at least four days before weighing to the nearest 0.1 mg.

Plant cover by species was estimated using a modified Daubenmire approach in four permanent 0.25-m² quadrats per plot (n = 7 plots per treatment) in 2000 and 2001. Aerial percent cover of each species was estimated using the following cover classes: 0-1%, 2-5%, 6-25%, 26-50%, 51-75%, 76-95%, and 96-100%. ANPP (excluding C. drummondii in shrub islands) was estimated by harvesting four 0.1-m² quadrats per plot (n = 7 plots per treatment) during late September to late October of 2000 and 2001. Current year’s plant biomass was separated into graminoid, forb and woody components, dried at 60 °C for one week and weighed to the nearest 0.01g. The four quadrats for cover and production assessments were randomly located within the grassland plots and in the grass-shrub ecotone of the shrub islands and shrub removal plots. Only cover and ANPP of the graminoid component are presented in this analysis.

**Data analyses**

Two way ANOVA was used to analyze the seasonal mean (Ψ, PFD, inorganic N, SLM and A_{net}), seasonal maximum (N_leaf), or end of season (graminoid ANPP and cover) values of each response variable. Individual plots were the experimental units. Fire (burned or unburned) and plant community type (grassland, shrub island or shrub removal) were the main effects (six treatments in total). Data from each year were analyzed separately because fire only occurred in the first year. Graminoid ANPP and A. gerardii SLM data were log transformed to improve normality, although untransformed means are shown for clarity. If the fire × plant community interaction was not significant in 2000, the community main effect was the focus for comparison of means, as the main effect of fire on resource availability and plant community dynamics has been well documented (Abrams et al. 1986; Knapp & Seastedt 1986; Gibson & Hulbert 1987; Blair 1997; Knapp et al. 1998). No plots were burned in 2001, thus only the community main effect could be considered. This pooling of unburned plots in 2001 was further justified because there were no significant differences (P ≥ 0.05) between the burned (in 2000) and unburned shrub island or shrub removal communities in any of the response variables measured. Fisher’s protected LSD procedure was used to determine significant differences among means (using least-squares means). Water (WUE = A_{net} / transpiration) and N (NUE = A_{net} / N_leaf) use efficiencies of A. gerardii were calculated for each plant community, and simple regression analyses were used to relate A_{net} to transpiration and N_leaf. All analyses were performed using SAS v.8.1 (Anon. 2000), and the level of significance for all tests was P < 0.05. All values presented are means ± 1 s.e.
Results

Resource availability

Concentrations of Mg, Ca and K and CEC in soils did not differ among the six treatments (burned and unburned grassland, burned and unburned shrub island, and burned and unburned shrub removal) in 2000. Soil P concentration (data not shown), however, was greater in the shrub island community relative to the open grassland in both 2000 and 2001 (P < 0.01), while that in the shrub removal community was intermediate and did not differ significantly from either the grassland or shrub island communities (P > 0.05). Due to the strong and similar effects of shrub cover and removal in both burned and unburned plots, the main effect of fire on resource availability was not significant, contrary to expectations for this grassland (Knapp et al. 1998). Fire × plant community interactions were likewise not significant (P > 0.05) in 2000 for light, water, or inorganic N seasonal means; therefore, only community main effects are emphasized (Table 1). Among the three plant communities, there were no significant differences in seasonal mean predawn Ψ in 2000 and 2001 or midday Ψ in 2000 for A. gerardii (Table 1). In 2001, however, the seasonal mean midday Ψ of A. gerardii in the shrub islands was significantly higher than that in both the shrub removal and open grassland communities (P < 0.001), indicating less water stress under the shade of shrubs.

Given the rapid resprouting and growth of C. drummondii in the ecotone of shrub islands after the fire in 2000, seasonal mean PFD at 15 cm above the soil surface (% of maximum; Table 1) was significantly reduced relative to that in the open grassland in both years (P < 0.001), with an 87% reduction in 2001. PFD in the shrub removal plots reached 73% of maximum (above canopy) values and was significantly greater than that in both the shrub islands and open grassland in 2000 (P < 0.001). Due to the rapid growth of herbaceous vegetation in the second growing season, seasonal mean PFD in the shrub removal plots was similar to that in the open grassland (ca. 40% of maximum) in 2001 (P = 0.7052).

