

Soil organic carbon and black carbon storage and dynamics under different fire regimes in temperate mixed-grass savanna

R. J. Ansley, T. W. Boutton, and J. O. Skjemstad³

Received 12 December 2005; revised 14 April 2006; accepted 11 May 2006; published 19 July 2006.

[1] We quantified the effects of repeated, seasonal fires on soil organic carbon (SOC), black carbon (BC), and total N in controls and four fire treatments differing in frequency and season of occurrence in a temperate savanna. The SOC at 0–20 cm depth increased from 2044 g C m $^{-2}$ in controls to 2393–2534 g C m $^{-2}$ in the three treatments that included summer fire. Similarly, soil total N (0–20 cm) increased from 224 g N m $^{-2}$ in the control to 251–255 g N m $^{-2}$ in the treatments that included summer fire. However, winter fires had no effect on SOC or total N. Plant species composition coupled with lower δ^{13} C of SOC suggested that increased soil C in summer fire treatments was related to shifts in community composition toward greater relative productivity by C_3 species. Lower δ^{15} N of soil total N in summer fire treatments was consistent with a scenario in which N inputs > N losses. The BC storage was not altered by fire, and comprised 13–17% of SOC in all treatments. Results indicated that fire and its season of occurrence can significantly alter ecosystem processes and the storage of C and N in savanna ecosystems.

Citation: Ansley, R. J., T. W. Boutton, and J. O. Skjemstad (2006), Soil organic carbon and black carbon storage and dynamics under different fire regimes in temperate mixed-grass savanna, *Global Biogeochem. Cycles*, 20, GB3006, doi:10.1029/2005GB002670.

1. Introduction

[2] Fire is an integral component of the disturbance regime of most terrestrial ecosystems [Collins and Wallace, 1990], and has significant consequences at both ecosystem and global scales [Bond and Keeley, 2005]. At the global scale, fires modify biogeochemical cycles and climate by volatilizing climatically active trace gases, injecting particulate matter into the atmosphere, and modifying the albedo of the terrestrial surface [Crutzen and Andreae, 1990; Pinty et al., 2000; Andreae and Merlet, 2001]. Fires affect approximately 600 Mha of grassland, savanna, and forest each year [Mouillot and Field, 2005], and transfer 1.7-4.1 Pg (10¹⁵ g) of carbon [Lavorel et al., 2001; van der Werf et al., 2003] and 12-28 Tg (10¹² g) of nitrogen [Lobert et al., 1990] to the atmosphere annually. In addition, incomplete combustion of biomass results in the storage of approximately 0.05-0.2 Pg yr⁻¹ as black carbon (BC) or "char" in soils [Kuhlbusch, 1998; Schmidt and Noack, 2000]. Because BC is relatively inert and resistant to decay, it represents an important sink for atmospheric carbon, and may comprise a significant fraction of the "missing carbon" in the global carbon budget [Kuhlbusch, 1998].

[3] At the ecosystem level, fire can alter plant species diversity and dominance by changing microclimate and the

[4] Fire has the potential to alter soil carbon storage by influencing rates of net primary productivity, carbon allocation patterns, plant tissue chemistry, and rates of organic matter decomposition [Ojima et al., 1994; Rice et al., 1998; Reich et al., 2001]. Despite the temporary loss of photosynthetic tissue, fire generally stimulates aboveground net primary productivity relative to comparable unburned areas in grasslands and savannas [Rice and Owensby, 2000; Ansley et al., 2002; Santos et al., 2003]. In some grasslands and savannas, fire also appears to accelerate root production, increase root biomass, and increase C/N ratios of root tissue [Blair, 1997; Rice et al., 1998; Johnson and Matchett, 2001; Reich et al., 2001]. Collectively, these phenomena would appear to favor soil carbon accumulation in burned

Copyright 2006 by the American Geophysical Union. 0886-6236/06/2005GB002670\$12.00

GB3006 1 of 11

availability of limiting resources (light, water, and nutrients). These changes in ecosystem structure and the abiotic environment often modify key functional characteristics of ecosystems (primary productivity, hydrologic and nutrient fluxes) that have the potential to alter the storage and turnover of carbon and nitrogen in plants and soils [Ojima et al., 1994; Rice and Owensby, 2000; Reich et al., 2001]. However, the direction and magnitude of these changes is difficult to predict, and depends on specific ecosystem characteristics, fire frequency, season of occurrence, and the timing and duration of post-fire sampling. Much of the uncertainty regarding the role of fire in global biogeochemical cycles is a result of our limited understanding of the biogeochemical consequences of fire at the ecosystem scale, and several reviews have highlighted the need for more quantitative assessments of the role of fire in grasslands and savannas [Crutzen and Andreae, 1990; Hao and Liu, 1995; Lavorel et al., 2001].

¹Texas Agricultural Experiment Station, Vernon, Texas, USA.

²Department of Rangeland Ecology and Management, Texas A&M University, College Station, Texas, USA.

³CSIRO Land and Water, Glen Osmond, South Australia, Australia.

grasslands and savannas. On the other hand, warmer soil temperatures may increase rates of organic matter decomposition and diminish or negate the effects of greater aboveground and belowground organic carbon inputs.

- [5] Because net annual carbon fluxes in ecosystems are small relative to the mass of soil organic carbon (SOC), changes in soil carbon storage occur slowly. Consequently, few controlled studies have been of sufficient duration to observe changes in SOC in response to fire regime. In a tropical savanna in southeastern Brazil, biannual fires for 21 years had no effect on SOC storage in the upper 1 m of the profile [Roscoe et al., 2000]. In contrast, 50 years of annual fire in a subhumid savanna in Zimbabwe reduced SOC storage in the upper 30 cm of the profile by 30% relative to unburned controls [Bird et al., 2000]. In the North American tallgrass prairie, SOC has been predicted to decline with annual burning over a period of 10–20 years [Ojima et al., 1990].
- [6] Fire effects on N storage and dynamics are also of great interest because N is a limiting nutrient in most terrestrial ecosystems [Vitousek and Howarth, 1991]. Field and laboratory studies indicate that about 70-90% of biomass N is volatilized during vegetation fires [Raison, 1979; Lobert et al., 1990; Ojima et al., 1990], and further losses may result from postfire wind and/or water erosion. In general, warmer soil temperatures accelerate microbial activity and significantly increase soil pools of NH₄ and NO₃ for approximately 1 year post-fire [Wan et al., 2001]. These enlarged substrate pools accelerate rates of nitrification and denitrification, resulting in elevated loss rates of N as NO, N₂O, and N₂ [Levine et al., 1988; Serca et al., 1998] which may persist for as long as 1 year post-fire [Poth et al., 1995]. However, it should be noted that frequent (annual) fires in some grasslands may reduce available N and reduce rates of N mineralization [Blair, 1997; Turner et al., 1997]. On the other hand, fires promote the presence of leguminous forbs capable of symbiotic N₂ fixation in grasslands [Leach and Givnish, 1996], and laboratory studies indicate that rates of asymbiotic cyanobacterial N2 fixation are stimulated by ash deposition [Eisele et al., 1989]. Although both N inputs and N losses may be more rapid following fire, a recent meta-analysis of previous studies in grasslands, shrublands, and forests revealed that fire generally results in no net change in soil N storage [Wan et al., 2001]. However, simulation modeling of tallgrass prairie indicates that soil total N decreases significantly within a few years under an annual fire regime [Risser and Parton, 1982; Ojima et al., 1990]
- [7] In the southern Great Plains and southwestern United States, prescribed fire is used to suppress the encroachment of honey mesquite (*Prosopis glandulosa* Torr.) into areas that have historically been grasslands or savannas [*Wright and Bailey*, 1982]. Mesquite is a highly productive tree legume capable of symbiotic N₂ fixation [*Johnson and Mayeux*, 1990; *Zitzer et al.*, 1996], and exerts strong control over ecosystem biogeochemistry [*Schlesinger et al.*, 1990; *Boutton et al.*, 1999; *Archer et al.*, 2001]. Mesquite sprouts from stem bases following fire, and it is necessary to apply repeated burns to maintain suppression [*Ansley and Jacoby*, 1998].

