GRASSLAND CARBON AND NITROGEN DYNAMICS: EFFECTS OF SEASONAL FIRE AND CLIPPING IN A MIXED-GRASS PRAIRIE OF THE SOUTHERN GREAT PLAINS

A Dissertation

by

WYLIE HARRIS

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

May 2005

Major Subject: Rangeland Ecology and Management

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Approved as to style and content by:

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May 2005

Major Subject: Rangeland Ecology and Management

ABSTRACT

Grassland Carbon and Nitrogen Dynamics: Effects of Seasonal Fire and Clipping in
a Mixed-Grass Prairie of the Southern Great Plains.
(May 2005)
Wylie Harris, B.A., Reed College
Chair of Advisory Committee: Dr. Thomas W. Boutton

Plant production and soil microbial biomass (SMB) in grassland ecosystems are linked by flows of carbon (C) and nitrogen (N) between the two groups of organisms. In native mixed grasslands of the southern Great Plains, these cycles are strongly influenced by climate. They may also be modulated by the timing and intensity of disturbances such as fire and clipping. We assessed the relative influence of climate and disturbance on plant community and soil C and N dynamics. Combined effects of fire and clipping were assessed in a 2x3 factorial design including spring fire and light clipping or continuous clipping. Seasonal fire effects were evaluated in a one-way analysis incorporating spring and fall fire in unclipped plots. Plant cover and biomass (by functional type), litter mass, SMB C and N, soil density fraction concentration and composition, soil organic C, total N, and inorganic N, soil temperature and moisture, soil respiration, and net N mineralization were measured at monthly intervals. C_4 grasses were unaffected by fire or clipping, probably as a result of summer drought in both study years. Clipping reduced cover of C_3 annual grasses but increased that of C_3 perennials, resulting in no net change in C_3 grass biomass. Fire did not affect C_3 grass cover or biomass. Both fire and clipping reduced litter mass. This was reflected in seasonal declines in SMB C in fire treatments, suggesting that the primary input of microbial C in this ecosystem occurs by decomposition of current-season plant litter. Litter removal offers a single mechanism by which fire-induced increases in soil temperature and reductions in light soil density fraction concentration, soil moisture, and net N mineralization rates may be explained. Lack of treatment effects on soil respiration rates suggest that plant roots represent an important component of the plant-soil C cycle, not quantified in this research. Overall, treatment effects were relatively minor compared to seasonal climate-related changes in response variables, particularly in light of repeated summer drought.

I dedicate this dissertation to my father,

Pat Harris

who saw me through, but did not see me finish.

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CHAPTER I

INTRODUCTION

Carbon and nitrogen dynamics in grassland ecosystems depend on interactions between plant tissue quantity and quality, size and availability of soil nutrient pools, and the timing, frequency, and nature of disturbance. Differences in tissue chemistry between plant species and functional groups can create differences in the rate of return of nutrients to the soil from decomposing plant material (Hobbie 1992; Chapin et al. 1997; Heal et al. 1997; Hooper and Vitousek 1997; Bardgett et al. 1999; Cebrian 1999). Thus, plant communities can exert a direct influence on soil nutrient status in some ecosystems. The assemblage of plant species present in grassland ecosystems varies in response to timing and intensity of integral disturbance events such as fire and herbivory. An understanding of the way in which these disturbances modulate the interactions between the plant and soil compartments of nutrient cycles is central to an effective conceptual framework of grassland C and N dynamics. These shifts in the ecosystem flux of C and N have the potential to generate local feedbacks in relative species and functional group abundance (Westoby 1985; Wedin 1995; Wedin 1996; Wedin and Tilman 1996). Integrated over larger spatiotemporal scales, these same processes can have consequences for regional budgets of these elements, with implications for global phenomena such as nitrogen loading and greenhouse warming

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This dissertation follows the style and format of the journal Ecology.

(Raich and Potter 1995; Burke et al. 1997; Epstein et al. 2002). This research evaluates impacts of herbivory and fire on plant-soil carbon and nitrogen dynamics in native grasslands of the southern Great Plains.

A variety of conceptual models have been put forth to account for observed patterns of nutrient cycling in a variety of North American grassland ecosystems. The primary cleavage between these alternate schema stems from the degree of importance assigned to feedbacks between plant tissue quality and soil N mineralization rates in determining overall rates of C and N cycling. Models attributing relatively greater importance to feedbacks have hypothesized both positive and negative mechanisms. Meanwhile, those in which feedbacks are less dominant have specified varying factors as damping influences on feedbacks. These have included climatic variables (moisture and/or temperature) as well as a partial decoupling of C and N cycles.

Several researchers (Wedin 1995, 1996; Pastor and Cohen 1997) have proposed models in which fire and herbivory induce positive feedbacks in grassland soil-plant nutrient dynamics. In soils beneath experimental monocultures of C_3 grasses (low tissue C:N), net N mineralization was high, while in C_4 plots (high tissue C:N), net immobilization of N resulted (Wedin and Tilman 1990; Wedin and Pastor 1993). These divergent outcomes were attributed to the fact that the N-rich C_3 litter supplies decomposers with an excess of N which is released to the soil in available mineral forms, whereas microbes must immobilize available nitrogen from the surrounding soil as they slowly decompose lower-quality C_4 litter.

Based on these data, Wedin (1995; 1996) hypothesized that plant tissue composition drives soil N availability, and is in turn modulated by plant-herbivore interactions. In this conception, herbivores preferentially graze sites dominated by higher-quality C_3 grasses and deposit N-rich manure on these sites. The rapid breakdown of the low-C:N fecal material and the C_3 plant litter releases relatively large quantities of mineral N to the soil. Increased abundance of C_3 species, in turn, makes the site more likely to be selected again by grazers in the future, establishing a feedback loop towards increasing dominance of C_3 species and ever-higher availability of mineral N in the soil. In contrast, sites dominated by less-nutritious C_4 grasses will be less frequently grazed, resulting in an accumulation of lower-quality litter which will tend to be passed over by herbivores and eventually be removed instead by fire. The heat of combustion volatilizes N from aboveground plant biomass, limiting N inputs to the soil and shifting the competitive balance toward C_4 species. This tips the nutrient cycling regime into an alternate positve feedback loop towards reduced availability of N, increased C:N ratios in plant tissue, and replacement of herbivory by fire as the dominant means of biomass removal.

The predictions of this positive-feedback model were questioned by Chapin et al. (1997). These authors argue for negative feedbacks between plant tissue quality and soil N availability based on species differences in N use efficiency (NUE). In their model, quickly-growing plant species have high NUE and tissue C:N ratios, so that litter from these plants decomposes slowly, reducing N mineralization and soil levels of available N. More slowly-growing plants, by contrast, have lower NUE and higher tissue quality, and produce litter which decomposes relatively more rapidly, fostering higher rates of N mineralization and levels of soil available N. Species with widely differing growth rates and NUE, then, can ultimately cause convergence of N mineralization rates and soil N pools, in contrast to the predictions of the positive-feedback model. Chapin et al. (1997) offer an interpretation of earlier data (Wedin and Tilman 1990; Tilman and Wedin 1991) which is consistent with their negative-feedback model. However, they attempt only cursory extrapolation from these modeled plant-soil C:N dynamics to potential consequences of biomass removal by fire and herbivory in ecosystems.

An “indeterminate dominance model” (Vinton and Burke 1995; Vinton and Burke 1997; Burke et al. 1998; Epstein et al. 1998; Burke et al. 1999) depicts an alternative nutrient cycling regime in which moisture limitation reduces the importance of plant-soil feedback loops in grassland C and N dynamics. According to this model, in mesic grasslands, any one of several factors may be limiting to plant productivity and N mineralization at any given point in time. However, in the shortgrass steppe, where moisture is more consistently limiting, the effects of N availability may be more rarely expressed in the structure and function of the plant community. Furthermore, moisture as well as temperature gradients in active SOM pools are well documented (Amelung et al. 1998; Franzluebbers et al. 2001), and thus climate must play an important role in the modulation of predictions from feedback-based models (Zak et al. 1994). Similarly, the feedback-based models implicitly assume the potential co-occurrence of plant species differing widely in tissue chemistry. As such, these models’ predictions are couched in terms of replacement of one species by another in response to changing soil nutrient relations or aboveground disturbance regimes. However, over most of the Great Plains, climatic constraints render one photosynthetic pathway dominant over the other (Tieszen et al. 1997). In these cases, where fundamental shifts in the functional composition of the community are unlikely or even impossible, it is uncertain whether equivalent shifts in nutrient dynamics can occur based solely on changes in the tissue chemistry of a single plant functional group.

Knops et al. (2002) proposed an alternative model of plant-soil C:N dynamics which concurs with the indeterminate dominance model in the relatively minor importance it assigns to feedback mechanisms. However, in this case, feedback effects are damped not (at least directly) by climatic factors, but rather by a decoupling between factors limiting to microbial activity and those controlling availability of mineral N. In this scheme, microbial growth is limited by inputs of plant C to the soil, but levels of available soil N are determined by microbially-mediated release from a large pool of soil organic N. The influences of climatic factors, as well as those of aboveground biomass removal by fire and herbivory, are integrated in their effects on the amount of aboveground plant C entering the soil. Negative feedbacks, in which increased plant productivity provides greater C inputs for microbial growth and thereby postpones microbial release of mineral N, can be envisioned within this conceptual framework. However, these feedbacks operate independently of interspecific differences in NUE, and are thus distinct from earlier models of plant-soil nutrient dynamics in which plant tissue chemistry drives nutrient cycles (Wedin 1995; Wedin 1996; Tateno and Chapin

1997). Knops et al. (2002) also depart from earlier models in their explicit focus on the microbial component of plant-soil C and N cycles.

Each of the models of plant-soil C and N dynamics discussed above was developed to account for observed patterns in particular ecosystems. As such, their respective predictions are not always mutually exclusive, and data from a range of ecosystems can be invoked to support one or another to varying degrees. For instance, intense herbivory and fecal deposition by lesser snow geese reinforce sedge dominance in lakeshore ecosystems of the Hudson Bay, constituting a case in which the concept of grazing-induced positive feedbacks between plant tissue quality and N mineralization appear to be operating (Ruess et al. 1989; Pastor and Cohen 1997). Positive feedbacks have also been reported along a gradient of increasing productivity, N mineralization, root turnover, and decreasing fire frequency from forest to grassland (Reich et al. 2001).

In grasslands, a wealth of data exists on relationships between large ungulate herbivory, fire regime, plant community structure, and nutrient cycling, and climate, but results are inconclusive. Feeding preferences of large ungulate herbivores in native North American tallgrass prairie (Knapp et al. 1999) as well as in grasslands of the Serengeti (McNaughton 1988; McNaughton et al. 1988; McNaughton et al. 1989; McNaughton 1990) create distinctive, frequently-revisited grazing lawns. In these grazed areas, grass root growth, root C:N ratios, and soil respiration all decrease, suggesting circumstantial support for the grazing-induced positive feedbacks model (Johnson and Matchett 2001). However, in tallgrass prairie, bison exhibit a marked preference for C_4 rather than C_3 grasses, in contrast to the model's predictions.

Temporal variation in forage quality between plants of differing photosynthetic pathways is a key factor which must be accounted for by any model based on plant NUE. This is particularly important in grasslands of the southern Great Plains, which have a more equal mixture of C_3 and C_4 grasses than grassland ecosystems elsewhere in North America (Epstein et al. 1997b). The role of fire in grassland nutrient dynamics is similarly complex. A sharp and transient increase in available N follows fire due to stimulation of microbial activity, but this may not be sufficient to balance volatilization losses, leading to a decline in soil N over extended periods of repeated fire (Towne and Owensby 1984; Ojima et al. 1990; Seastedt and Ramundo 1990; Hobbs et al. 1991; Seastedt and Knapp 1993; Ojima et al. 1994; Turner et al. 1997; Coppedge et al. 1998; Sanchez and Lazzari 1999). Annual burning in tallgrass prairie leads to increased root growth, root C:N ratios, and soil respiration, again meeting the predictions of the positive-feedbacks model (Johnson and Matchett 2001).

Temporal variation in nutrient dynamics stemming from the fire-herbivory interaction creates a more complex pattern than the linear bifurcation envisioned in the positive-feedback model (Seastedt and Ramundo 1990). Bison preferentially graze areas which have been recently burned (Coppedge et al. 1998). At this stage of post-fire regrowth, the C_4 grasses have higher tissue N concentrations than unburned C_4 grasses. Continued bison grazing in frequently-burned, C_4-dominated areas eventually leads to an increase in C_3 forbs, though whether this is due to grazing pressure alone or to nutrient dynamics is unclear (Knapp et al. 1999). While grazing and fire in isolation have opposite effects on soil C and N dynamics in tallgrass prairie (Blair 1997; Johnson and

Matchett 2001), the preference of the bison for recently-burned areas creates a landscape-level interaction in which herbivory closely follows fire in time, generating a negative feedback loop which maintains a homeostatic nutrient regime (Hobbs et al. 1991; Knapp et al. 1999).

