

Influence of shrub encroachment on aboveground net primary productivity and carbon and nitrogen pools in a mesic grassland

Michelle S. Lett, Alan K. Knapp, John M. Briggs, and John M. Blair

Abstract: The clonal shrub *Cornus drummondii* C.A. Mey. is rapidly increasing in cover and displacing mesic grassland species in the central USA as a consequence of fire suppression. We assessed the impact of *C. drummondii* on carbon (C) and nitrogen (N) pools and C fluxes in a tallgrass prairie in eastern Kansas, USA, through a comparison of both burned and unburned *C. drummondii* islands with open grassland areas. Allometric equations relating *C. drummondii* foliage and wood biomass to basal stem diameter were developed to estimate aboveground biomass and net primary productivity (ANPP) of *C. drummondii*. Within *C. drummondii* islands, ANPP was $496 \pm 45 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$, nearly three times that within open grassland ($167 \pm 13 \text{ g C}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$). As a result of greater aboveground biomass, aboveground C and N storage within shrub islands ($3270 \pm 466 \text{ g C}\cdot\text{m}^{-2}$, $37.9 \pm 5.3 \text{ g N}\cdot\text{m}^{-2}$) was substantially greater than that within open grassland ($241 \pm 33 \text{ g C}\cdot\text{m}^{-2}$, $6.1 \pm 0.8 \text{ g N}\cdot\text{m}^{-2}$). No change in soil organic C or total N to 10-cm depth was evident; however, soil CO₂ flux was significantly reduced in *C. drummondii* islands relative to the open grassland. The storage of C in aboveground biomass of *C. drummondii* represents a significant short-term increase in C storage relative to open grassland. However, potential alterations in belowground processes must be quantified before the long-term net effect of shrub encroachment on C and N pools within this mesic grassland can be determined.

Key words: aboveground biomass, *Cornus drummondii*, net primary productivity, shrub encroachment, tallgrass prairie.

Résumé : Suite aux effets suppressifs du feu dans le centre des États-Unis, l'arbuste clonal *Cornus drummondii* C.A. Mey. augmente rapidement sa couverture, en déplaçant des espèces de la prairie mésique. Les auteurs ont évalué l'impact sur les réserves en carbone (C) et en azote (N) ainsi que sur les flux du C, dans une prairie de hautes herbes de l'est du Kansas, aux E.U., en comparant des îlots brûlés et non-brûlés du *C. drummondii* ainsi que des surfaces de prairie ouverte. Afin d'évaluer la biomasse épigée et la productivité primaire nette (ANPP) du *C. drummondii*, les auteurs ont développé des équations allométriques reliant le feuillage du *C. drummondii* et sa biomasse ligneuse, avec le diamètre basal de la tige. Dans les îlots du *C. drummondii*, l'ANPP est de $496 \pm 45 \text{ g C}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$, presque trois fois celui retrouvé dans la prairie ouverte ($167 \pm 13 \text{ g C}\cdot\text{m}^{-2}\cdot\text{an}^{-1}$). Suite à une augmentation de la biomasse épigée, la réserve épigée en C et en N dans les îlots arbustifs ($3270 \pm 466 \text{ g C}\cdot\text{m}^{-2}$; $37.9 \pm 5.3 \text{ g N}\cdot\text{m}^{-2}$) est substantiellement plus grande que celle de la prairie ouverte ($241 \pm 33 \text{ g C}\cdot\text{m}^{-2}$; $6.1 \pm 0.8 \text{ g N}\cdot\text{m}^{-2}$). On observe aucun changement évident du C organique ou du N total dans les 10 premiers cm du sol; cependant, le flux de CO₂ du sol est significativement réduit dans les îlots du *C. drummondii*, comparativement à la prairie ouverte. L'accumulation du C dans la biomasse épigée du *C. drummondii* représente une augmentation significative à court terme de la réserve en C, comparativement à la prairie. On doit cependant quantifier les perturbations potentielles dans les processus hypogés, avant de pouvoir déterminer l'effet net à long terme de l'envahissement arbustif sur les réserves en C et en N dans cette prairie mésique.

Mots clés : biomasse épigée, *Cornus drummondii*, productivité primaire nette, envahissement, prairie de hautes herbes.

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Introduction

The density and cover of the C₃ shrub *Cornus drummondii* C.A. Mey. (rough-leaved dogwood) within mesic grasslands (tallgrass prairies) of the central USA has increased substantially within recent history, primarily because of fire suppression (Briggs et al. 2002). *Cornus drummondii*

is a clonal shrub with an aerial cover of less than 0.1% in annually burned grasslands, but with fire suppression it expands and forms discrete "islands" of woody vegetation within the grassland matrix. These islands can cover more than 11% of the area of grassland sites in which fire has been excluded for over 10 years (Briggs et al. 2002) and can rapidly eliminate the dominant vegetation (mostly C₄ gram-

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inoids) in the understory because of reductions in light availability (Lett and Knapp 2003).

