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VEGETATION-MEDIATED CHANGES IN MICROCLIMATE REDUCE SOIL RESPIRATION AS WOODLANDS EXPAND INTO GRASSLANDS

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Abstract. This study compared annual and growing-season in situ soil respiration and soil C cycling in paired juniper woodland and C_4-dominated grassland sites in eastern Kansas (USA) to determine if, under similar edaphic and regional climate conditions, vegetation change alters soil CO_2 dynamics. We found marked differences in soil respiration related to vegetation: Growing season mean woodland soil respiration rates (4.6 μmoles·m^{-2}·s^{-1}) averaged 38% less than paired grassland sites. Soil moisture did not explain the difference in soil respiration between woodlands and grasslands. Soil temperatures at the 10-cm depth were 5°C cooler in woodlands during the growing season and significantly different between woodlands and grasslands throughout the year, explaining most of the low soil respiration in woodlands. However, there were subtle intrinsic differences in the response of soil respiration to temperature between woodlands and grasslands: Woodland and grassland respiration response was significantly different at the $P = 0.05$ level, also indicated by a grassland Q_{10} of 2.4 compared to 2.2 in woodlands. We found no significant differences between woodlands and grasslands in long-term (82-week) laboratory incubations of potentially mineralizable soil C and short-term incubations for microbial biomass C. Similarly, root biomass did not differ between woodlands and grasslands and could not explain the lower in situ woodland soil respiration. Thus, vegetation-mediated reduction in soil temperature under the canopy explained much of the lower in situ woodland soil respiration. Lower soil respiration in the woodland resulted in an annual flux of 533.6 (±21.7) compared to 858.4 (±14.5) g C·m^{-2}·yr^{-1} in grasslands, nearly 38% lower in the woodland (means ± 1 SE). Assuming root respiration is 50% of soil respiration, we estimate that the turnover of woodland soil C stocks may be slowed by 15 years relative to grassland. This suggests that, if juniper expansion (now occurring across nearly 5 million hectares in the Great Plains) proceeds to canopy closure, annual soil C flux may be potentially reduced by as much as 19×10^6 Mg of C below C flux rates that occurred historically from tallgrass prairie soils.

Key words: afforestation; soil carbon cycling; soil respiration; tallgrass prairie; woody encroachment.

INTRODUCTION

Soil respiration is a major component of the terrestrial carbon (C) cycle (Schlesinger 1977, Raich and Schlesinger 1992, Raich and Potter 1995). Indeed, the current global soil respiration flux to the atmosphere is estimated to be >10 times that of annual fossil fuel emissions (Schlesinger 1997, Schlesinger and Andrews 2000). Thus, understanding controls over belowground cycling of C becomes critical if we are to successfully predict soil respiration responses to global climate change (Schimel et al. 2001). Environmental factors, such as soil temperature and moisture (Rayment and Jarvis 2000, Fang and Moncrieff 2001, Thornley and Cannell 2001), and substrate quality (Tewary et al. 1982, Raich and Potter 1995) are known to control the rate of soil CO_2 efflux (Rustad et al. 2001) and litter decomposition (Norris et al. 2001*a*). Thus, a major shift in the type of vegetation (e.g., grassland to woodland) can be expected to change some or all of these environmental determinants of soil C cycling.

The expansion of juniper (*Juniperus virginiana* L.) in the prairies of North America provides a unique opportunity to study the role of vegetation physiognomy in regulating soil C cycling. In fact, the expansion of woody vegetation into grasslands is occurring throughout the world (Archer et al. 1995, Moleele and Perkins 1998, Fang et al. 2001, Hibbard et al. 2001, Pacala et al. 2001, Jackson et al. 2002), and recent reports indicate that woody plant encroachment in North America may comprise a part of the missing terrestrial C sink (Houghton et al. 1999, Pacala et al. 2001, Scholes and Noble 2001). Thus, studies of the effects of woody encroachment on soil C efflux become critical for an improved understanding of the relationship among terrestrial C cycles, atmospheric CO_2 concentrations, and vegetation change (Archer et al. 1995, Raich and Potter 1995, Gaudinski et al. 2000, Schlesinger and Andrews 2000).

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In spite of the potential importance of juniper and other woody plant encroachments in modifying ecosystem dynamics, few studies have specifically addressed the belowground consequences of encroachment. Our study is one of few (Hibbard et al. 2001, Jackson et al. 2002, Hibbard et al. 2003) that quantify alterations in belowground C cycling resulting from woody plant encroachment into Great Plains and southwestern U.S. grasslands. Most studies that have compared woodland and grassland respiration from geographically and climatically different areas show lower soil respiration in woodlands relative to grassland. Raich and Potter (1995) reported annual soil C flux in temperate evergreen woodlands to be 53–59% that of perennial grasslands. Raich and Tufekcioglu (2000), found grasslands to have >20% higher soil respiration rates than woodlands, with coniferous woodlands lower than both grasslands and deciduous woodlands. Another study showed 15% higher soil CO_2 efflux rates under bunchgrass vegetation than in nearby pine woodlands (Kaye and Hart 1998).

This project expanded on these studies to examine soil CO_2 fluxes as woody species encroach into grasslands with the same regional climate and similar edaphic conditions. *J. virginiana* has been expanding throughout the lower Midwest in the last four decades (Graf et al. 1965, Owensby et al. 1973, Engle et al. 1987, Gehring and Bragg 1992, Schmidt and Wardle 1998) in response to fire suppression due to suburbanization (Hoch et al. 2002) and land fragmentation. Indeed, in much of the eastern Great Plains and lower Midwest, precipitation is adequate (700–1000 mm at Konza Prairie, Manhattan, Kansas, USA) to support woodland, provided that fire is suppressed (Hayden 1998).

The encroachment of woodland into tallgrass prairie alters many aspects of the physical and biological environment. Ecological changes reported to accompany juniper expansion include a reduction in native grassland species (Bragg and Hulbert 1976, Engle et al. 1987, Smith and Stubendieck 1990, Gehring and Bragg 1992), lower intensity of solar radiation at the soil surface (Hoch and Briggs 1999), an accumulating litter layer (Norris et al. 2001*a*), and changes in soil chemistry and physical properties (Spurr 1940, Broadfoot 1951). Juniper expansion into tallgrass prairie has been shown to reduce herbaceous plant diversity and its effect is directly proportional to juniper canopy coverage (Hoch et al. 2002). On the other hand, juniper encroachment increased ecosystem C sequestration. At our paired woodland-grassland sites, aboveground productivity in closed-canopy juniper woodland is double to triple that of tallgrass prairie, and aboveground biomass C stocks are from 10- to 20-fold that of tallgrass prairie (Norris et al. 2001*b*). This study, set in the Flint Hills of northeastern Kansas, USA, compared soil C cycling (in situ soil respiration and laboratory indices) in closed-canopy (40–60 year old) woodlands and tallgrass prairie to determine if vegetation type and fire suppression alters belowground C cycling. For our study, we used ''over the fence'' site comparisons of soil C cycling to minimize the confounding effects of topography and soil type on soil C cycling. Our objectives were to compare instantaneous and annual in situ soil respiration rates in woodlands and grasslands, and to evaluate the possible mechanisms behind differences in soil respiration.

