

Soil Carbon and Nitrogen Storage in Response to Fire in a Temperate Mixed-Grass Savanna

X. Dai,* T. W. Boutton, M. Hailemichael, R. J. Ansley, and K. E. Jessup

ABSTRACT

Vegetation fires may alter the quantity and quality of organic matter inputs to soil, rates of organic matter decay, and environmental factors that influence those processes. However, few studies have evaluated the impacts of this land management technique on soil organic carbon (SOC) and total N in grasslands and savannas. We evaluated the impact of repeated fires and their season of occurrence on SOC and total N storage in a temperate mixed-grass-mesquite savanna where fire is used to control woody plant encroachment. Four fire treatments varying in season of occurrence were examined: summer only (SF), winter only (WF), alternate summer and winter fires (SWF), and unburned controls. In each treatment, soils were sampled to 1 m under three vegetation types: C₃ grasses, C₄ grasses, and mesquite trees. The SOC storage at 0 to 20 cm was significantly greater in SF (2693 g C m⁻²) and SWF (2708 g C m⁻²) compared to WF (2446 g C m⁻²) and controls (2445 g C m⁻²). The SWF treatment also increased soil total N (271 g N m⁻²) relative to all other treatments (228–244 g N m⁻²) at 0 to 20 cm. Fire had no effect on SOC or total N at depths of >20 cm. Vegetation type had no significant influence on SOC or total N stocks. The $\delta^{13}\text{C}$ value of SOC was not affected by fire, but increased from -21‰ at 0 to 10 cm to -15‰ at depths of >20 cm indicating that all treatments were once dominated by C₄ grasses before woody plant encroachment during the past century. These results have implications for scientists, land managers, and policymakers who are now evaluating the potential for land uses to alter ecosystem C storage and influence atmospheric CO₂ concentrations and global climate.

WOODY PLANT INVASION into grasslands and savannas has been widespread in North and South America, Australia, Africa, and Southeast Asia over the past century due primarily to fire suppression and livestock grazing (Archer et al., 2001). This encroachment may adversely affect about 20% of the world's population by jeopardizing grassland biodiversity, and threatening the sustainability of pastoral, subsistence, and commercial livestock grazing (Rappole et al., 1986; Turner et al., 1990; Noble, 1997). Fire has long been recognized as a disturbance that maintains grasslands and savannas and prevents invasion of woody species (Axelrod, 1985; Wright, 1980; Archer et al., 1988, 2001). Therefore, prescribed fire is often employed as a land management

tool to suppress the encroachment of woody plants into grass-dominated ecosystems.

Fire has the potential to influence ecosystem carbon storage and dynamics by changing plant species diversity and dominance, plant tissue chemistry, primary productivity, decomposition of soil organic matter (SOM), and characteristics of the physical environment. In savanna ecosystems, the balance between trees and grasses, stand structure and dynamics, and shrub cover and abundance is determined to a large extent by fire frequencies and interactions between fire and other disturbance factors (Scholes and Archer, 1997; Peterson and Reich, 2001; Heisler et al., 2003; Van Langevelde et al., 2003). Above- and belowground productivity often increase following fire as a result of microclimatic modification due to removal of litter and standing crop, and changes in nutrient availability and distribution (Raison, 1979; Ojima et al., 1990, 1994; Blair, 1997; Rice and Owensby, 2000; Johnson and Matchett, 2001; Wan et al., 2001). In many ecosystems, microbial C and N increase after the first year of burning and decrease after prolonged annual burning compared to unburned controls (Ojima et al., 1990; Pietikäinen and Fritze, 1995; Fritze et al., 1994; Anderson et al., 2004). Vegetation fires have also been observed to alter plant tissue chemistry by increasing C to N ratio of shoots and roots (Ojima et al., 1994; Johnson and Matchett, 2001), potentially modifying the decomposability of SOM. In contrast, increased soil temperatures resulting from elimination of shading by vegetation and litter have the potential to increase the decomposition rate of SOM (Ojima et al., 1990). Although fires have demonstrated potential to alter the physical environment, the quantity and quality of organic matter inputs to the soil, and the decay rates of SOM, few studies have evaluated the impacts of this land management technique on SOM storage in temperate savannas that include deep-rooted woody plants as a component of the plant community, and the direction and magnitude of these effects are unknown.

In the southern Great Plains, fire is used to control encroachment of honey mesquite (*Prosopis glandulosa* Torr.) into grasslands and savannas. The purpose of this study was to evaluate the impact of repeated prescribed fire and its season of occurrence on the storage and vertical distribution of soil organic C and N in a mixed-grass savanna in the Rolling Plains region of north-central Texas. The specific objectives of this study were to: (i) quantify organic C and total N stocks in the upper meter of the soil profile in response to fire and vegetation composition, and (ii) utilize the natural

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Abbreviations: SF, summer fire; SOC, soil organic carbon; SOM, soil organic matter; SWF, alternate summer and winter fire; WF, winter fire.

isotopic signature ($\delta^{13}\text{C}$) of soil organic carbon (SOC) to identify sources of SOC and evaluate the potential for fire-induced vegetation changes in this mixed-grass savanna ecosystem.