Similarly ambiguous dynamics occur in the Serengeti ecosystem (Ruess and McNaughton 1987; McNaughton et al. 1988). Wetter, more productive areas at the northern end of the Serengeti plains are characterized by proportionally lower levels of herbivory and rates of nutrient turnover between producer, consumer, and decomposer components. Large migratory herbivores concentrate their feeding activity at the dry (shortgrass) southern end of the plains during the wet season, perhaps in response to the nutrient requirements of pregnant and lactating females (Ruess and McNaughton 1987; McNaughton 1988). These distinct regional variations in nutrient dynamics within the Serengeti point up three further variables lacking from present models: large-scale climatic gradients (with corresponding clines of climate, productivity, decomposition, nutrient availability), the dominance of a single photosynthetic pathway (C_4), and movement (or lack thereof) of herbivores, across those gradients. The historic mass migrations of large herds of native ungulate herbivores, along with pre-Columbian fire regimes, have been interrupted by human activity in North American grassland ecosystems. Data from the Konza Prairie and the Serengeti plains, which preserve this spatiotemporal pattern of herbivory, may thus bear limited relevance to contemporary systems of grazing management. McNaughton et al. (1988) assert that “Slow cycles will be created by fencing and firebreaking in any landscape, regardless of the prevailing natural patterns."

As summarized in Hobbie (1992), numerous factors interact in a complex manner to produce surface phenomena of nutrient dynamics in any given system. While certain large-scale trends in the patterns of fire (Wan et al. 2001) and herbivory (Milchunas and Lauenroth 1993) effects on C and N cycling have been revealed via meta-analysis of multiple datasets, it is uncertain whether any of the current set of conceptual models, in its current formulation, can be extended to provide a robust and comprehensive theory of plant-soil C and N cycling across a broad range of ecosystem types. Further data from different ecosystems are necessary to evaluate the applicability of these models. This dissertation research investigates the relationships between nutrient dynamics and vegetation removal by fire and simulated grazing in a mixed-grass prairie ecosystem of the southern Great Plains of North America. C and N dynamics in this ecoregion have been relatively little studied (Ansley et al. unpublished manuscript). Further research on these topics in southern mixed-grass prairie ecosystems is essential due to their extensive area and potential for management decisions to impact nutrient cycles at large spatial scales. An evaluation of extant models of plant-soil C and N dynamics in this ecoregion is necessary to advance relevant ecological theory. By informing ecosystem management strategies at local and regional scales, such an evaluation may have bearing on global processes of soil and atmospheric C storage (Seastedt et al. 1994; Wedin 1995; Wedin 1996; Derner et al. 1997; Campbell et al. 2000; Conant et al. 2001; Derner et al. unpublished manuscript). However, intensive data collection is necessary to determine whether and to what extent the various conceptual models accurately predict ecological processes in southern mixed-grass prairie ecosystems.

Several such foci of investigation are underrepresented in published studies, and are thus of particular relevance for refining the understanding of disturbance effects on plant-soil C and N cycles in grasslands. First, interactive effects of fire and herbivory/clipping can produce outcomes contrary to the results of studies examining the effect of a single disturbance in isolation (Hobbs et al. 1991; Vinton and Hartnett 1992; Vinton et al. 1993; Hobbs 1996; Hubbard 2003). For example, even in a case where N losses due to fire create a context for negative feedbacks on plant productivity and soil N availability (Wedin 1995; Wedin 1996), a preference of herbivores for feeding on the nitrogen-rich regrowth following fire may exert a stabilizing counterinfluence (Knapp et al. 1999; Johnson and Matchett 2001). Second, seasonality of disturbance is increasingly acknowledged as a factor of similar importance to its nature and intensity in determining grassland plant community composition (Hulbert 1988; Howe 1994; Howe 1995; Howe 2000; Engle and Bidwell 2001). However, while the potential implications of that role for nutrient cycling are apparent, few studies have addressed them (Ansley et al. unpublished manuscript). Finally, although the importance of regional climatic variation as the context in which disturbance effects are acknowledged (Vinton and Burke 1997; Burke et al. 1998; Derner et al. in preparation), datasets with comprehensive and contemporaneous representation of relevant responses are available from relatively few sites. Though mesic mixed-grass prairie ecosystems may represent the greatest potential of any grassland type for the manifestation of interactive disturbance effects (Seastedt et al. 1994), such data from them are sparse (Raich and Schlesinger 1992).

The several aims of this dissertation research are thus unified in their attempt to characterize, at as many points as possible in their respective cycles, the interactive effects of seasonal disturbance, in the form of fire and clipping, on plant-soil C and N dynamics in the understudied mixed-grass prairie of the southern Great Plains. Carbon flows were traced at approximate monthly intervals from initial atmospheric fixation into plant tissue (as both foliar cover, by species, and biomass, by functional type) through senesence into the litter pool, into incorporation in soil microbial biomass (SMB). Of particular interest was the assessment of shifts in the rapidly-cycling active or labile fraction of soil organic matter (SOM), which controls the balance between net immobilization and mineralization of N despite its small size relative to the total SOM pool (Christensen 1992; Wedin and Pastor 1993; Pastor and Cohen 1997). The active fraction has been variously defined as that portion of SOM associated with a range of coarser (size fractionation) or lighter (density fractionation) soil separates. It is a labile and transitory SOM pool, dominated by incompletely decomposed plant and animal residues (Oades 1988; Christensen 1992). The size of the overall SOM pool varies predictably with climate, soil texture, and management; however, the portion of total SOM represented by the active fraction varies widely even over small spatial and temporal scales (Post et al. 1982; Oades 1988; Burke et al. 1989; Christensen 1992; Amelung et al. 1998; Skjemstad et al. 1998; Franzluebbers et al. 2001). In spite of this inconstant pool size, the active fraction is consistently correlated with mineralization rates of C and N from a range of soils worldwide (Vanlauwe et al. 1994; Barrios et al. 1996; Curtin and Wen 1999; Alvarez and Alvarez 2000; Franzluebbers et al. 2000; Parfitt and Salt 2001).

The interactive responses of these variables to spring fire and clipping are detailed in Chapter II, while seasonal fire effects are treated in Chapter III. Soil density fractions and soil inorganic N were quantified on the same schedule. In addition, elemental analyses of plant tissue and soil at the beginning and end of the study allowed an evaluation of net longer-term change in the total ecosystem stocks of C and N, and the same analyses were performed on litter samples at approximate monthly intervals during the second half of the study. The interactive effects of spring fire and clipping on all these responses are covered in Chapter IV, while Chapter V presents an account of those resulting from seasonal fire. Finally, losses of both elements from the plant-soil system were monitored via regular *in situ* measurements of soil C efflux and net N mineralization, along with soil temperature and moisture content, which regulate their rates. Patterns of these variables in response to interactive effects of clipping and spring fire are presented in Chapter VI, while their behavior following fires in different season is described in Chapter VII. Chapter VIII synthesizes the relevance of these findings for an evaluation of the various conceptual models of disturbance effects on plant-soil grassland dynamics as applied to mixed native grasslands of the southern Great Plains.

CHAPTER II

PLANT COMMUNITY AND SOIL MICROBIAL RESPONSES TO FIRE AND CLIPPING IN A SOUTHERN MIXED GRASSLAND

INTRODUCTION

Disturbance is an important determinant of production, community composition, and plant-soil flows of C and N in grassland ecosystems (McGill et al. 1986; Howe 1994). Varied effects of fire and clipping on plant and soil microbial biomass (SMB) and nutrient content have been reported. In many cases the range of responses appears to be due to site-specific differences in climate, plant community composition, and seasonality of both plant production and disturbance. Mesic mixed grasslands may have the highest potential for interactive effects of fire and clipping on these responses to be expressed (Seastedt et al. 1994; Hobbs 1996).

The bulk of extant literature on effects of fire and clipping on grassland dynamics consists of single-factor experiments addressing one or the other of these disturbance types individually (Coppedge et al. 1998; Engle and Bidwell 2001). Complex interactions between fire and herbivory influence vegetation responses at individual (Vinton and Hartnett 1992), community (Collins 1987; Hobbs et al. 1991; Collins et al. 1998), and landscape (Hobbs 1996; Coppedge et al. 1998; de Mazancourt et al. 1998; Biondini et al. 1999; de Mazancourt et al. 1999; Knapp et al. 1999) scales. All these responses may in turn impact soil microbes (Woodmansee and Wallach 1981; Schuman et al. 2002). In Hobbs et al's (1991) seminal experiments on community-level responses to fire and herbivory in tallgrass prairie, mowing in unburned treatments increased the likelihood that the mown area would be grazed, though no similar pattern was observed in burned treatments. Meanwhile, fire temperature and energy release, as well as N losses, were greater from ungrazed than grazed treatments (Ewing and Engle 1988; Hobbs et al. 1991).

Effects of herbivory and fire on plant and SMB are modulated by climatically induced interannual variation in ANPP (Vinton and Burke 1995; Vinton and Burke 1997; Burke et al. 1998; Copeland et al. 2002). That variation is higher in grasslands than in any other biome (Knapp and Smith 2001), a direct consequence of high variability in interannual precipitation (Burke et al. 1991; Fuhlendorf et al. 2001). In addition to causing such interannual variability in vegetation dynamics within a single site, climatic variation over regional scales alters the context within which disturbance effects are manifested (Burke and Lauenroth 2002). In the U.S. Great Plains, regional climatic patterns correspond to gradients in primary production (Burke et al. 1991; Burke et al. 1997; Epstein et al. 1997a), canopy architecture (Lane et al. 2000), C_3-C_4 composition (Paruelo and Lauenroth 1996; Epstein et al. 1997b; Tieszen et al. 1997; Epstein et al. 1998), and SMB (Wardle 1992; Zak et al. 1994). As with disturbance, seasonality of climatic variables also has far-reaching but understudied consequences for grassland vegetation dynamics (Ojima et al. 1993; Epstein et al. 1999). This climatic background must be fully acknowledged in any attempt to understand responses to biomass removal, whether within a single site or in comparisons between different sites.

Responses of single species to fire and herbivory are often idiosyncratic, leading researchers to adopt a variety of classifications for aggregating species into functional groups whose responses to these treatments are more generalized and predictable. This study adopts a set of plant response groups similar to that of Coffin and Lauenroth (1996), incorporating growth form, photosynthetic pathway (C_3 vs. C_4), and life history (annual versus perennial).

This study examines effects of seasonal fire and simulated herbivory on plant functional composition, plant production, and SMB in a mixed-grass prairie of the southern Great Plains. This region is climatically intermediate between tallgrass prairie and shortgrass steppe sites where the relative influences of climate and disturbance on plant-soil dynamics have been more thoroughly assessed (Burke et al. 1998). We hypothesized that spring fire would increase the absolute biomass and relative proportion of C_4 grasses in the plant community relative to control and clipped treatments. This shift in aboveground community composition, combined with losses of volatilized N, would lead to lower SMB and higher microbial biomass C:N ratios. Clipping was hypothesized to moderate these impacts by reducing fuel loads and fire intensity, as evidenced by SMB levels and C:N ratios intermediate between those of fire and control treatments.

METHODS

Study site

Research was conducted on a 1 ha grazing exclosure on the W.T. Waggoner Ranch in Wilbarger County, Texas (33° 51'N, 99° 26' W, elevation 381 m). Mean annual precipitation for the site is 665 mm, bimodally distributed, with peaks in May (18% of annual total) and September (12% of annual total). Mean annual temperature is 16.1° C, with monthly average extremes ranging from 36° C in July to -2.5° C in January. Soils are classified as fine, mixed, thermic Typic Paleustolls of the Tillman series.

Dominant cool season (C_3) grasses include Texas wintergrass (*Nasella leucotricha* (Trin & Rupr) Pohl), a native perennial bunchgrass, and Japanese brome (*Bromus japonicus* Thunb. ex Murr.), an exotic annual grass. Dominant warm season (C_4) grasses include the perennial bunchgrass sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), and the stoloniferous, sod-forming buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.). The study site was root-plowed and seeded with sideoats grama in 1974. It has not been burned since that time. The site was grazed by cattle at a moderate stocking rate (1 cow 12 ha^{-1}) from the late 1800s to 1988, when livestock were removed.

Experimental design

Vegetation and soil microbial dynamics were evaluated on experimental plots in a 2 x 3 factorial design (fire x clipping). Treatments were randomly assigned to thirty 6x6-m plots (n= 5 replicates/treatment combination). The following treatments were implemented annually beginning in 1999: 1) control (no fire, no clipping), 2) continuous clipping, 3) spring clipping, 4) spring fire, 5) spring fire + spring clipping, and 6) spring fire + continuous clipping. Plots in the spring clipping treatment were mown to 5 cm height once per year in late April, and those in the continuous clipping treatment were mown monthly (except during drought). Clipped plant material was transported offsite. Plots in the fire treatment were subjected to prescribed fires in February/March 1999, 2000, 2001, and 2002. Fire intensity for all fires in all years was classified as low to moderate, with flame heights not exceeding 1.5 m. Rainfall was measured at the site.

Sampling and analysis

Sampling was carried out at approximately monthly intervals from June 2000 through May 2002. During each sampling period, a 1x1 m subplot was randomly chosen from each of the 30 6x6 m treatment plots. Since sampling was destructive, no subplots were resampled. The following sampling procedures were performed on each 1x1 m subplot.

Ocular estimates of foliar cover were recorded on each subplot, distinguishing the following cover classes: C_3 grasses by species, C_4 grasses by species, forbs, litter, and bare ground. Since various cover classes overlapped at different levels within the canopy, cover percentages may total to more than 100 on a given subplot.

Vegetation was clipped to ground level within a square 0.125 m^2 quadrat centered within the subplot. (Clipping only was carried out on the subplot from the previous sampling interval in order to prevent disruption of concurrent *in situ* N-mineralization assays.) Clipped vegetation was bagged by category (C_3 grass, C_4 grass, forb, and litter) and dried for 5 d at 60 °C. Dried vegetation was then separated into live and dead and weighed to estimate biomass.

