



Soil C and N responses to woody plant expansion in a mesic grassland

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Abstract

Changes in land management and reductions in fire frequency have contributed to increased cover of woody species in grasslands worldwide. These shifts in plant community composition have the potential to alter ecosystem function, particularly through changes in soil processes and properties. In semi-arid grasslands, the invasion of shrubs and trees is often accompanied by increases in soil resources and more rapid N and C cycling. We assessed the effects of shrub encroachment in a mesic grassland in Kansas (USA) on soil CO₂ flux, extractable inorganic N, and N mineralization beneath shrub communities (*Cornus drummondii*) and surrounding undisturbed grassland sites. In this study, a shift in plant community composition from grassland to shrubland resulted in a 16% decrease in annual soil CO₂ flux (4.78 kg CO₂ m⁻² year⁻¹ for shrub dominated sites versus 5.84 kg CO₂ m⁻² year⁻¹ for grassland sites) with no differences in total soil C or N or inorganic N. There was considerable variability in N mineralization rates within sites, which resulted in no overall difference in cumulative N mineralized during this study (4.09 g N m⁻² for grassland sites and 3.03 g N m⁻² for shrub islands). These results indicate that shrub encroachment into mesic grasslands does not significantly alter N availability (at least initially), but does alter C cycling by decreasing soil CO₂ flux.

Introduction

In the last few decades, there has been increasing concern about the consequences of land-cover change and its effects on the Earth's ecosystems (Vitousek 1994). Indeed, ecosystem function can be altered dramatically if the dominant species are replaced by species of a different growth form (Evans et al. 2001; Naeem et al. 1994). These shifts in plant community composition, often resulting from land management practices, are likely to be associated with changes in soil properties in a manner similar to alterations that occur during succession as species assemblages replace one another (e.g., Ehrenfeld et al. 2001). Plant community composition also has been shown to alter chemical and biological properties of soils within natural and constructed ecosystems (Hooper and Vit-

ousek 1998; Naeem et al. 1994; Tilman et al. 1996; Wedin and Tilman 1990), with alterations in plant lifespan, biomass allocation patterns, and tissue chemical composition having significant effects on ecosystem processes such as soil organic matter and nutrient dynamics (Hobbie 1992).

In many grasslands of the world, there has been a dramatic shift in the composition and turnover of the dominant species due to the invasion or expansion of woody species (Archer et al. 2001). Expansion of woody vegetation has also occurred at the prairie-forest ecotone in central North America following European settlement in the mid-1800s (Abrams 1986; Archer 1994; Knight et al. 1994). Fire suppression related to land management practices has caused landscape fragmentation in these grassland ecosystems and has been considered a primary factor responsible for the increase in abundance of C₃ woody species in C₄-dominated tallgrass prairies (Abrams 1986; Bragg and

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Hulbert 1976; Daubenmire 1968; Hoch and Briggs 1999; Hulbert 1986). Although many woody species are native to tallgrass prairies and are present even in frequently burned grasslands, their historical abundance was low and often limited to stream banks and areas sheltered from fire (Abrams 1986; Hulbert 1986). In the absence of fire, shrub invasion and expansion typically precedes forest development and may facilitate conversion of grasslands to forest (Petranka and McPherson 1979; Weaver 1968). Although many woody species are intolerant of fire, once established, those native to tallgrass prairie can persist with occasional fires and respond vigorously after fire by re-sprouting abundant vegetative shoots (Adams et al. 1982; Briggs et al. 2002; Knapp 1986; McCarron and Knapp in press). Patterns and rates of woody plant expansion into mesic grasslands have been well documented (Abrams 1986; Briggs and Gibson 1992; Bragg and Hulbert, 1976; Briggs et al. 2002; Hoch and Briggs 1999; Kucera 1960; Loehle et al. 1996), and significant changes in soil properties resulting from conversion of grasslands to forest have been reported (Wilson and Kleb 1996). However, the consequences of the initial grass-shrub transition phase in mesic grasslands on soil properties and processes remains to be evaluated.