The shift from a C_4 grass to a C_3 shrub-dominated ecosystem is likely to significantly affect plant productivity and the pools and fluxes of C within this ecosystem (Jackson et al. 2002). Tallgrass prairies are characterized by high net primary productivity (NPP), high belowground allocation of NPP (>50%), large quantities of soil organic matter, high microbial biomass and activity, and high soil CO_2 flux (J_{CO_2}) (Kucera et al. 1967; Zak et al. 1994; Briggs and Knapp 1995; Bremer et al. 1998; Knapp et al. 1998a). These attributes are expected to change as *C. drummondii* encroaches, with alterations in both the cycling and storage of C in this ecosystem. Due to the structure of *C. drummondii*, both aboveground biomass and net primary productivity (ANPP) are expected to be greater within shrub islands relative to adjacent grassland, resulting in greater storage of C aboveground, at least temporarily. However, *C. drummondii* may allocate less NPP belowground, ultimately reducing belowground C storage and perhaps offsetting gains in aboveground biomass C (Jackson et al. 2002). Given that grasslands occupy a large fraction of the Earth's land area (approx. 30%) and shrub encroachment within grasslands is a worldwide phenomenon, a better understanding of how shrub encroachment in grasslands alters C dynamics is important for quantifying and balancing the global C budget (Archer 1990; Scholes and Archer 1997; Van Auken 2000; Roques et al. 2001; Silva et al. 2001).

Nitrogen dynamics are also expected to change as shrub encroachment proceeds in grasslands. *Cornus drummondii*, a C_3 species, likely has relatively high leaf N concentrations, while the dominant species being displaced are C_4 graminoids, characterized by relatively low leaf N concentrations (Knapp 1985). This shift in tissue quality, along with a shift toward greater aboveground biomass, will alter aboveground N pools and soil C and N pools, as well as litter dynamics (Wedin and Pastor 1993; Norris et al. 2001a).

The objectives of the present study were to quantify changes in aboveground productivity, aboveground biomass C and N pools, soil C and N pools, and J_{CO_2} that accompany *C. drummondii* encroachment into a mesic grassland.

Materials and Methods

Site description

Research was conducted during the 2000 and 2001 growing seasons at the Konza Prairie Biological Station (KPBS) in northeast Kansas, USA (39°05'N, 96°35'W). Konza Prairie is a native mesic grassland (3487 ha) representative of the Flint Hills region of the central USA (Knapp and Seastedt 1998). The Flint Hills contains the largest remaining tract of unplowed tallgrass prairie and extends throughout much of eastern Kansas from the Kansas–Nebraska border south to northeastern Oklahoma. The KPBS is characterized by highly dissected terrain with deep lowland soils and shallow upland soils. Mean annual air temperature is 12.8 °C, with a mean monthly high of 29.3 °C in July and a mean monthly low of –3 °C in January. Mean annual precipitation is 835 mm, with 75% falling during the growing season (April to September). The KPBS is dominated by the C_4 (warm-season) grasses *Andropogon gerardii* Vitman, *A. sco-*

parius Michx., *Sorghastrum nutans* (L.) Nash, and *Panicum virgatum* L. Forbs are much less abundant, but account for the majority of plant species richness. Gallery forests dominated by *Quercus macrocarpa* Michx. and *Q. muehlenbergii* Engelm. have expanded in lowland areas in recent years (Abrams 1986; Knight et al. 1994). Shrubs (primarily *C. drummondii* and *Rhus glabra* L.) have expanded throughout this grassland (Briggs et al. 2002; Heisler et al. 2003), but are predominant on slopes with shallow soils.

Experimental design

To assess the effects of shrub encroachment on C and N dynamics, pools of plant and soil C and N were compared between open grassland areas and areas of similar topography and soils dominated by *C. drummondii*. Fourteen *C. drummondii* islands were selected in the spring of 2000. Seven of the 14 islands had been burned once every four years since 1992 (including April of 2000), while the other seven had been burned only twice since 1980 (1980 and 1991) and, because fire had been excluded for nine years, are referred to as “unburned” for the present study. Fourteen grassland plots were established in close proximity to the shrub islands in areas that were not yet affected by shrub encroachment. These plots were similar in size to the shrub islands and were also located on similar soils and topographic position. These plots were burned at a frequency identical to that of the shrub islands, with seven burned in April of 2000, while the other seven had not been burned for nine years. The same plots were used in 2001, but no plots of any treatment were burned. The shrub islands were delineated into “ecotone” and “center” areas based on existing patterns of understory cover. The “ecotone” was defined as that area within which graminoids and shrubs coexisted, while the “center” was defined as that area nearly devoid of herbaceous vegetation. Including the ecotone area, the selected shrub islands averaged 39 ± 2 m² in size, with ecotone and center locations of equal areas. Owing to vigorous resprouting following fire, *C. drummondii* stem density was significantly greater in the burned shrub islands (43 stems·m⁻²) relative to the unburned shrub islands (22 stems·m⁻², $P = 0.0014$).