A composite soil sample consisting of 8, 2.5-cm diameter cores taken 10 cm deep was taken from each subplot. Soil samples were immediately placed on ice for transport to the laboratory and subsequently stored at 4 °C until analysis. Samples were homogenized prior to laboratory analysis. A 30 g, field moist soil subsample was brought to 50 % water holding capacity, and analyzed for soil microbial biomass (SMB) C and N using the chloroform fumigation-incubation method (Horwath and Paul 1994; Franzluebbers et al. 1999).

SMB-C, SMB-N, and SMB-N:C were calculated as:

$$\text{SMB-C} = C_f/K_c \qquad \text{(Voroney and Paul 1984)}$$

$$\text{SMB-N:C} = 0.56\,(N_f/C_f) + 0.095 \qquad \text{(Harris et al. 1997)}$$

$$\text{SMB-N} = \text{SMB-C (SMB-N:C)} \qquad \text{(Harris et al. 1997)}$$

where C_f and N_f are the flushes of mineralized C and N, respectively, from fumigated soils, and $K_c = 0.43$.

Data analysis

Data were analyzed using SAS Version 9.0 (SAS Institute 2002). Each response variable was separately analyzed using a three-way ANOVA factorial design with sampling date, fire, and clipping as factors. For all variables where treatment effects and treatment-by-date interactions were significant, the analysis was also carried out within each sampling date, excluding sampling date as a factor. Significant differences between treatment effects were evaluated via pairwise comparisons of least squares means.

RESULTS

In 2000, precipitation from April through September was below normal in every month. In 2001, precipitation was below normal for five of the sixth months, with only August precipitation exceeding normal. Total precipitation for this six month period was 38 % of normal in 2000, and 50 % of normal in 2001. During the remaining six months, by contrast, precipitation was 162 % of normal in 2000, and 123 % of normal in 2001 (Figure 1).

Sampling date was a significant factor for all response variables. Three-way interactions (sampling date x fire x clipping) were not significant for any response except C_3 annual grass cover and forb biomass.

Overall, total cover of live vegetation was reduced by clipping, with reductions occurring during late winter and early spring. Fire had no significant effect on total cover of live vegetation (Table 1). During the winter months of 2001 and 2002, cover was higher in unclipped treatments, regardless of fire treatment (Figure 2A). Overall, both fire and clipping significantly increased the area of bare ground, with the difference increasing over time throughout the study. Due to significant interactions between fire and clipping in the bare ground response, clipping significantly increased the area of bare ground only in combination with fire (Figure 2B; Tables 1,2B).

Overall, continuous clipping significantly increased the cover of C_3 perennial grasses, with the differences occurring in April/May and November 2001 and May 2002 (Figure 3A, Table 1). Both spring and continuous clipping reduced the cover of C_3 annual grasses, with a significant clip-by-date interaction (Figure 3B, Table 1). Overall, fire did not affect the cover of either C_3 grass functional type. Neither fire nor clipping affected the cover of C_4 grasses (Figure 3C, Table 2).

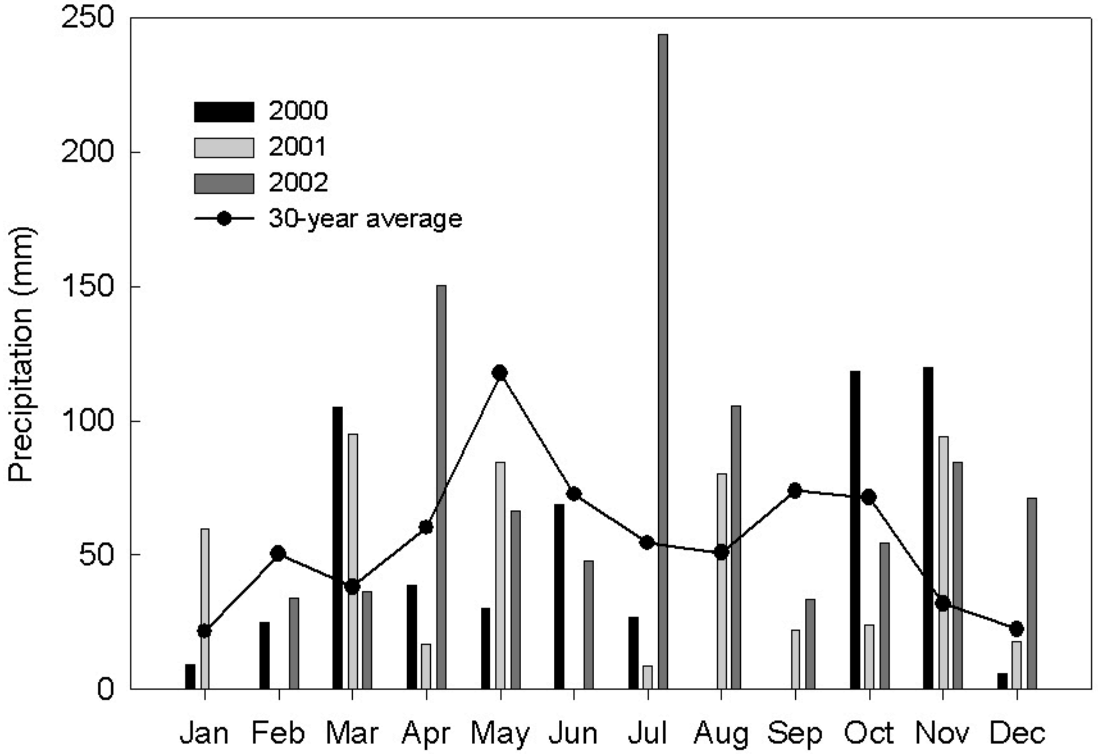

Figure 1. Monthly precipitation for 2000-2002, relative to the 30-year average precipitation at the study site.

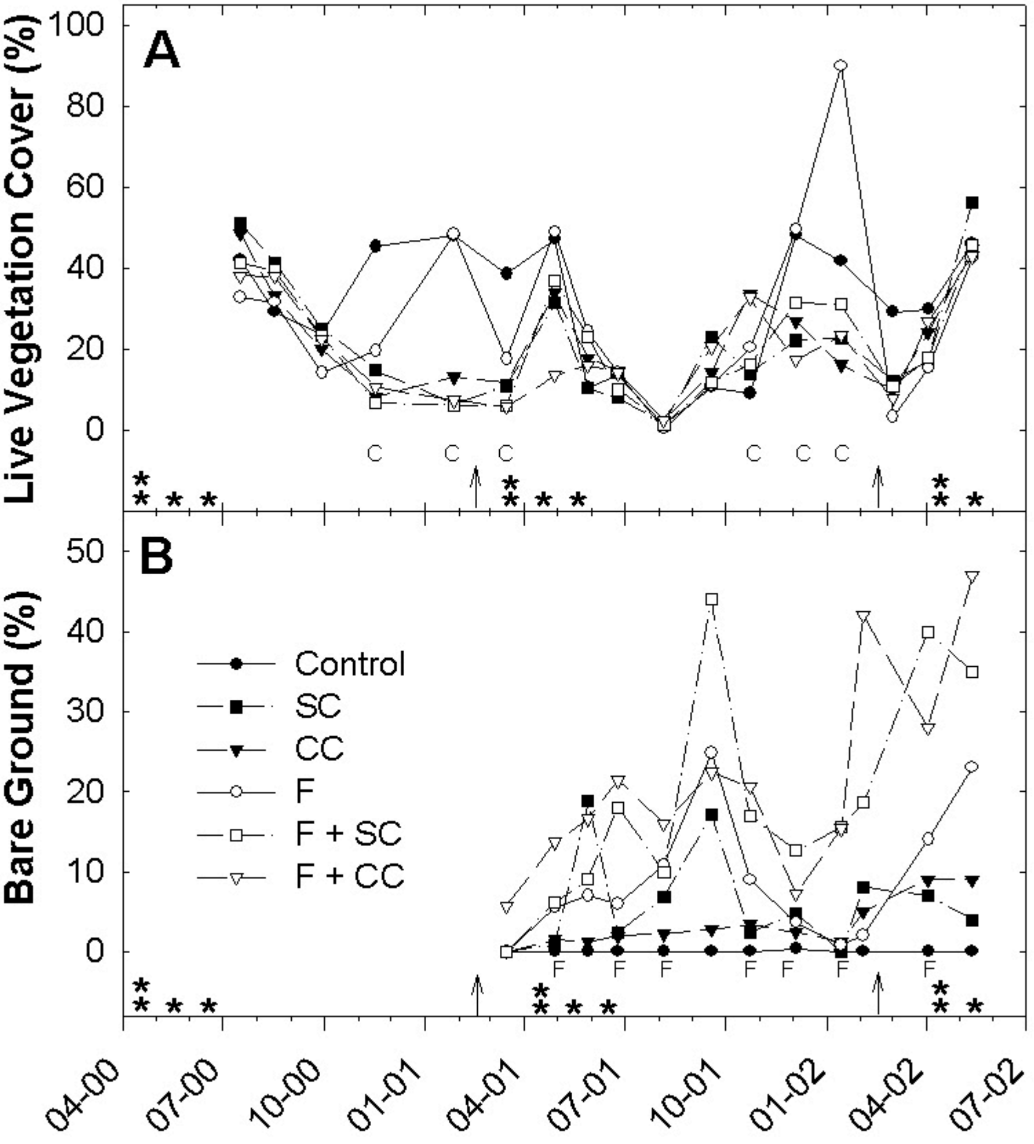

Figure 2. Per cent cover of live vegetation (Panel A) and bare ground (Panel B) , June 2000-May 2002. Values are means of five replicates. Significant ($p \leq 0.05$) treatment effects within individual sampling dates are indicated by C (clipping) and F (fire) along the x-axis. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis. Treatments are control (no fire, no clipping), SC (spring clipping), CC (continuous clipping), F (fire only), F + SC (fire and spring clipping), and F + CC (fire and continuous clipping).

TABLE 1. ANOVA results for the effects of fire and clipping on different cover variables, once sampling date effects are considered.

	Fire	Clipping	Fire x clipping	Fire x date	Clipping x date
Response	*P*	*P*	*P*	*P*	*P*
Live vegetation	0.4337	0.0007	0.9189	0.0100	<0.0001
Bare ground	< 0.0001	0.0001	0.0379	< 0.0001	0.2338
C_3 perennial grasses	0.3910	0.0042	0.0595	0.1917	0.0002
C_3 annual grasses	0.9981	< 0.0001	0.6757	0.0011	< 0.0001
C_4 perennial grasses	0.7583	0.5084	0.0794	0.0348	0.4539

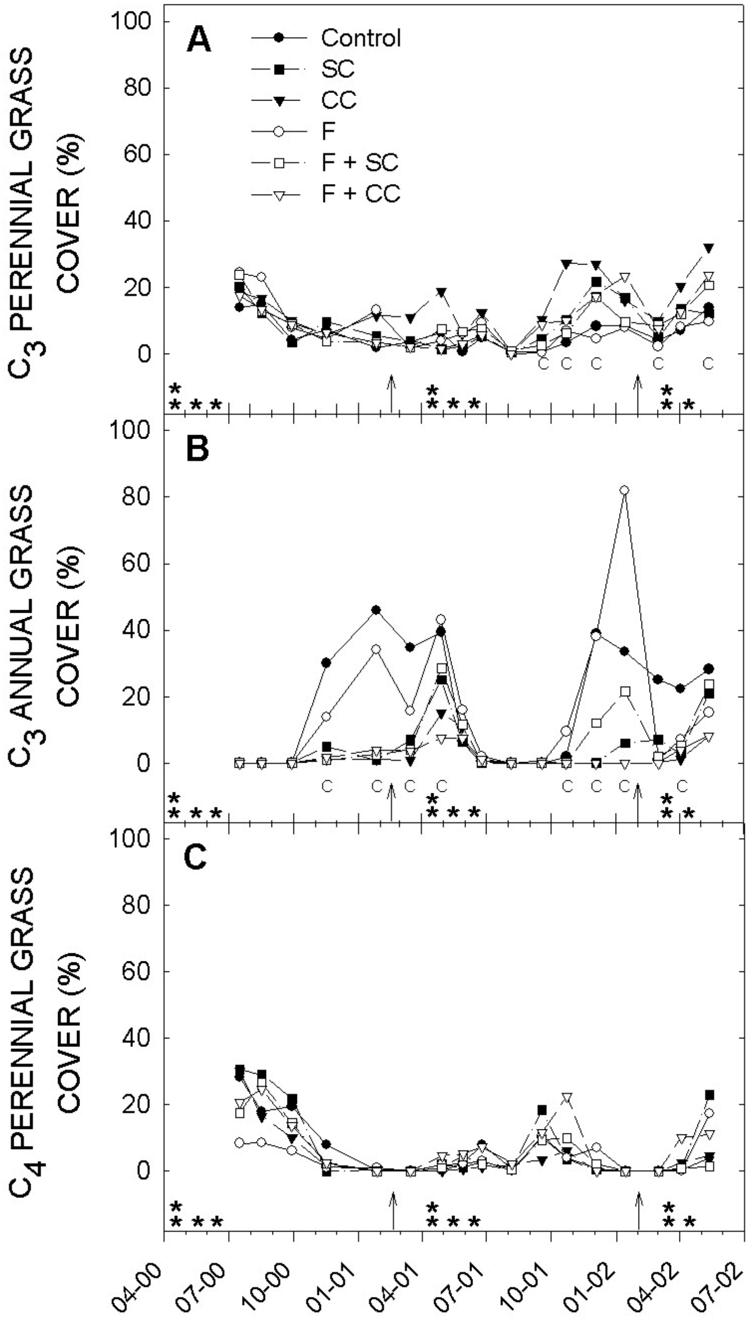

Figure 3. Per cent live cover of C_3 perennial grasses (Panel A), C_3 annual grasses (Panel B), and C_4 perennial grasses (Panel C), June 2000-May 2002. Values are means of 5 replicates. Significant ($p \leq 0.05$) treatment effects within individual sampling dates are indicated by C (clipping) along the x-axis. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis.