Soils of the mesic grasslands of the central US (tallgrass prairie) are noted for their relatively high organic content and nutrients per unit volume compared with forest ecosystems (Jenny 1930; Seastedt and Knapp 1993). These conditions exist because the tallgrass prairie generally has high annual net primary productivity (Briggs and Knapp 1995), the dominant C_4 grasses allocate >50% of this productivity belowground, and decomposition rates are relatively slow (Seastedt 1988; Seastedt and Knapp 1993). Additionally, the soil microbial biomass C pool and microbial activity are among the highest in native ecosystems of the United States (Zak et al. 1994) and are 10–50% greater than in agricultural lands (Garcia and Rice 1994). These characteristics result in soil CO_2 flux rates that can be quite high relative to many other ecosystems (Knapp et al. 1998). Forest communities are noted for their comparatively higher plant biomass and soil moisture than in adjacent grasslands (Briggs et al. 1989; Wilson and Kleb 1996), but generally lower soil CO_2 flux (Raich and Schlesinger 1992; Raich and Tufekcioglu 2000).

The primary objectives of this study were to examine patterns of soil CO_2 flux and N availability and mineralization during the conversion of undisturbed

(unburned) C_4 -dominated grassland to a C_3 shrubland. Soil CO_2 flux, or soil respiration (J_{CO_2}), is a product of the combined respiration activities of roots and soil heterotrophs and can be an integrative index of belowground processes and C cycling capacity of soils (Raich and Potter 1995; Raich and Schlesinger 1992).

Material and methods

Study site

Research was conducted at the Konza Prairie Biological Station (KPBS) in northeast Kansas (39°05'N, 96°35'W) during the 1999 and 2000 growing seasons. The KPBS is a 3487-ha native tallgrass prairie preserve located within the Flint Hills of Kansas. Elevation at KPBS varies from 320 to 444 m above sea level. Average annual rainfall is 835 mm with 75% falling between April and September (Hayden 1998). Plant communities are dominated by warm season C_4 grasses *Andropogon gerardii* Vitman, *A. scoparius* Michx. and *Sorghastrum nutans* (L.) Nash (Freeman 1998). Shrubs (C_3), such as *Cornus drummondii* C. A. Mey, *Rhus glabra* L., and to a lesser extent *Prunus americana* Marsh., can be found as monospecific 'islands' within the matrix of grass or as large multispecies communities. Densities of shrub populations are greater along seeps and intermittent lowland streams, becoming less dense with distance from streams, and shrub cover and island sizes tend to increase with a decrease in fire frequency (Briggs et al. 2002). For this study, the clonal shrub species *C. drummondii* was selected due to the large number of monospecific, distinct islands of this species on most watersheds on the KPBS.

Experimental design

Four large (> 140 m²) monospecific *C. drummondii* islands embedded in a matrix of prairie grasses were selected for study. The shrubs and surrounding grassland had not been burned for > 10 years and the islands were estimated to be > 15 years old. Each island was at least 10 m from its nearest neighbor island. Since soil respiration and N mineralization rates can vary with topographic position (Knapp et al. 1998; Turner et al. 1997), care was taken to select islands that were in the same topographic location and same soil type. In each island, a north to south transect was established running from 5 m into the grassland, through

the island and 5 m out the opposite side. Along this transect, 1 × 1-m plots were established within the grassland (two sites, 5 m from shrub island border with 100% grass cover), within the shrub-grass ecotone (two sites, shrub stems approximately 1 m height and 100% grass cover), and at the shrub island center (one site, shrub stems only with no grass cover). Within each plot type per island, nine permanent soil thermocouples were buried, three each at ground level, at 5 cm, and at 15 cm below soil surface.