- [8] The historical fire regime in the southern Great Plains included both late winter and summer fires [Frost, 1998], although most "management" burns are applied in late winter (February–March) [Ansley et al., 1998]. There is some concern that fires applied repeatedly during the same season may shift the C_3 (cool season) versus C_4 (warm season) composition of the plant community and alter key aspects of ecosystem function. An alternate-season fire regime may more closely mimic natural historical conditions and thus be better suited to maintain the biodiversity of these mixed C_3 – C_4 systems. Therefore it is critical to understand the impact of repeated fires and their season of occurrence on the carbon and nitrogen cycles of these mesquite savannas.
- [9] The purpose of this study was to evaluate the biogeochemical consequences of fire in a temperate mixed-grass/mesquite savanna in the southern Great Plains, United States. More specifically, our objectives were to: (1) quantify changes in SOC, BC, and soil total N in response to fire frequency and season of occurrence; (2) determine if gains/losses of SOC are attributable to shifts in the functional composition (i.e., C_3 versus C_4 species) of plant communities by measuring δ^{13} C of SOC; and (3) determine if changes in soil N could be linked to specific changes in N-cycling processes by measuring δ^{15} N of soil total N.

2. Materials and Methods

2.1. Study Site

[10] The experiment was conducted from 1991 to 1996 in mixed-grass savanna in north-central Texas (34°00'N, 99°20′W). Mean annual precipitation is 665 mm. Mean annual temperature is 16.9°C, with mean monthly temperatures ranging from 3.8°C in January to 29.1°C in July. Soils are fine, mixed, thermic Typic Paleustolls of the Tillman series, 0-1% slope, which are alluvial clay loams from 0 to 3-4 m depth, underlain by Permian sandstone/ shale parent material [Koos et al., 1962]. Texture is 32% clay, 52% silt and 16% sand at 0-10 cm depth, and 43% clay, 41% silt and 16% sand at 10-20 cm depth. Soil pH is 7.0-7.2. Prior to burning, the site was dominated by honey mesquite (2-4 m tall; 20-40% canopy cover). Herbaceous understory was a mixture of short and mid grasses with approximately equal proportions of C₃ and C₄ species. Primary C3 grass was Texas wintergrass (Nassella leucotricha [Trin. and Rupr.] Pohl.). Dominant C₄ grasses were buffalo grass (Buchloe dactyloides [Nutt.] Engelm.), and vine mesquite (Panicum obtusum H.B.K.). Livestock were excluded from the site since 1988. Prior to this, cattle were grazed at a moderate continuous level (i.e., removing approximately 50% of net primary production annually) for at least 70 years.

2.2. Fire Treatments and Behavior

[11] The study consisted of three replicates each of five fire treatments. The size of each replicate plot ranged from 1 to 6 ha. Fire treatments were: (1) repeated winter fires in 1991, 1993 and 1995 (w91w93w95); (2) repeated summer fires in 1992 and 1994 (s92s94); (3) repeated summer fires

Table 1. Number of Months Following the Most Recent Fire in Each Fire Treatment at the Time Soil Samples Were Obtained in December 1996^a

Fire Treatment	Months After Last Fire			
w91w93w95	22			
s92s94	27			
s93s94	27			
w91s92w94	34			

^aAbbreviations: s, summer fire; w, winter fire.

in 1993 and 1994 (s93s94); (4) alternate-season fires in winter 1991, summer 1992 and winter 1994 (w91s92w94); and (5) unburned controls. Winter fires were applied from late January to mid-March, and summer fires were applied in September. All fires were conducted as headfires [Ansley and Jacoby, 1998]. None of the plots had burned for at least 30 years prior to this study. Mesquite trees were in full foliage during summer fires but without leaves during winter fires.

[12] Air temperature, relative humidity (RH) and wind speed were measured on site a few minutes prior to each fire. Herbaceous fine fuel amount (litter + grass and forb standing crop) was estimated in each plot by harvesting 15 quadrats (0.25 m²) of herbaceous material in interstitial spaces between mesquite trees. Fire temperatures were measured at 1-s intervals at three to five locations per plot and at four vertical positions (ground level, and 0.1, 0.3, and 1.0 m above ground) per location using thermocouples and a data logger [after Ansley et al., 1998]. In addition, soil temperature at 1 cm depth was measured during the winter 1991, winter 1993 and summer 1992 fires at the same locations in each plot using the same equipment. All locations were in grass communities in interstitial spaces between mesquite trees. Flame length was estimated by videotaping the flame front as it passed four metal standards in each plot [Ansley et al., 1998], and used to compute fire intensity using the equation of Byram [1959].

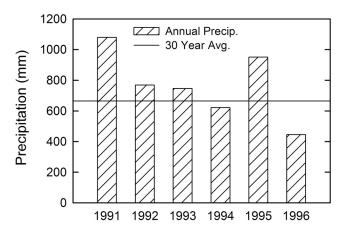


Figure 1. Annual precipitation from 1991 to 1996 (bars) relative to the 30-year mean (line).

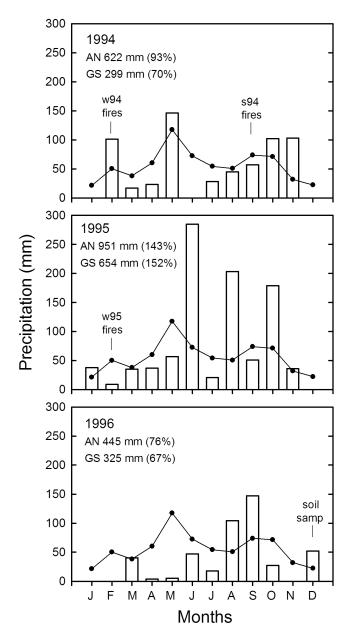


Figure 2. Monthly precipitation from 1994 to 1996 (bars) versus 30-year mean (line). Each panel displays annual (AN) and growing season (GS) totals relative (%) to the 30-year mean.

2.3. Vegetation Measurements

[13] Fifty to 100 mesquite in each replicate plot were evaluated at the end of the first full growing season following each fire in each repeated fire treatment along permanently marked line transects. Response variables included percent canopy reduction, percent of trees with complete above ground mortality (top-kill), percent of trees that were partially top-killed, and percent dead trees [after *Ansley and Jacoby*, 1998].

[14] Herbaceous cover was determined in 1994 and 1995 by visually estimating percent foliar cover of each species within a 0.25 m² frame placed at five points along each of

Table 2. Weather and Fine Fuel Amount Immediately Prior to Burning and Fire Behavior Averaged Over All Fires in Each Treatment^a

Fire Treatment ^b	Air Temp., °C	Relative Humidity, %	Wind Velocity, m s ⁻¹	Herbaceous Fine Fuel, g m ⁻²	Peak Fire Temp., °C	Fireline Intensity, kW m ⁻¹
w91w93w95	20.2 ± 1.9	29.6 ± 2.9	4.5 ± 0.8	281 ± 30	558 ± 31	2687 ± 1326
s92s94	32.9 ± 0.7	36.2 ± 4.7	2.6 ± 0.4	282 ± 29	641 ± 15	3257 ± 342
s93s94	33.8 ± 0.6	35.8 ± 4.8	5.0 ± 0.3	202 ± 18	571 ± 18	5327 ± 712
w91s92w94	27.1 ± 1.6	32.9 ± 2.8	4.5 ± 0.7	276 ± 44	534 ± 52	3507 ± 1214

^aMeans are followed by standard errors (n = 6 or 9; 3 reps \times 2 or 3 fires treatment $^{-1}$).

six 50-m transect lines in each plot. Data for the s93s94 treatment were obtained in 1993 (preburn) and 1995. In addition, in 1995, many plots became dominated by the C₃ annual forb, *Amphiachyris dracunculoides* DC (annual broomweed) that grew to canopy heights of 0.5 to 0.7 m. Foliar cover of this species was estimated as a separate layer above the graminoid layer. Herbaceous data for the alternate-season fire treatment were not available in 1995.