TABLE 2. Percent cover (± 1 SE) of total live vegetation (A), bare ground (B), C3 perennial grasses (C), C_3 annual grasses (D), and C_4 perennial grasses (E), June 2000 - May 2002.

A) Total live vegetation

	No clipping[a]	Spring clipping[b]	Continuous clipping[b]
No fire	30.4 ± 2.1	21.6 ± 2.1	22.0 ± 2.1
Spring fire	28.6 ± 2.1	21.2 ± 2.1	20.0 ± 2.1

B) Bare ground

	No clipping	Spring clipping	Continuous clipping
No fire	0.0 ± 1.7[c]	4.8 ± 1.7[bc]	3.3 ± 1.7[c]
Spring fire	8.9 ± 1.7[b]	18.8 ± 1.7[a]	21.3 ± 1.7[a]

C) C_3 perennial grasses

	No clipping[b]	Spring clipping[b]	Continuous clipping[a]
No fire	6.2 ± 1.5	8.8 ± 1.5	15.0 ± 1.5
Fire	8.0 ± 1.5	9.1 ± 1.5	9.8 ± 1.5

D) C_3 annual grasses

	No clipping	Spring clipping	Continuous clipping
No fire	18.1 ± 2.0	4.8 ± 2.0	2.3 ± 2.0
Spring fire	16.3 ± 2.0	6.6 ± 2.0	4.9 ± 2.0

E) C_4 perennial grasses

	No clipping	Spring clipping	Continuous clipping
No fire	6.1 ± 1.3	8.0 ± 1.3	4.7 ± 1.3
Spring fire	4.3 ± 1.3	5.4 ± 1.3	8.0 ± 1.3

Note: Different superscript lowercase letters indicate significantly different means ($P < 0.05$). Letters follow values if a significant fire x clipping interaction is present. Otherwise, letters follow treatment labels and indicate differences between the relevant rows and/or columns.

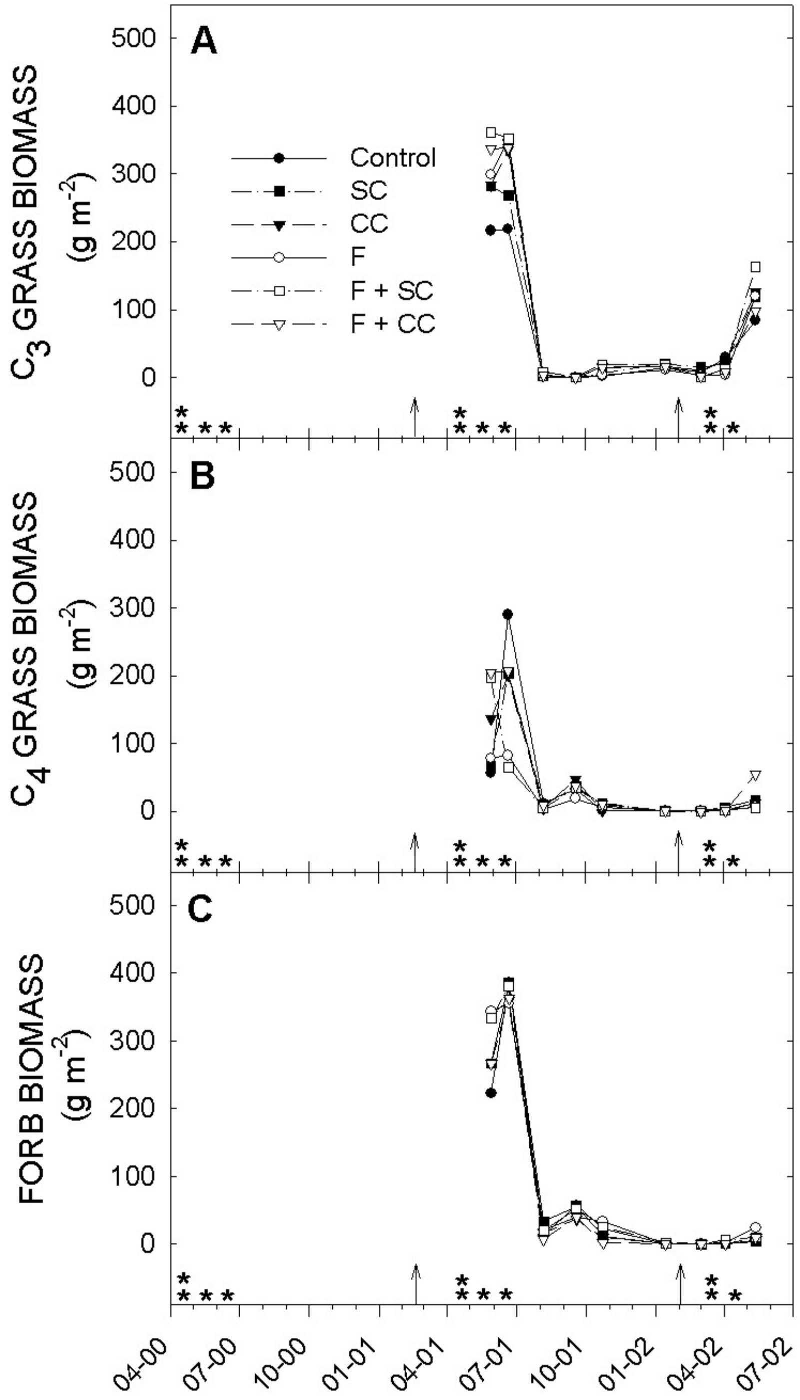

Figure 4. Live biomass of C_3 grasses (Panel A), C_4 grasses (Panel B), and forbs (Panel C), May 2001-May 2002. Values are means of 5 replicates. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis.

TABLE 3. ANOVA results for the effects of fire and clipping on different biomass variables, once sampling date effects are considered.

	Fire	Clipping	Fire x clipping	Fire x date	Clipping x date
Response	*P*	*P*	*P*	*P*	*P*
C_3 grasses	0.0784	0.1179	0.4428	0.0647	0.8470
C_4 grasses	0.6798	0.3610	0.5459	0.0143	0.3147
Forbs	0.4584	0.6093	0.2582	0.4163	0.9810
Total standing crop	0.1961	0.9778	0.4995	0.0474	0.2110
Live standing crop	0.3253	0.0777	0.9085	0.0015	0.1291
Litter	< 0.0001	0.0523	0.1092	0.0016	0.2419

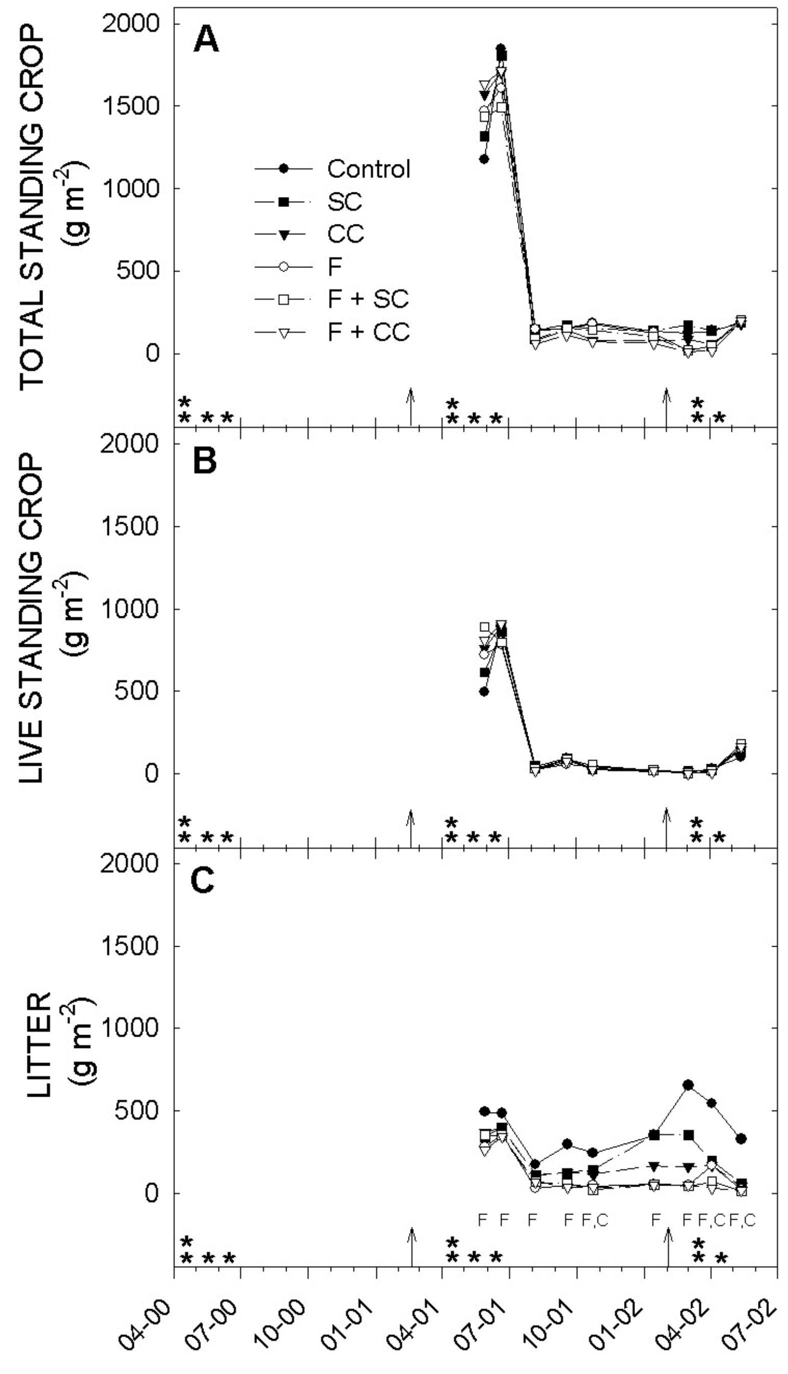

Figure 5. Total standing crop (Panel A), live standing crop (Panel B), and litter (Panel C), May 2001-May 2002. Values are means of 5 replicates. Significant ($p \leq 0.05$) treatment effects within individual sampling dates are indicated by F (fire) along the x-axis. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis.

TABLE 4. Mean biomass (± 1 SE) of C_3 grasses (A), C_4 grasses (B), forbs (C), total standing crop (D), live standing crop (E), and litter (F).

A) C_3 grass biomass (g m^{-2})

	No clipping	Spring clipping	Continuous clipping
No fire	67.1 ± 8.7	86.6 ± 8.7	90.5 ± 8.7
Spring fire	87.9 ± 8.7	104.0 ± 8.7	90.7 ± 8.7

B) C_4 grass biomass (g m^{-2})

	No clipping	Spring clipping	Continuous clipping
No fire	38.8 ± 14.4	46.0 ± 14.4	44.7 ± 14.4
Spring fire	21.8 ± 14.4	35.0 ± 14.4	58.0 ± 14.4

C) Forb biomass (g m^{-2})

	No clipping	Spring clipping	Continuous clipping
No fire	78.5 ± 6.7	83.2 ± 6.7	85.4 ± 6.7
Fire	90.8 ± 6.7	92.1 ± 6.7	76.6 ± 6.7

D) Total standing crop (g m^{-2})

	No clipping	Spring clipping	Continuous clipping
No fire	449.8 ± 25.7	471.8 ± 25.7	441.2 ± 25.7
Spring fire	435.9 ± 25.7	408.4 ± 25.7	430.1 ± 25.7

E) Live standing crop (g m^{-2})

	No clipping	Spring clipping	Continuous clipping
No fire	184.3 ± 14.9	215.8 ± 14.9	220.5 ± 14.9
Spring fire	200.6 ± 14.9	231.1 ± 14.9	225.3 ± 14.9

F) Litter (g m^{-2})

	No clipping^{a}	Spring clipping^{ab}	Continuous clipping^{b}
No fire^{a}	396.2 ± 49.7	261.7 ± 28.4	182.9 ± 19.3
Spring fire^{b}	116.1 ± 19.8	113.9 ± 19.9	98.2 ± 18.6

Note: Different superscript lowercase letters within treatment headings indicate significantly different means ($P < 0.05$).