Soil CO₂ flux and environmental measurements

Soil CO₂ flux, soil temperature and soil moisture were measured approximately bi-weekly during the growing season (April–November) and monthly during the winter months from May 1999 to March 2001 using a dynamic-chamber method described by Norman et al. (1992). At each island, four J_{CO_2} measurements were made adjacent to each of the permanent plots (eight measurements for shrub center plots). The system employed a LI-6200 portable closed-flow gas exchange system (Li-Cor, Lincoln, NE, USA) equipped with a cylindrical chamber with a 850-cm³ volume and a 40.7-cm² circular area exposed to soil surface. Measurements were made by sampling for ambient CO₂ concentrations at the soil surface first and then pressing the chamber lightly into the soil to form a seal. Care was taken not to excessively disturb the soil, because it can cause a rapid release of CO₂ resulting in an artificially high estimation of CO₂ soil flux. Additionally, since standing detritus and soil surface litter can be significant in unburned grasslands (Knapp and Seastedt 1986), all standing dead biomass was temporarily moved aside and the chamber was placed between plants such that no living biomass was within the chamber. Soil CO₂ flux was measured until chamber CO₂ concentration had increased by 10–20 ppm over approximately 15–30 s intervals. Pressure equilibrium between the air and the chamber was maintained by a 0.2-cm inside diameter tube (10.5 cm long) that vented the chamber to the atmosphere (Norman et al. 1992). Soil temperature was measured using a digital thermometer (Omega Engineering, Stamford, CT, USA). Soil moisture was measured within all permanent plots ($n=5$) integrated between 0–15 cm soil depths using a HydroSense soil volumetric water content measurement system (Campbell Scientific, Logan, UT, USA). All measurements were made between 11:00 and 15:00 h CST, to minimize diurnal fluctuation, and measurements were not

made during periods of rain or when snow covered the soil surface. Data for both years were combined to produce average seasonal responses at monthly intervals. Annual J_{CO_2} was calculated by summing the products of monthly mean flux rates and the number of days within each month.

Inorganic soil N and net N mineralization

In situ net N mineralization was measured four times during the 2000 growing season and once during the 2000–2001 winter using a modification of the buried soil core technique (Raison et al. 1987). Two sharpened PVC (polyvinyl chloride plastic) cores (5 cm internal diameter × 20 cm long) were driven 15 cm into the ground within 2 m of each plot (four around island center plots) per island. Small holes were drilled into the aboveground portion of each core to allow for gas exchange, and lids were placed over cores to minimize leaching losses. Prior to insertion of cores, litter was moved to the side and then replaced after core placement. Cores were incubated in the field for approximately 40 days during the growing season and 61 days during the winter. At the beginning of the incubation period, two similar sized soil cores per plot were taken adjacent to the PVC cores to measure initial soil inorganic N content. Each field moist soil core was sieved through a 4-mm screen, and a subsample was extracted with a 2 mol L⁻¹ KCl solution. Concentration of inorganic N (NH₄-N and NO₂/NO₃-N) for both the initial N extraction ($N_{initial}$) and the final N extraction from postincubation cores (N_{final}) were determined colorimetrically using an Alpkem FlowSolution analyzer (OI Analytical, College Station, TX, USA). A second subsample of soil from each core was dried at 60 °C to determine gravimetric soil water content, and to calculate extractable soil N concentrations as N mass per unit mass of dry soil. Extractable soil N was converted to mass per unit area using an average soil bulk density of 1 g cm⁻³ (Seastedt and Ramundo 1990). Net N mineralization rates were calculated as $(N_{final} - N_{initial})/(\text{incubation time in days})$ for each incubation period. Cumulative N mineralized over the growing season (May–November) was calculated by summing net N mineralization rates from each incubation period, and interpolating values for the periods between incubations.

Total soil C and N content was measured during November 2000 by collecting soil cores (5 cm diameter × 5 cm deep), three each from the shrub center, shrub-grassland ecotone, and adjacent grassland of the

four shrub islands and two additional shrub islands having similar soil types. Individual soil cores were sieved through a 4-mm screen, dried at 60 °C, and analyzed for total C and N content using a Carlo-Erba C/N analyzer (Carlo-Erba, Milan, Italy).