Based on earlier studies (Raich and Potter 1995, Kaye and Hart 1998), we hypothesized that grassland soil respiration rates would exceed those of woodlands. Specifically, we expected that the woodland canopy would alter microclimatic factors such as soil temperature and moisture, because both autotrophic (root) and heterotrophic (microbial) respiration are closely tied to soil physical and environmental conditions (Keith et al. 1997, Boone et al. 1998, Craine et al. 1999, Hanson et al. 2000). Secondly, we hypothesized that there would be differences between woodland and grassland soil heterotrophic activity due to poor substrate quality of woodland litter (Neill et al. 1996, Norris et al. 2001*a*). Thus, we also carried out long-term (82 week) laboratory soil incubations to assess differences in potentially mineralizable C between woodland and grassland soils. Finally, due to the dominance of belowground productivity in tallgrass prairie (Rice et al. 1998, Gill et al. 1999, Johnson and Matchett 2001), we hypothesized that lower root biomass would occur in woodlands relative to prairie.

Materials and Methods

Paired woodland and grassland sites

Our studies were conducted in the Flint Hills of northeastern Kansas, USA (39° N, 96° W), where climate is temperate mid-continental (mean 13°C), with July mean temperature of 27°C and mean January minimums of −3°C. Precipitation averages 835 mm annually, with 75% falling during spring and early summer (Hayden 1998). Rainfall and soil conditions will support woodland if fire is suppressed, or row-crop agriculture if soils are plowed (Appendix A). However, the remaining Flint Hills prairies are too rocky and sloping for cultivation, and are now being threatened by woody plant encroachment. A mix of C_4 tallgrasses—*Andropogon gerardii* (big bluestem), *Schizachrium scoparium* (little bluestem), *Sorghastrum nutans* (Indiangrass), and *Panicum virgatum* (switchgrass)—dominate the native vegetation along with other grasses and forbs (Hartnett and Fay 1998).

Our approach for studying vegetation-induced changes in soil C dynamics was to make side-by-side comparisons of in situ soil respiration in three woodlands and grasslands under similar edaphic condition, aspect and slope. All three grasslands were managed with long-term grazing and burning, and were grazed and burned twice between 1996 and 2000. The closed-

canopy woodland sites are on areas formerly covered with tallgrass prairie. Presently, there is minimal understory in these woodlands. The age of the woodland at each site was initially determined using aerial photographs from the Natural Resources Conservation Service (Natural Resources Conservation Service Offices, Federal Building, Manhattan [Cowley County], Kansas, USA). Tree increment coring corroborated ages (Norris et al. 2001*b*).

The study sites are described in detail elsewhere (Norris et al. 2001*a*, *b*, Hoch et al. 2002, Smith and Johnson 2003). Mean tree density at these closed-canopy woodland sites is 1498 trees/ha and the mean basal area is 36 m^2/ha (Norris et al. 2001*a*). The first woodland–grassland site (elevation 119 m above sea level) included a 40-year-old woodland near the airport west of Manhattan, Kansas (referred to as the Scenic Drive site). Both the woodland and grassland were on sloping, cherty silt loam, a clayey–skeletal, montmorillonitic, mesic Udic Argiustoll (U.S. Department of Agriculture Soil Conservation Service 1975). The woodland at the second site (elevation 366 m, referred to as the Randolph site) was also 40 years old. Both the woodland and grassland soils at this location were silty clay loams: fine, mixed, mesic Pachic Argiustolls, and fine, mixed mesic Udic Haplustolls, respectively. Soil depth at this site was >1 m. At these sites, property fences separated the woodlands and grasslands. At the third site (elevation 366 m, referred to as the Tuttle Creek site), the 60-year-old woodland and native grassland were on adjacent hills with the same silty clay loam soil, a fine, mixed, mesic Udorthentic Haplustoll (U.S. Department of Agriculture Soil Conservation Service 1987). All sites were located on well-drained uplands, and unconsolidated rock occurred below 25 cm at two sites.

Previous study of the soils at these sites indicated that soil organic carbon (SOC) derived from juniper trees has permeated the surface layers of the original prairie-derived SOC (Smith and Johnson 2003). Isotopic study of the C^{12}:C^{13} ratios at grassland sites reflected C isotopic ratios that were enriched in C^{13} inputs from prairie vegetation ($-15.6‰ \pm 0.37$, at 0–2.5 cm). In contrast, woodland soils strongly reflected juniper C isotope ratios ($-20.5‰ \pm 0.42$, at 0–2.5 cm). Furthermore, both woodland and grassland soils showed ratios enriched with C^{13} at depth. We were able to use these contrasting C ratios to show that woodland soils developed over former prairie contained 42% juniper-derived SOC from 1–2.5 cm depth, which decreased to 6% at 25 cm. Therefore, we have clear evidence that juniper encroachment is altering SOC at these sites.

In situ soil CO_2 flux, soil temperature, and moisture

From June 1999 through November 2000 we measured soil respiration for a total of 14 dates in 1999 and 13 dates in 2000, with more measurements obtained during the growing season (we arbitrarily designate the ''growing season'' as being from mid-April through mid-October, typically considered the frost-free period of the year in eastern Kansas). Carbon dioxide efflux from the soil surface of the three closed-canopy woodlands was measured along 200-meter transects. Grassland transects were established that mirrored the direction, length, slope, and aspect in each woodland.

We collected clusters of four measurements at five locations along each woodland and grassland transect, for a total of 20 per transect. Measurements were obtained at random positions within a 2 m^2 area in each cluster to better capture the heterogeneity of the grasslands. Measurements were made in new, random locations at each measurement date. Because of the large number of measurements obtained and distance between sites, we could not obtain respiration at the same time each day. Instead we alternated the location of the first measurements of the day between woodland and grassland. Measurements at each woodland occurred within four hours of those from its paired grassland. Measurements were taken between 09:00 and 17:00 h.

Soil CO_2 flux was measured using a dynamic-chamber method (Norman et al. 1992). The system utilized a cylindrical chamber (850 cm^3) enclosing a 40.7 cm^2 circular area of soil surface. The chamber was designed in the micrometeorology laboratory of Dr. Jay Ham, Kansas State University, under the advisement of Li-Cor (Li-Cor, Lincoln, Nebraska, USA). The chamber was coupled to a closed-flow gas exchange system (Li-Cor 6200), that circulated air from the infrared gas analyzer to the chamber; CO_2 from the soil increased the concentration in the chamber. Pressure between the air and the chamber was maintained at equilibrium by a 0.2 cm inside diameter tube (10.5 cm long) that vented the chamber to the atmosphere (Norman et al. 1992).