There was no significant difference in seasonal mean soil inorganic N among the shrub islands and open grassland in either 2000 or 2001 (P > 0.1); values ranged from 1.44 to 7.41 µg g⁻¹ in the open grassland and 1.80 to 5.35 µg g⁻¹ in the shrub islands (Table 1). As is typical of disturbances, removal of above-ground shrub biomass created a large pulse in inorganic N in 2000 (seasonal mean of 18.75 ± 1.96 µg g⁻¹). In 2001, the availability of inorganic N within the removal plots had decreased to 4.12 ± 0.33 µg g⁻¹, presumably a result of decreased rates of N mineralization and greater graminoid tiller density, but was still greater than that in the undisturbed grassland (P = 0.0002).

Patterns of A. gerardii N_leaf differed from those of inorganic N availability (Table 1). There was a significant fire × plant community interaction for seasonal maximum N_leaf in 2000 (P = 0.0102), with A. gerardii N_leaf greater in the unburned vs burned grassland community (1.55 ± 0.09% and 1.31 ± 0.03%, respectively; P = 0.0415) and lower within the unburned vs burned shrub island community (1.81 ± 0.07% and 2.05 ± 0.08%, respectively; P = 0.0415). There was no significant difference in A. gerardii N_leaf among the burned and unburned shrub removal communities (2.02 ± 0.08% and 1.82 ± 0.09%, respectively; P = 0.0776). The community main effect was significant in both years (P < 0.03; Table 1), with seasonal maximum N_leaf in the shrub islands (2000: 1.93 ± 0.07%; 2001: 2.13 ± 0.09%) greater than that in the open grassland (2000: 1.43 ± 0.06%; 2001: 1.85 ± 0.07%). After shrub removal in 2000, maximum N_leaf of A. gerardii remained similar to that in the shrub islands at 1.92 ± 0.07% (P = 0.8975). In 2001, however, maximum N_leaf within the shrub removal plots

Table 1. Responses of water, light and nitrogen to fire in 2000 and plant community type in 2000 and 2001. The fire × community interaction of all responses in 2000 (except N_leaf) was not significant (P > 0.05). No plots were burned in 2001. Values represent seasonal means ± 1 s.e., except for N_leaf (seasonal maximum ± 1 s.e.). Within each year, means with different letters are significantly different at P < 0.05.

<table>
<thead>
<tr>
<th>Main effect</th>
<th>Water</th>
<th>Light</th>
<th>Nitrogen</th>
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<tr>
<td>Fire</td>
<td>Ψ_pre (MPa)</td>
<td>Ψ_mid (MPa)</td>
<td>PFD (% of max.)</td>
</tr>
<tr>
<td>2000</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Burned</td>
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<td>-1.97 ± 0.09*</td>
<td>47 ± 5*</td>
</tr>
<tr>
<td>Unburned</td>
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<td>-1.87 ± 0.08*</td>
<td>43 ± 5*</td>
</tr>
<tr>
<td>Plant Community</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Grassland</td>
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<td>-2.00 ± 0.08*</td>
<td>44 ± 5*</td>
</tr>
<tr>
<td>Shrub island</td>
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<td>-1.95 ± 0.14*</td>
<td>18 ± 4*</td>
</tr>
<tr>
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<td>-1.81 ± 0.08*</td>
<td>73 ± 4*</td>
</tr>
<tr>
<td>2001</td>
<td></td>
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</tr>
<tr>
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<td>39 ± 5*</td>
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<tr>
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<tr>
<td>Shrub removal</td>
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<td>-1.72 ± 0.05*</td>
<td>38 ± 4*</td>
</tr>
</tbody>
</table>
(1.92 ± 0.05%) was significantly lower than that in the shrub islands \((P = 0.0462)\) and was similar to that in the open prairie \((P = 0.5264)\).