Data analysis

For J_{CO_2} , soil temperature, and soil moisture, bi-weekly measurements averaged into monthly values. Analysis of variance (ANOVA) with repeated measures was used to assess plot, location, and date as main effects for each response variable using SAS (SAS 1989). Within each month, means were separated using the least significant difference means comparison. Shrub center and shrub-grassland ecotone locations were not significantly different for any of the measured variables, thus data for these areas were pooled.

Results

Soil CO₂ flux

Average maximum monthly values of midday soil CO₂ flux were ~16% greater in open undisturbed grassland than in shrub islands (Figure 1), with grassland rates typically greater during the April through November growing season. This resulted in a greater annual cumulative J_{CO_2} in grassland vs. shrub communities (5.84 versus 4.78 kg CO₂ m⁻² year⁻¹, respectively; $P=0.0031$). This difference in J_{CO_2} , however, was not reflected in differences in soil organic C between sites (47.9 ± 0.94 g kg⁻¹ all sites combined).

Soil CO₂ flux was strongly correlated with soil temperature, at all soil depths, for both shrub and grassland locations (Figure 2a) with the greatest variance in J_{CO_2} explained by soil temperatures at 5 cm. Shrub communities had greater variability in J_{CO_2} at a given temperature, which resulted in a smaller coefficient of determination ($r^2 = 0.70$) compared to grassland sites ($r^2 = 0.88$). Nevertheless, for a given soil temperature, J_{CO_2} was greater in grasslands than beneath shrub islands ($P=0.0316$, with no difference between slopes $P = 0.9979$) although there were no seasonal differences in soil temperature between the two sites.

There was also a significant non-linear relationship between soil moisture and J_{CO_2} both in grassland and beneath shrub islands (Figure 2b); however, this relationship was most apparent when non-growing

season measurements (November through April) were removed from the analyses. Only for shrub islands was J_{CO_2} significantly related to soil moisture when winter values were included ($r^2 = 0.18$, $P = 0.003$). Additionally, soil moisture (integrated between 0 and 15cm) was only significantly different between sites during summer months, at which time grasslands had ~10% greater soil moisture than shrub sites. When only growing seasonal values were used, J_{CO_2} in shrub islands was lower compared to grassland sites for a given level of soil moisture (Figure 2b).

N-availability

Seasonal patterns of extractable inorganic N indicated greatest N availability in the spring, with a decline throughout the growing season (Figure 3a). There were no significant differences between sites for total N (3.7 ± 0.07 g kg⁻¹ all sites combined) or for seasonal inorganic N, NH₄-N, and NO₃-N, except for one sampling date (August 11). In contrast, N mineralization rates were significantly greater in grasslands during the spring (Figure 3b), but these differences were not apparent during the rest of the study. Seasonal patterns of N mineralization were also greatest during the spring and early summer and decreased by the end of the growing season. There was a considerable amount of variability in N mineralization within sites, which resulted in no overall difference in cumulative N mineralized during the study (4.09 g N m⁻² for grassland sites and 3.03 g N m⁻² for shrub islands).

Discussion

The encroachment of shrubs into arid and semi-arid grasslands is often associated with higher resource concentrations beneath shrubs than in the dominant grass matrix and/or open spaces, creating 'islands of fertility' (Belsky 1994; Schlesinger et al. 1990; Scholes and Archer 1997). In more mesic grasslands, patterns of increased N and C cycling have been noted for encroaching forest communities as well (Mordelet et al. 1993; Reich et al. 2001; Wilson 1993; Wilson and Kleb 1996). However, in this study, a shift in plant community composition from grassland to shrubland resulted in a 16% decrease in annual soil J_{CO_2} for shrub dominated sites with no differences in total soil C, N availability, or N mineralization between sites. These results are consistent with two other recent studies in a nearby tallgrass prairie that assessed the effects