During the measurements, the bottom edge of the chamber was gently pressed against a foam rubber gasket to improve the seal with the litter layer, and the chamber volume was adjusted accordingly. Grassland measurements were made over minimal litter accumulations due to frequent burning. At the grassland sites, the chamber and gasket were placed between plants so that no green biomass was enclosed within the chamber during the measurement. Twenty seconds after the chamber was placed, we made three consecutive 22-s measurements of CO_2 flux, and the three measurements were averaged to comprise one of the four measurements in each cluster. Concurrently with each respiration measurement, we recorded soil temperature from a soil thermometer inserted in the soil to 10 cm. Soil cores (2.5 cm diameter) were collected, sealed in plastic bags, and taken to the laboratory to determine gravimetric moisture content (using 105°C oven-drying).

Long-term soil incubations and potentially mineralizable C

A total of 60 soil samples were collected in May 2000 from transects in each woodland and paired grassland site, from 0–10 and 10–20 cm depths. We chose these depths because previous isotopic studies (Smith and Johnson 2003) showed that most of the isotopic signature from the juniper C was found in the shallow surface layer (0–10 cm depth). To remove plant fragments (leaves, twigs, and roots) and rocks while maintaining aggregate structure of the soil, samples were sieved to pass through a 4-mm mesh. The soils were placed on top of a glass fiber filter contained in Falcon funnels (Falcon sterile bottle top filters, Becton-Dickinson, Franklin Lakes, New Jersey, USA). The soils and Falcon funnels were placed inside glass mason jars for long-term incubation. Forty-five grams of soil (field moist) were used in the 0–10 cm depth incubations, and 60 grams in 10–20 cm depth incubations. (Note that the organic horizon in the woodland soil cores was not incubated; incubated samples were mineral horizons only). The grassland and woodland soils were maintained at uniform soil moisture and temperature (60% moisture, 25°C).

Soils were leached periodically. Prior to incubation (and thereafter monthly) the samples were leached with 50 mL of 0.01 mol/L $CaCl_2$ solution (Ajwa et al. 1998). For leaching, the Falcon funnels were fitted with Gelman membrane filters (0.45 μm). After 15 minutes, the $CaCl_2$ solution was filtered under vacuum. All samples were adjusted to 60–63% moisture after leaching. Falcon funnels were set into 490 mL glass mason jars and incubated at 25°C.

Heterotrophic microbial respiration was determined at weeks 2, 4, 6, 14, 19, 31, 46, and 82 from the start of the incubation. Respiration rates were determined with a series of three syringe measurements of CO_2 concentrations in the headspace of the jars. Carbon dioxide concentrations were determined using a Shimadzu GC-14A gas chromatograph (Shimadzu North America, Columbia, Maryland, USA) equipped with a thermal conductivity detector. Standards for CO_2 analyses on the gas chromatograph were 300 and 10 000 ppm CO_2 in N_2 gas (Scott Specialty Gases, Plumsteadville, Pennsylvania, USA). Rates were calculated as the slope of change in CO_2 over time. Starting concentrations of CO_2 in the incubation jars was typically 2000 ppm. R^2 values for change in CO_2 concentration over time were >0.99.

Microbial biomass C

Ten soil cores (5 cm diameter, 0–10 cm depth) from each woodland and grassland were collected in June and October 1999 (early and late growing season, respectively) for microbial biomass C determination. The results for potentially mineralizable C from a shorter incubation were the same as the results of the long-term incubation, and so only the long-term incubations are shown. Samples were processed as those for the long-term incubations. To assess differences in microbial biomass, we determined microbial biomass C by a direct extraction method (Vance et al. 1987). Chloroform was filtered through alumina powder to remove ethanol contaminants. A vial containing chloroform was placed into each glass mason jar, sealed, and evacuated with a vacuum pump to promote boiling of chloroform. The soils were allowed to fumigate for 24 h. Soils from both fumigated and unfumigated control jars were extracted by shaking for two hours with 100 mL of 0.5 mol/L K_2SO_4, and then filtered through Gelman 0.45 μm membrane filters. The K_2SO_4 solution was analyzed for dissolved organic C (DOC) on a Shimadzu Total Organic Carbon (TOC) 5000. Because both grassland and woodland soils were originally of the same grassland origins, we used an efficiency factor of 0.41 for both prairie and woodland soils (Anderson and Domsch 1978).

Root biomass

Living roots removed from soil cores used for microbial biomass determination provided an estimate of root biomass in woodlands and grasslands. Roots were washed, dried, sorted by size (0–1 and 1–2 mm diameter), and weighed. Living roots were distinguished by their light color and firm texture. Rhizomes were removed from grassland soil samples and processed in the same manner.

Statistical analysis

In situ soil respiration, soil temperature, and moisture were grouped into growing season and non-growing season data and analyzed by ANOVA (SAS Institute 2001) and tested for site and treatment × site interactions. In addition, we tested for comparison of slopes in the temperature response of soil respiration in woodlands and grasslands using SAS analysis of covariance. SAS multiple regression was also used to analyze the combined effects of temperature and moisture on soil respiration. For all the statistical analysis of in situ soil respiration rates, data were $\log_{10}$ transformed before analysis. Soil moisture data was transformed before analysis using the arc sine of the square root of the percent gravimetric soil moisture. Root biomass and microbial biomass C were analyzed using both ANOVA and *T* tests to detect significant differences. The long-term soil incubations were analyzed using a repeated measures analysis of variance using Superanova (Abacus Concepts 1989).

RESULTS

Grassland respiration rates during the growing season (15 April–15 October) were significantly higher ($P < 0.0001$) than woodland rates (Table 1; Fig. 1). Mean grassland soil efflux (±1 SE) was 4.60 ± 0.15 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ during the growing season, while the

TABLE 1. Results of ANOVA analyses for differences between woodland and grassland in instantaneous rates of soil respiration, soil temperature (10-cm depth), and soil moisture (gravimetric) averaged (A) over the year and (B) during the growing season (15 April–15 October).

Factor	Soil respiration (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)	Soil temperature (10-cm depth)	Soil moisture (%, gravimetric)
A) Annual			
Vegetation type	<0.0001	<0.0001	0.06
Site	0.0004	0.0002	<0.0001
Vegetation type × site	<0.0001	NS	<0.0001
B) Growing season			
Vegetation type	<0.0001	<0.0001	NS
Site	0.0031	0.0001	0.0004
Vegetation type × site	<0.0001	0.0001	0.0002

Notes: *P* values are provided in the table. NS indicates ''not significant.'' Vegetation refers to the woodland–grassland comparison; site indicates location for the paired woodland–grassland comparison ($n = 3$ sites).

woodland rate was 38% less (2.87 ± 0.07 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$). However, differences between respiration rates narrowed both early and late in the growing season. The mean non-growing season (15 October–15 April) rates were nearly identical ($P = 0.5$), although on two measurement dates, there were significant differences. During June 1999, heavy rains (denoted R in Fig. 1) preceded observations where grassland and woodland respiration rates converged (17, 24, 30 June 1999). Statistical analysis also revealed a site effect ($P = 0.0004$) attributed to the Scenic Drive site. At the Scenic Drive site, respiration for both woodland and grassland was always higher relative to the other two sites. Presumably Scenic Drive soil temperatures were higher because of a more southeastern aspect, which exposed the soil to more intense solar radiation early in the day compared to the other relatively level sites.