**Graminoid responses**

There was a significant fire × plant community interaction in seasonal mean \(A_{\text{net}}\) for \(A.\ gerardii\) (Fig. 1a) in 2000 \((P = 0.0199)\), as photosynthesis was reduced by 37% in unburned shrub islands relative to unburned grassland plots \((P = 0.0337)\). In contrast, there was no significant difference in \(A_{\text{net}}\) of \(A.\ gerardii\) between burned shrub islands and burned grassland plots \((P = 0.1552)\). Following shrub removal, photosynthetic rates of \(A.\ gerardii\) were increased by 43 - 47% relative to the open grassland \((P < 0.01)\). By 2001 (all plots unburned) photosynthetic rates in the shrub removal plots were no longer significantly different from those of the open grassland \((P = 0.1878)\). The effect of shrub cover in unburned shrub islands was similar in both years, with a 38% reduction in \(A_{\text{net}}\) relative to that in the open grassland in 2001 \((P < 0.0001)\).

In 2000, there were significant differences in seasonal mean SLM of \(A.\ gerardii\) among the three plant communities \((P = 0.0001;\) Fig. 1b), with the highest SLM in grassland plots \((7.23 ± 0.24 \text{ mg cm}^{-2})\) and the lowest in \(A.\ gerardii\) tillers within shrub islands \((5.71 ± 0.30 \text{ mg cm}^{-2})\). There was partial recovery in SLM in the shrub removal plots in 2000, with the seasonal mean \((6.32 ± 0.18 \text{ mg cm}^{-2})\) intermediate between the grassland and shrub island values. By 2001, SLM in the shrub removal plots \((6.66 ± 0.17 \text{ mg cm}^{-2})\) was not significantly different \((P = 0.3483)\) from that in the grassland \((6.94 ± 0.17 \text{ mg cm}^{-2})\). Specific leaf mass of \(A.\ gerardii\) remained significantly lower in the shrub islands \((4.66 ± 0.15 \text{ mg cm}^{-2})\) relative to the open grassland in 2001 \((P < 0.0001)\).

We calculated leaf-level WUE and NUE as metrics of resource use by \(A.\ gerardii\). Seasonal mean WUE of \(A.\ gerardii\) (Fig. 2a) within the shrub removal community was significantly greater than that in the other two communities \((P < 0.001)\) at \(2.6 ± 0.1 \mu\text{mol mmol}^{-1}\), with \(A_{\text{net}}\) and transpiration strongly correlated in all communities.
In contrast, the open grassland exhibited the only significant relationship between $A_{\text{net}}$ and $N_{\text{leaf}}$ ($P = 0.0028$; Fig. 2a), with no relationship in the shrub islands and shrub removal plots. Seasonal mean NUE in A. gerardii (Fig. 2a) was significantly lower in the shrub island community at $13.1 \pm 1.0$ $\mu$mol-CO$_2$.g$^{-1}$.s$^{-1}$ relative to both the grassland and removal communities ($19.4 \pm 0.9$ $\mu$mol-CO$_2$.g$^{-1}$.s$^{-1}$ and $18.3 \pm 1.0$ $\mu$mol-CO$_2$.g$^{-1}$.s$^{-1}$, respectively; $P < 0.005$).

As expected, fire generally increased graminoid ANPP in the burned plots relative to the unburned plots in 2000 ($P = 0.0028$; Knapp et al. 1998); however, the fire x plant community interaction was not significant for either graminoid ANPP or cover in 2000. Graminoid ANPP in the ecotone of the shrub island community (2000: $49 \pm 11$ g m$^{-2}$; 2001: $90 \pm 11$ g m$^{-2}$) was significantly lower than that in the open grassland (2000: $342 \pm 39$ g.m$^{-2}$; 2001: $288 \pm 22$ g.m$^{-2}$) in both years ($P < 0.0001$; Fig. 3a). A similar pattern occurred for total cover of graminoids in both years ($P < 0.0001$; Fig. 3b). Graminoid ANPP within the former ecotone of the shrub removal community (162 $\pm$ 34 g.m$^{-2}$) was significantly greater than that in the shrub island community in 2000 ($P < 0.0001$) but lower than that in the grassland ($P < 0.0001$). In 2001, however, graminoid ANPP in the shrub removal community had increased to $378 \pm 33$ g.m$^{-2}$ and was not significantly different from that in the open grassland ($P = 0.3506$). In 2000, total cover of graminoids within the shrub removal community remained similar to that in the shrub island community at $87 \pm 7\%$ ($P = 0.8261$), significantly lower than that in the open grassland ($P < 0.0001$). Similar to graminoid ANPP, by the end of the 2001 growing season, total cover of graminoids within the shrub removal community had increased to $149 \pm 7\%$, equivalent to that in the grassland ($P = 0.4491$).