MATERIALS AND METHODS

Study Area and Fire Treatments

The research was conducted on a private ranch (Waggoner Ranch, Wilbarger County; 33°51'20" N, 99°26'50" W; elevation 381 m) near Vernon in north-central Texas. Mean annual precipitation is 665 mm and mean annual temperature is 16.9°C. The mean monthly temperatures range from 3.8°C in January to 29.1°C in July. Soils are fine, mixed, thermic Typic Paleustolls of the Tillman series, 0 to 1% slope, which are alluvial clay loams from 0 to 3–4 m depth, underlain by Permian sandstone/shale parent material (Koos et al., 1962). The soil particle size distribution in the surface (0–10 cm) is comprised of 32% clay, 52% silt, and 16% sand, and the 10- to 20-cm depth is 43% clay, 41% silt, and 16% sand. Before burning, vegetation was a mixture of C_3 and C_4 grass species in the herbaceous layer, and honey mesquite in the tree layer. The dominant C_3 grass species is Texas wintergrass [*Nassella leucotricha* (Trin. & Rupr.) R. W. Pohl], and the dominant C_4 grass species are the midgrasses vine mesquite (*Panicum obtusum* Kunth) and meadow dropseed [*Sporobolus compositus* (Poir.) Merr.] and the rhizomatous shortgrass, buffalograss [*Bouteloua dactyloides* (Nutt.) Columbus]. Texas wintergrass, buffalograss, and vine mesquite tend to occur in small monoculture patches while other C_4 grasses are dispersed throughout the site. Livestock grazing has been excluded from the study area since 1988, and fire did not occur on the site for at least 30 yr before the establishment of fire treatments.

This study was comprised of four fire treatments: (i) repeated summer fires in 1992, 1994, and 2002 (SF); (ii) repeated winter fires in 1991, 1993, 1995, and 2002 (WF); (iii) alternate-season fires in winter 1991, summer 1992, winter 1994, and summer 2002 (SWF); and (iv) an unburned control. Each fire treatment had three replicates, with plot sizes ranging from 1 to 6 ha. All treatments were on the same soil series on level, upland surfaces. Winter fires were conducted between late-January through mid-March, and summer fires between late-August through September. All fires were conducted as headfires using methods described by Wright and Bailey (1982). Herbaceous fine fuel loads (standing crop + litter) ranged from 1300 to 3083 kg ha⁻¹ for winter fires and 1632 to 4285 kg ha⁻¹ for summer fire (Ansley and Jacoby, 1998). Most of the fires, both winter and summer, were of moderate to high intensity (Ansley and Jacoby, 1998). The winter 1993, 1995, and 2002, and summer 1992 and 1994 fires approached the maximum intensities that were possible given the herbaceous fine fuel loads in this mixed grass savanna.

Soil and Litter Sampling and Processing

Soil was collected in January 2003 by coring (3.2-cm diameter \times 100 cm deep) in three functionally distinct vegetation types within each plot: (i) patches dominated by cool season C_3 grass species ($n = 3$), (ii) patches dominated by warm season C_4 grass species ($n = 3$), and (iii) patches of the C_3 N-fixing tree honey mesquite ($n = 6$). Litter samples were collected within a 0.25 \times 0.25-m area centered over the core location within each vegetation type before extracting each core. Litter samples were then dried at 60°C, pulverized, and saved for isotopic and elemental analyses. Soil cores were divided into six depth increments (0–10, 10–20, 20–40, 40–60,

60–80, and 80–100 cm). Each depth increment was weighed, and a subsample was dried at 105°C to determine bulk density. The remainder of each increment was air-dried for 3 d and passed through a 2-mm sieve to remove gravel and large organic fragments. Soil cores were then pooled by vegetation type within each replicate plot, dried at 60°C for 48 h, homogenized thoroughly, and pulverized in a centrifugal mill before elemental and isotopic analyses.

Elemental and Isotopic Analyses

Soil samples were weighed into silver foil capsules, and then exposed to an HCl atmosphere for 6 to 8 h in a desiccator to volatilize carbonate carbon (Harris et al., 2001). Soil organic C, soil total N, and $\delta^{13}\text{C}$ of SOC were then determined using a Carlo Erba EA-1108 elemental analyzer interfaced with a Delta Plus isotope ratio mass spectrometer operating in continuous flow mode (ThermoElectron, Woburn, MA). The $\delta^{13}\text{C}$ values were reported relative to the international V-PDB standard by calibration through NBS-19 (Hut, 1987; Coplen, 1995). Precision was $<0.1\text{‰}$ for $\delta^{13}\text{C}$. The fraction of SOC derived from C_4 sources (F_{C_4}) was estimated by the mass balance equation:

$$F_{\text{C}_4} = (\delta_{\text{sample}} - \delta_{\text{C}_3}) / (\delta_{\text{C}_4} - \delta_{\text{C}_3})$$

where δ_{sample} is the $\delta^{13}\text{C}$ value of the SOC, δ_{C_3} is the average δ_{C_3} value of the C_3 plant litter, and δ_{C_4} is the average δ_{C_4} value of the C_4 plant litter (Boutton et al., 1999).

Statistical Analyses

A linear mixed model ANOVA was used to analyze this data set using SPSS Version 12.0 (SPSS, 2003). The experimental design was a split plot with fire treatment as the main plot and vegetation type as the split plot. Soil depth was treated as a repeated measures variable with covariance structure first order autoregressive AR(1). Replicated plots were nested within fire treatments and were considered a random effect. Fire treatment, vegetation type, and soil depth were considered fixed effects. A posteriori means separation tests were performed using the Bonferroni procedure (SPSS, 2003).