2.4. Soil Sampling and Analysis

[15] Soil samples were collected at 0–10 cm and 10–20 cm depths in December 1996 within small patches of Texas wintergrass in interstitial spaces between mesquite trees. At the time of soil sampling, 22 to 34 months had passed since the most recent fire in each treatment (Table 1). Ten 2.5-cm-diameter soil cores were collected in each plot and mixed into two subsamples (five cores per subsample) prior to analysis. Litter was removed from the soil surface before coring. Samples were oven-dried at 50°C for 24 hours, and passed through a 2-mm sieve to remove coarse organic debris [Nelson and Sommers, 1982]. Soils were then homogenized thoroughly and pulverized for elemental and isotopic analyses.

[16] The SOC and total N concentrations in all soil samples were determined by combustion/gas chromatography using a Carlo-Erba NA-1500 (Milan, Italy) elemental analyzer. Samples containing CaCO₃ were pretreated with HCl according to the method of *Nieuwenhuize et al.* [1994]. C/N ratios were calculated by dividing SOC by total N. Soil bulk density was used to convert concentrations (g kg⁻¹) of SOC and total N to mass per unit area (g m⁻²). Bulk density (determined by the core method of *Blake and Hartge* [1986]) averaged 1.3 g cm⁻³ (range 1.23 to 1.42 g cm⁻³) over all treatments with no significant difference between treatments

[17] Soils were also analyzed for $\delta^{13}C$ and $\delta^{15}N$ using a Carlo Erba EA-1108 (Milan, Italy) elemental analyzer interfaced with a Delta Plus (Thermo-Finnigan, San Jose, California) isotope ratio mass spectrometer operating in continuous flow mode. Samples containing CaCO₃ were pretreated with HCl to volatilize inorganic C [*Nieuwenhuize et al.*, 1994]. Precision was <0.1% for $\delta^{13}C$, and <0.2% for $\delta^{15}N$. The $\delta^{13}C$ values were expressed relative to the V-PDB standard [*Coplen*, 1995], while $\delta^{15}N$ values were expressed relative to atmospheric N₂ [*Mariotti*, 1983].

2.5. Black Carbon Analyses

[18] Soils from three treatments (control, w91w93w95, and s92s94) were analyzed for BC using a combination of

physical separation, high-energy photo-oxidation, and solidstate ¹³C nuclear magnetic resonance (NMR) spectroscopy [*Skjemstad et al.*, 1999]. Three replicates per treatment were analyzed for the 0- to 10-cm depth interval, while the three replicates for the 10- to 20-cm interval were pooled, homogenized, and analyzed as a single sample.

[19] Soil samples (10 g) were shaken overnight in 50 mL of sodium hexametaphosphate (5 g L⁻¹) before being passed through a 200-μm and a 53-μm sieve in series. Fractions >53 μm were dried, weighed, and inspected microscopically to ensure that no aggregates or pieces of BC remained. Previous studies showed that the fraction >53 μm is dominated by less decomposed plant debris, whereas nearly all of the BC is concentrated in the <53 μm fraction [Skjemstad et al., 1999; Schmidt et al., 2002; Glaser and Amelung, 2003]. Aliquots of each size fraction were analyzed for organic C concentration as described above.

[20] The <53-µm suspension was made to 500 mL with water. Aliquots (<20 mL) containing 2–3 mg C were placed in quartz tubes, made to 20 mL with water, and photo-oxidized using high-energy ultraviolet radiation for 2 hours to remove labile fractions of organic C. Photo-oxidized samples were treated with 2% hydrofluoric acid to remove magnetic and paramagnetic materials that interfere with NMR. Treated samples were packed into 7-mm zirconia rotors, and solid-state ¹³C Cross Polarization/Magic Angle Spin (CP/MAS) NMR spectra obtained at 50.3 MHz on a Varian Unity 200 spectrometer with a 2.7 T wide-bore Oxford superconducting magnet using a Doty Scientific MAS probe. The chemical shift regions 0–45 ppm, 45–110 ppm, 110–140 ppm, 140–165 ppm, 165–190 ppm,

Table 3. Mesquite Responses to Repeated Winter, Summer, or Alternate-Season Fires, 1991–1995^a

Fire Treatment ^b	Stand-Level Canopy Reduction, %	Trees With Complete Aboveground Mortality (Top Kill), ^b %	Partially Top-Killed Trees, %	Dead Trees, %
w91w93w95 ^c	88 ± 2	61 ± 1	39 ± 1	0 ± 0
s92s94	98 ± 2	92 ± 8	6 ± 6	2 ± 2
s93s94	100 ± 0	94 ± 3	2 ± 1	4 ± 2
w91s92w94	97 ± 2	86 ± 6	13 ± 7	1 ± 1

^aValues represent cumulative responses to all fires in each treatment. Means are followed by standard errors (n = 3).

^bAbbreviations: w, winter fire (January–March); s, summer fire (September); for example, "w91" is winter fire in January–March 1991.

bValues in 3 columns to the right add to 100%

^cAbbreviations: w, winter fire (January-March); s, summer fire (September).

Table 4. Foliar Cover of C₃ and C₄ Perennial Grasses, 1993–1995, and Amphiachyris dracunculoides (Amdr) in 1995^a

	C	C ₃ Perennial Grasses, %		C ₄ Perennial Grasses, %			Amdr, %
Fire Treatment	1993 ^b	1994°	1995 ^d	1993	1994	1995	1995
Control		26 ± 8	24 ± 7		28 ± 3	41 ± 12	0
w91w93w95		29 ± 6	50 ± 7		41 ± 4	37 ± 5	1 ± 1
s92s94		17 ± 6	31 ± 8		49 ± 7	42 ± 6	18 ± 3
s93s94	29 ± 5		62 ± 14	28 ± 5		17 ± 6	16 ± 5
w91s92w94		29 ± 3			43 ± 4		

^aMeans are followed by standard errors (n = 3).

and 190–220 ppm were assigned to alkyl-C, O-alkyl-C, aryl-C, O-aryl-C, carbonyl-C, and aldehyde/ketone-C, respectively. The BC content of the <53-μm fraction was estimated using the aryl-C content of the sample as described by *Skjemstad et al.* [1999, 2002]. For BC calculations, a Bloch decay correction was applied on the aryl-C fraction following photo-oxidation, as documented previously [*Skjemstad et al.*, 1999].

2.6. Statistical Analyses

[21] Soils responses were analyzed using a split-plot ANOVA with fire treatment as whole plot and soil depth as subplot [SAS Institute, 1996]. We used the replicate by fire treatment mean square as the error term in testing for effects of fire treatment, and the pooled error to test for effects of depth and treatment by depth interactions. If a significant treatment by depth interaction occurred, one-way ANOVAs were conducted within each soil depth to test for treatment effects. Mean comparisons were conducted using LSD ($P \le 0.05$ unless otherwise noted).

3. Results

3.1. Precipitation

[22] Annual precipitation was near or above-average for most of the study duration, with the exception of 1996 (Figure 1). Average to above-average rainfall from 1991 through 1994 stimulated herbaceous growth and the accumulation of sufficient amounts of herbaceous fine fuel to conduct fires. Monthly precipitation during the 1995 growing season following the final fires in each fire treatment (either s94 or w95) was above normal (Figure 2) and stimulated herbaceous growth. Precipitation in 1996 was below normal, other than a pulse of moisture in August and September prior to the December 1996 soil sample date.