Allometric equations

We developed allometric equations for estimating peak aboveground biomass (g·m⁻²) and productivity (g·m⁻²·year⁻¹) of *C. drummondii* in our study plots. These values were converted to grams of C per square metre and grams of C per square metre per year, respectively, using the C concentration of *C. drummondii* wood and foliage (discussed later in text). A total of 166 stems were cut at ground level at the time of peak *C. drummondii* foliage biomass (July) within randomly placed 0.1-m² quadrats spanning the ecotone and center of four additional *C. drummondii* islands. Basal stem diameter (cm) was measured and all leaves were removed from each stem, dried at 60 °C, and weighed to the nearest 0.01 g. Stems and branches were cut into 10-cm to 12-cm sections, dried at 60 °C, and weighed to the nearest 0.01 g. Separate allometric equations relating *C. drummondii* foliage and wood biomass (stems + branches) to basal stem diameter were then developed as log–log functions using SAS version 8.1 (SAS Institute Inc. 2000).

Aboveground biomass and net primary productivity

Peak aboveground biomass in the grassland sites was determined by harvesting biomass in late September to October within four randomly placed 0.1-m² quadrats within each plot ($n = 7$ plots per treatment) in both 2000 and 2001. Understory biomass in the shrub islands was also harvested in four randomly placed 0.1-m² quadrats in both the ecotone and center of each plot ($n = 7$ plots per treatment). All biomass was sorted into current and previous year's growth, dried at 60 °C, and weighed to the nearest 0.01 g. To non-destructively estimate *C. drummondii* biomass in the shrub islands, the basal diameters of all live *C. drummondii* stems within the four center and four ecotone quadrats were measured for use with the allometric equations. Foliage and wood biomass values for each stem were summed to estimate total *C. drummondii* aboveground biomass within each quadrat. Total aboveground biomass within each quadrat was then estimated by summing understory and *C. drummondii* biomass.

Annual aboveground net primary productivity for all plots was estimated for 2001. In the grassland and understory of shrub islands, it was estimated using the mass of current year's biomass produced in each quadrat. Aboveground net primary productivity of *C. drummondii* in the shrub islands was determined using the equation $ANPP = \Delta B + F$, where ΔB is the annual increase in aboveground wood biomass (wood productivity) and F is annual foliage productivity. Foliage biomass in 2001 (as determined from the respective allometric equation) was used to estimate foliage productivity. Because quadrats were randomly placed in both 2000 and 2001, different stems and varying numbers of stems/quadrat were measured each year. Thus, direct comparisons of quadrat data between years were not possible for estimating wood production. Instead, we quantified the average diameter increase in stems measured across all shrub islands over the two sample years and used stem densities from 2001 to estimate the increase in biomass/area with the allometric equation relating *C. drummondii* wood biomass to basal stem diameter. This is a minor variation of permanent plot or tree-based methods to estimate wood production (Norris et al. 2001b), and although shrub mortality was not quantified, it was rare in these young, expanding islands. Foliage and wood productivity of each stem were added to compute an estimate of aboveground productivity for each stem. Total ANPP was then estimated by summing *C. drummondii* and understory ANPP within each quadrat.

Carbon and nitrogen pools

Mid-season C and N concentrations of *C. drummondii* foliage ($n = 14$) and wood ($n = 4$) and *A. gerardii* foliage ($n = 8$) were determined by dry combustion and gas chromatography with a Carlo Erba NA 1500 analyzer (Carlo Erba, Milano, Italy). Aboveground biomass (g·m⁻²) was converted to grams of C per square metre using the C concentrations of *C. drummondii* and *A. gerardii*. To estimate aboveground biomass C and N in the open grassland and *C. drummondii* understory, aboveground biomass values were multiplied by the C and N concentrations of *A. gerardii*, as this and other C₄ grasses comprise 90% of total cover and biomass in frequently burned tallgrass prairie (Briggs and Knapp 1995; Silletti and Knapp 2002). However, aboveground biomass N

was likely underestimated (more in unburned relative to burned grassland) because of greater biomass of C₃ forbs in unburned grassland (15–20%), which have relatively higher foliage N concentrations compared to C₄ grasses. Aboveground biomass C and N of *C. drummondii* were determined by summing the products of *C. drummondii* C and N concentrations and aboveground biomass of both foliage and wood components. *Cornus drummondii* C and N was then added to that of the understory to estimate total aboveground biomass C and N within *C. drummondii* islands. Similarly, ANPP (g·m⁻²·year⁻¹) was converted to grams of C per square metre per year using the C and N concentrations of *C. drummondii* and *A. gerardii*.