RESULTS

Litter Characteristics

Nitrogen concentrations were generally highest in mesquite litter ($>2\%$ N) and lowest in C_4 grass litter ($<1.3\%$ N) (Table 1). The C to N ratios were greater in C_4 (30–46) and C_3 (23–39) grass litter than in mesquite tree litter (10–18). The C_4 grass litter had the highest $\delta^{13}\text{C}$ values (-14 to -16‰), followed by C_3 grass (-27 to -28‰), and mesquite tree litter (-24 to -29‰).

Concentrations and Densities of Soil Organic Carbon and Total Nitrogen

The SOC and total N concentrations ranged from 1.4 to 13.5 g C kg⁻¹ and 0.2 to 1.3 g N kg⁻¹, respectively, and decreased exponentially with soil depth (Fig. 1). Neither fire treatment nor vegetation type had significant main effects on SOC and total N concentrations; however, the interactions between fire \times depth and vegetation \times depth both affected SOC and total N concentration

Table 1. Carbon, nitrogen, C to N ratio, and $\delta^{13}\text{C}$ values (means \pm standard errors) of litter in different fire treatments and vegetation types.

Vegetation	Measure	Fire treatment†			
		Control	SF	WF	SWF
C ₃ grasses	C, %	39.0 \pm 1.5	41.7 \pm 0.9	39.6 \pm 0.9	42.1 \pm 0.8
	N, %	1.5 \pm 0.09	1.7 \pm 0.10	1.0 \pm 0.07	1.8 \pm 0.13
	C/N	26.2 \pm 2.5	24.7 \pm 2.1	38.7 \pm 2.7	23.1 \pm 1.2
	$\delta^{13}\text{C}$	−27.2 \pm 0.4	−28.1 \pm 0.8	−26.6 \pm 0.4	−28.5 \pm 0.1
C ₄ grasses	C, %	39.5 \pm 2.4	39.4 \pm 4.6	37.3 \pm 0.9	45.1 \pm 0.6
	N, %	1.3 \pm 0.13	1.3 \pm 0.03	1.0 \pm 0.05	1.0 \pm 0.14
	C/N	30.5 \pm 4.9	30.1 \pm 3.1	36.7 \pm 1.9	45.6 \pm 6.1
	$\delta^{13}\text{C}$	−16.3 \pm 0.2	−14.9 \pm 0.5	−16.1 \pm 0.8	−13.7 \pm 0.2
Mesquite trees	C, %	40.0 \pm 1.1	35.5 \pm 0.9	37.6 \pm 0.8	30.0 \pm 1.7
	N, %	2.5 \pm 0.03	2.4 \pm 0.02	2.1 \pm 0.1	2.0 \pm 0.13
	C/N	15.7 \pm 0.2	10.0 \pm 5.0	17.6 \pm 0.8	14.9 \pm 0.2
	$\delta^{13}\text{C}$	−27.0 \pm 0.1	−28.6 \pm 1.3	−24.2 \pm 0.3	−26.6 \pm 0.7

† Control, no fire; SF, summer fire; WF, winter fire; SWF, alternate summer and winter fire.

significantly (Table 2). The SF and SWF treatments had significantly higher SOC concentrations than WF ($p < 0.05$), but only in the 0- to 10-cm depth increment. Soil total N concentrations were significantly greater ($p < 0.01$) in SW than in controls at 0 to 10 and 10 to 20 cm, and greater in both SF and SWF than in WF ($p < 0.01$) at 0 to 10 cm. The SOC and soil total N concentrations were significantly higher ($p < 0.001$) under mesquite trees than under C₃ and C₄ grasses at 0 to 10 cm. The fire treatment \times depth interaction had a significant effect ($p < 0.02$) on soil C to N ratio (Fig. 1; Table 2). Summer fires increased C to N ratio significantly ($p < 0.05$) only at 60 to 80 cm, while WF increased C to N ratio significantly ($p < 0.05$) at both 60 to 80 and 80 to 100 cm compared to that of the unburned control.

Densities of SOC ranged from $>2500 \text{ g C m}^{-2}$ in the upper 20 cm of the profile to $<700 \text{ g C m}^{-2}$ at 80 to 100 cm, while those for soil total N ranged from $>250 \text{ g N m}^{-2}$ in the upper 20 cm of the profile to $<75 \text{ g N m}^{-2}$ at 80 to 100 cm (Fig. 2). Approximately 37 to 40% of SOC and total N stocks were located in the upper 20 cm of the profile. Total stocks of SOC in the upper 1 m of the soil profile ranged from 6363 to 7321 g C m^{-2} across all treatment combinations, while those of total N ranged from 585 to 747 g N m^{-2} (Fig. 2). However, these differences in SOC and total N stocks in the upper 1 m were not significant.

The responses of SOC and total N densities (g m^{-2}) to fire treatment, vegetation type, soil depth, and their interactions were generally similar to those outlined above for SOC and total N concentrations (Fig. 2). The fire \times depth interaction had a significant ($p < 0.001$) effect on both SOC and total N (Table 2). The SOC densities were greater ($p < 0.01$) in SF (2693 g C m^{-2}) and SWF (2708 g C m^{-2}) than in WF (2446 g C m^{-2}) and the unburned control (2445 g C m^{-2}) at the 0- to 20-cm depth only. Nitrogen density in the SWF treatment (271 g N m^{-2}) was significantly greater ($p < 0.001$) than that of all other treatments (228–244 g N m^{-2}) in the 0- to 20-cm depth increment. Vegetation type had no effect on SOC and N density.