We tested to see if there was a difference in soil respiration rates between woodland and grassland that could be attributed to vegetation-induced differences in soil temperature and microclimate. During the growing season, daytime soil temperature at 10 cm depth was significantly higher (25 ± 0.2°C) in grasslands compared to woodland (20 ± 0.3°C) (Fig. 2; Table 1).

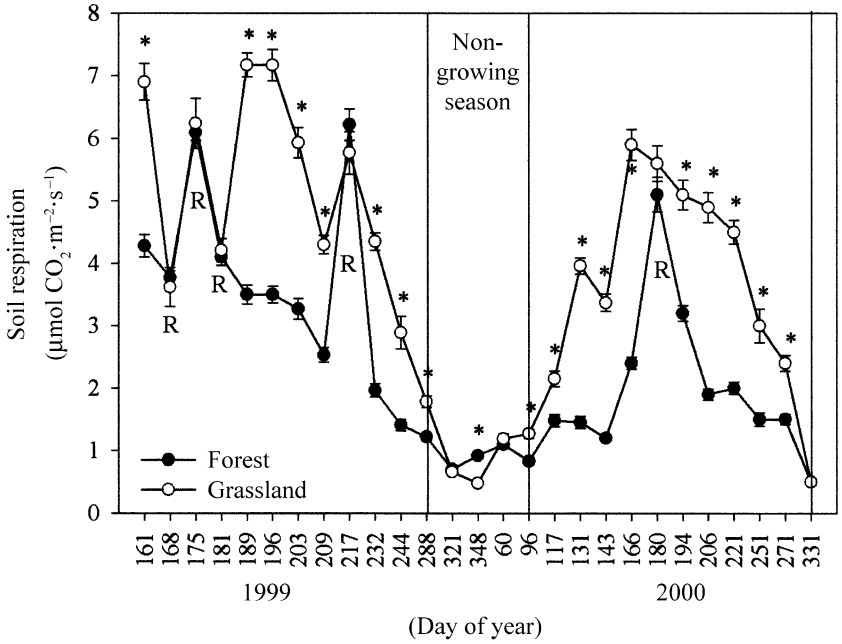

FIG. 1. Respiration rates in three juniper woodlands and paired grasslands from June 1999 to November 2000. Bars represent ±1 SE. Heavy rains within five days are represented by ''R.'' Vertical lines mark beginning and end of the growing season. Asterisks indicate significant differences ($P < 0.05$) between grassland and forest respiration data for a particular date.

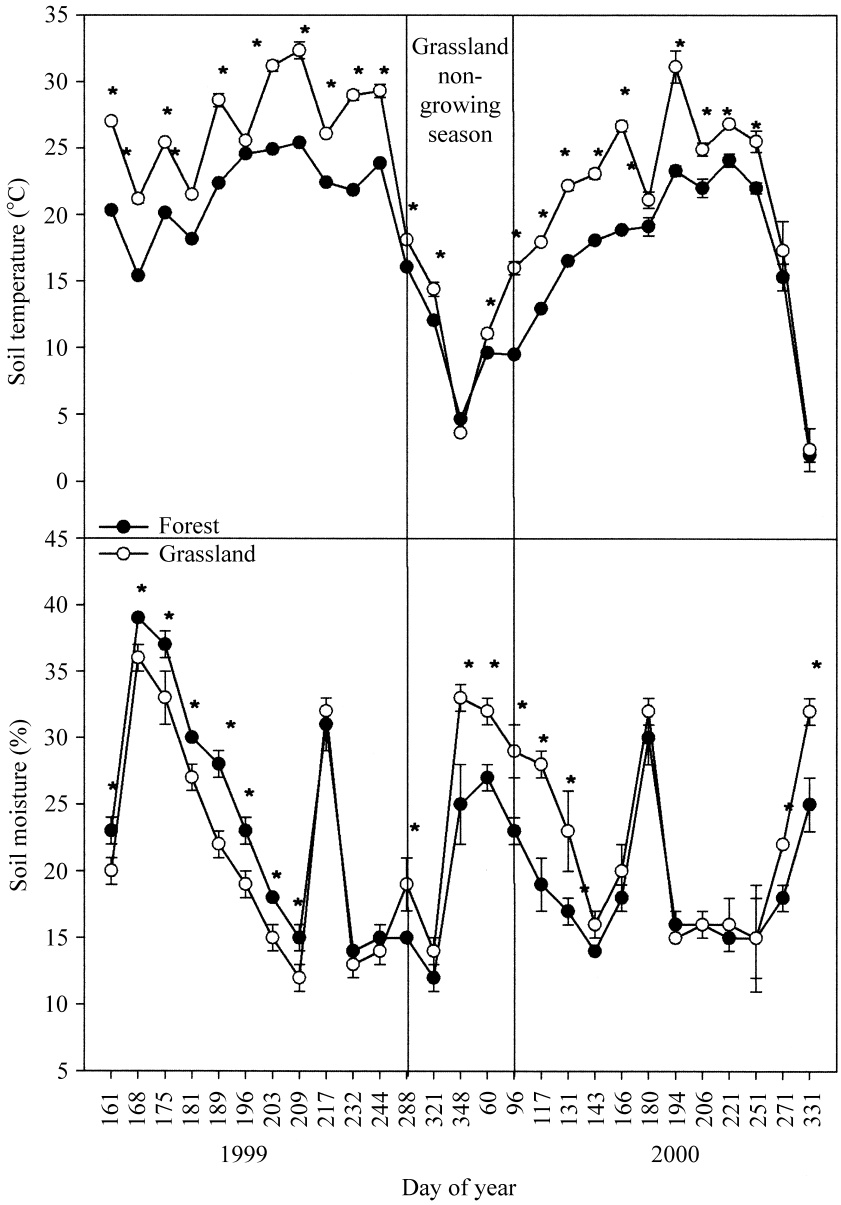

FIG. 2. Soil temperature (top) measured at 10 cm and gravimetric soil moisture (bottom; percentage) from 0–10 cm depth, from June 1999 to November 2000, in three juniper woodlands and paired grasslands. Bars represent ±1 SE; asterisks indicate days with significant treatment (vegetation type) effects ($P = 0.05$). Vertical lines mark the beginning and end of the growing season.

During the non-growing season, grassland soil temperatures averaged 10°C (±1.5), compared to 8 ± 0.3°C in woodlands ($P = <0.0001$). There was a significant site effect during both seasons ($P = <0.0001$). Soil temperature explained from ~40% to almost 70% of the variation in soil respiration rates. Furthermore, soil respiration was more highly correlated with soil temperature at grassland sites ($r^2 = 0.67$) than at woodland sites ($r^2 = 0.37$) (Fig. 3a, b).