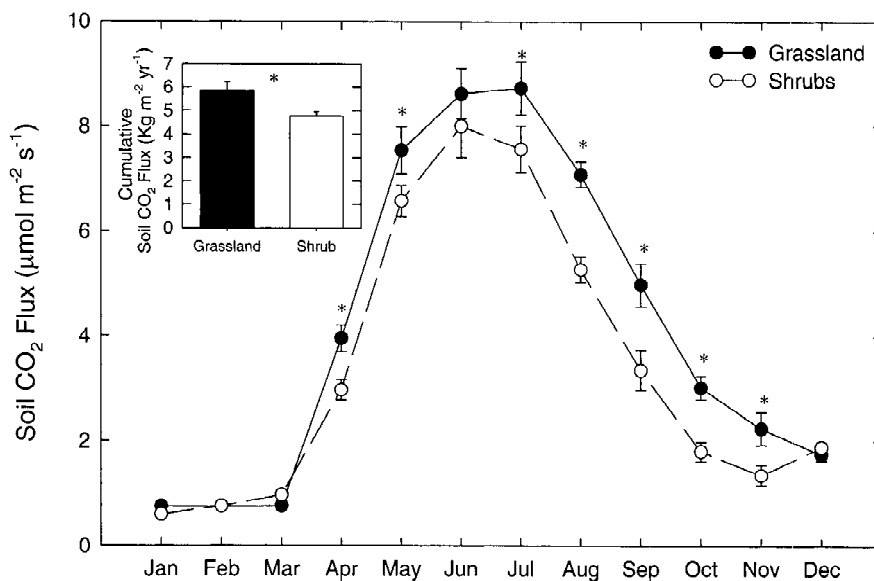


Figure 1. Seasonal course of soil CO₂ flux (J_{CO_2}) from undisturbed grassland sites and beneath *Cornus drummondii* shrub islands in tallgrass prairie. Values are averaged for monthly periods over two growing seasons (1999–2000). Inserted panel depicts cumulative annual J_{CO_2} for grassland and shrub sites over both growing seasons. Asterisks represent significant differences between adjacent upper and lower data points ($P < 0.05$) and vertical bars represent ± 1 SE.

of juniper (*Juniperus virginiana*) forest invasion on C and N cycling. Smith (2001) reported a decrease of 38% in growing season soil CO₂ in forested sites compared to adjacent grazed grassland sites, although there were no differences in total soil C between sites. In a related study, Norris (2000) found that after >40 years of forest establishment there were only minor differences in N availability or N mineralization between forest and grassland sites.

In arid grasslands, the increase in soil resources beneath shrubs and their loss from intershrub spaces are partly the result of a redistribution of resources by wind and water (Kieft et al. 1998). Schlesinger et al. (1990) suggest that this increase in soil resource heterogeneity is likely to provide positive feedback that will increase the dominance of shrubs within these arid grasslands. Conversely, nitrogen availability in the tallgrass prairie is strongly dependent on fire frequency. In the absence of fire, grass productivity becomes constrained by light limitation due to increases in leaf litter, which results in lower productivity of grasses and an increase in available soil N relative to burned sites (Seastedt and Knapp 1993; Turner et al. 1997). Shrubs and woody species are less limited by light penetration of the detrital layer and can take advantage of increased N resources in unburned grasslands (McCarron and Knapp, in Press). Reich et

al. (2001) found in the North American oak savanna, that as fire frequency decreased, increases in woody species and N availability resulted in a linear increase in aboveground net primary productivity. They suggest that high woody species dominance leads to high rates of N cycling and further alters resource dynamics in grasslands resulting in a positive-feedback for woody species dominance. The shrub islands used in this study were approximately 15 years old and may have occupied the landscape for too short a period to cause any measurable change in N availability in this grassland system. This study, along with the two similar studies of >40-year-old Juniper forests, suggest that for this grassland, a shift from a C₄-dominated ecosystem to one more dominated by C₃ shrubs and trees, is not associated with an increase in available soil N, at least over several decades.