$\delta^{13}\text{C}$ Values of Soil Organic Carbon

The $\delta^{13}\text{C}$ of SOC increased from 0 to 10 cm to 20 to 40 cm, and then decreased gradually from 20 to 40 cm to

80 to 100 cm in all vegetation types and fire treatments (Fig. 3), and there was a significant vegetation \times depth interaction (Table 2). The $\delta^{13}\text{C}$ values of SOC under mesquite trees (-22‰) were significantly lower ($p < 0.001$) than those under grasses (-20 to -19‰), but only at 0 to 10 cm. Soils under C₃ grasses (-20.3‰) had significantly lower $\delta^{13}\text{C}$ values ($p < 0.05$) than C₄ grasses (-19.3‰) at 0 to 10 cm only. Fire had no significant impact on $\delta^{13}\text{C}$ values of SOC. The estimated proportion of SOC derived from C₄ plants increased with depth (Fig. 3), ranging from 40 to 65% at 0 to 10 cm and 60 to 90% below 10 cm, indicating that C₄ grasses were dominant before woody plant invasion during the past century.

DISCUSSION

Carbon and Nitrogen Stocks in Temperate Mixed-Grass Savanna

Pool sizes of SOC (6363 to 7321 g C m^{-2}) and total N (585 to 747 g N m^{-2}) in the upper 1 m of the soil profile were consistent with previous estimates for this bioclimatic region. Based on global data sets of SOC and total N coupled with the Holdridge life-zone classification system, Post et al. (1982, 1985) estimated that this region should store approximately 7000 g C m^{-2} and 600 g N m^{-2} . Although there have been few measurements of soil C and N stores in the southern Great Plains region, Jackson et al. (2002) found that SOC was 6500 to 7240 g C m^{-2} and total N was 840 to 940 g N m^{-2} in the upper 1 m of the profile at a site located within 5 km of our study area. In addition, the vertical distribution of SOC in this temperate mixed-grass savanna is remarkably similar to that described for temperate grasslands around the world (Jobbagy and Jackson, 2000), with approximately 40% of SOC in the upper 20 cm and 65% in the upper 40 cm of the profile. Thus, the mass and distribution of soil C and N documented in this study are consistent with model predictions and other direct measurements for the region.

Influence of Fire on Soil Carbon and Nitrogen

This study revealed a significant interaction between fire treatment and soil depth, indicating that fire altered