3.2. Weather Conditions and Fire Behavior

[23] Air temperature just prior to burning was higher in summer than winter fires (Table 2). Relative humidity was slightly higher in summer than winter fires. Wind velocity ranged from 2.6 to 5.0 m s⁻¹. Herbaceous fine fuel amount ranged from 202 to 282 g m⁻². Peak fire temperatures occurred at 0.1 or 0.3 m above ground and were slightly higher in summer than winter fires. Fire intensity was greater in the repeated summer and alternate-season than the repeated winter fire treatment. The winter 1991 fires

were of low intensity (<600 kW m⁻¹) in both the repeated winter and the alternate-season fire treatments, but intensity of all other fires reached levels that would be considered near the maximum for typical native mixed-grass herbaceous fuel loads in this ecosystem [*Ansley and Jacoby*, 1998]. Soil temperatures at 1 cm soil depth (measured during winter 1991, winter 1993 and summer 1992 fires only) were 19.5 (±1.0)°C and 29.5 (±0.8)°C just prior to burning, and increased to 35.9 (±4.0)°C and 50.5 (±5.0)°C during winter and summer fires, respectively.

3.3. Vegetation Responses

[24] Stand-level tree canopy reduction was slightly lower in the repeated winter than the other fire treatments following completion of the last fire in each treatment (Table 3). All treatments that included a summer fire had >97% canopy reduction. There were considerably more trees with complete aboveground mortality (top-kill) in the repeated summer and alternate-season fire treatments than the repeated winter fire treatment. Conversely, the repeated winter fire treatment had more partially top-killed trees than any treatment that included a summer fire. Whole plant mortality was <5% in all treatments. Most of the mesquite that had either total or partial above ground mortality sprouted from dormant buds at stem bases. Thus, at the time of soil sampling in December 1996, plots that included summer fires appeared as open grasslands with standing stems of the original mesquite trees and each tree with 0.5 to 1.5 m tall multistemmed basal regrowth. In contrast, the repeated winter fire plots appeared more as a savanna with 60% of the trees completely top-killed with basal regrowth and the remaining trees partially top-killed (although foliage remaining on these partially top-killed trees was usually <30% of the original preburn canopy).

[25] Foliar cover of C₃ perennial grasses increased in all fire treatments except the control from 1993 or 1994 to 1995 (Table 4). During the same time, cover of C₄ grasses decreased in the fire treatments but increased in the control. At the end of the 1995 growing season, cover of the C₃ forb *Amphiachyris* was greater in the repeated summer fire treatments than in the control or winter fire treatment.

3.4. Soil Responses

3.4.1. SOC and Total N

[26] The SOC and total N at 0-10 cm depth increased significantly in the s92s94 and alternate season fire treatments relative to the unburned control (Figure 3). The C/N

^bThe 1993 data recorded prior to the s93 summer fires.

^cThe 1994 data recorded prior to s94 summer fire (in s92s94 and s93s94 treatments).

^dThe 1995 data recorded in October 1995, after all fire treatments.

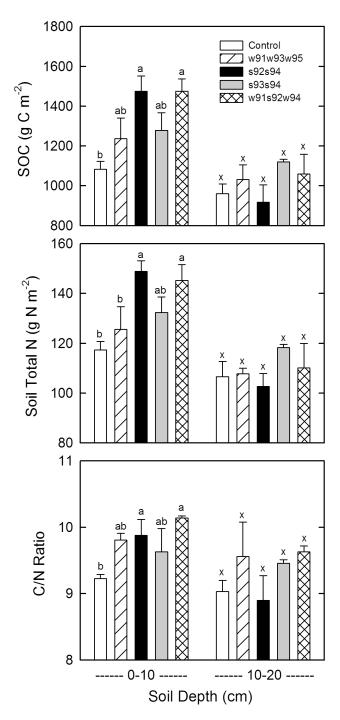


Figure 3. SOC (g C m⁻²), soil total N (g N m⁻²), and C/N ratio at two soil depths in fire treatments during 1996. Vertical lines are ± 1 standard error. Means with similar letters within each depth are not significantly different (P \leq 0.05).

ratio at 0-10 cm was significantly greater in s92s94 and alternate season fire treatments relative to the control, indicating that SOC increased relatively more rapidly than did total N in those same treatments. Although SOC, total N, and C/N ratio were generally higher in fire treatments

than in the control at 10-20 cm, these differences were not significant.

3.4.2. Isotopic Composition of SOC and Total N

[27] The δ^{13} C value of SOC at 0–10 cm was -18.4% in the unburned control, while those in fire treatments were lower (more negative) and ranged from -19.2 to -20.2% (Figure 4). However, only the s92s94 fire treatment was significantly different than the control. The δ^{13} C values of SOC at 10-20 cm were lower in the summer fire treatments than the other treatments. The δ^{13} C values of SOC were significantly lower at 0-10 cm than at 10-20 cm in all treatments.

[28] The $\delta^{15}N$ of soil total N at $0{\text -}10$ cm was approximately +7% in unburned controls and in the repeated winter fire treatment, and +6% in the three other treatments that included summer fires (Figure 4); however, only the winter fire treatment and two treatments with summer fire differed significantly from each other. At $10{\text -}20$ cm, the s93s94 treatment had significantly lower $\delta^{15}N$ than the unburned control. A regression that included all treatments and both

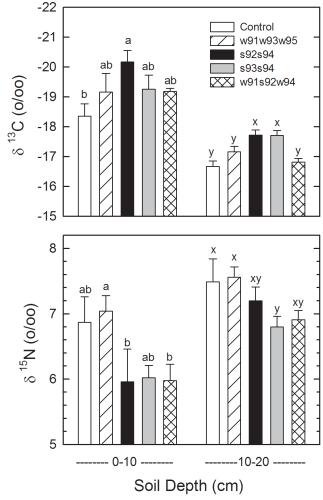


Figure 4. The $\delta^{13}C_{V\text{-PDB}}$ values of SOC and $\delta^{15}N_{AIR}$ values of soil total N in fire treatments. Vertical lines are ± 1 standard error. Means with similar letters within each depth are not significantly different (P ≤ 0.05).

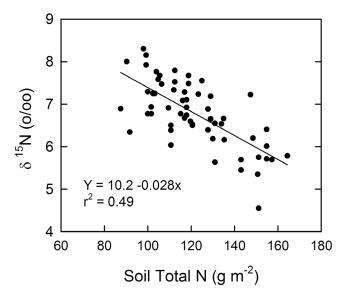


Figure 5. Regression between soil total N and $\delta^{15}N_{AIR}$ values of soil total N, all fire treatments and soil depths included.

soil depths indicated that as total N increased, $\delta^{15}N$ decreased (Figure 5).

3.4.3. Black Carbon

[29] Soil BC concentrations at 0–10 cm ranged from 1.4 to 1.7 g kg⁻¹, but did not differ between the control and the fire treatments (Table 5). BC concentrations were slightly lower at 10-20 cm $(1.0-1.3 \text{ g kg}^{-1})$, and differed little between controls and fire treatments. BC comprised approximately 13-17% of SOC in both 0-10 cm and 10-20 cm depth increments, and this proportion did not differ between treatments. BC densities were not significantly different between controls and fire treatments at 0-10 cm (185-225 g m⁻²). Although densities in the 10- to 20-cm depth increment were greater in the fire treatments (150-179 g m⁻²) than in the unburned controls (133 g m⁻²), these differences could not be evaluated statistically because only one composite sample per treatment was analyzed for that increment. However, each sample was a composite of 10 soil cores and should have been representative of the treatments. Total BC densities for the upper 20 cm of the profile were lower in unburned controls (344 g m⁻²) than in the winter fire (365 g m⁻²) or summer fire (375 g m^{-2}) treatments.