Soil CO₂ flux is the combined respiration of soil heterotrophs and roots and has been shown to be correlated with soil temperature, moisture, organic content of the soil, and activities of the microbial biomass and roots themselves (Buchmann 2000; Davidson et al. 1998; Lloyd and Taylor 1994; Luo et al. 2001; Mielnick and Dugas 2000; Raich and Potter 1995; Rustad et al. 2000). In this study, we found a significant correlation of J_{CO_2} with both soil temperature and moisture, with soil CO₂ flux rates consistently

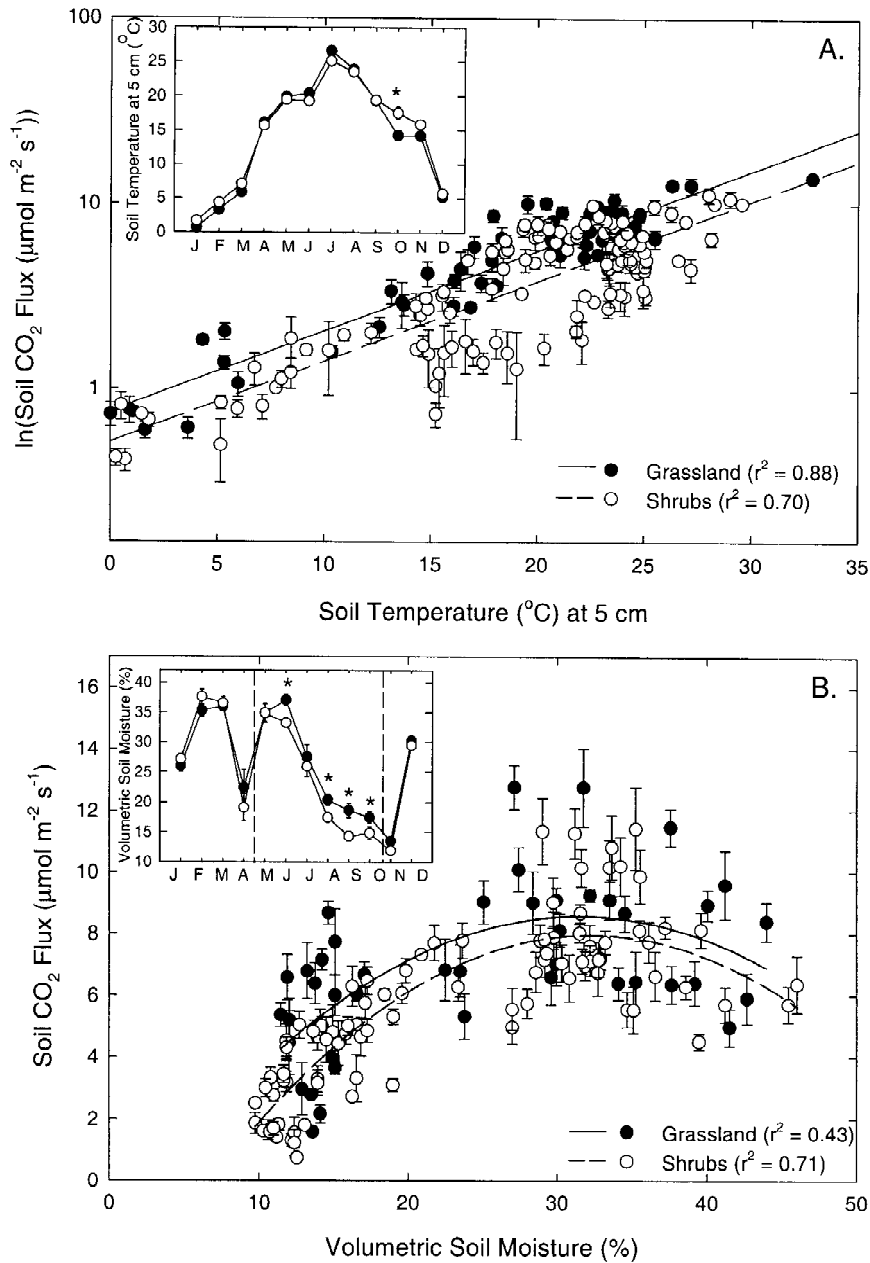


Figure 2. Relationship between soil CO₂ flux (J_{CO_2}) and soil temperature at 5 cm (A) and growing season volumetric soil moisture (B) for grassland sites and *Cornus drummondii* shrub islands. Inserted panel depicts monthly soil temperature at 5 cm (A) and monthly volumetric soil moisture (B; 0–15 cm) for grassland and shrub sites over both growing seasons. Asterisks represent significant differences between adjacent upper and lower data points ($P < 0.05$) and vertical bars represent ± 1 SE.

lower beneath shrub islands. The relationship between J_{CO_2} and soil temperature was best described by an exponential function, which is similar to results reported for other studies (Fang and Moncrieff 2001; Knapp et al. 1998; Lloyd and Taylor 1994; Luo et al. 2001; Mielnick and Dugas 2000). Grassland sites

were generally more sensitive to changes in soil temperature than shrub sites and this was more apparent with increasing temperatures. The effects of temperature and water content on soil respiration are often statistically confounded, however field studies have demonstrated that the temperature effect is often more