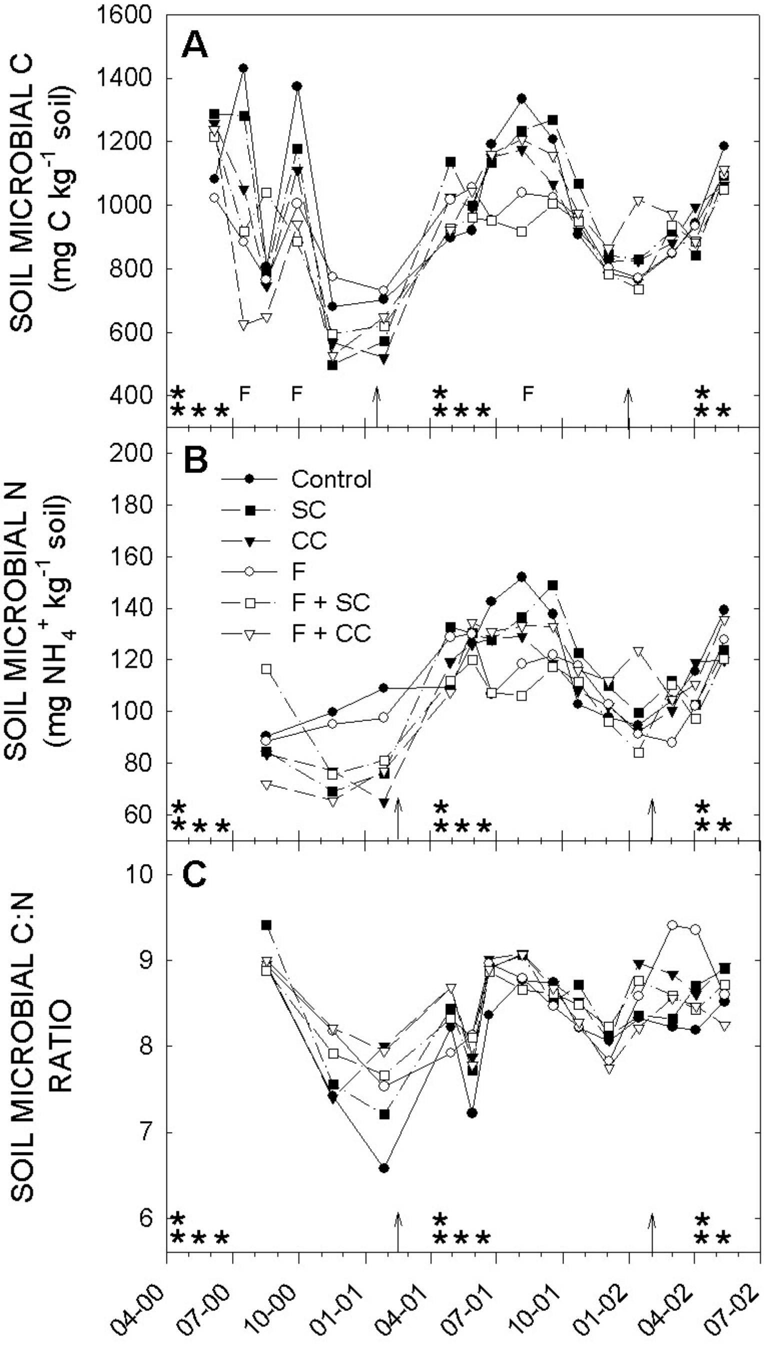

Figure 6. Soil microbial biomass carbon (Panel A), nitrogen (Panel B), and carbon:nitrogen ratio (Panel C) , May 2001-May 2002. Values are means of five replicates. Significant ($p \leq 0.05$) treatment effects within individual sampling dates are indicated by F (fire) along the x-axis. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis.

Neither fire nor clipping had no effect on any plant biomass response. (Figure 4A, Table 3). All components of plant biomass declined substantially over the period June-August 2001.

Both fire and clipping reduced litter mass overall (Figure 5C; Tables 3,4).

Soil microbial biomass C and N displayed similar seasonal fluctuations, peaking once per year from late summer to late fall. Soil microbial C:N ratios showed less amplitude in seasonal change, and appear to have had a separate and higher peak in early spring and early summer, while otherwise paralleling the pattern seen in SMB-C and –N. Overall, fire reduced soil microbial biomass C, while clipping had no effect. Fire and sampling date interacted significantly in the microbial C response, with fire effects appearing within three to sixth months following fire, in July and September 2000 and August 2001 (Figure 6A, Table 5). Neither fire nor clipping significantly affected soil microbial biomass N (Figure 6B) or soil microbial C:N ratios (Figure 6C; Tables 5,6).

TABLE 5. ANOVA results for the effects of fire and clipping on different microbial variables, once sampling date effects are considered.

	Fire	Clipping	Fire x clipping	Fire x date	Clipping x date
Response	*P*	*P*	*P*	*P*	*P*
Microbial C	0.0271	0.8516	0.3864	< 0.0001	0.0656
Microbial N	0.3878	0.7048	0.2754	0.2610	0.0275
Microbial C:N	0.3508	0.2692	0.0469	0.0085	0.3181

TABLE 6. Mean (± 1 SE) microbial biomass C (A) and N (B), and microbial C:N ratio (C).

A) Microbial C (mg C kg^{-1} soil)

	No clipping	Spring clipping	Continuous clipping
No fire[a]	1002.6 ± 32.2	999.9 ± 32.2	949.8 ± 32.2
Spring fire[b]	923.0 ± 31.7	905.1 ± 32.2	939.5 ± 31.9

B) Microbial N (mg NH_4^+ kg^{-1} soil)

	No clipping	Spring clipping	Continuous clipping
No fire	116.9 ± 5.3	112.6 ± 5.3	106.0 ± 5.2
Spring fire	108.0 ± 5.1	103.9 ± 5.4	112.2 ± 5.4

C) Microbial C:N

	No clipping	Spring clipping	Continuous clipping
No fire	8.11 ± 0.11	8.41 ± 0.11	8.55 ± 0.10
Fire	8.50 ± 0.11	8.43 ± 0.11	8.39 ± 0.11

Note: Different superscript lowercase letters within treatment headings indicate significantly different means ($P < 0.05$).

DISCUSSION

The results of this study show that disturbance in the form of fire and clipping is strongly modulated by climate, and varies across plant functional types due both to that modulation and to other factors related to the nature and timing of disturbance. Those factors are also important in the translation of aboveground plant community responses into effects on soil microbes. Of particular importance in that translation are the relative magnitudes of plant contributions to soil microbial C and N.

Summer drought during both study years reduced cover and biomass of C_4 grasses relative to years with average growing-season precipitation, limiting treatment effects to other plant functional types. The significance of sampling date as a factor in all response variables further illustrates the strong seasonal variation in plant production and soil microbial dynamics in this ecosystem.

Treatment-related reductions in total live vegetation cover were due to clipping alone, as a result of reductions in cover of C_3 annuals in the late winter and early spring. Both fire and clipping increased the area of bare ground, and interacted significantly in that clipping-related increases in bare ground were much greater in the presence of fire. Fire probably contributed more to the increase in bare ground via the removal of virtually all surface litter, with clipping's smaller role attributable to the prevention of current-season standing vegetation from entering subsequent seasons' litter pool.

The interpretation of litter removal as the primary mode of fire effects on bare ground is further supported by the finding that fire did not significantly affect the cover of any individual plant functional type. The lack of any significant response to fire or clipping in C_4 grasses contrasts with the literature (Towne and Owensby 1984; Collins 1987; Howe 1994; Howe 1995; Howe 2000; Engle and Bidwell 2001), and is likely due to low C_4 grass production caused by successive extreme summer droughts. That spring and continuous clipping reduced the cover of C_3 annual grasses while fire did not suggests that the timing as well as the mode of biomass removal is important to the system response. In late winter, when fire treatments were applied, C_3 annual grasses were still in a state of vegetative growth. However, when clipping began in April, seeds had already begun to form. Thus, the observed reduction in C_3 annual grass cover in response to clipping may be primarily due to a large reduction in the subsequent season's seed bank. In addition, more of the biomass is removed by clipping in spring than by fire in winter. It is also possible that reductions of the litter layer rendered conditions less favorable for germination of *B. japonicus* seeds (Whisenant 1990), though the lack of significant fire effects on C_3 annual cover suggests that this is a minor mechanism. The increase of C_3 perennial grass cover in response to continuous clipping raises the possibility that they are competitively excluded by C_3 annuals (Whisenant et al. 1984b), but the methods employed in this study permitted no direct assessment of that hypothesis. However, since C_3 perennial grasses increased significantly under continuous but not spring clipping, repeated clipping may have reduced C_3 annual grasses below some threshold level at which competitive interactions cease.

The lack of treatment effects on C_3 grass biomass suggests that the clipping-induced decreases in C_3 annual cover, and accompanying increases in C_3 perennial cover, may amount to net compensation in terms of biomass. Again, lack of treatment response in C_4 biomass is presumably attributable to repeated summer droughts. Taken together, these response patterns also account for the lack of treatment effects on total standing crop and total live standing crop. In unburned tallgrass prairie, neither clipping nor grazing produced any net change in individual plant biomass of *Andropogon gerardii* or *Panicum virgatum* (due to compensation via increased relative growth rate). However, in burned areas, the response to clipping and grazing was increased in *A. gerardii* (resulting in increased biomass), but absent from *P. virgatum* (Vinton and Hartnett

1992). A simulation model (de Mazancourt et al. 1998), applied to an African savanna grassland (de Mazancourt et al. 1999), found that grazing optimization (i.e. compensatory growth) occurred only when herbivory reduced ecosystem losses of N relative to the amount that would have left the system had the biomass been burned rather than consumed by herbivores. Although no direct measurements of insect numbers were made, anecdotal observations suggest that high abundance of and intense herbivory by grasshoppers may be the most likely explanation for the parallel decline in all plant biomass components across all treatments between June and August 2001 (Callaham et al. 2000).

Both fire and clipping reduced litter mass, but fire's larger relative reduction in litter mass may explain why soil microbial biomass C declined in response to fire, but not to clipping. That decline occurred 3-6 months following fire, suggesting that the combustion of recent litter that would otherwise be decomposed by soil microbes is indeed responsible (Bruulsema and Duxbury 1996). Contrary to hypothesized results, fire did not reduce soil microbial biomass N. This may be due to differing relative importance of sources of microbial C and N; microbes tightly retain, and dominate the cycling of, N derived primarily from soil inorganic pools, but are limited by inputs of plant C to drive those processes (Knops et al. 2002).

Fire in tallgrass prairie has been found to reduce both SMB-C and –N (Ajwa et al. 1999). However, this finding is not consistent across all studies (Garcia and Rice 1994), probably due to indirect effects stemming from interactions with climatic variables (Groffman et al. 1993). In New Zealand tussock grasslands, fire reduced SOC, SMB-C, and SMB-N up to 30 months after burning (Ross et al. 1997). In tallgrass prairie, SMB-C and -N declined in response to clipping generally, and to fire in dry years, with differences occurring during a period of a few months following treatments (Garcia and Rice 1994). Hamilton and Frank (2001) found increased SMB-C in response to clipping, presumably via stimulation of microbial growth in response to increased root exudation from defoliated plants.

Contrary to our initial hypothesis, fire had no impact on cover or biomass of C_4 grasses during the study period. This result, a consequence of consecutive summer droughts, made clipping the dominant disturbance type in terms of impacts on the plant community. However, fire's more severe impacts on surface litter gave it a relatively greater influence on soil microbes, highlighting the importance of plant C inputs as a principal driver of microbial dynamics. Avenues for further research in this system include assessment of the effects of disturbance on C_4 grasses during years of normal growing-season precipitation, the potential for competitive interactions between C_3 annual and perennial grasses, and the implications of these patterns for the relative roles of quantity versus quality (C:N ratio) of litter inputs in regulating the soil microbial community.

CHAPTER III

PLANT COMMUNITY AND SOIL MICROBIAL RESPONSES TO SEASONAL FIRE IN A SOUTHERN MIXED GRASSLAND

INTRODUCTION

Fire is an important disturbance in grassland ecosystems, with impacts on plant production, community composition, and, by consequent effects on flows of C and N from plants to soils, on soil microbial pools of those nutrients (Woodmansee and Wallach 1981; Hobbie 1992; Howe 1994; Wedin 1996). Variation in climate, season of disturbance, and the suite of plant functional types present at the site have produced varied reports on the direction and degree of response of these variables to fire.

These dynamics have been studied in depth in both the tallgrass prairie, and the shortgrass steppe, at opposite ends of the Great Plains' precipitation gradient (Blair 1997; Burke et al. 1998). However, they have not been extensively evaluated in the mixed grass prairie of the southern Plains. In this region, precipitation is intermediate between, and mean annual temperature higher than, those of short- and tallgrass prairie. Large-scale climatic gradients give rise to corresponding clines in ANPP (Burke et al. 1991; Lauenroth and Sala 1992; Burke et al. 1997; Epstein et al. 1997a; Tieszen et al. 1997; Paruelo et al. 1999; Lane et al. 2000), the balance between grass species possessing the C_3 and C_4 photosynthetic pathways (Paruelo and Lauenroth 1996; Epstein et al. 1997b; Tieszen et al. 1997; Epstein et al. 1998), and soil microbial biomass (Wardle 1992; Zak et al. 1994). Data on these variables' response to fire in southern Plains mixed grasslands thus constitute a necessary addition to the understanding of the interplay between climate and disturbance.

Additionally, the bulk of studies on fire in grasslands have focused on cool-season fire, and neither they nor the smaller number that have addressed fire in other seasons have typically compared fire season as a treatment in replicated designs (Engle and Bidwell 2001). Given that the historic fire regime consisted predominantly of more intense fires in drier and warmer periods of the year, this emphasis may overlook key elements of native plant species' adaptive responses to fire-induced disturbance (Howe 1994).

Individual plant species and functional types display a range of responses to fire, complicating interpretation and prediction of fire effects at community and ecosystem levels. The combination of a) strongly seasonal patterns of precipitation and temperature and b) a mixture of plant functional types whose phenologies are differently keyed to that variation, and whose responses to disturbance vary both between and within types, highlights the importance of seasonality in determining the ultimate impact of disturbance. This study adopts an approach parallel to that of Coffin and Lauenroth's (1996) modelling of C_3 and C_4 plant functional type responses to climatic change in shortgrass steppe.