We also determined if there was an intrinsic difference in the manner in which woodland and grassland soil respiration responds to soil temperature. We analyzed slopes of the respiration rates (data $\log_{10}$ transformed) vs. temperature to determine if woodland and grassland respiration rates have intrinsic differences in their response to temperature. A comparison of the slopes (ANCOVA) of linear regressions of soil temperature vs. soil respiration in woodlands and grasslands (Fig. 3) indicated that the woodland and grassland response to temperature was significantly different at the $P = 0.05$ level. This difference in slope indicated that soil temperature affected respiration differently in

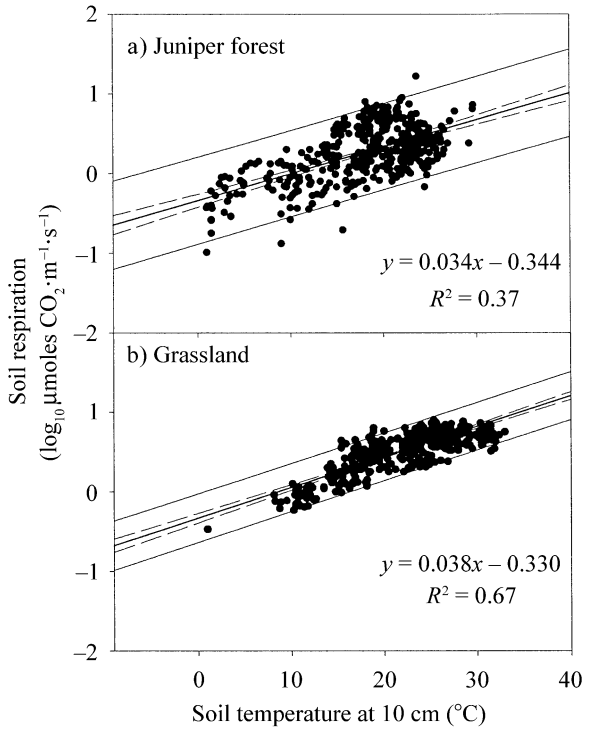

FIG. 3. Linear regressions of soil temperature at 10-cm depth with $\log_{10}$-transformed soil respiration rates in (a) juniper woodlands and (b) grasslands. Dashed lines are 95% confidence limits; solid lines are prediction intervals. Slopes are significantly different at $P < 0.05$.

woodlands than in grasslands. That is, for a given temperature, grassland respiration was slightly higher than in woodlands.

The rate at which many biological processes proceed, including soil respiration, is often expressed as a relationship to environmental temperature change (Winkler et al. 1996, Boone et al. 1998). Q_{10} predicts an approximate doubling of biological processes with each 10°C temperature increase (Luo et al. 2001). The values of Q_{10} for soil respiration in woodlands and grasslands were calculated using the following equation:

$$Q_{10} = R_{T+10}/R_T$$

where R_{T+10} is equal to respiration at an initial soil temperature (R_T) plus 10°C (Winkler et al. 1996). We calculated these values using our derived regression equations for soil respiration vs. temperature (Fig. 3a, b). As expected, the difference between woodland and grassland soil respiration was also reflected in higher Q_{10} values in grasslands (2.4) than in woodlands (2.2).

Gravimetric soil moisture did not differ between prairie and woodland sites over the year ($P = 0.06$) or during the growing seasons (Fig. 2; Table 1). However, during the non-growing season, soil moisture was 19% less in woodland than in grassland. Apparently, grass senescence alleviated the grassland demand for soil water during the non-growing season.

Linear regression of soil moisture vs. soil respiration explained 21% of the variability in woodlands, but showed no relationship in grasslands (Fig. 4). Multiple regression of soil respiration vs. soil moisture and temperature indicated a relationship between these two factors and their effect on respiration rates in both woodland and grassland soils ($P = 0.0001$). In woodlands, these two factors explained 58% of the variation in respiration rates, compared to 37% by soil temperature alone (Fig. 3a). In grasslands, temperature and moisture together explained 67% of the variation in soil respiration rates. However, considering that linear regression of soil respiration with soil temperature alone also explained 67% (Fig. 3b) of the variability, this study suggests that soil moisture had little or no effect on tallgrass prairie respiration.

Long-term laboratory incubations (82 weeks) to assess differences in potentially mineralizable C between woodland and grassland soils indicated no significant difference in microbial respiration over either the short or long term (Fig. 5). However, there were anticipated differences in respiration, depending on depth and time (incubation week). Both woodland and grassland sur-

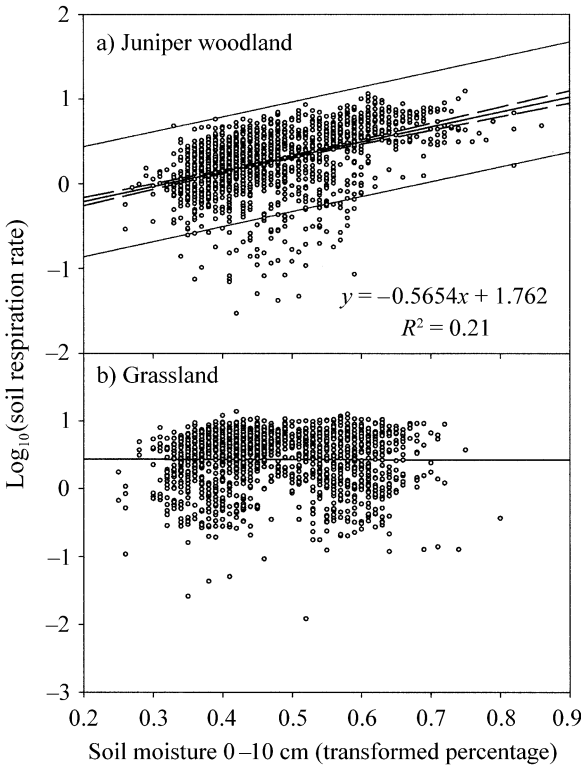

FIG. 4. Linear regressions of gravimetric soil moisture (%) from 0 to 10 cm depth and $\log_{10}$ soil respiration rates (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) in (a) juniper woodlands and (b) grasslands. In panel (a), dashed lines are 95% confidence limits, and solid lines are prediction intervals. [No significant relationship was found for the data in panel (b).] Soil moisture was transformed from percentages.