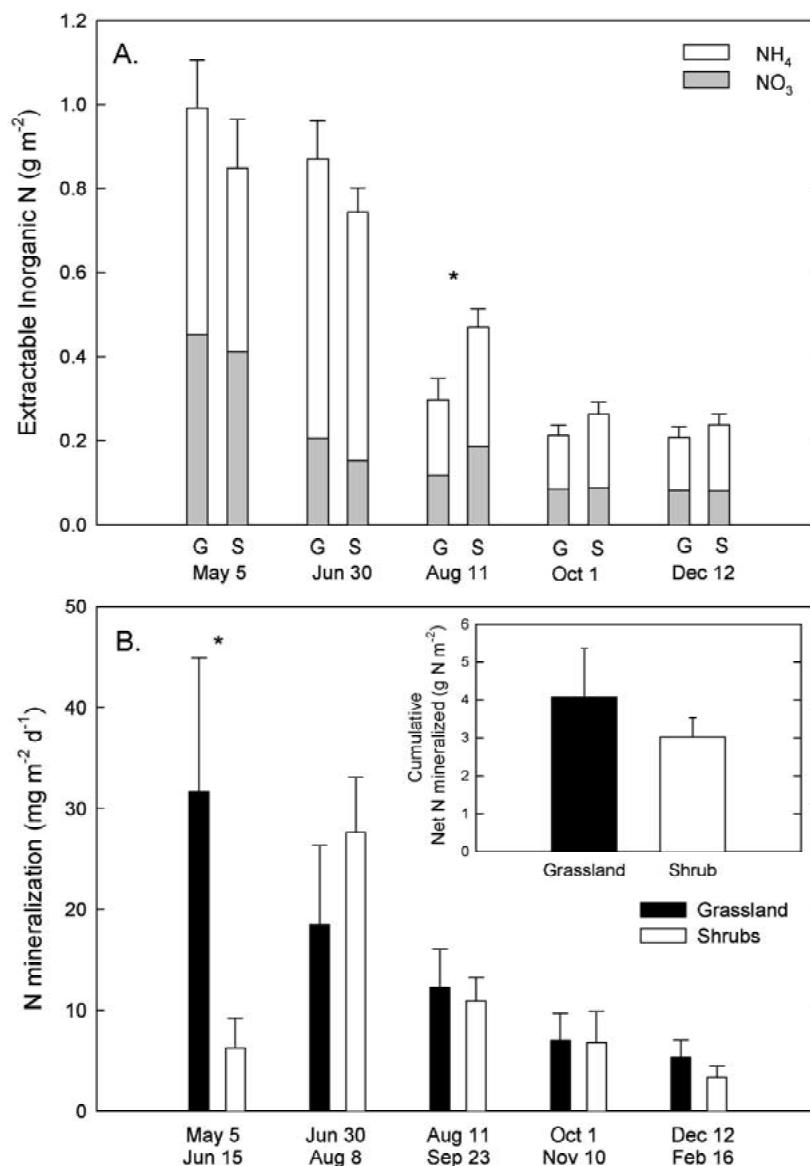


Figure 3. Extractable inorganic N (NH₄-N and NO₃-N; A) and N mineralization rates (B) for grassland sites and *Cornus drummondii* shrub islands. Inserted panel (A) depicts seasonal cumulative net N mineralization for grassland and shrub sites. Asterisks represent significant differences between adjacent upper and lower data points ($P < 0.05$) and vertical bars represent ± 1 SE.

pronounced than that of water (Davidson et al. 1998, 2000). During the winter, this was evident when low soil temperatures had a greater effect on J_{CO_2} than soil water content. When only growing season values were used, the relationship between soil moisture and J_{CO_2} was best fit with a quadratic function. This is similar to the results of Mielnick and Dugas (2000) for tallgrass prairies; J_{CO_2} was greatest at intermediate soil moistures and decreased under both dry condi-

tions (<20% soil moisture) and wet conditions (>45% soil moisture). Soils were usually wetter at grassland sites, however. Kucera and Kirkham (1971) and Herman (1977) both estimated that ~30–40% of the total J_{CO_2} in tallgrass prairie was due to root respiration. Since there were no differences in N mineralization rates (a microbial process) but there were differences in J_{CO_2} (a combined plant and microbial process) this reduction in J_{CO_2} in shrub dominated sites may have

resulted from a shift from fine roots systems characteristic of grassland species, to those of more coarse roots associated with woody vegetation (Jackson et al. 1996).

Differences in land management practices such as fire frequency and grazing can produce considerable heterogeneity in annual J_{CO_2} within grassland systems (Knapp et al. 1998; Raich and Potter 1995; Raich and Tufekcioglu 2000). Raich and Tufekcioglu (2000) found in a paired comparison