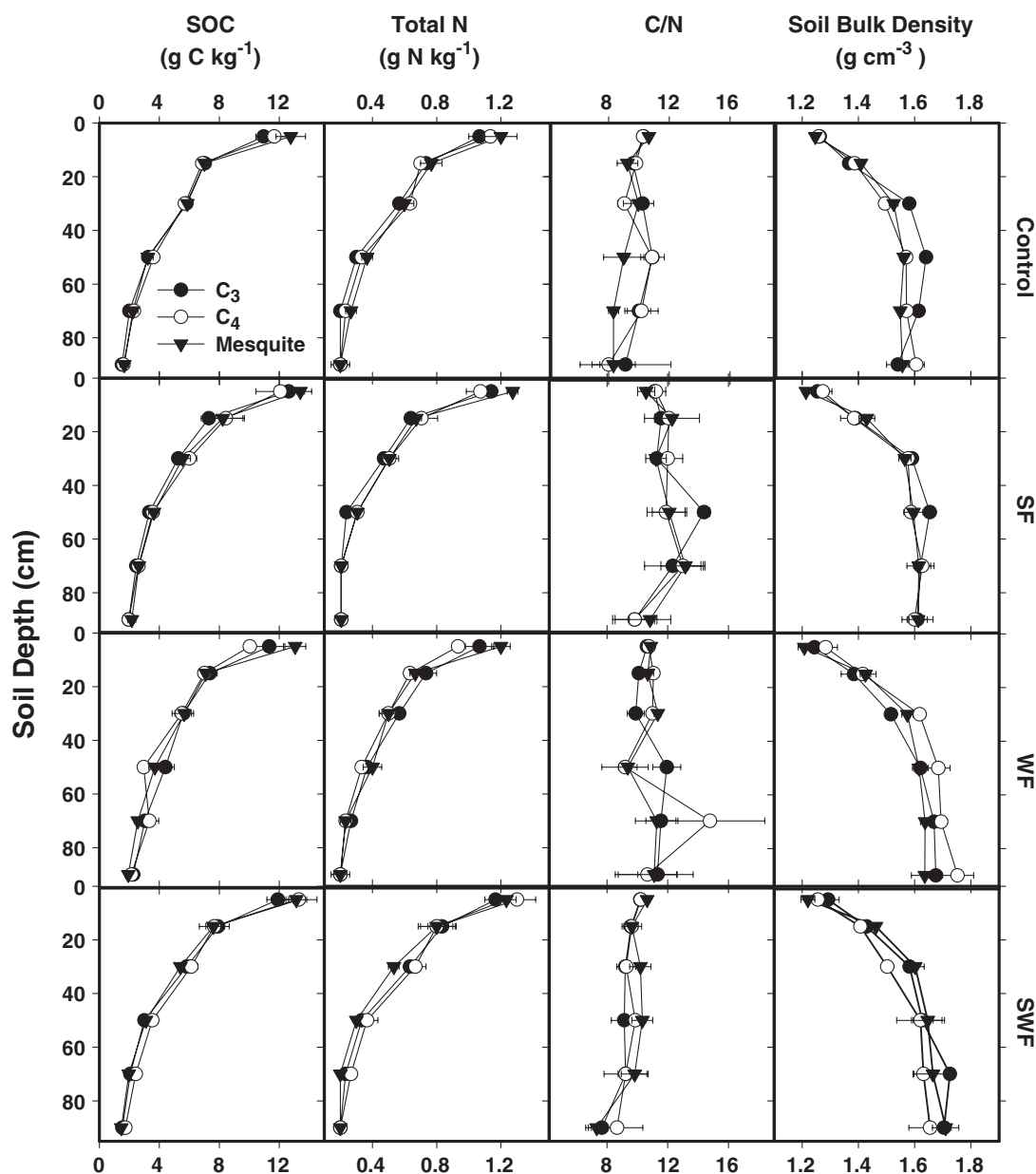


Fig. 1. Soil organic C and N concentration (g kg^{-1}), C to N ratio, and soil bulk density (g cm^{-3}) relative to fire treatments, vegetation types, and soil depth. Data are means \pm standard errors, and are plotted at the midpoint of each depth interval. SF, summer fire; WF, winter fire; SWF, alternate summer and winter fire.

the concentration, mass, and depth distribution of SOC. More specifically, the two treatments that included summer fires (SF and SWF) had approximately 13% more SOC in the upper 20 cm of the profile compared to the WF and control treatments. There were no changes in SOC at depths of >20 cm. We speculate that these changes in SOC storage in the surface soil could be due to: (i) increased rates of above- and/or belowground primary production; (ii) changes in the quality of organic matter inputs to the soil system; (iii) modifications to the physical environment of the soil and soil surface due to removal of litter and vegetation; and (iv) change in the rates of organic matter decay due to the second and third reasons above. It seems likely that all of these mecha-

nisms have interacted to shape the responses documented in this study.

Previous studies have shown that annual dry matter production, both above- and belowground, is usually greater under regular burning than unburned controls in mesic grasslands (Rice et al., 1998; Rice and Owensby, 2000; Ojima et al., 1994). Johnson and Matchett (2001) reported that annual burning caused a 25% increase in root growth compared to unburned controls, and hypothesized that plants increased allocation to roots to compensate for N limitation in burned areas. It is also observed that fire induces a higher C to N ratio in above- and belowground biomass and litter (Ojima et al., 1994; Johnson and Matchett, 2001), and these higher C to N

Table 2. Results of ANOVA for each soil response variable.

Source of variation	SOC†	Total N	C to N ratio	SOC	Total N	$\delta^{13}\text{C}$
	g C kg ⁻¹	g N kg ⁻¹		g C m ⁻²	g N m ⁻²	‰
Fire (F)	0.742	0.305	0.060	0.638	0.284	0.652
Plot (fire)	0.057*	0.007*	0.005*	0.001*	0.001*	0.034*
Vegetation (V)	0.585	0.468	0.859	0.745	0.837	0.000*
Soil depth (D)	0.000*	0.000*	0.000*	0.000*	0.000*	0.000*
F × V	0.888	0.119	0.925	0.623	0.180	0.986
F × D	0.051*	0.003*	0.016*	0.001*	0.000*	0.154
V × D	0.007*	0.010*	0.260	0.208	0.059	0.000*
F × V × D	0.315	0.612	0.621	0.578	0.995	0.435

* Significant at the 0.05 probability level.

† Soil organic carbon.

ratios have the potential to increase N limitation and reduce soil organic matter decomposition rate.

Aboveground net primary productivity during 2003 and 2004 in this mixed-grass savanna was approximately 25% higher in fire treatments (approximately 294 g m⁻²) than in unburned controls (approximately 222 g m⁻²) (E. Hollister, T. Boutton, and J. Ansley, unpublished data), suggesting that the increases in SOC observed in this study may be at least partially attributable to increased aboveground production. In addition, the increase in SOC after summer fires may be due to increased fine root production. Recent studies immediately adjacent to our study area indicated that summer fires increased the productivity and biomass of roots during the subsequent growing season, particularly in the spring; however, winter fires had no effect on root production (Hubbard, 2003). Hence, our observation that SF and SWF (but not WF) increase SOC storage may be attributable to differential response of root productivity to summer vs. winter fire (Hubbard, 2003). Collectively, these studies suggest that increased above- and belowground productivity are likely to be among the mechanisms responsible for the increases in SOC in SF and SWF treatments.

Fire also altered the concentration, mass, and depth distribution of soil total N. Concentrations and densities of N were generally greater in SF and SWF than in WF or control treatments, but these effects were evident only in the upper 20 cm of the profile. It is conceivable that these increases in soil total N were simply a function of greater organic matter inputs through increased above- and belowground productivity discussed above (Hubbard, 2003; E. Hollister, T. Boutton, and J. Ansley, unpublished data). In addition, fires are known to promote the presence of N-fixing leguminous forbs in grasslands (Leach and Givnish, 1996), and other studies have shown that asymbiotic N fixation in soil is stimulated by fire ash (Eisele et al., 1989). Finally, mesquite trees are known to be capable of symbiotic N fixation (Johnson and Mayeux, 1990; Zitzer et al., 1996), and it is possible that regrowing mesquite trees in fire treatments have increased N-fixing activity. Photosynthetic rates of mesquite regrowth following fire can be three times those of unburned plants (Ansley et al., 2002), and some of that increased photosynthetic income may be allocated to support increased symbiotic N fixation. Thus, increased organic matter inputs and/or accelerated

rates of symbiotic or asymbiotic N fixation appear to be plausible mechanisms by which N stocks could increase in response to fire treatments.