4. Discussion

4.1. Soil Organic Carbon

[30] Changes in SOC storage in response to ecosystem perturbation are generally difficult to detect over short time periods because of the large quantity of carbon stored in soil. In this study, SOC at 0–20 cm depth increased from 2044 g C m⁻² in unburned controls to 2393–2534 g C m⁻² in the three treatments that included summer fire (by adding SOC values from 0–10 cm and 10–20 cm depths from Figure 3), implying rates of carbon accumulation of 58–82 g C m⁻² yr⁻¹ in those treatments during the 6 years of the study. These rates are comparable to those found on

abandoned agricultural soils in temperate regions allowed to return to native grassland vegetation [Gebhart et al., 1994; Schlesinger, 1997]. Our results suggest that summer-season fires may have strong effects on rates of organic matter inputs and/or decomposition in this ecosystem.

[31] Direct measurements of aboveground annual net primary productivity during 2003 and 2004 indicate that primary production is on average 25% higher in fire treatments (\approx 294 g m⁻²) than in unburned controls (\approx 222 g m⁻²) (E. Hollister, T. W. Boutton, R. J. Ansley, unpublished data, 2006), suggesting that observed increases in SOC may be at least partially attributable to increased aboveground production in fire treatments. In addition, the increase in SOC after summer fires may be due to increased production of very fine roots of grasses that may have passed through the 2-mm sieve. The increase in C/N ratio at 0-10 cm depth in the fire treatments suggests an increase in root biomass. Recent studies adjacent to our study area indicate that latesummer fires increased root productivity and biomass during the subsequent growing season, particularly in the spring. In contrast, winter fires had no effect on annual root production compared to unburned controls [Hubbard, 2003]. Therefore it seems possible that observed differences in soil carbon response may be attributable to differential response of root productivity to summer vs. winter fire. The lower response of SOC accumulation in the s93s94 treatment may be attributable to a slower recovery of herbaceous vegetation following summer fires in two consecutive years, as the fine fuel data in Table 2 indicate. This treatment was the only one in which fire killed a significant portion of C₄ grasses and greatly stimulated growth of C3 Texas wintergrass (data not shown).

[32] The herbaceous composition of the plant community showed that C₃ grass and forb cover increased while C₄ grass cover decreased in response to all fire treatments. Thus changes in soil carbon storage may be related to increased relative productivity of the C₃ component of the plant community. This seems reasonable because both late-summer fires (September–October) and winter fires (January–March) occur at a time when C₄ grasses are largely dormant, but C₃ grasses and forbs are actively growing. Hence fires occurring between September and March will

Table 5. SOC and BC in Soils Collected From the Unburned Control and Two Fire Treatments in 1996^a

Fire Treatment	Soil Depth, cm	SOC, g kg ⁻¹	BC, g kg ⁻¹	Percent of SOC as BC	BC, g m ⁻²
Control	0 - 10	9.4 ± 0.6	1.6 ± 0.1	17 ± 2	211 ± 13
	10-20	7.7	1.0	13	133
	0 - 20				344
w91w93w95	0 - 10	9.8 ± 1.1	1.4 ± 0.4	14 ± 3	185 ± 51
	10 - 20	8.1	1.3	16	179
	0 - 20				364
s92s94	0 - 10	12.7 ± 1.3	1.7 ± 0.3	13 ± 1	225 ± 41
	10 - 20	7.7	1.1	14	150
	0 - 20				375

^aValues for the 0- to 10-cm depth increment are means±standard deviations (n = 3). Values for the 10- to 20-cm increment are composite values for three replicates pooled to comprise a single well-mixed sample.

remove litter accumulations, leave a nutrient-rich ash, and warm the soil surface when C₃ grasses and forbs are actively growing but when C4 grasses are dormant and incapable of responding to greater resource availability. The trend toward lower δ^{13} C values for SOC in burned areas suggests that these changes in the C_3 ($\delta^{13}C \approx -27\%$) versus C_4 ($\delta^{13}C \approx -13\%$) composition of the herbaceous community may have altered the relative rates at which these functional groups contribute to the SOC pool. Lower δ¹³C may also result from a stimulation of root production by resprouting mesquite (C₃). Photosynthetic rates of mesquite regrowth following fire can be $3 \times$ those of unburned plants [Ansley et al., 2002], and some of that increased photosynthetic income may be allocated to increased root production. Decreasing δ^{13} C values after burning may also be due to δ^{13} C depletion of the charring process itself [*Turney et al.*, 2006].

4.2. Black Carbon

[33] Fires also influence the carbon cycle by converting a proportion of biomass carbon into black carbon (BC) [Kuhlbusch, 1998]. In grasslands and savannas, approximately 0.6-4% of biomass carbon is converted to BC [Kuhlbusch et al., 1996, J. O. Skjemstad, unpublished data, 2006]. Because BC has a highly aromatic structure with few functional groups, it is highly resistant to decay and therefore contributes to the recalcitrant fraction of soil carbon. At the global scale, formation of BC transfers fast-cycling carbon from the atmosphere-biosphere system to much slower cycling geological forms that may persist for millennia, and therefore represents a sink for atmospheric CO₂ [Kuhlbusch, 1998; Masiello and Druffel, 1998]. However, there is some evidence that a portion of the BC pool in soils may be degraded on decadal to centennial timescales [Bird et al., 1999; Hamer et al., 2004].

[34] In this study, we found that two to three fires over a period of 6 years had no significant effect on concentrations of BC in either the 0-10 cm $(1.4-1.7 {\rm g kg^{-1} soil})$ or 10- to 20-cm depth increments $(1.0-1.3 {\rm g kg^{-1} soil})$, indicating that the changes in SOC discussed above cannot be attributable to production of new BC. Nonetheless, observed concentrations of BC comprised a significant proportion of the total SOC pool in both burned (13-16%) and unburned control plots (13-17%). Given that BC is generally regarded as chemically and biologically inert, and given that about 50% of SOC is considered to be recalcitrant (i.e., mean residence time = 250 to >1000 years) [Paul et al., 2001], it seems likely that a significant proportion of this recalcitrant soil carbon pool must consist of BC.

[35] BC concentrations obtained in this study are comparable to but near the lower end of the range of values reported previously for soils in the United States (0.6–13.6 g kg⁻¹ soil; 5–35% of SOC) [Skjemstad et al., 2002; Glaser and Amelung, 2003]. Lower values in this mixed-grass savanna may reflect a lower BC production potential compared to the sites measured by Skjemstad et al. [2002], most of which were within the tallgrass prairie region where fire frequency and primary production were significantly greater than at our site prior to human settlement. In addition, soils evaluated by Skjemstad et al. [2002] were

from cultivated agroecosystems where the more labile portion of the soil carbon pool may have been greatly reduced [e.g., *Harrison et al.*, 1993], thereby increasing the concentration of the more recalcitrant BC fraction.

[36] In a previous study at this same site, we used benzenepolycarboxylic acids (BPCA) as molecular markers to quantify BC [Dai et al., 2005]. This analytical method also revealed that the fire regimes examined in this study had no effect on soil BC concentrations. However, the BPCA method yielded BC concentrations that were, on average, 45% lower than those documented in the present study, ranging from approximately 0.55-1.07 g kg⁻¹ soil in both the 0- to 10-cm and 10- to 20-cm depth intervals. These results emphasize the fact that the true concentration of BC in soil is difficult to quantify in absolute terms because BC exists as a continuum of thermally altered materials [Schmidt et al., 2001; Glaser and Amelung, 2003]. A standardized method for measuring BC is needed to improve the accounting of this important component of the carbon cycle at the ecosystem and global scales [Simpson and Hatcher, 2004; Masiello, 2004].