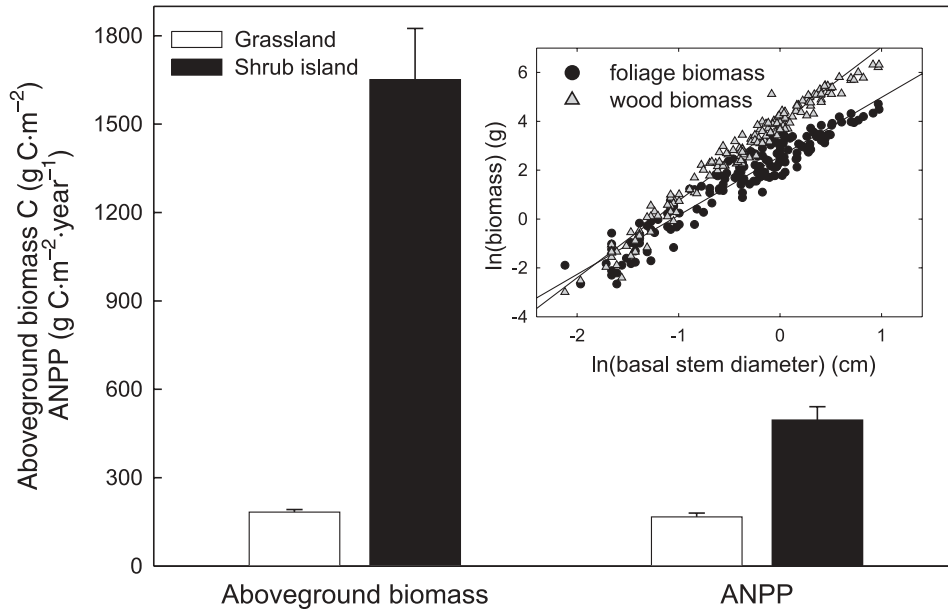
Soil organic C (SOC) and total N were measured in June and August of 2000 and June, July, and August of 2001 in all plots. Five soil cores of 2-cm diameter were taken to a depth of 10 cm within the center of each plot ($n = 7$ plots per treatment) and composited. The soil samples were sieved to remove roots, aboveground litter, and rocks; dried at 60 °C; ground for homogenization; and analyzed for C and N concentration by dry combustion and gas chromatography. Using an average soil bulk density of 1 g·cm⁻³ (Seastedt and Ramundo 1990), percent C and N values were converted to grams of C per square metre and grams of N per square metre, respectively, in the upper 10 cm of soil.

Soil CO₂ flux was measured with an infrared gas analyzer system (LI-6200 IRGA, LI-COR Inc., Lincoln, NE, USA) operated in the closed mode (Knapp et al. 1998a). Measurements were made by placing an 850-cm³ chamber on an area of soil surface devoid of any live plant material. Loose surface litter was carefully removed to avoid disruption of the soil surface and allow for the chamber to seal to the surface. Three measurements were made in both the ecotone and center of each plot in 2000 ($n = 7$ plots per treatment) and a sub-set of randomly chosen plots in 2001 ($n = 4$ plots per treatment). Measurements were made five times throughout the 2000 growing season and three times throughout the 2001 growing season. On each sampling date, soil J_{CO_2} was measured in all plots within a consecutive two-day period, during which changes in soil temperature and moisture were minor.

Data analyses

All statistical analyses were performed using SAS version 8.1 (SAS Institute Inc. 2000). Aboveground biomass C and N, ANPP, and plant tissue C and N concentrations were assessed using a two-way ANOVA, with fire (burned and unburned) and vegetation type (grassland and shrub island) as the main effects. Seasonal mean values of soil J_{CO_2} and SOC and total N were analyzed in a similar manner. In all tests, individual plots were the experimental units. Separate analyses were performed for each year and for both the ecotone and center locations of each treatment. Data from the grassland plots (in which there was no ecotone and center distinction) were used in both ecotone and center analyses for comparative purposes. The effects of fire in 2000 were assessed by pairwise comparisons between the burned and unburned grassland and shrub island vegetation types. If these pairwise comparisons were not significant, the vegetation type main effect was the focus for comparison of means, as the main effect of fire on ecosystem processes has been

Fig. 1. Aboveground biomass C and net primary productivity (ANPP) of the grassland and shrub island vegetation types. Values are averaged over location, burn treatment, and year (ANPP data available for 2001 only). The inset shows the allometric regressions relating the log of *Cornus drummondii* foliage biomass and *C. drummondii* wood biomass (total organic matter) to the log of *C. drummondii* basal stem diameter. For foliage, $\log(\text{biomass, g}) = 2.57 + 2.42 \log(\text{diameter, cm})$, and, for wood, $\log(\text{biomass, g}) = 3.90 + 3.15 \log(\text{diameter, cm})$. These regressions were used to determine both peak aboveground biomass ($\text{g}\cdot\text{m}^{-2}$) and ANPP ($\text{g}\cdot\text{m}^{-2}\cdot\text{year}^{-1}$) of *C. drummondii*.



well-documented (Abrams et al. 1986; Briggs and Knapp 1995; Blair 1997; Knapp et al. 1998b; Rice et al. 1998). With the exception of aboveground biomass C and N, only the vegetation type main effect was considered in the second year (2001) when no plots were burned.