Relatively few studies have examined the impact of fire on soil C and N storage in grassland and savanna ecosystems. In the North American tallgrass prairie, SOC and total N storage have remained unchanged after 15 yr of annual fire (Rice and Owensby, 2000). In the Brazilian cerrado, biannual fires for 21 yr had no effect on SOC storage in the upper 1 m of the profile (Roscoe et al., 2000). In contrast, 30 to 50 yr of annual or biennial fire in grasslands and savannas in Zimbabwe (Bird et al., 2000) and South Africa (Aranibar et al., 2003; Fynn et al., 2003; Mills and Fey, 2004) reduced SOC by 10 to 30%, whereas soil total N remained constant or decreased by up to 20% in the upper 30 cm of the profile relative to unburned controls. A recent meta-analysis of previous studies in grasslands, shrublands, and forests revealed that fire generally results in no net change in soil total N (Wan et al., 2001). Although a diversity of responses have been documented, it appears that C and N stocks generally decrease or remain unchanged after 15 to 50 yr of annual-biennial fire treatment. Thus, our results are unique in that SF and SWF treatments have increased soil C and N stocks by approximately 10 to 15% relative to controls. We hypothesize that the discrepancies between our study and previous fire studies in grassland-savanna ecosystems may be due to the presence of N-fixing mesquite trees as an important component of the plant community. If symbiotic N fixation by this species is stimulated following fire, then mesquite may be providing an important limiting resource (fixed N) that increases rates of primary production and soil organic matter storage.

Influence of Vegetation on Soil Carbon and Nitrogen

Woody plant encroachment into grasslands and savannas is one of the most extensive land cover changes occurring around the world today (Archer et al., 2001; Jackson et al., 2002), and has the potential to alter soil C and N stocks through changes in primary production, above- vs. belowground biomass allocation, rooting patterns, and modifications to the physical environment. In this study, we found that concentrations (g kg⁻¹) of SOC and total N in the upper 10 cm of the profile were significantly higher under mesquite canopies than under C₃ or C₄ grass canopies; however, there were no significant differences in densities (g m⁻²) of SOC or total N.

Jackson et al. (2002) found that the influence of woody encroachment (mainly by mesquite) on soil C and N storage varied along a precipitation gradient in the southwestern USA, with soil C and N accumulation at sites with annual precipitation of <400 mm but C and N loss at sites with precipitation of >600 mm. At a site within 5 km of our study area, Jackson et al. (2002) found that soils beneath mesquite canopies stored 10% less SOC and 11% less total N than soils under grassland. It is not clear why their results differ from those of our study, but potential differences in soil texture and prior