This study compares the effects of spring and fall fire on plant functional composition and production and soil microbial biomass in a native mixed-grass community of the southern Great Plains. In studies of tallgrass prairie, spring fire increased the abundance of C_4 relative to C_3 grasses (Towne and Owensby 1984; Collins 1987), with fall fire having the opposite result (Howe 1994; Howe 1995; Howe 2000; Engle and Bidwell 2001). Spring fire also decreased the relative microbial content of N relative to C, perhaps via shifts in the elemental composition of litter inputs (Turner et al. 1997; Johnson and Matchett 2001). We hypothesized that spring fire would increase the proportional representation of C_4 grasses, and thereby the C:N ratio of microbial biomass, in the study system. Fall fire, by increasing the relative proportion of production from C_3 grasses, was expected to decrease microbial C:N ratios.

METHODS

Study site

Research was conducted on a 1 ha grazing exclosure on the W.T. Waggoner Ranch in Wilbarger County, Texas (33° 51'N, 99° 26' W, elevation 381 m). Mean annual precipitation for the site is 665 mm, bimodally distributed, with peaks in May (18% of annual total) and September (12% of annual total). Mean annual temperature is 16.1° C, with monthly average extremes ranging from 36° C in July to -2.5° C in January. Soils are classified as fine, mixed, thermic Typic Paleustolls of the Tillman series.

Dominant cool season (C_3) grasses include Texas wintergrass (*Nasella leucotricha* (Trin & Rupr) Pohl), a native perennial bunchgrass, and Japanese brome (*Bromus japonicus* Thunb. ex Murr.), an exotic annual grass. Dominant warm season (C_4) grasses include the perennial bunchgrass sideoats grama (*Bouteloua curtipendula* (Michx.)

Torr.), and the stoloniferous, sod-forming buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.). The study site was root-plowed and seeded with sideoats grama in 1974. It has not been burned since that time. The site was grazed by cattle at a moderate stocking rate (1 cow 12 ha^{-1}) from the late 1800s to 1988, when livestock were removed.

Experimental design

Vegetation and soil microbial dynamics were evaluated on experimental treatment plots in a single-factor design. Treatments were randomly assigned to fifteen 6x6-m plots (n= 5 replicates/treatment combination/year). The following treatments were implemented annually beginning in 1999: 1) control (no fire), 2) spring fire, and 3) fall fire. Plots in the spring fire treatment (typical management fire) were subjected to prescribed fires in February/March 1999, 2000, 2001, and 2002, while those in the fall fire treatment (typical wildfire) were burned in September/October 1999, 2000, and 2001. Fire intensity for all fires in all years was classified as low to moderate, with flame heights not exceeding 1.5 m. Rainfall was measured at the site.

Sampling and analysis

Sampling was carried out at approximately monthly intervals intervals from June 2000 through May 2002. During each sampling period, a 1x1 m subplot was randomly chosen from each of the 15, 6x6 m treatment plots. Since sampling was destructive, no subplots were resampled. The following sampling procedures were performed on each 1x1 m subplot.

Ocular estimates of foliar cover were recorded on each subplot, distinguishing the following cover classes: C_3 grasses (live/dead) by species, C_4 grasses (live/dead) by species, forbs, litter, and bare ground. Since various cover classes overlapped at different levels within the canopy, cover percentages may total to more than 100 on a given subplot.

Vegetation was clipped to ground level within a square 0.125 m^2 quadrat inside the subplot. Clipping only was carried out on the subplot from the previous sampling interval in order to prevent disruption of concurrent *in situ* N-mineralization assays. Clipped vegetation was bagged by category (C_3 grass, C_4 grass, forb, litter) and dried for 5 d at 60 °C. Dried vegetation was then separated into live and dead and weighed to estimate biomass.

A composite soil sample consisting of 8, 2.5-cm diameter cores sampled 10 cm deep was taken from each subplot. Soil samples were immediately placed on ice for transport to the laboratory and subsequently stored at 4 °C until analysis. Samples were homogenized prior to laboratory analysis. A 30 g, field moist soil subsample was brought to 50 % water holding capacity, and analyzed for soil microbial biomass (SMB) C and N using the chloroform fumigation-incubation method (Horwath and Paul 1994; Franzluebbers et al. 1999).

SMB-C, SMB-N, and SMB-N:C were calculated as:

$$\text{SMB-C} = C_f/K_c \qquad \text{(Voroney and Paul 1984)}$$

$$\text{SMB-N:C} = 0.56\,(N_f/C_f) + 0.095 \qquad \text{(Harris et al. 1997)}$$

$$\text{SMB-N} = \text{SMB-C (SMB-N:C)} \qquad \text{(Harris et al. 1997)}$$

where C_f and N_f are the flushes of mineralized C and N, respectively, from fumigated soils, and $K_c = 0.43$.

Data analysis

Data were analyzed using SAS Version 9.0 (SAS Institute 2002). Each response variable was separately analyzed using a two-way ANOVA with sampling date and fire as factors. For responses where fire effects and fire-by-date interactions were significant, the analysis was repeated within each sampling date, excluding sampling date as a factor. Significant differences between treatment effects were evaluated via pairwise comparisons of least squares means.

RESULTS

In 2000, precipitation from April through September was below normal in every month. In 2001, precipitation was below normal for five of the six months, with only August precipitation exceeding normal. Total precipitation for this six month period was 38 % of normal in 2000, and 50 % of normal in 2001. During the remaining six months, by contrast, precipitation was 162 % of normal in 2000, and 123 % of normal in 2001 (Figure 1).

All responses showed pronounced seasonal variation, as reflected by the significance of sampling date as a factor for all variables measured.

Overall, fall fire significantly reduced live vegetation cover (Table 7), though significant interactions with sampling date preclude a direct comparison of overall means. Within individual sampling dates (Figure 7A), live vegetation cover was never significantly greater in fall fire than in spring fire or no fire treatments. The fire-by-sampling date interaction stems from the fact that in late 2000, live vegetation cover in the no fire treatment increased above that in spring and fall fire treatments. During the same period of 2001, by contrast, live vegetation cover was highest in the spring fire treatment (see discussion of C_3 annual cover below). By January of both years, live vegetation cover in the spring fire treatment was greater than that in the fall fire treatment, and equal to or greater than that in the no fire treatment, but declined sharply following fire in February/March.

Overall, fire in either season significantly increased the area of bare ground (Figure 7B; Table 7) relative to that in the no fire treatment. However, significant fire by sampling date interactions prevent a direct assessment of these effects. This interaction is due to the fact that increases in the area of bare ground in both fire treatments began immediately after fire, and continued for a period of several months before declining again until the next fire.

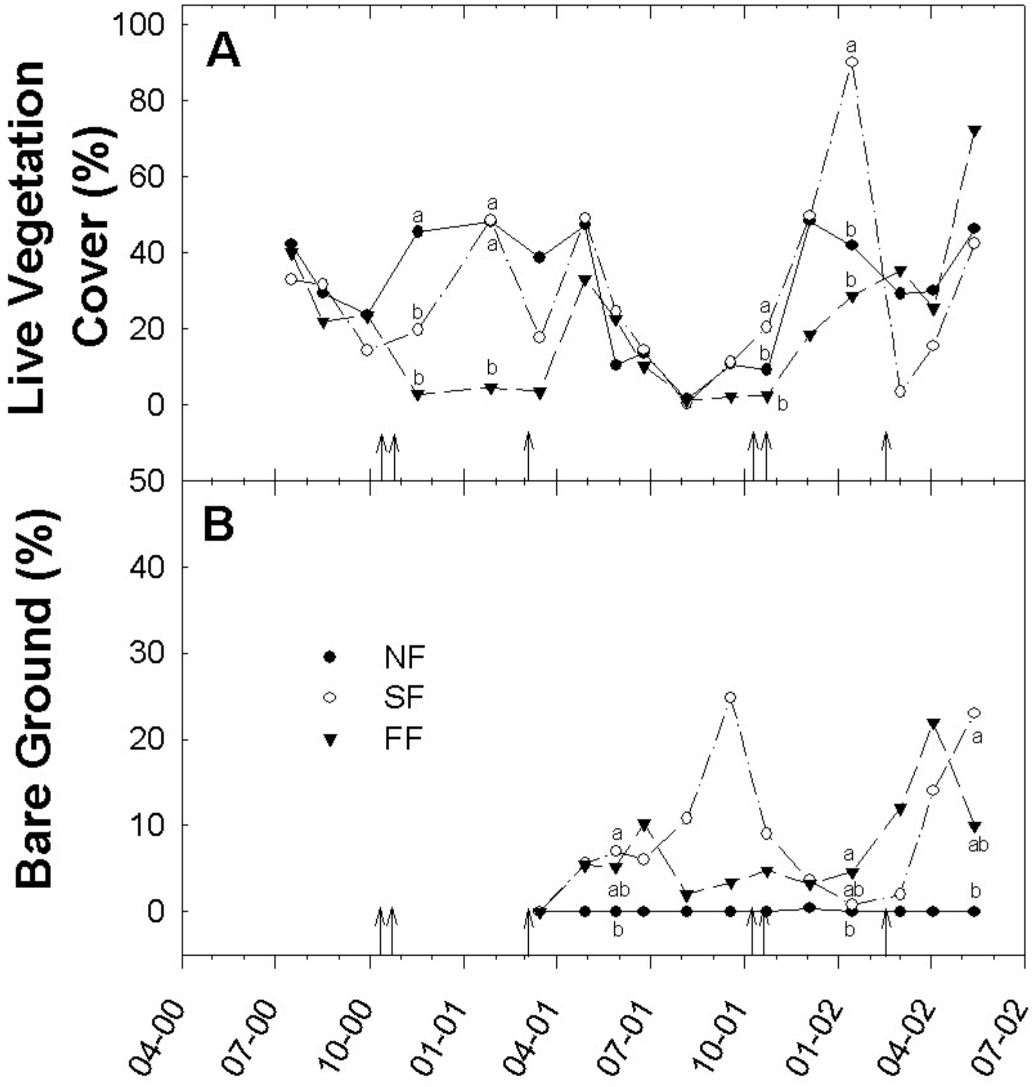

Figure 7. Per cent cover of live vegetation (Panel A) and bare ground (Panel B) under seasonal fire, June 2000-May 2002. Values are means of five replicates; values sharing one or more letters in the same sampling date are not significantly different ($p \leq 0.05$). Arrows indicate timing of fire treatments (single arrow = spring fire; double arrow = fall fire). Note that 2 spring fires and one fall fire had already occurred before the start of the period shown in the plot (see Methods). Treatments are NF (no fire), SF (spring fire), and FF (fall fire).

TABLE 7. ANOVA results for the effects of fire and sampling date on different cover variables under seasonal fire.

	Fire	Date	Fire x date
Response	*P*	*P*	*P*
Live vegetation	0.0395	< 0.0001	< 0.0001
Bare ground	0.0136	0.0029	0.0068
C_3 perennial grasses	0.7036	< 0.0001	0.0721
C_3 annual grasses	0.2357	< 0.0001	< 0.0001
C_4 perennial grasses	0.1051	< 0.0001	0.0976

The responses of individual plant functional types correspond to the observed patterns of total live vegetation cover and area of bare ground. Fire did not significantly affect the cover of C_3 perennial or annual, or C_4 perennial, grasses (Tables 7,8; Figure 8). However, the response of C_3 annual grass cover to fire was similar in character to that of total live vegetation cover.

In contrast with the cover results, fire in both seasons increased the live biomass of C_3 grasses, though this was significant only for fall fire (Table 9; Figure 9A). In another difference from the cover response, fire had no significant effect on C_4 grass biomass (Table 9; Figure 9B).

There was also no significant effect of fire on biomass of forbs (Table 9; Figure 9C), total standing crop, or live standing crop (Table 9; Figure 10A,B). However, fire in both seasons significantly reduced the mass of surface litter by more than 60 % (Figure 10C; Table 10).