The plant tissue percent C and N data were transformed to improve normality. Fisher's LSD procedure was used to determine significant differences between means, with the level of significance at $P < 0.05$. All values reported are means ± 1 SE, with backtransformed means reported for plant percent C and N.

Results

Basal stem diameter was a good predictor of both foliage and wood biomass (Fig. 1). Foliage and wood biomass allometric regressions were highly significant ($P < 0.001$), with coefficients of determination (r^2) of 0.91 and 0.97, respectively.

Typically, fire increases leaf N concentration in *A. gerardii*, although the increase is short-lived and detectable only in the spring (Knapp et al. 1998b). At the time of collection of foliage and wood samples in the present study, there were no significant differences in C or N concentrations between the burned and unburned plots. Both C and N concentrations varied between the foliage and wood components of *C. drummondii*. Total C concentration within *C. drummondii* was significantly greater in the wood component (49%) than the foliage component (47%, $P < 0.0001$). Total N concentration exhibited the opposite pattern, with N concentration in the foliage (1.6%) four-fold greater than that in wood (0.4%, $P < 0.0001$). Total C concentration within *A. gerardii* foliage was 47%, similar to *C. drum-*

mondii foliage and significantly lower than that in *C. drummondii* wood ($P < 0.0001$). Total N concentration within *A. gerardii* foliage (1.2%) was intermediate between that of *C. drummondii* wood and foliage ($P < 0.0001$).

In the tallgrass prairie, fire increases productivity, especially that of the dominant C₄ grasses (Knapp et al. 1998b) and perhaps also that of *C. drummondii*, as this shrub resprouts rapidly when it has been top-killed by fire. However, in the present study, ANPP was only measured in the second year, when no plots were burned, so the effects of fire on productivity of the shrub islands can not be evaluated. Across both the ecotone and center, ANPP in 2001 within the shrub island vegetation type was 496 ± 45 g C·m⁻²·year⁻¹ (Fig. 1) and was significantly greater ($P < 0.001$) in both the ecotone (376 ± 46 g C·m⁻²·year⁻¹) and center (615 ± 63 g C·m⁻²·year⁻¹) relative to grassland sites (167 ± 13 g C·m⁻²·year⁻¹, Table 1). *Cornus drummondii* accounted for 83% (312 ± 49 g C·m⁻²·year⁻¹) of total ANPP in the ecotone of shrub islands and 99% (607 ± 64 g C·m⁻²·year⁻¹) in the center, where understory vegetation was nearing complete exclusion. Allocation between foliage and wood productivity was similar in *C. drummondii*: 46% and 54%, respectively, in the ecotone of shrub islands and 53% and 47%, respectively, in the center.

Detritus accumulates in the absence of fire in tallgrass prairie, resulting in greater aboveground biomass in unburned relative to burned grassland (Abrams et al. 1986; Briggs and Knapp 1995). In the present study, there was a significant fire \times vegetation type interaction ($P < 0.01$) for peak aboveground biomass C in both the ecotone and center locations in the first year of study (Table 2). In both the ecotone and center, aboveground biomass C was significantly greater in unburned shrub islands (ecotone: $1617 \pm$

Table 1. Aboveground net primary productivity (ANPP) of the grassland and shrub island vegetation types in 2001 (mean \pm SE).

	ANPP (g C·m ⁻² ·year ⁻¹)	
	Ecotone	Center
Grassland*	167 \pm 13b	167 \pm 13b
Shrub island total	376 \pm 46a	615 \pm 63a
<i>Cornus drummondii</i>		
Foliage	142 \pm 23	322 \pm 35
Wood (stem + branches)	170 \pm 26	285 \pm 29
Total	312 \pm 49	607 \pm 64
Shrub island understory	63 \pm 9	8 \pm 3

Note: Within shrub islands, ANPP is allocated among *Cornus drummondii* and the understory community. Within each location, means with different letters are significantly different at $P < 0.05$.

*Grassland plots were not delineated into ecotone and center locations, but productivity data were included in both analyses for comparative purposes.

484 g C·m⁻², center: 3270 \pm 466 g C·m⁻²) compared to burned shrub islands (ecotone: 205 \pm 25 g C·m⁻², center: 1595 \pm 236 g C·m⁻²) and burned (241 \pm 33 g C·m⁻²) and unburned (154 \pm 20 g C·m⁻²) grassland. In the center location, aboveground biomass C was also significantly greater ($P < 0.005$) in burned shrub islands relative to both burned and unburned grassland. In the second year of study, the effect of the previous year's fire remained evident, and the patterns of peak aboveground biomass C were identical to those in year one. In both the ecotone and center of burned and unburned shrub islands, *C. drummondii* accounted for the bulk of peak aboveground biomass C (data not shown). Understory biomass C accounted for only 1–29% of the total in the ecotone of shrub islands and only 0.1–2.4% in the center.