4.3. Soil Total Nitrogen

[37] Soil total N (0-20 cm) increased from 224 g N m⁻² in the control to 251-255 g N m⁻² in the treatments that included summer fire (by adding total N values from 0–10 cm and 10-20 cm depths from Figure 3), indicating N accumulated at 4-5 g N m⁻² yr⁻¹ in those treatments during the 6 years of observation. Fire ash that is rich in phosphorus has been shown to stimulate N₂ fixation by cyanobacteria in the tallgrass prairie, and could add as much as $2 \text{ g N m}^{-2} \text{ yr}^{-1}$ to that ecosystem type following fire [Eisele et al., 1989]. It is also conceivable that the pulse of phosphorus in fire ash may stimulate symbiotic N₂ fixation by resprouting mesquite trees. Mesquite has been shown to possess effective root nodules across its distribution range [Johnson and Mayeux, 1990], and it obtains approximately 60% of its N from fixation [Shearer et al., 1983]. Rates of N fixation in ecosystems with 30-50% mesquite cover have been estimated to range from 4–15 g N m⁻² yr⁻¹ [Rundel et al., 1982; Johnson and Mayeux, 1990]. These rates are clearly adequate to account for rates of N accumulation in treatments with summer fires. However, it is not clear how fire could promote soil N accumulation via N2 fixation to a greater degree in summer than winter fire treatments. The slightly greater soil temperature during summer fires (51°C) than winter fires (36°C) had a negligible effect on soil total N.

[38] The δ^{15} N values of soil total N (0–10 cm) decreased from +7‰ in unburned controls to +6‰ in treatments that included summer fires, but remained unchanged in the winter fire treatment. Because ecosystem N inputs via atmospheric deposition and N₂ fixation are generally ¹⁵N-depleted (δ^{15} N = -2 to +1‰), and because gaseous N losses via microbial transformations (NH₃, NO_X, N₂O, N₂) are also ¹⁵N-depleted (δ^{15} N = -40 to 0‰), changes in input and/or loss rates can alter the δ^{15} N of the soil total N pool [*Hogberg*, 1997; *Robinson*, 2001]. When inputs exceed losses, the soil total N pool should become ¹⁵N-depleted (i.e., lower δ^{15} N); conversely, when losses exceed inputs,

the soil total N pool should become $^{15}N\text{-enriched}$ (i.e., higher $\delta^{15}N$). Therefore the lower $\delta^{15}N$ values for soil total N in treatments with summer fire indicate that inputs exceeded losses during the period of study, consistent with elevated N concentrations and densities observed in those treatments. The negative relationship between total N and $\delta^{15}N$ values supports the view that new additions of N were from $\delta^{15}N\text{-depleted}$ sources.

[39] Alternatively, N inputs could remain unchanged across all treatments, but N losses might be diminished in summer fire treatments. This might occur if plant uptake and/or microbial immobilization of NH₄ and NO₃ were elevated in the summer fire but not winter fire treatments, thereby reducing the potential for those inorganic N species to serve as substrate for N-losing processes such as nitrification and denitrification. The observation that root productivity and biomass are increased in summer but not winter fire treatments in a grassland adjacent to our study area [Hubbard, 2003] indicates that increased uptake of inorganic N by grasses and other herbaceous vegetation in summer fire treatments is a plausible hypothesis. In addition, C/N ratios of root tissue in burned portions of the North American tallgrass prairie have been shown to be significantly greater than those in unburned areas [Blair et al., 1998; Johnson and Matchett, 2001], suggesting increased microbial immobilization of inorganic N during decomposition of these lower quality roots. In fact, Dell and Rice [2005] showed that immobilization of inorganic N was greater in burned than unburned tallgrass prairie, and hypothesized that greater immobilization in burned areas was due to decay of litter inputs with high C/N ratios. More detailed mechanistic studies are needed to evaluate the mechanisms by which soil total N increased in response to summer fire in our study area.

4.4. Ecological Implications

[40] While there is perhaps some threshold of fire frequency at which SOC and total N losses may exceed gains [e.g., Risser and Parton, 1982; Ojima et al., 1990], findings from this study suggest that two or three fires within 5 years either increased or had no effect on SOC and total N in a mixed-grass/mesquite savanna. Soil microbial biomass and rates of nutrient mineralization in grasslands, savannas, and other ecosystem types are often correlated positively with pool sizes of SOC and total N [e.g., Abbadie and Lensi, 1990; Zak et al., 1990; Franzluebbers et al., 2001]. Although these relationships need direct evaluation in this ecosystem, enlarged SOC and total N pools in repeated summer fire treatments might enhance nutrient availability and have positive feedbacks on primary and secondary productivity in livestock production systems in this region. On the other hand, enhanced fertility could alter plant species interactions and lead to changes in community composition that might be economically and/or ecologically undesirable [Wedin and Tilman, 1996].

5. Conclusions

[41] Many dryland ecosystems throughout the world have been invaded by woody plants that threaten biodiversity,

modify ecosystem function and diminish livestock production. Fire is a common land management tool that reduces the cover of woody species and favors conservation of native perennial grasses and other components of the biota. However, little is known regarding the impact of fire on C and N cycles in these systems. In this study, repeated summer fires appeared to alter ecosystem processes in a manner that led to increased SOC and total N in the surface soil of a mixed-grass/mesquite savanna in the southern Great Plains. In contrast, repeated winter fires had no effect on SOC and total N. Differences induced by summer fires became evident after two or three fires and within 6 years after treatments were initiated. Changes in herbaceous cover in conjunction with the δ^{13} C values of SOC suggested that these changes in SOC and total N storage were related to shifts in the functional composition of the plant community toward greater relative productivity by C₃ grasses and forbs. Changes in soil $\delta^{15}N$ were small but consistent with a scenario in which N inputs were greater than losses, and suggested stimulation of symbiotic or asymbiotic N₂ fixation, reduced gaseous N losses due to lower transformation rates, and/or greater immobilization of inorganic N. BC comprised 13-17% of total SOC across all treatments, but was not altered significantly by the fire regimes in this study. Collectively, these results indicated that fire and the season during which it occurs can play a significant role in the biogeochemistry of mixed-grass/mesquite savannas. Longer-term studies that assess whole-ecosystem response (i.e., storage and turnover rates of C and N in aboveground and belowground biomass and the entire soil profile) are required to assess more comprehensively the impact of fire frequency and season of occurrence on the biogeochemistry of C and N in this ecosystem. Nonetheless, results of the present study will have implications not only for land managers, but also for scientists and policy makers who are now evaluating the potential for land management practices to alter ecosystem carbon storage and influence atmospheric CO₂ concentrations and global climate.

[42] Acknowledgments. This research was supported by grants from the USDA-NRICGP Agricultural Systems (94-04256), the USDA/CSREES CASMGS Program, and the E. Paul and Helen Buck Waggoner Foundation (Vernon, Texas). We thank Betty Kramp, David Jones, and Tim Tunnell, who assisted with the fires and field sampling. Technical assistance in the Stable Isotope Biogeochemistry Laboratory was provided by Alison Hoskisson, Julia Liao, and Paul Jurena. Statistical consultation was provided by Mike Longnecker, Department of Statistics, Texas A&M University.

References

Abbadie, L., and R. Lensi (1990), Carbon and nitrogen mineralization and denitrification in a humid savanna of West Africa (Lamto, Cote d'Ivoire), *Acta Oecol.*, 11, 717–728.

Andreae, M. O., and P. Merlet (2001), Emission of trace gases and aerosols from biomass burning, *Global Biogeochem. Cycles*, 15, 955–966.
Ansley, R. J., and P. W. Jacoby (1998), Manipulation of fire intensity to

Ansley, R. J., and P. W. Jacoby (1998), Manipulation of fire intensity to achieve mesquite management goals in north Texas, in *Fire in Ecosystem Management: Shifting the Paradigm From Suppression to Prescription, Tall Timbers Fire Ecol. Conf.*, vol. 20, edited by T. L. Pruden and L. A. Brennan, pp. 195–204, Tall Timbers Res. Stn., Tallahassee, Fla.