**Discussion**

*Corncorncorncornus drummondii* expansion and grassland displacement

The expansion of *C. drummondii* in mesic grasslands of the central United States does not affect patterns of resource availability consistent with the expansion of woody species in other grassland ecosystems. The primary effect of *C. drummondii* on resource availability in tall-grass prairie was a significant reduction in the amount of light that reaches the understory, which ultimately resulted in a near complete loss of the dominant *C_4* grasses. The effects of *C. drummondii* expansion on water and nitrogen were marginal, which contrasts with other grasslands in which increasing dominance of woody vegetation results in greater availability of these two soil resources (Schlesinger et al. 1990).

Within shrub islands that had been burned, there was no effect of *C. drummondii* on carbon gain of *A. gerardii* growing in the grass-shrub ecotone. The *C. drummondii* stems in the ecotone were top killed, which increased light availability to the growing grass canopy early in the growing season and allowed for high photosynthetic rates. However, within unburned shrub islands, light availability was reduced up to $87\%$ relative to open grassland. This reduction in light led to significant declines in carbon gain by the dominant grass *A. gerardii*, as net photosynthetic rates were reduced by about $40\%$. The effects of reduced light underneath the *C. drummondii* canopy were probably mediated through significant modifications in leaf structure (reduced SLM) of *A. gerardii*. Low light availability had significant effects on the use of other resources by *A. gerardii*, as well. Seasonal maximum $N_{\text{leaf}}$ (leaf N concentration) of *A. gerardii* in the *C. drummondii* understory was significantly greater than that in open grassland. However, *A. gerardii* in the understory was unable to efficiently use N because of the overriding limitation of low light, as
indicated by the lack of a significant relationship between *A. gerardii* ANPP and *N* leaf within the shrub island community.

In contrast to light availability, water availability (measured as *A. gerardii* leaf water potential) and soil inorganic N availability were similar within shrub islands and open grassland. This lack of an effect of *C. drummondii* on water and inorganic N suggests that these soil resources, unlike light, are not likely to limit graminoid growth in shrub islands, perhaps because shrub encroachment occurs in unburned prairie, which is usually not water or N limited (Blair 1997; Knapp et al. 1998). In many grassland ecosystems, the availability of water and soil inorganic N are higher under woody vegetation relative to open grassland (Petranka & McPherson 1979; Belsky et al. 1989; Schlesinger et al. 1990; Wilson 1993; Köchy & Wilson 2000; Archer et al. 2001; Hibbard et al. 2001). Soil moisture is often higher under woody vegetation because evapotranspiration may be reduced by shade, stem flow may concentrate water underneath shrubs/trees or hydraulic lift may move water from deep in the soil profile to upper soil layers (Scholes & Archer 1997). However, in our study, lack of significant differences between predawn leaf water potential of *A. gerardii* in the shrub island and grassland communities suggests that soil moisture does not differ between the two communities. The high transpirational area of intact *C. drummondii* islands may have contributed to this result by offsetting gains in soil moisture associated with reduced soil temperatures (data not shown) and consequent low evaporation from the soil surface. Soil inorganic N was expected to be higher within *C. drummondii* islands because of large inputs of high quality (*C*₃) litter. Similar soil inorganic N availability between the shrub island and grassland communities may be the result of lower N mineralization rates within shrub islands compared to open grassland or greater uptake of N by *C. drummondii*.