In both years of study, patterns of aboveground biomass N accumulation (Table 3) within the shrub island and open grassland vegetation types were consistent with those of aboveground biomass C (Table 2). Aboveground biomass N ranged from 3.6 \pm 0.4 g N·m⁻² to 6.1 \pm 0.8 g N·m⁻² in the grassland and from 3.7 \pm 0.3 g N·m⁻² (ecotone) to 37.9 \pm 5.3 g N·m⁻² (center) in the shrub islands.

Total soil N to a depth of 10 cm ranged from 350–385 g N·m⁻² over both years, with no significant difference between the two vegetation types ($P > 0.07$, Table 4). Similarly, SOC to a depth of 10 cm did not vary significantly between the open grassland and shrub islands in either year ($P > 0.9$), ranging from 4691–4740 g C·m⁻².

Soil J_{CO_2} is higher in burned relative to unburned grassland (Knapp et al. 1998a); however, the fire \times vegetation type interaction was not significant in the first year of study for soil J_{CO_2} in either the ecotone or center locations ($P > 0.08$). Soil CO₂ flux in the grassland (0.08–0.10 mg C·m⁻²·s⁻¹) was significantly greater than in both the ecotone and center of the shrub islands (ecotone: 0.06 – 0.08 mg C·m⁻²·s⁻¹, center: 0.06 – 0.07 mg C·m⁻²·s⁻¹) in years one and two ($P < 0.01$), with slightly higher fluxes in the second year (Fig. 2).

Discussion

The displacement of the dominant C₄ herbaceous vegetation of tallgrass prairies by *C. drummondii* can have dra-

matic effects on plant community structure through reductions in species richness and diversity (Lett and Knapp, in press). In the present study, substantial changes in ecosystem structure and function (C and N pools and C cycling) were also evident.

Including both *C. drummondii* and understory productivity, ANPP in 2001 within shrub islands was 496 \pm 45 g C·m⁻²·year⁻¹ (averaged over the entire island, Fig. 1). In comparison, ANPP within the grassland sites was only 167 \pm 13 g C·m⁻²·year⁻¹, or about one-third of average shrub island productivity. Furthermore, our estimate of shrub island ANPP was nearly two times greater than the 22-year average of ANPP in the most productive of herbaceous areas on the study site (Knapp et al. 1998b). The importance of additional productivity from woody species is further emphasized by noting that understory (primarily herbaceous) ANPP contributed only 63 \pm 9 g C·m⁻²·year⁻¹ and 8 \pm 3 g C·m⁻²·year⁻¹ to the respective totals in the ecotone (376 \pm 46 g C·m⁻²·year⁻¹) and center (615 \pm 63 g C·m⁻²·year⁻¹) within the shrub islands.

The dramatic, albeit localized, increase in ANPP within areas of shrub encroachment is consistent with the observation that the leaf-area index of *C. drummondii* is 2–3 times greater than that of the open grassland (data not shown). The capacity to fix C was clearly not reduced, but rather was enhanced with *C. drummondii* encroachment, as ANPP of *C. drummondii* more than accounted for losses in ANPP associated with the elimination of herbaceous vegetation. A similar result was reported by Harcombe et al. (1993) in a comparison of Texas coastal grasslands and woodlands composed of the invasive tree *Sapium sebiferum* (Chinese tallow). However, in more arid grasslands, net losses of ANPP have been reported with woody plant encroachment (Aguiar et al. 1996; Huenneke et al. 2002). This suggests that only in more mesic grasslands will ANPP associated with encroaching shrubs and (or) trees offset that of the herbaceous vegetation being displaced.

Our estimates of ANPP within shrub islands are somewhat greater than comparable estimates of *Juniperus virginiana* (eastern red cedar) woodland ANPP on nearby sites in the Flint Hills (Norris et al. 2001b). The high density of *C. drummondii* stems (33 stems·m⁻²) and the relative young age of *C. drummondii* islands used in the present study (6–11 years) suggest this was a period of peak productivity for these shrubs. Our estimate of ANPP within the center of *C. drummondii* islands (615 \pm 63 g C·m⁻²·year⁻¹, Table 1) is very similar to ANPP of *S. sebiferum* woodland on the coastal prairie of Texas (Harcombe et al. 1993) and to that of *Baccharis pilularis* stands invading annual grasslands in California (Hobbs and Mooney 1986). In contrast, our estimate of shrub island ANPP is greater than that reported for *Prosopis glandulosa* (honey mesquite) woodlands in southern Texas (Archer et al. 2001), likely a consequence of differences in growing season climate.

Averaged over location, burn treatment, and year, peak aboveground biomass C within shrub islands was 1651 \pm 174 g C·m⁻² (Fig. 1). The corresponding value within the open grassland sites was 183 \pm 9 g C·m⁻². Due to greater aboveground biomass and the perennial nature of woody vegetation, shrub islands stored more than nine times the amount of C and four times the amount of N aboveground

Table 2. Peak aboveground biomass C (g C·m⁻²) of the grassland and shrub island vegetation types (mean ± SE).