Ansley, R. J., D. L. Jones, T. R. Tunnell, B. A. Kramp, and P. W. Jacoby (1998), Honey mesquite canopy responses to single winter fires: Relation to fine fuel, weather and fire temperature, *Int. J. Wildland Fire*, 8, 241– 252.

Ansley, R. J., W. A. Dugas, M. L. Heuer, and B. A. Kramp (2002), Bowen ratio/energy balance and scaled leaf measurements of CO₂ flux over burned *Prosopis* savanna, *Ecol. Appl.*, 12, 948–961.

- Archer, S., T. Boutton, and K. Hibbard (2001), Trees in grasslands: Biogeochemical consequences of woody plant expansion, in Global Biogeochemical Cycles in the Climate System, edited by E. D. Schulze et al., pp. 115-137, Elsevier, New York.
- Bird, M. I., C. Moyo, E. M. Veenendaal, J. Lloyd, and P. Frost (1999), Stability of elemental carbon in a savanna soil, Global Biogeochem. Cycles, 13, 923-932.
- Bird, M. I., E. M. Veenendaal, C. Moyo, J. Lloyd, and P. Frost (2000), Effects of fire and soil texture on soil carbon in a sub-humid savanna (Matapos, Zimbabwe), Geoderma, 94, 71-90.
- Blair, J. M. (1997), Fire, N availability, and plant response in grasslands: A test of the transient maxima hypothesis, *Ecology*, 78, 2359–2368. Blair, J. M., T. R. Seastedt, C. W. Rice, and R. A. Ramundo (1998),
- Terrestrial nutrient cycling in tallgrass prairie, in Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie, edited by A. K. Knapp et al., pp. 222-243, Oxford Univ. Press, New York
- Blake, G. R., and K. H. Hartge (1986), Bulk density, in Methods of Soil Analysis: Part I. Physical and Mineralogical Methods, edited by A. Klute, pp. 364-370, Soil Sci. Soc. of Am., Madison, Wis.
- Bond, W. J., and J. Keeley (2005), Fire as a global 'herbivore': The ecology and evolution of flammable ecosystems, Trends Ecol. Evol., 20, 387
- Boutton, T. W., S. A. Archer, and A. J. Midwood (1999), Stable isotopes in ecosystem science: Structure, function, and dynamics of a subtropical savanna, Rapid Commun. Mass Spectrom., 13, 1263-1277
- Byram, G. M. (1959), Combustion of forest fuels, in Forest Fire: Control and Use, edited by K. P. Davis, pp. 61-89, McGraw-Hill, New York.
- Collins, S. L., and L. L. Wallace (1990), Fire in North American Tallgrass Prairie, Univ. of Okla. Press, Norman.
- Coplen, T. B. (1995), Reporting of stable carbon, hydrogen, and oxygen isotopic abundances, in Reference and Intercomparison Materials for Stable Isotopes of Light Elements, pp. 31-34, Int. Atom. Energy Agency,
- Crutzen, P. J., and M. O. Andreae (1990), Biomass burning in the tropics: Impact on atmospheric chemistry and biogeochemical cycles, Science, 250, 1669-1678.
- Dai, X., T. W. Boutton, B. Glaser, R. J. Ansley, and W. Zech (2005), Black carbon in a temperate mixed-grass savanna, Soil Biol. Biochem., 37, 1879-1881.
- Dell, C. J., and C. W. Rice (2005), Short-term competition for ammonium and nitrate in tallgrass prairie, Soil Sci. Soc. Am. J., 69, 371-37
- Eisele, K. A., D. S. Schimel, L. A. Kaputska, and W. J. Parton (1989), Effects of available P and N:P ratios on non-symbiotic dinitrogen fixation in tallgrass prairie soils, Oecologia, 79, 471-474.
- Franzluebbers, A. J., R. L. Haney, C. W. Honeycutt, M. A. Arshad, H. H. Schomberg, and F. M. Hons (2001), Climatic influences on active fractions of soil organic matter, Soil Biol. Biochem., 33, 1103-1111.
- Frost, C. C. (1998), Presettlement fire frequency regimes of the United States—A first approximation, in Fire in Ecosystem Management: Shifting the Paradigm From Suppression to Prescription, Tall Timbers Fire Ecol. Conf., vol. 20, edited by T. L. Pruden and L. A. Brennan, pp. 70-81, Tall Timbers Res. Stn., Tallahassee, Fla.
- Gebhart, D. L., H. B. Johnson, H. S. Mayeux, and H. W. Polley (1994), The CRP increases soil organic carbon, J. Soil Water Conserv., 49, 488-492
- Glaser, B., and W. Amelung (2003), Pyrogenic carbon in native grassland soils along a climosequence in North America, Global Biogeochem. Cycles, 17(2), 1064, doi:10.1029/2002GB002019
- Hamer, U., B. Marschner, S. Brodowski, and W. Amelung (2004), Interactive priming of black carbon and glucose mineralization, Org. Geochem., 35, 823-830.
- Hao, W., and M. Liu (1995), Spatial and temporal distribution of tropical
- biomass burning, *Global Biogeochem. Cycles*, 8(4), 495–503. Harrison, K. G., W. S. Broecker, and G. Bonani (1993), The effect of changing land use on soil radiocarbon, *Science*, 262, 725–726. Hogberg, P. (1997), Tansley Review No. 95: ¹⁵N natural abundance in soil-
- plant systems, New Phytol., 137, 179-203.
- Hubbard, J. A. (2003), Interactive effects of fire and grazing on plant productivity and soil respiration in a mixed-grass savanna, Ph.D. dissertation, Texas A&M Univ., College Station.
- Johnson, H. B., and H. S. Mayeux (1990), Prosopis glandulosa and the nitrogen balance of rangelands: Extent and occurrence of nodulation, Oecologia, 84, 176-185.
- Johnson, L. C., and J. R. Matchett (2001), Fire and grazing regulate belowground processes in tallgrass prairie, Ecology, 82, 3377-3389.
- Koos, W. M., J. C. Williams, and M. L. Dixon (1962), Soil survey at Wilbarger County, Texas, Soil Surv. Ser. 1959-18, USDA Soil Conserv. Ser., Fort Worth, Texas.