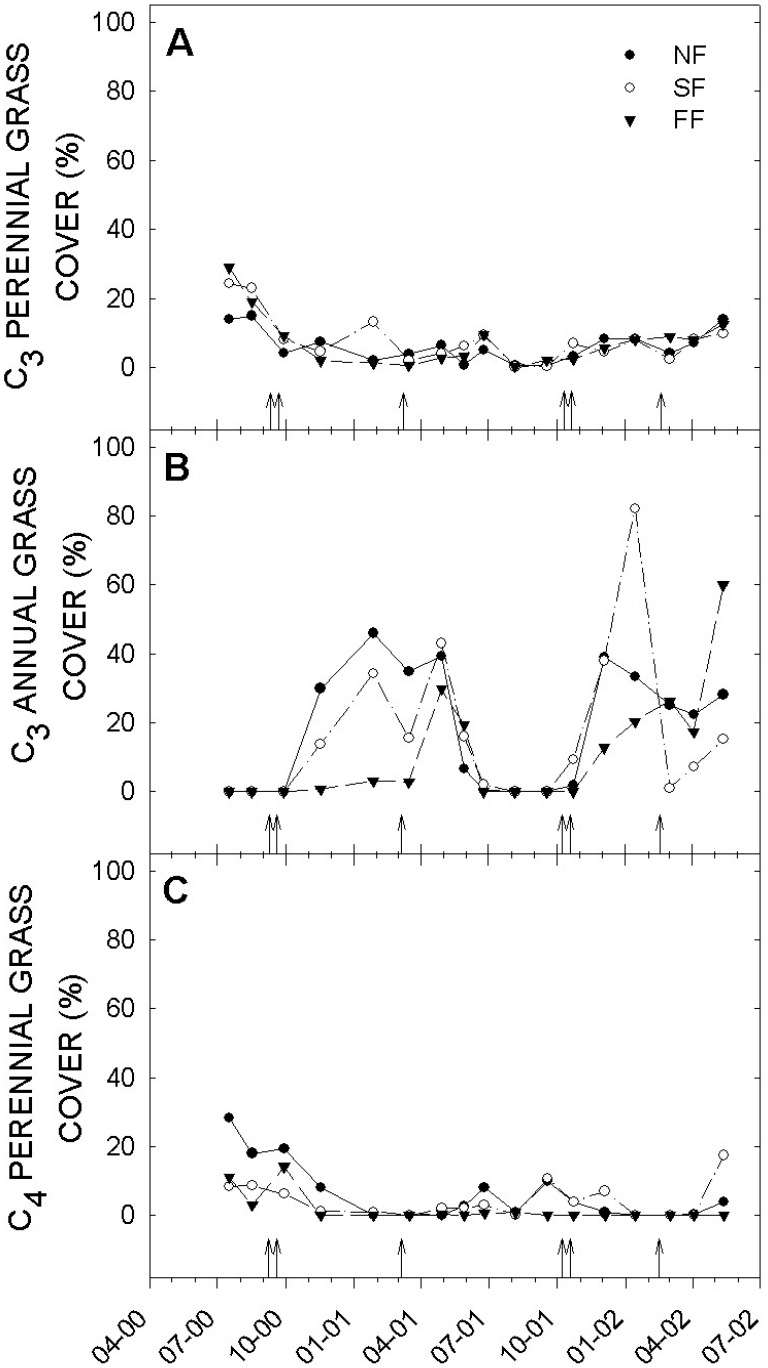

Figure 8. Per cent live cover of C_3 perennial grasses (Panel A), C_3 annual grasses (Panel B), and C_4 perennial grasses (Panel C) under seasonal fire, June 2000-May 2002. Values are means of five replicates; values sharing one or more letters in the same sampling date are not significantly different ($p \leq 0.05$). Arrows indicate timing of fire treatments (single arrow = spring fire; double arrow = fall fire).

TABLE 8. Percent cover (± 1 SE) of total live vegetation, bare ground , C_3 perennial grasses (C), C_3 annual grasses (D), and C_4 perennial grasses (E) under seasonal fire, June 2000 - May 2002.

	No fire	Spring fire	Fall fire
Total live vegetation	30.4 ± 2.5	28.6 ± 2.5	20.5 ± 2.5
Bare ground	0.0 ± 1.9	8.9 ± 1.9	6.9 ± 1.9
C_3 perennial grasses	6.2 ± 1.5	8.0 ± 1.5	7.4 ± 1.5
C_3 annual grasses	18.1 ± 2.7	16.3 ± 2.7	11.4 ± 2.7
C_4 perennial grasses	6.1 ± 1.3	4.3 ± 1.3	1.8 ± 1.3

TABLE 9. ANOVA results for the effects of fire and sampling date on different biomass variables under seasonal fire.

	Fire	Date	Fire x date
Response	*P*	*P*	*P*
C_3 grasses	0.0396	< 0.0001	0.0879
C_4 grasses	0.3116	< 0.0001	0.0334
Forbs	0.3335	< 0.0001	0.1162
Total standing crop	0.2983	< 0.0001	0.0166
Live standing crop	0.2109	< 0.0001	0.2252
Litter	< 0.0001	< 0.0001	0.1158

TABLE 10. Mean biomass (g m^{-2} ± 1 SE) of C_3 grasses, C_4 perennial grasses, forbs, total standing crop, live standing crop, and litter under seasonal fire, June 2000 - May 2002.

	No fire	Spring fire	Fall fire
C_3 grasses	67.1 ± 9.2^{a}	87.1 ± 9.0^{ab}	103.9 ± 9.0^{b}
C_4 grasses	38.8 ± 10.3	21.8 ± 10.1	16.7 ± 10.1
Forbs	78.5 ± 8.6	90.8 ± 8.5	97.1 ± 8.5
Total standing crop	445.2 ± 20.4	435.9 ± 20.1	400.9 ± 20.1
Live standing crop	183.7 ± 12.8	200.6 ± 12.6	217.7 ± 12.6
Litter	391.1 ± 57.7^{a}	116.1 ± 56.8^{b}	151.5 ± 56.8^{b}

Note: Different superscript lowercase letters within rows indicate significantly different means ($P < 0.05$).

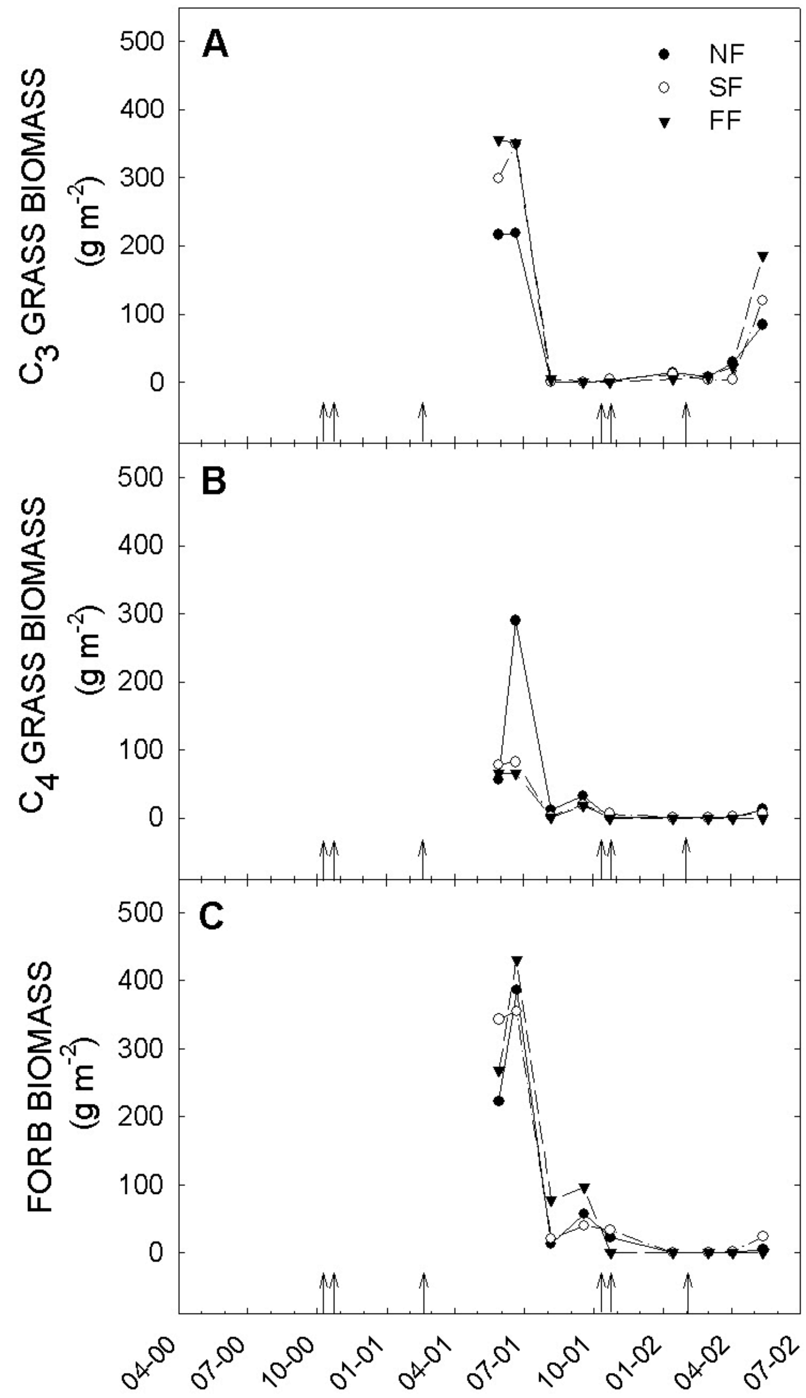

Figure 9. Live biomass of C_3 grasses (Panel A), C_4 grasses (Panel B), and forbs (Panel C) under seasonal fire, May 2001-May 2002. Values are means of 5 replicates; values sharing one or more letters in the same sampling date are not significantly different ($p \leq 0.05$). Arrows indicate timing of fire treatments (single arrow = spring fire; double arrow = fall fire).

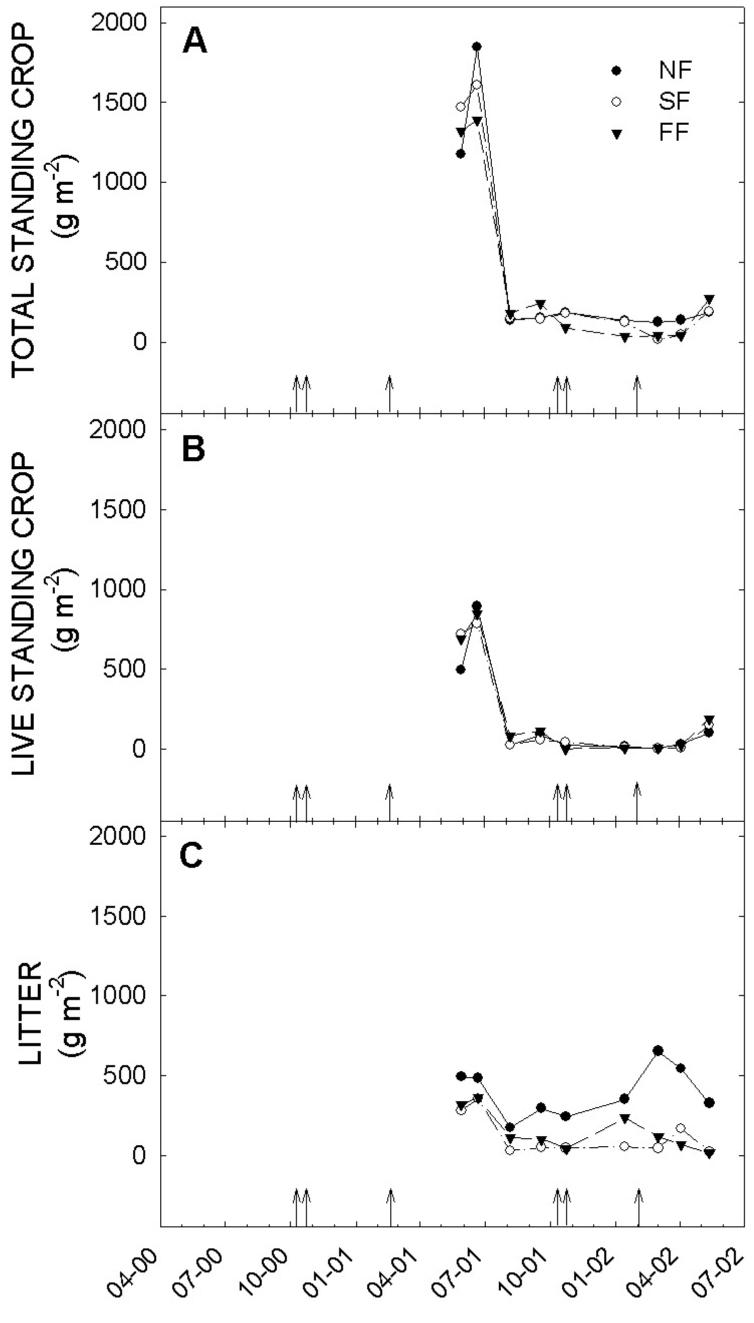

Figure 10. Total standing crop (Panel A), live standing crop (Panel B), and litter (Panel C) under seasonal fire, May 2001-May 2002. Values are means of 5 replicates; values sharing one or more letters in the same sampling date are not significantly different ($p \leq 0.05$). Arrows indicate timing of fire treatments (single arrow = spring fire; double arrow = fall fire).

The trend of response in both microbial C and N was a nonsignificant decline in both fire treatments (Tables 11,12). Soil microbial C was reduced relative to other treatments in the summers following spring fires (2000 and 2001). A similar, but more rapid, decline in microbial C following fall fire occurred in 2000, but not in 2001 (Figure 11A,B). In general, soil microbial C:N ratios were greater in spring fire than in fall fire or no fire treatments. However, significant fire-by-sampling date interactions preclude direct statistical interpretation of this effect (Table 11). Mean soil microbial C:N ratios in no fire and fall fire treatments tended to be closer, and lower than those in spring fire treatments, over the course of the study (Table 12). The interaction effect stems from a reversal of this pattern in April 2001, with higher values in the fall fire treatment persisting through the following month (Figure 6C).

TABLE 11. ANOVA results for the effects of fire and sampling date on different microbial variables under seasonal fire.

	Fire	Date	Fire x date
Response	*P*	*P*	*P*
Microbial C	0.1882	< 0.0001	0.0695
Microbial N	0.2279	< 0.0001	0.1820
Microbial C:N	0.0461	< 0.0001	0.0131

TABLE 12. Mean (± 1 SE) microbial C, N, and C:N ratio under seasonal fire, June 2000 - May 2002.