Vegetation type	2000		2001	
	Ecotone	Center	Ecotone	Center
Burned grassland*	241±33b	241±33c	195±16b	195±16c
Burned shrub island	205±25b	1595±236b	634±106b	1792±365b
Unburned grassland*	154±20b	154±20c	140±16b	140±16c
Unburned shrub island	1617±484a	3270±466a	1234±352a	2859±464a

Note: The fire × vegetation type interaction was significant in both the ecotone and center locations in 2000 ($P < 0.01$). Although no plots were burned in 2001, the effect of fire remained evident. Within each location and year, means with different letters are significantly different at $P < 0.05$.

*Grassland plots were not delineated into ecotone and center locations, but biomass data were included in both analyses for comparative purposes.

Table 3. Peak aboveground biomass N (g N·m⁻²) and C:N ratios in the shrub island and grassland vegetation types (mean ± SE).

Vegetation type	2000				2001			
	Ecotone		Center		Ecotone		Center	
	Biomass N	C:N	Biomass N	C:N	Biomass N	C:N	Biomass N	C:N
Burned grassland*	6.1±0.8b	40	6.1±0.8c	40	5.0±0.4b	39	5.0±0.4c	39
Burned shrub island	3.7±0.3b	55	20.3±2.8b	79	9.5±1.3ab	67	22.4±4.3b	80
Unburned grassland*	3.9±0.5b	40	3.9±0.5c	40	3.6±0.4b	39	3.6±0.4c	39
Unburned shrub island	19.7±5.2a	82	37.9±5.3a	86	15.3±3.9a	81	32.5±5.0a	88

Note: The fire × vegetation type interaction was significant in both the ecotone and center in 2000 for aboveground biomass N ($P < 0.01$). Although no plots were burned in 2001, the effect of fire remained evident. For calculation of C:N ratios, biomass C was taken from Table 2. Within each year, means with different letters are significantly different at $P < 0.05$.

*Grassland plots were not delineated into ecotone and center locations, but biomass data were included in both analyses for comparative purposes.

Table 4. Soil organic C (SOC) and total soil N in the center of the grassland and shrub island vegetation types (mean ± SE).

Vegetation type	SOC (g C·m ⁻²)	Total soil N (g N·m ⁻²)
2000 Grassland	4721±213a	350±7a
Shrub island	4740±129a	383±10a
2001 Grassland	4691±168a	355±5a
Shrub island	4699±111a	385±9a

Note: Soil samples were taken to a depth of 10 cm from the center of each plot. Burned and unburned values were combined because there were no significant fire × vegetation type interactions in 2000, and no plots were burned in 2001. Within each year, means with different letters are significantly different at $P < 0.05$.

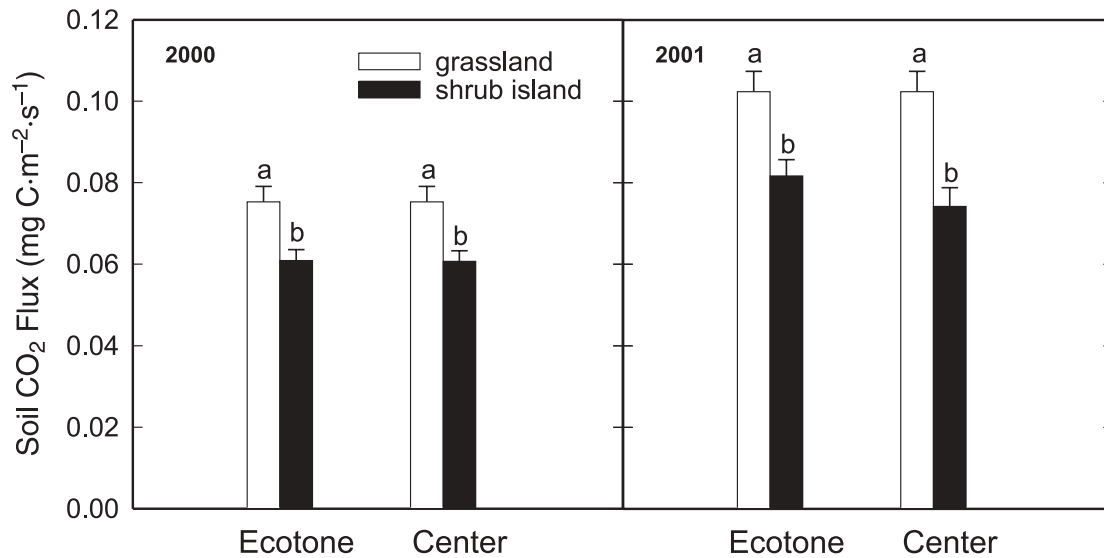
than did the open grassland (Table 3). Furthermore, C:N ratios (Table 3) indicate that shrub islands store up to twice the amount of C aboveground per unit of N relative to open grassland.