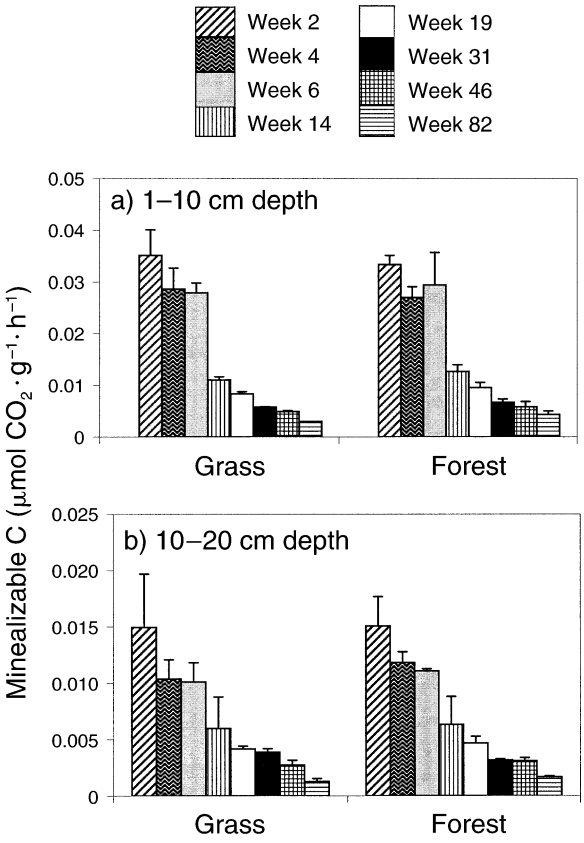

FIG. 5. Potentially mineralizable C over time (2, 4, 6, 14, 19, 31, 46, and 82 weeks) from long-term laboratory incubations of woodland and grassland soils: (a) 0–10 cm depth; (b) 10–20 cm depth. Bars represent one standard error, $N = 3$. For panel (a), grass, $y = 0.0727x^{-0.7145}$, $r^2 = 0.97$; forest, $y = 0.0607x^{-0.5973}$, $r^2 = 0.95$; for panel (b), grass, $y = 0.0267x^{-0.6206}$, $r^2 = 0.95$; forest, $y = 0.0272x^{-0.5962}$, $r^2 = 0.97$.

face soils (0–10 cm) had respiration rates twice those observed in subsurface soils (10–20 cm). Both woodland and grassland microbial respiration also decreased ~10-fold from the start to week 82. Power functions explained >95% of the variation in rates over time for both woodland and grassland soils at both depths. Furthermore, after 82 weeks, microbial respiration in both woodland and grassland soils leveled off to ~0.004 μmol $CO_2 \cdot (g\ soil)^{-1} \cdot h^{-1}$ in the surface soils and ~0.002 μmol $CO_2 \cdot (g\ soil)^{-1} \cdot h^{-1}$ in the subsurface soils.

Similarly, microbial biomass C did not differ between woodlands and grasslands in either the June or October soil sampling. Woodland microbial biomass C was 0.41 (±0.16) and 0.51 (±0.12) mg CO_2/g soil for the growing and non-growing seasons, respectively. Grasslands were similar, with 0.38 (±0.04) and 0.46 (±0.03) mg C/g during the growing and non-growing seasons, respectively.

We focused on estimates of living fine root biomass in woodland and grassland because it was expected to be more biologically active than larger size classes of roots (Fig. 6). Based on our limited sampling, fine root biomass (0–1 mm) did not differ between woodland and grassland (range ~450–456 g/m^2), and thus could not explain the lower in situ soil respiration in woodlands. The 1–2 mm size class was significantly different, with >90% more of the larger size class found in woodlands. Some larger coarse woody roots were found in the woodland soil samples, but this size class was not quantified.

We estimated annual C budgets of soil respiration based on soil temperature at 10 cm (Table 2). To quantify the cumulative flux of C from woodlands and grasslands, we utilized continuous data sets of air temperatures from the Manhattan (Kansas, USA) Airport Weather Station, and soil temperatures from D. Bremer (*unpublished data*) obtained as ancillary data from flux towers in a related study. Air temperatures were found to correlate with our grassland soil temperatures ($R^2 = 0.73$), and we used that regression equation to predict diurnal soil temperatures based on air temperature data. Then the equation describing the relationship between soil temperatures and respiration at each grassland site was used to predict diurnal CO_2 flux rates across our sampling months. Woodland predictions were calculated similarly, except that diurnal soil temperatures at 10 cm were available from one of our woodlands. This continuous data set correlated closely with the instantaneous soil temperatures obtained at the time of our respiration measurements (continuous vs. instantaneous, $R^2 = 0.94$). We applied the continuous vs. instantaneous temperature regression to the entire set of woodland soil temperatures. Daily fluxes from both woodlands and grasslands were summed for the growing season and non-growing season. These estimates indicated that annual woodland C flux (533 ± 21.7 g C/m^2) was 62% lower than grassland C flux (858 ± 14.5 g C/m^2) (Table 2).

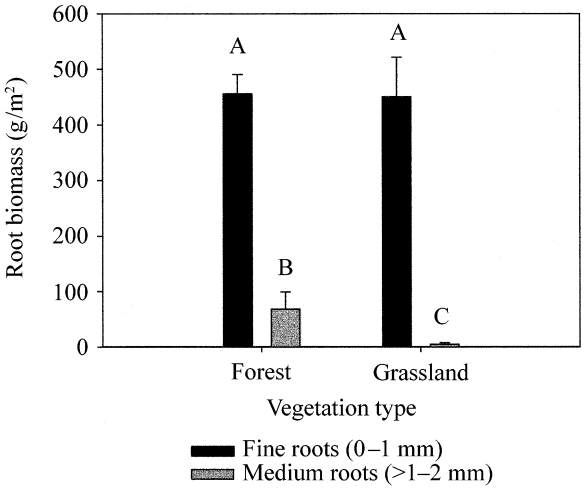

FIG. 6. Root biomass removed from woodland and grassland soil cores from 0–10 cm depth. Bars represent +1 SE ($N = 8$).

TABLE 2. Predicted cumulative C flux (g C/m^2) from soils.

Season	Grassland sites				Woodland sites			
	Tuttle	Randolph	Scenic	Mean (± 1 SE)	Tuttle	Randolph	Scenic	Mean (± 1 SE)
Growing season (June–October 1999)	602	645	669	639 (20)	419	396	364	*393 (16)
Non-growing season (October 1999–April 2000)	239	165	154	186 (27)	152	134	130	*139 (7)
Growing season (April–October 2000)	648	681	686	672 (12)	420	398	367	*395 (16)
Annual (October 1999–October 2000)	887	847	841	858 (15)	572	532	497	534 (22)

Notes: These C flux predictions were derived from regressions of soil temperature and soil respiration rates. The growing season in this region is between 15 April and 15 October. The 1999 growing season measurements were not initiated until June 1999. Therefore, C flux during the June–October 1999 growing season was based on 4.5 months and does not include the low respiration rates in early spring. Consequently, the flux in the 1999 growing season, though lower than the 2000 growing season, is probably slightly overestimated.

DISCUSSION

Juniper encroachment slows soil respiration

The presence of a closed canopy juniper woodland reduced instantaneous (Fig 1; Table 1) and annual soil respiration (Table 2) relative to grassland (by ~38%), resulting in a greatly slowed soil C cycling in woodlands. In general, our data concurred with others who found slower rates in woodlands relative to grassland in the few published ''across the fence'' comparisons and in geographically different regions. Our tallgrass prairie and woodland rates fall in the middle of the range of other reported results (Appendix A). Indeed, tallgrass prairie has yielded some of the highest soil respiration rates of any ecosystem (Zak et al. 1994, Knapp et al. 1998). What factors could be responsible for the 38% decline in soil respiration rates in woodland as observed in this study? Below we consider biotic (root biomass, microbial biomass, and mineralizable C) and abiotic factors (soil temperature and moisture) as possible causes for low soil respiration in woodlands.