The presence of *C. drummondii* reduced tiller density of graminoids (as reflected by graminoid cover). Consequently, ANPP was reduced up to 86% at the grass-shrub ecotone of shrub islands relative to open grassland. Similar declines in herbaceous production have been reported in other grasslands following shrub/tree encroachment (Hobbs & Mooney 1986; Harrington & Johns 1990; McPherson & Wright 1990; Scholes & Archer 1997; Wilson 1998). This reduction in graminoid ANPP represents a loss in ecosystem function with respect to the ability of tall-grass prairie to support ungulate grazers and may also result in loss of annual carbon inputs if *C. drummondii* ANPP does not fully account for the loss of graminoid ANPP (Aguiar et al. 1996; Hueneke et al. 2002).

With the exception of increasing *N* leaf of *A. gerardii* in burned relative to unburned shrub islands, fire did not have any significant effects on the seasonal availability of light, water and N in the first year of study in either the shrub island or shrub removal communities. The lack of a fire effect on resource availability is surprising for this grassland (Knapp et al. 1998). However, fire effects on resource availability are transient and strongest early in the growing season (Seastedt & Knapp 1993). In this study, calculating mean values for resource availability over the growing season may have obscured early season effects of fire.

*Coronarius drummondii* removal and grassland recovery

It appears that *C. drummondii* dominance in tall-grass prairie is a biotically maintained alternative stable state, since removal of *C. drummondii* eliminated light limitations for graminoid growth and resulted in a full recovery of graminoid production and cover at the ecotone where graminoid rhizomes were still present. This increase in graminoid growth after shrub removal was consistent with recovery of herbaceous vegetation in other shrub/tree removal studies (Harrington & Johns 1990; Bates et al. 2000; Köchy & Wilson 2000). Although graminoid cover and production in the ecotone of shrub removal areas recovered to ‘pre-invasion’ values within two growing seasons, recovery within the center, where graminoid tiller density was very low, will take multiple growing seasons, as the dominant grasses reproduce primarily through clonal expansion at a slow rate (Hartnett 1993; Hartnett & Keeler 1995). Indeed, two years after shrub removal, graminoid ANPP in central areas was still less than 10 g m⁻². This lag in recovery indicates that the legacy effect of *C. drummondii* dominance is manifest primarily through loss of rhizomes of the dominant grasses.

Recovery of graminoid vegetation after *C. drummondii* removal was facilitated by a pulse in light and N availability, which increased carbon gain in *A. gerardii*. These increases were short-lived, however, as PFD, *N* leaf, and soil inorganic N within the shrub removal community were comparable to values in open grassland in the second year of study. These results suggest there is no legacy effect of *C. drummondii* dominance on resource availability.

In other ecosystems, removal of woody plants often results in greater water and N availability as a result of reduced demand for these resources (Bates et al. 2000; Köchy & Wilson 2000; Peltzer & Köchy 2001). Indeed, *C. drummondii* removal resulted in an increase in inorganic N availability. This increase may reflect elimination of N uptake by shrubs. It may also reflect greater N mineralization due to warmer soil temperatures and a large mineralizable pool of N created by removal of the
shrub canopy and mortality of *C. drummondii* roots and rhizomes. In contrast to soil inorganic N, removal of *C. drummondii* did not increase either Ψ or N_leaf of *A. gerardii* relative to intact shrub islands and may again be related to the fact that shrub invasion occurs in sites that are usually not water or N-limited (Blair 1997; Knapp et al. 1998).

**Conclusion**

The probability of moving from a shrub/woodland state back to grassland in response to a return to high fire frequency is low, as the shift in dominant growth form renders substantial changes in ecosystem and community properties that fire alone cannot reverse. More labour intensive means of shrub removal can facilitate recovery in grasslands. However, the energy inputs required to accomplish this reversal are prohibitive over a large scale and represent significant costs of woody plant expansion in mesic grasslands. Therefore, prevention of woody plant expansion through frequent burning is a preferred management option in remnant tall-grass prairies.

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**References**


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