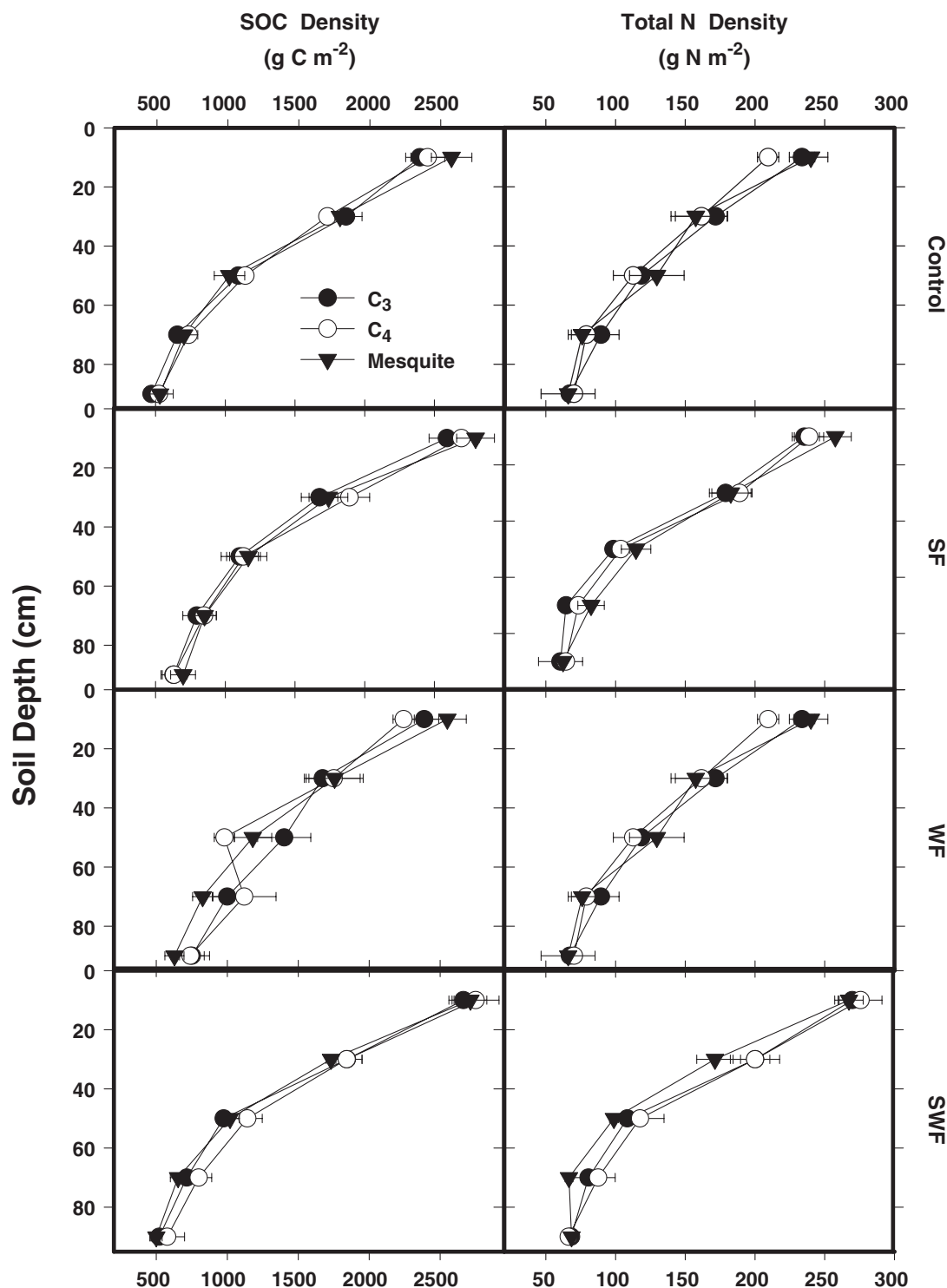


Fig. 2. Soil organic C and N density (g m^{-2}) relative to fire treatments, vegetation types, and soil depth. Data are means \pm standard errors, and are plotted at the midpoint of each depth interval. SF, summer fire; WF, winter fire; SWF, alternate summer and winter fire.

land use–disturbance histories between the two sites could be important factors. In contrast with the results of the present study and that of Jackson et al. (2002), other studies in the southern Great Plains and in the Rio Grande Plains of southern Texas at sites where annual precipitation is >600 mm have shown that soils beneath

mesquite canopies generally store significantly more SOC and total N than adjacent grasslands (Geising et al., 2000; Archer et al., 2001, 2004). Given that mesquite now covers approximately 45 million ha of the southwestern United States and northern Mexico, it will be important to develop a better understanding of the role of this plant