of published daily flux rates, that there was a ~20% decrease in J_{CO_2} from soil in areas occupied by woodland species compared to grassland systems. In our study, annual estimates of soil CO_2 ranged from 5.84 kg CO_2 m⁻² year⁻¹ in unburned grasslands to 4.78 kg CO_2 m⁻² year⁻¹ in shrub dominated sites. Knapp et al. (1998), reported similar values for unburned grasslands (5.29 kg CO_2 m⁻² year⁻¹), which on average were 30% lower than for annually burned grasslands (7.31 kg m⁻² year⁻¹). Although J_{CO_2} was lower in sites with shrubs, these rates were still greater than in many forested sites (2.6–3.11 kg CO_2 m⁻² year⁻¹, Davidson et al. 1998; 2.7–3.4 kg CO_2 m⁻² year⁻¹, Hanson et al. 1993; 1.9 kg CO_2 m⁻² year⁻¹, Smith 2001). Because shrub invasion and expansion often precedes forest development (Petranka and McPherson 1979; Weaver 1968) it might be expected that their influence on soil processes would be intermediate between grassland and forest.

In summary, with the absence of fire there has been an increase in the abundance of woody species in central US grassland ecosystems. Results from this study, indicate that shrub encroachment into undisturbed tallgrass prairie does not alter N availability (at least initially), but does change C cycling by decreasing soil CO_2 loss. These patterns were also clearly evident at the shrub-grass ecotone (data not shown), suggesting soil C processes are affected very early during this transition from grassland to shrub/woodland. Grasslands are one of the most widespread vegetation types worldwide, covering approximately 24 million km², and accounting for around 10–30% of the world's carbon (Anderson 1991). Thus, even modest changes to these grasslands may have significant implications to global C cycling (e.g., Jackson et al. 2002).

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