- Kuhlbusch, T. A. J. (1998), Black carbon and the carbon cycle, Science, 280, 1903-1904.
- Kuhlbusch, T. A. J., M. O. Andreae, H. Cachier, J. G. Goldammer, J. P. Lacaux, R. Shea, and P. J. Crutzen (1996), Black carbon formation by savanna fire: Measurements and implications for the global carbon cycle, J. Geophys. Res., 101, 23,651-23,665.
- Lavorel, S., E. F. Lambin, M. Flannigan, and M. Scholes (2001), Fires in the Earth system: The need for integrated research, IGBP Global Change Newsl., 48, 7-10.
- Leach, M. K., and T. J. Givnish (1996), Ecological determinants of species loss in remnant prairies, *Science*, *273*, 1555–1558.
- Levine, J. S., W. R. Cofer, D. L. Sebacher, E. L. Winstead, S. Sebacher, and P. J. Boston (1988), The effects of fire on biogenic soil emissions of nitric oxide and nitrous oxide, Global Biogeochem. Cycles, 2, 445-449.
- Lobert, J. M., D. H. Scharffe, W. M. Hao, and P. J. Crutzen (1990), Importance of biomass burning in atmospheric budgets of nitrogen-containing gases, Nature, 346, 552-554.
- Mariotti, A. (1983), Atmospheric nitrogen is a reliable standard for natural ¹⁵N abundance measurements, *Nature*, *303*, 685–687.
- Masiello, C. A. (2004), New directions in black carbon research, *Mar. Chem.*, 92, 201–213.
- Masiello, C. A., and E. R. M. Druffel (1998), Black carbon in deep-sea sediments, Science, 280, 1911-1913.
- Mouillot, F., and C. B. Field (2005), Fire history and the global carbon budget: A 1° × 1° fire history reconstruction for the 20th century, Global Change Biol., 11, 398-420.
- Nelson, D. W., and L. E. Sommers (1982), Total carbon, organic carbon, and organic matter, in Methods of Soil Analysis: Part 2. Chemical and Microbiological Properties, edited by A. L. Page, R. H. Miller, and D. R. Keeney, pp. 539-579, Soil Sci. Soc. of Am., Madison, Wis.
- Nieuwenhuize, J., Y. E. Maas, and J. J. Middelburg (1994), Rapid analysis of organic carbon and nitrogen in particulate materials, Mar. Chem., 45, 217 - 224.
- Ojima, D. S., W. J. Parton, D. S. Schimel, and C. E. Owensby (1990), Simulated impacts of annual burning on prairie ecosystems, in Fire in North American Tallgrass Prairies, edited by S. L. Collins and L. L. Wallace, pp. 118-137, Univ. of Okla. Press, Norman.
- Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby (1994), Long- and short-term effects of fire on nitrogen cycling in tall grass prairie, Biogeochemistry, 24, 67-84.
- Paul, E. A., H. P. Collins, and S. W. Leavitt (2001), Dynamics of resistant soil carbon of midwestern agricultural soils measured by naturally occur-⁴C abundance, *Geoderma*, 104, 239–256.
- Pinty, B., M. M. Verstraete, and N. Gobron (2000), Do man-made fires affect Earth's surface reflectance at continental scales?, Eos Trans AGU, 81, 381-389.
- Poth, M., I. Cofman, H. Miranda, A. Miranda, and P. Riggan (1995), The magnitude and persistence of soil NO, N₂O, CH₄, and CO₂ fluxes from burned tropical savanna in Brazil, Global Biogeochem. Cycles, 9, 503-513
- Raison, R. J. (1979), Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformations: A review, Plant Soil, 51, 73-108.
- Reich, P. B., D. W. Peterson, D. A. Wedin, and K. Wrage (2001), Fire and vegetation effects on productivity and nitrogen cycling across a forestgrassland continuum, Ecology, 82, 1703-1719.
- Rice, C. W., and C. E. Owensby (2000), The effects of fire and grazing on soil carbon in rangelands, in The Potential of U.S. Grazing Lands to Sequester Carbon and Mitigate the Greenhouse Effect, edited by R. Follet et al., pp. 323-342, CRC Press, Boca Raton, Fla.
- W., T. C. Todd, J. M. Blair, T. R. Seastedt, R. A. Ramundo, and G. W. T. Wilson (1998), Belowground biology and processes, in Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie, edited by A. K. Knapp et al., pp. 244–264, Oxford Univ. Press, New York.
- Risser, P. G., and W. J. Parton (1982), Ecosystem analysis of the tallgrass prairie: Nitrogen cycle, *Ecology*, 63, 1342–1351. Robinson, D. (2001), δ^{15} N as an integrator of the nitrogen cycle, *Trends*
- Ecol. Evol., 16, 153-162.
- Roscoe, R., P. Buurman, E. J. Velthorst, and J. A. A. Pereira (2000), Effects of fire on soil organic matter in a "cerrado sensu-stricto" from southeast Brazil as revealed by changes in δ^{13} C, Geoderma, 95, 141–160.
- Rundel, P., E. Nilsen, and M. Sharifi (1982), Seasonal dynamics of nitrogen cycling for a Prosopis woodland in the Sonoran Desert, Plant Soil, 67,
- Santos, A., G. Silva, H. Miranda, A. Miranda, and J. Lloyd (2003), Effects of fire on surface carbon, energy and water vapor fluxes over Campo Sujo savanna in central Brazil, Funct. Ecol., 17, 711-719.
- SAS Institute (1996), Version 6.11 for Windows, Cary, N.C.

- Schlesinger, W. H. (1997), Biogeochemistry: An Analysis of Global Change, Elsevier, New York.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford (1990), Biological feedbacks in global desertification, *Science*, 247, 1043–1048. Schmidt, M. W. I., and A. G. Noack (2000), Black carbon in soils and
- sediments: Analysis, distribution, implications and current challenges, Global Biogeochem. Cycles, 14, 777-793.
- Schmidt, M. W. I., J. O. Skjemstad, C. Czimczik, B. Glaser, K. M. Prentice, Y. Gelinas, and T. A. J. Kuhlbusch (2001), Comparative analysis of black carbon in soils, Global Biogeochem. Cycles, 15, 163-167.
- Schmidt, M. W. I., J. O. Skjemstad, and C. Jager (2002), Carbon isotope geochemistry and nanomorphology of soil black carbon: Black chernozemic soils in central Europe originate from ancient biomass burning, Global Biogeochem. Cycles, 16(4), 1123, doi:10.1029/2002GB001939.
- Serca, D., R. Delmas, X. LeRoux, D. Parsons, M. Scholes, L. Abbadie, R. Lensi, O. Ronce, and L. Labroue (1998), Comparison of nitrogen monoxide emissions from several African tropical ecosystems and influence of season and fire, Global Biogeochem. Cycles, 12, 637-651.
- Shearer, G., D. Kohl, R. Virginia, B. Bryan, J. Skeeters, E. Nilson, M. Sharifi, and P. Rundel (1983), Estimates of N₂-fixation from variations in the natural abundance of ¹⁵N in Sonoran Desert ecosystems, *Oecologia*, *56*, 365–373.
- Simpson, M. J., and P. G. Hatcher (2004), Overestimates of black carbon in soils and sediments, Naturwissenschaften, 91, 436-440.
- Skjemstad, J. O., J. A. Taylor, and R. J. Smernik (1999), Estimation of charcoal (char) in soils, Commun. Soil Sci. Plant Anal., 30, 2283-2298.
- Skjemstad, J. O., D. C. Reicosky, A. R. Wilts, and J. A. McGowan (2002), Charcoal carbon in U.S. agricultural soils, Soil Sci. Soc. Am. J., 66, 1249 - 1255
- Turner, C. L., J. M. Blair, R. J. Schartz, and J. C. Neel (1997), Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie, Ecology, 78, 1832-1843.

- Turney, C. S. M., D. Wheeler, and A. R. Chivas (2006), Carbon isotope fractionation in wood during carbonization, Geochim. Cosmochim. Acta, 70(4), 960-964.
- van der Werf, G., J. Randerson, G. Collatz, and L. Giglio (2003), Carbon emissions from fires in tropical and subtropical ecosystems, Global Change Biol., 9, 547-562.
- Vitousek, P. M., and R. W. Howarth (1991), Nitrogen limitation on land and in the sea: How can it occur?, Biogeochemistry, 13, 87-115.
- Wan, S., D. Hui, and Y. Luo (2001), Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: A meta-analysis, Ecol. Appl., 11, 1349 - 1365.
- Wedin, D. A., and D. Tilman (1996), Influence of nitrogen loading and species composition on the carbon balance of grasslands, Science, 274, 1720 - 1723
- Wright, H. A., and A. W. Bailey (1982), Fire Ecology, Wiley-Intersci., Hoboken, N. J.
- Zak, D. R., D. F. Grigal, S. Gleeson, and D. Tilman (1990), Carbon and nitrogen cycling during old-field succession: Constraints on plant and microbial biomass, Biogeochemistry, 11, 111-129.
- Zitzer, S. F., S. R. Archer, and T. W. Boutton (1996), Spatial variability in the potential for symbiotic N2 fixation by woody plants in a subtropical savanna ecosystem, J. Appl. Ecol., 33, 1125-1136.
- R. J. Ansley, Texas Agricultural Experiment Station, P.O. Box 1658, Vernon, TX 76384, USA. (r-ansley@tamu.edu)
- T. W. Boutton, Department of Rangeland Ecology and Management, Texas A&M University, College Station, TX 77843-2126, USA.
- J. O. Skjemstad, CSIRO Land and Water, Private Bag 2, Glen Osmond, S.A. 5064, Australia.