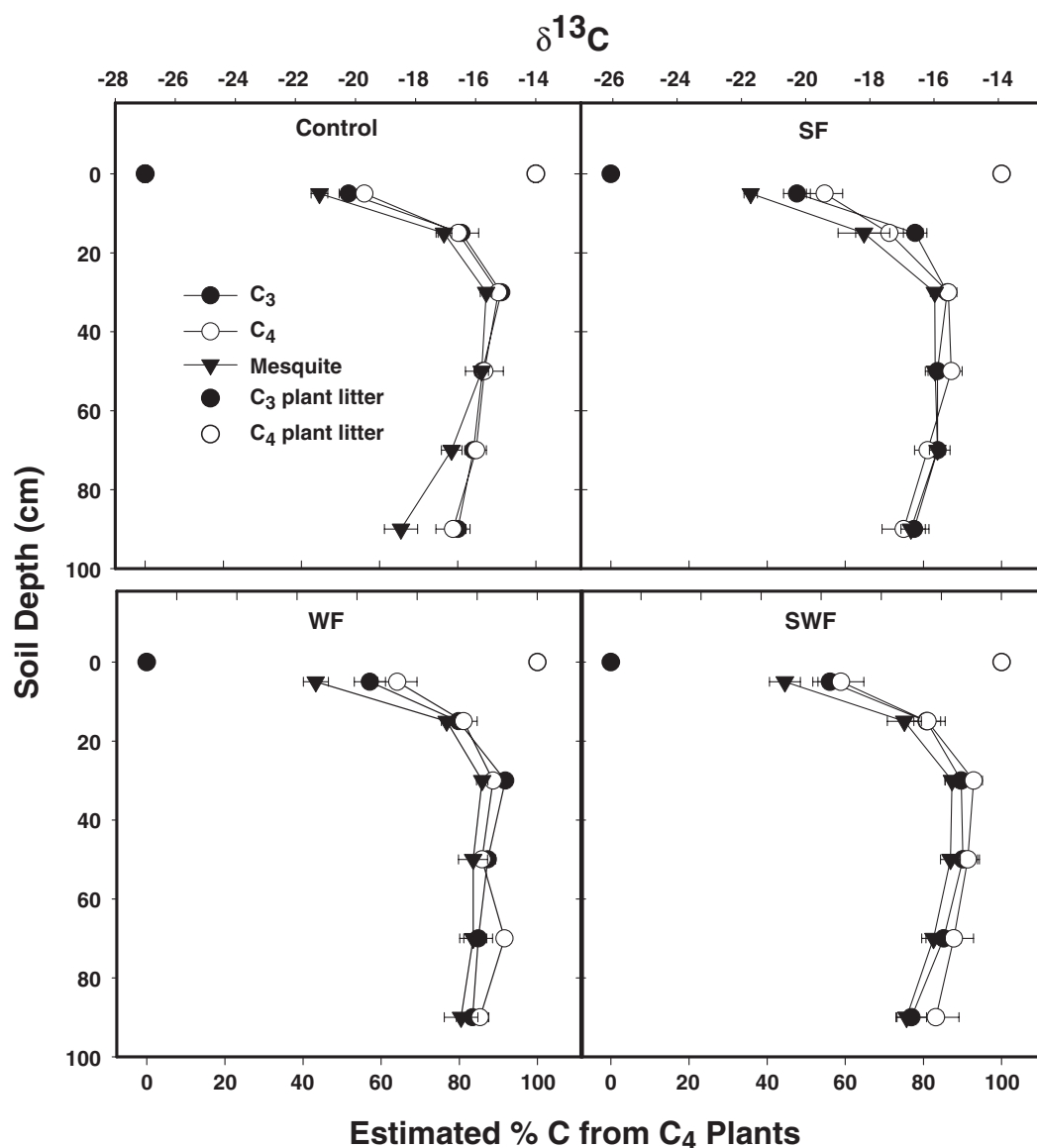


Fig. 3. The $\delta^{13}\text{C}$ values and estimated percent C from C₄ plants in soils beneath three vegetation types and four fire treatments at soil depth intervals. Data are means \pm standard errors, and are plotted at the midpoint of each depth interval. SF, summer fire; WF, winter fire; SWF, alternate summer and winter fire.

in SOC and total N storage in burned and unburned grassland and savanna ecosystems.

Sources of Soil Organic Carbon and Vegetation Change: Evidence from $\delta^{13}\text{C}$

It is generally predicted that the season of fire occurrence can influence the functional composition of plant communities in the Great Plains, with late winter–early spring fires favoring C₄ warm-season grasses and late summer fires potentially favoring C₃ cool-season grasses due to differences in their phenologies. The $\delta^{13}\text{C}$ values of SOC reflect relative inputs of C₃ vs. C₄ organic matter to the soil, and this index is well-suited for evaluating shifts in C₃–C₄ composition (Boutton et al., 1998, 1999). Fires applied during different seasons over a period of 13 yr did not change $\delta^{13}\text{C}$ values of SOC significantly in this mixed-

grass savanna, indicating that the relative above- and belowground productivity of C₃ vs. C₄ functional groups was not altered by this fire regime.

Although fire treatments have apparently not altered the C₃–C₄ composition of this ecosystem over the past 13 yr, there were significant changes in $\delta^{13}\text{C}$ values of SOC with respect to depth in the soil profile that indicate substantial changes have occurred in the C₃–C₄ composition of the vegetation over longer periods of time. The $\delta^{13}\text{C}$ values of SOC in the upper 10 cm of the profile generally range from -23 to -19‰ , indicating that approximately 40 to 60% of SOC was derived from C₄ grass inputs in that depth increment. However, the older SOC present at depths of >10 cm had $\delta^{13}\text{C}$ values of SOC ranging from -18 to -14‰ , indicating that 75 to 95% of that SOC was derived from C₄ sources. These data indicate that this mixed-grass savanna was once

much more strongly dominated by C_4 grasses than at present. Since the mean residence time of SOC at 0 to 10 cm in Mollisols is generally on the order of 50 yr, while that of SOC at depths of >10 cm is generally on the order of hundreds to thousands of years (e.g., Scharpenseel and Neue, 1984), it seems probable that this increase in relative C_3 productivity has occurred over the past 100 yr or so. This shift toward increased C_3 plant importance is likely related to increased abundance of the C_3 woody plant mesquite due to fire suppression (Archer et al., 2001), and to the increased abundance of the C_3 Texas wintergrass due to livestock grazing (Boutton et al., 1993). In addition, rising atmospheric CO_2 concentrations over the past century may have improved the carbon–water relations of C_3 plants, enabling them to be more competitive in C_4 -dominated grassland ecosystems (Polley, 1997; Polley et al., 1997).

CONCLUSIONS

The effects of fire on SOC and total N varied with fire seasonality, vegetation type, and soil depth in this temperate mixed-grass savanna. Both SF and SWF significantly increased SOC density in the 0- to 20-cm interval compared to WF and unburned controls. The SWF treatment also increased N density significantly at 0 to 20 cm. Soil organic C and N decreased exponentially with soil depth in all treatment combinations, with 40% of SOC and N concentrated in the upper 20 cm of the soil profile. Stable carbon isotope ratios of SOC showed that the frequency and seasonality of the prescribed fires applied to this mixed-grass savanna site over the past 13 yr did not significantly alter the relative proportions of C_3 vs. C_4 organic matter inputs, even though most of the fires were of high intensity. The $\delta^{13}C$ values of SOC in the 0- to 10-cm interval indicated that a significant proportion of SOC is now derived from C_3 plants due to increased abundances of woody plants and cool-season grasses during the past century; however, $\delta^{13}C$ values of SOC at depths of >10 cm suggested that primary productivity in this ecosystem was once almost exclusively dominated by C_4 grasses. Although the primary intent of prescribed fire as a land management tool in the southern Great Plains is generally to control the encroachment of woody plants and other weedy or invasive plant species, this study demonstrates that fires applied at 2- to 4-yr intervals have the potential to significantly increase SOC and total N storage in the upper soil profile over decadal time frames. Results of the present study will have implications for scientists, land managers, and policymakers who are now evaluating the potential for land uses to alter ecosystem carbon storage and influence atmospheric CO_2 concentrations and global climate.

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