Mineralizable C and microbial C cannot explain the low respiration in woodlands

We anticipated lower potentially mineralizable C and microbial biomass in woodland relative to grassland. Several lines of evidence initially suggested that there might be lower levels of heterotrophic activity in woodland soils, leading to lower soil respiration in woodland: (1) juniper litter is a poorer substrate for microbial utilization based on high lignin and C:N (Norris et al. 2001*a*); a reciprocal litterbag transplant study found decomposition rates of juniper litter were lower than rates of tallgrass prairie detritus (Norris et al. 2001*a*) due to litter quality differences; and (2) microbial biomass was reported to be relatively high in tallgrass prairie compared to other ecosystems (Rice and Garcia 1994, Zak et al. 1994). Thus, we expected this to be so in our paired site comparison of soil C cycling. However, although we hypothesized that a lower microbial biomass or potentially mineralizable C might explain part of the reduced woodland soil respiration, we found no significant differences in microbial biomass or the mineralizable C from long-term laboratory incubations (Fig. 5). Unfortunately, these microbial assays do not address potential changes in microbial diversity and the balance between fungal and bacterial contribution to mineralized soil.

Nor can root biomass explain the low respiration in woodlands

We anticipated that lower fine-root biomass in woodland relative to grassland may partially explain the low soil respiration in woodland relative to grassland based on the characteristically high root biomass and productivity in prairies (Johnson and Matchett 2001). Based on our limited sampling of root biomass in woodland and grassland, we found no difference in fine root biomass between these two vegetation types. However, it is possible that root-related activity (root respiration) was different between vegetation types. A literature review of root respiration rates indicated grasses have respiration rates per gram of root biomass that are comparable to, and often higher than, those of trees (Hanson et al. 2000). Thus, it is possible that higher root respiration in grasslands could explain some of the differences in in situ soil respiration observed between woodland and grassland (Fig. 3a, b). Similarly, higher root turnover in the grassland compared to the woodland could also result in higher soil respiration in grasslands. Studies of root productivity and root turnover in grassland and woodland are currently being conducted.

Subtle, differential effects of soil moisture on soil respiration

Soil moisture is also known to be a highly correlated environmental driver of soil biological processes (Hartel 1999), specifically soil respiration (Kelting et al. 1998). Large differences in soil moisture between woodland and grassland could potentially explain low respiration rates in woodland if woodland soils were drier than grassland. However, there were no differences in growing season soil moisture between woodland and grassland soils from 0–10 cm, but there was

a moderate reduction in non-growing season soil moisture in woodland soils.

However, there were subtle differences in woodland and grassland response to soil moisture. Our results indicate that moisture did not significantly affect soil respiration rates in grassland, as reported by others (Reiners 1968, Anderson 1973, Kaye and Hart 1998, Knapp et al. 1998). In contrast, multiple regressions of woodland soil temperature and moisture improved the regression by 21%. Therefore, moisture together with temperature explained 58% of the variation in soil respiration in woodlands.

Soil temperature accounts for the reduction in soil respiration in juniper woodlands

Our study concurred with others that soil temperature is a highly correlated environmental driver of soil respiration rates (Lloyd and Taylor 1994, Holland et al. 1995, Raich and Potter 1995, Winkler et al. 1996, Boone et al. 1998, Kaye and Hart 1998, Londo et al. 1999). The relationship between temperature and respiration varies between studies, but frequently temperature explains a large portion of the variability in soil respiration. Soil temperature explained 75–90% of the respiration variability in Minnesota woodlands (Reiners 1968), 75–89% in pine plantations (Ewel et al. 1987), 81% in eucalyptus woodland (Keith et al. 1997), 58 and 71% in burned and unburned tallgrass prairie, respectively (Knapp et al. 1998), 75% in boreal woodland (Rayment and Jarvis 2000), 76 and 85% in farmland and woodland, respectively (Fang and Moncrieff 2001), and 43 and 58%, respectively, in intact and clearcut woodlands (Toland and Zak 1994). In our study, soil temperature explained 67 and 37% of the variability in grassland and woodland soil respiration, respectively.

Soil respiration is comprised of microbial (heterotrophic) and root (autotrophic) respiration (Raich and Nadelhoffer 1989). Our study did not attempt to partition soil respiration into autotrophic and heterotrophic fluxes, although others have attempted this difficult task (Kelting et al. 1998). Hanson et al. (2000) summarized many efforts to estimate root respiration and suggested that 38–50% of total respiration may be associated with root and rhizosphere respiration. Högberg et al. (2001) estimated 50% of soil respiration is due to roots. Furthermore, a recent study of temperature sensitivity of roots and heterotrophic processes (Boone et al. 1998) indicated that roots were more sensitive to temperature than microbes; they found that living root and rhizosphere respiration had a Q_{10} of 4.6, and was significantly higher than their control Q_{10} of 3.5 (soil without roots). Further research in juniper woodlands will attempt to partition autotrophic and heterotrophic soil processes.

Vegetation-mediated microclimate drives low soil respiration in woodland

Changes in the physical environment accompany juniper expansion through shading of the surface and near-surface environment, which, in turn, reduces soil temperatures. In this study, an overriding change in the physical environment brought about by the shading of the juniper canopy (Hoch et al. 2002) resulted in a reduction of soil temperatures in woodland. Thus, soil temperatures during the growing season were 5°C lower in the woodland than in adjacent grassland (Fig. 2). In a related study, microclimate was also shown to influence other soil processes such as litter decomposition. In a reciprocal litterbag transplant study, Norris et al. (2001*a*) found slower decomposition rates in the woodland relative to adjacent prairies (irrespective of litter type).

In order to predict differences in soil respiration rates related to vegetation-induced differences in microclimate, we used the temperatures vs. respiration regression equations for woodland and grassland soils (Fig. 3a, b). Recalling the 5°C difference between juniper woodland and paired grassland soils during the growing season (Fig. 2), we solved the equations for a growing season temperature of 20°C (woodland mean), and a growing season temperature of 25°C (grassland mean). The equations predicted that the mean soil respiration rates in woodland and grassland would be 2.19 and 4.17 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, respectively, a difference of 1.98 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$. We observed that mean respiration rates in woodland and grassland sites were actually 2.87 and 4.60 μmol of $CO_2 \cdot m^{-2} \cdot s^{-1}$, respectively, with a difference of 1.73 μmol of $CO_2 \cdot m^{-2} \cdot s^{-1}$. Therefore, the regression equations predicted a greater difference between woodland and grassland respiration than was actually observed. This suggests that much of the difference between woodland and grassland in situ respiration was attributable to a vegetation-induced difference in soil temperature caused by the shading of the soil surface by the juniper canopy. Thus, this microclimate effect apparently overrides the slight intrinsic difference between woodland and grassland plant respiration (Fig. 3a, b), as expressed by a slightly higher Q_{10} in grasslands (2.4) relative to woodlands (2.2).