The dramatic shift in aboveground C storage with *C. drummondii* encroachment is likely to increase overall C storage within the ecosystem, in spite of any shifts that may occur in belowground C storage. Tallgrass prairies allocate a large proportion of NPP to roots and rhizomes belowground, supporting root:shoot ratios from 2–4 (Risser et al. 1981) and belowground biomass as high as 1914 g m⁻² to a depth of 60 cm (Rice et al. 1998). Conversely, woody species typically allocate much less NPP belowground (Jackson et al. 1996; Cairns et al. 1997). Therefore, *C. drummondii* may support less root biomass than does the prairie, although little is known of differences in root turnover between grasses

and shrubs. Regardless, increases in aboveground biomass with *C. drummondii* encroachment likely outweigh potential losses in belowground biomass, leading to increased C storage in the short term. *Prosopis glandulosa* woodlands in southern Texas are reported to support greater fine and coarse root biomass in the top 10 cm than the remnant grasslands they are replacing (Archer et al. 2001; Hibbard et al. 2001). If such is the case with *C. drummondii*, even greater storage of C can be expected in the short term. It must be stressed, however, that short-term increases in aboveground C may not necessarily equate to long-term C storage. Jackson et al. (2002) reported that gains in aboveground biomass C associated with shrub encroachment in grasslands in the southwestern USA were exceeded by losses in SOC in the wettest sites assessed. In tallgrass prairies, inherently frequent fires may also rapidly oxidize aboveground C to the atmosphere.

We found no detectable differences in either SOC or total N between *C. drummondii* islands and the open grassland in the top 10 cm of the soil profile (Table 4). This is not surprising given the large size of the SOC pool in grasslands and the comparatively short residence time of shrub islands thus far (6–11 years). However, *P. glandulosa* woodlands in Texas savannas supported twice the amount of SOC in the top 10 cm of the soil profile relative to grazed grassland communities (2352 g m⁻² vs. 1165 g m⁻², Archer et al. 2001), as well as greater total soil C to a depth of 1 m (Gill and Burke 1999). Furthermore, Jobbágy and Jackson (2000) in a global analysis of the vertical distribution of SOC reported that SOC in the second and third meters in shrub-

Fig. 2. Seasonal mean soil CO₂ flux (J_{CO_2}) within the ecotone and center of the grassland and shrub island vegetation types in both 2000 and 2001. Grassland plots were not delineated into ecotone and center locations, but J_{CO_2} data were included in both analyses for comparative purposes. Burned and unburned values were combined because there were no significant fire \times vegetation type interactions in 2000, and no plots were burned in 2001. Within each location and year, means with different letters are significantly different at $P < 0.05$.



lands was 77% of that in the top 1 m, in contrast to only 43% for grasslands, a result of the deeper roots of shrubs relative to grasses. This suggests that longer-term sampling and an inventory of SOC throughout the soil profile will be necessary to more accurately assess the impact of *C. drummondii* expansion into these grasslands. One indication that SOC may be altered with shrub encroachment is that J_{CO_2} was significantly lower within shrub islands relative to open grassland (Fig. 2). This reduction in J_{CO_2} is indicative of a change in the cycling of C belowground. Although it may reflect reduced belowground productivity or species-specific differences in root or rhizosphere respiration, it may also reflect lower rates of decomposition, leading to greater C storage within shrub islands relative to the open grassland. Soil temperatures were lower within *C. drummondii* islands (22.3 ± 0.1 °C) relative to the open grassland (24.0 ± 0.2 °C), and this is consistent with presumed reduced rates of organic matter decomposition within shrub islands relative to grassland. The effect of *C. drummondii* on C cycling is, therefore, likely a product of the indirect effects of microclimate and also changes in belowground productivity and decomposition rate, perhaps influenced by substrate quality (Raich and Tufekcioglu 2000).

Conclusion

It is clear from the present study that with continued fire suppression in mesic grasslands, the displacement of herbaceous vegetation by *C. drummondii* and other woody species will substantially alter the dynamics of C and N pools. Although further investigation of belowground processes associated with *C. drummondii* encroachment is warranted, including the dynamics of decomposition, N mineralization, root productivity, and soil C and N, our data document large shifts in productivity and storage of C and N from belowground in open grassland to aboveground in *C. drummondii* islands. Furthermore, changes in the cycling of C with shrub

encroachment will likely affect the cycling of N within the ecosystem, largely through alterations in the rate of N mineralization (Wedin and Pastor 1993). The shift to greater aboveground C and N storage makes these pools more vulnerable to fire relative to stable organic matter complexes belowground in this grassland. Accordingly, the long-term net effect of shrub encroachment on C and N pools within mesic grassland ecosystems remains unresolved, but will be strongly dependent on fire frequency.

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