A recent paper (Högberg et al. 2001) indicated that current photosynthate was a highly correlated driver of soil respiration rates in boreal forest, based on an innovative tree girdling study. Unfortunately, we did not collect photosynthesis data in *J. virginiana* woodland and tallgrass prairie concomitant with our soil respiration measurements. A comparison of photosynthetic rates of *J. virginiana* and *A. gerardii* may provide some insight into the high grassland soil respiration rates. During the warm part of the growing season, photosynthetic rates of *A. gerardii* (a C_4 grass) were 3–5 times higher than those of *J. virginiana* for the same time period (A. Knapp et al., *unpublished data*). Similarly, Axmann and Knapp (1993) found photosynthetic rates of the grass species exceeded those of juniper trees, but only during wet periods. Clearly, further studies of controls over soil respiration should include measurement of photosynthetic rates.

TABLE 3. Annual soil carbon turnover calculated from carbon stocks in Smith and Johnson (2003).

Measure	Woodland	Grassland
Carbon stocks (g C/m^2)	8782 (810)	7699 (1004)
Soil respired C (g C·m^{-2}·yr^{-1})	267 (11)	429 (7)*
Time for turnover of soil C (yr)	33 (2)	18 (2)*

Note: Respired carbon was calculated from annual respiration (Table 2) minus 50% (midrange estimate attributed to root respiration; Högberg et al. 2001). Asterisks indicate significant differences ($P < 0.05$). One standard error is reported in parentheses.

Juniper woodland soil C cycles more slowly than in grasslands

We found that annual C flux in juniper woodlands lagged behind grassland flux by 325 g C·m^{-2}·yr^{-1} (Table 2). In a six-state Midwest region (Kansas, Oklahoma, Indiana, Iowa, Missouri, and Illinois), if all the areas now undergoing juniper encroachment continue to closed-canopy *J. virginiana* woodland, nearly 5 million hectares (Bidwell et al. 1989, Schmidt and Leatherberry 1995, Schmidt and Wardle 1998, Leatherberry et al. 1999, Drake and Todd 2002) of abandoned agricultural fields and pastures would exhibit a downward shift in soil C efflux. To estimate the potential reduction in C flux that is occuring across the land area where juniper is replacing grassland, we multiplied the difference in woodland and grassland C flux by the number of hectares involved in juniper encroachment in these states. Thus, if conversion of grassland to closed canopy woodlands continues, soil C efflux from soil respiration will potentially drop by 18.9×10^6 Mg C relative to soil respiration of historical tallgrass prairie. This extrapolation assumes that the juniper woodland sites (on which these calculations are based), are currently in steady state after to 40–60 years of growth. Thus, our calculation may be underestimating the total downward shift in soil C efflux.

Furthermore, lower fluxes of soil CO_2 in the juniper woodland also slowed the turnover of soil C stocks. Our estimate of soil C stocks was based on data from a study of these same paired grassland–woodland sites (Smith and Johnson 2003), in which we used the percent C and the soil bulk density to calculate soil organic carbon in g/m^2 stored in the 0–10 cm soil layer. We calculated soil carbon turnover (years) by dividing soil carbon stocks (g C/m^2) by the annual rate of soil respired CO_2 (g C·m^{-2}·yr^{-1}). We made the assumption that 50% of respiration is autotrophic based on a recent paper showing that new photosynthate from plants contributes half of the total soil respiration effluxed from soils (Högberg et al. 2001). Based on these estimates and assumptions, woodland turnover rates of soil C were 15 years slower than comparable grasslands, a significant difference in soil C turnover (Table 3). This difference in soil C turnover was attributable primarily to the reduced soil CO_2 efflux in woodlands.

We expected to find substantially greater soil carbon stocks in the woodland based on greater aboveground productivity (Norris et al. 2001*b*) and lower soil respiration rates in woodlands. However, Smith and Johnson (2003) did not detect a significant increase in soil C stocks in woodland stands that were 40–60 years old (perhaps due to small sample size). Additional intensive sampling in an ongoing study in a similar area indicated significantly greater concentrations of soil organic C and N in the upper 10 cm of *J. virginiana* woodland soils compared to adjacent prairie sites (24% higher C and 21% higher N concentrations in woodland compared to prairie soil; D. McKinley, *unpublished data*). Assuming similar bulk densities in grassland and woodland, these data suggest greater C storage in woodland soils compared to grassland soils.

Our results of soil C cycling with woody encroachment into mesic tallgrass prairie are corroborated by modeling (Hibbard et al. 2003) and observational studies (Hibbard et al. 2001) of grassland to savanna woodland transitions in semi-arid southwest Texas. In this southwest Texas *Prosopis* encroachment, soil carbon stocks are estimated to exceed those of the pristine grasslands they replaced by 1.3×. This is in sharp contrast to the recent study by Jackson et al. (2002). They report that along a gradient from arid to mesic (~1000 mm mean annual precipitation), woody encroachment into mesic grasslands resulted in a loss of soil C relative to the mesic grasslands they replaced. Clearly, the lack of agreement in results between Jackson et al. (2002) and those reported here and elsewhere (Hibbard et al. 2003, Smith and Johnson 2003) warrant additional field studies to evaluate the net effect of woody encroachment on the C cycle and its implications for regional C balance. These become imperative given that woody plant encroachment is a potentially significant, but highly uncertain, component of the North American carbon sink (Houghton et al. 1999, Pacala et al. 2001).

CONCLUSION

The vegetation-mediated reduction in soil temperature under juniper canopies (5°C cooler during the growing season) explained much of the lower instantaneous and annual in situ soil respiration observed in woodlands relative to adjacent grasslands. However, there were subtle intrinsic differences in the soil respiration response to temperature in woodlands and grasslands: grassland respiration responded more strongly to temperature than woodland respiration, re-

flected by a Q_{10} in grasslands of 2.4 compared to 2.2 in woodlands. We ruled out other biotic and abiotic factors that might have caused lower soil respiration in woodlands. Indices of soil C cycling (potentially mineralizable C and microbial biomass) showed no differences between woodlands and grasslands. Similarly, based on our limited sampling, root biomass also did not differ between woodland and grassland, and thus, could not explain the lower in situ soil respiration in woodland sites. Soil moisture also did not differ between woodland and grassland (at least during the growing season). On an annual basis, the lower soil respiration in the woodland resulted in a flux 38% reduced compared to adjacent grassland. Furthermore, we estimate that the turnover of woodland soil C stocks slowed by 15 years relative to grassland. This study suggests that if juniper expansion, now occurring across nearly 5 million hectares in the Great Plains, proceeds to canopy closure, annual soil C flux may be reduced as much as 18.9×10^6 Mg of C below C flux rates from tallgrass prairie soils.

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APPENDIX A

Study sites were across-the-fence comparisons of native grasslands and closed canopy juniper woodlands in north central Kansas, USA. A photograph of a study site is available in ESA's Electronic Data Archive: *Ecological Archives* E085-117-A1.

APPENDIX B

A table showing comparisons of soil respiration studies in woodlands and grasslands is available in ESA's Electronic Data Archive: *Ecological Archives* E085-117-A2.