	No fire	Spring fire	Fall fire
Microbial C (mg C kg^{-1} soil)	1002.6 ± 29.4	923.0 ± 29.0	948.6 ± 29.2
Microbial N (mg NH_4^+ kg^{-1} soil)	116.9 ± 5.0	108.0 ± 5.0	104.2 ± 4.9
Microbial C:N	8.1 ± 0.1	8.5 ± 0.1	8.4 ± 0.1

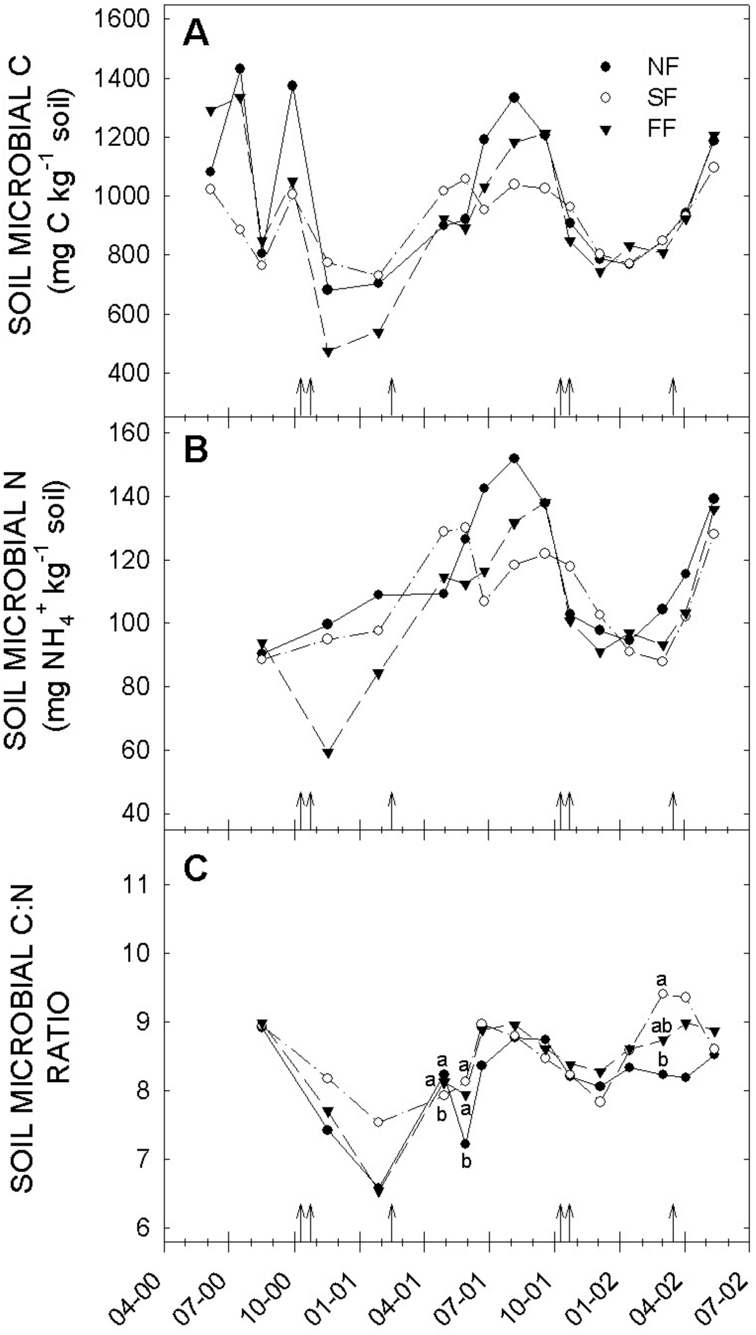

Figure 11. Soil microbial biomass carbon (Panel A), nitrogen (Panel B), and carbon:nitrogen ratio (Panel C) under seasonal fire, May 2001-May 2002. Values are means of five replicates; values sharing one or more letters in the same sampling date are not significantly different ($p \geq 0.05$). Arrows indicate timing of fire treatments (single arrow = spring fire; double arrow = fall fire).

DISCUSSION

These findings confirm that the role of fire as a disturbance is significant in its consequences for plant production and community composition in southern Great Plains mixed grasslands. That role is strongly contingent on climatic variation, and also varies with plant functional types and seasonality of disturbance. Climate, plant functional type, and season of fire also control the conversion of aboveground plant responses into effects on soil microbial dynamics.

The high significance of sampling date as a factor in all response variables highlights the importance of intraannual climatic variability for plant-soil dynamics in this system. The relative production of grasses of differing photosynthetic pathways in relation to above-normal winter and below-normal summer precipitation also indicates the large role of interannual climatic variability , as documented for grasslands in other regions of the Great Plains (Burke et al. 1991; Fuhlendorf et al. 2001; Knapp and Smith 2001).

On this site, C_3 annual grasses dominated the surface-cover dynamics of the plant community. This has been a recent trend in vegetation dynamics of the region (Ansley et al. 2004), and may be the result of the summer grazing by cattle and chronic lack of fire that have together reduced the competitive ability of C_4 grasses. The observed reduction in C_4 grass cover in response to fall fire, while not statistically significant, is consistent with the hypothesized result and with those reported for warm-season fire by other authors (Towne and Owensby 1984; Collins 1987; Howe 1994; Howe 1995; Howe 2000; Engle and Bidwell 2001). The lack of any observed increase in C_4 grass cover in spring fire treatments, however, was unexpected, and likely a result of water limitation during the period of active growth for this functional type due to consecutive summer droughts. Supporting this interpretation is the observation that cover of C_4 grasses in all treatments remained below typical levels throughout the study period.

Considering the lack of response by C_3 grass cover in fire treatments, the significant increase in (annual + perennial) C_3 biomass in response to fall fire at first seems counterintuitive. However, fire did increase the area of bare ground, making conditions less favorable for C_3 annual grass germination, and creating the possibility of compensatory or even overcompensatory growth by C_3 perennial grasses as an explanation for the C_3 biomass response. This study did not quantify biomass of C_3 annual and perennial grasses separately and so cannot confirm this supposition. However, Whisenant et al. (1984b) reported increased standing crops of C_3 perennial *N. leucotricha* following winter fire in areas where C_3 annual grasses were abundant, a result which they attributed to reduced competition. Such varied responses of different plant functional types are consistent with other reports from studies of warm-season fire (Ewing and Engle 1988; Biondini et al. 1989; Coppedge et al. 1998; Howe 2000; Copeland et al. 2002; Ansley et al. in preparation). Sharp declines in all categories of standing biomass, and across all treatments, between June and August 2001, may be the result of high levels of grasshopper herbivory (Callaham et al. 2000); grasshopper populations were not quantified but were anecdotally observed to be abnormally high during this period.

In general, declines in the biomass of certain plant functional types appeared to be balanced by increases in that of others, as evidenced by the lack of significant fire effects on either live or total standing crop. Given the intermediate precipitation and vegetational composition of the site relative to shortgrass steppe and tallgrass prairie ecosystems, this result is intuitively tractable. In tallgrass prairie, annual spring fire commonly (Seastedt and Ramundo 1990; Seastedt and Knapp 1993; Blair 1997; Briggs and Knapp 2001), though not always (Seastedt et al. 1991; Vinton and Hartnett 1992; Ojima et al. 1994), increases productivity over that of unburned sites. Summer fire also increased productivity, but to a lesser degree (Howe 2000). In shortgrass steppe, however, both dormant- and growing-season fires reduced aboveground biomass (Brockway et al. 2002).

At an annual frequency, both 4 consecutive spring fires and 3 consecutive fall fires significantly reduced the mass of surface litter, removing over 60 % of the cumulative total in unburned controls. This pattern offers a more consistent explanation than changes in standing crop of the observed microbial responses to fire treatments. Although both fire treatments were associated with higher levels of live C_3 grass biomass (significantly so only in the fall fire treatment), microbial biomass C and N were highest in the no fire treatment (albeit lower in spring fire than fall fire in the 2000 and 2001 growing seasons). Since most aboveground plant material presumably enters the soil microbial biomass via the decomposition of detached surface litter, fire's removal of the majority of that litter mass constitutes a more direct interruption of the conduit between aboveground plant litter and microbial tissue. This mechanism is consistent with the observed pattern of litter mass response to fire treatments (no fire > spring fire ≈ fall fire), and also with the 5-6 month offset between peaks in plant production and those in microbial C and N (Bruulsema and Duxbury 1996). Since the decrease in litter mass was statistically significant, and an order of magnitude greater than the nonsignificant declines in microbial C and N following fire, soil microbes in this system may obtain a significant portion of their substrate from belowground plant inputs, whose responses to fire were not assessed in this study. Earlier work at the same site suggested that spring fire did increase root length production and mortality early in the season (Hubbard 2003).

Other studies have reported reduced soil microbial C and N following fire in tallgrass prairie ecosystems (Ajwa et al. 1999). However, the pattern is not consistent either in the study system (see Chapter II) or in all studies of tallgrass prairie (Garcia and Rice 1994). Soil microbial C declined following fire in New Zealand tussock grasslands, but N showed no response (Ross et al. 1997). These variations in microbial C and N response to fire may stem from the modulating influence both of other disturbance types, such as clipping or grazing, and of climate (Groffman et al. 1993).

The observed values of microbial C:N ratios fall within the range typical of systems dominated by fungi, with a relatively small bacterial component (Harris et al. 1997; Wallander et al. 2003). Other work has shown an increase, rather than a decline, in soil microbial C:N ratios following fire (Ross et al. 1997), further highlighting the role of climate and plant functional type in determining the ultimate microbial response to this disturbance.

These results partly support the initial hypotheses concerning fire effects on relative abundance of plant functional types and microbial C and N stocks. As expected, fall fire reduced the cover of C_4 grasses, although – probably due to drought-induced constraints on production - no effects on biomass were observed. Also in keeping with predictions, fall fire increased the biomass of C_3 grasses, but via the unexpected mechanism of shifts in the relative abundance of annual and perennial components. Despite these shifts in plant community composition, fire's primary mode of effect on soil microbes appears to have been via its large reductions in surface litter, with corresponding increases in microbial C:N ratios. Further research on plant-soil interactions in this ecosystem is necessary for a direct assessment of the role of competition between C_3 annual and perennial grasses in their response to fire, the response of C_4 grasses in years when their growth is not drought-limited, and the consequences of that increased growth on the potential role of litter composition, as well as quantity, in influencing soil microbial dynamics. Additional data on root dynamics following fire would also advance the understanding of the links between plant and microbial responses to disturbance.

CHAPTER IV

SOIL CARBON AND NITROGEN RESPONSES TO SPRING FIRE AND CLIPPING IN A SOUTHERN MIXED GRASSLAND

INTRODUCTION

Disturbance has profound impacts on plant-soil C and N dynamics (Hobbie 1992; Asner et al. 1997; Wardle et al. 1998; Wali et al. 1999). The most pronounced effects of disturbance on nutrient cycling are indirect, exerted via changes in the quantity and quality of above- and belowground plant inputs to the soil (McGill et al. 1986; Hobbs 1996; Frank and Groffman 1998). The potential effects of disturbance are greater in grasslands than in any other biome; in temperate grasslands, soil organic matter (SOM) content averages 331 Mg/ha, 12 % of the earth's total (Ojima et al. 1993; Seastedt et al. 1994; Hobbs 1996; Conant et al. 2001). SOM is an important channel by which disturbance effects on nutrient cycles are translated from aboveground to belowground pools, and vice versa (Wedin 1996). It comprises a suite of related attributes, including total soil organic carbon (SOC) and total N, as well as various physical, chemical, and kinetic fractions of those pools (Gregorich et al. 1994).

Differing consequences of both herbivory and fire on plant productivity and quality and soil C and N pools have been documented. In some cases intensive grazing can lead to SOM losses, while in others it may stimulate ANPP and increase SOC (Augustine and McNaughton 1998; Ritchie et al. 1998). These increases in SOC are greatest for warm dry regions with high potential evapotranspiration that have with long histories of grazing (*sensu* Milchunas and Lauenroth (1993)). The trend is more pronounced as grazing intensity increases, and could be attributed to any of three different mechanisms: a) changes in community composition, leading to greater root:shoot ratios and increased belowground biomass, b) lower standing stocks of biomass but increased turnover and production, c) compensation for decreased plant production by increased manure inputs (Conant et al. 2001). Similarly, while increases in both ANPP (Schuman et al. 2002) and available N are common following fire, they are neither consistent (Ajwa et al. 1999) nor necessarily persistent (Towne and Owensby 1984; Ojima et al. 1990; Ojima et al. 1994; Blair 1997; Turner et al. 1997; Wan et al. 2001).

Most studies of disturbance's role in grassland plant-soil nutrient dynamics focus on fire or grazing as isolated factors, to the exclusion of addressing potential interactions between the two (Coppedge et al. 1998; Engle and Bidwell 2001). Such interactions mediate nutrient dynamics at scales of individual plants (Vinton and Hartnett 1992), communities (Collins 1987; Hobbs et al. 1991; Collins et al. 1998), and landscapes (Hobbs 1996; Coppedge et al. 1998; de Mazancourt et al. 1998; Biondini et al. 1999; de Mazancourt et al. 1999; Knapp et al. 1999). In tallgrass prairie, fire temperature and energy release, as well as N losses, were greater from ungrazed than grazed treatments (Ewing and Engle 1988; Hobbs et al. 1991). A variety of heuristic models has been put forth to address the interplay between disturbances. Shifts in dominance between functional groups of differing photosynthetic pathway, or even of differing palatability within a single photosynthetic pathway (Moretto et al. 2001; Moretto and Distel 2002), may have pronounced effects on pool sizes and turnover rates of C and N in the plant-soil system (Hobbie 1992; Chen and Stark 2000). Characteristic differences in plant tissue chemistry exist between these groups (Caswell et al. 1973; Levang-Brilz and Biondini 2003) and may be exacerbated by both species replacement (de Mazancourt et al. 1998; de Mazancourt et al. 1999; de Mazancourt and Loreau 2000a; de Mazancourt and Loreau 2000b) and intraspecific shifts in tissue quality (Johnson and Matchett 2001) in response to fire and herbivory. Hypothesized mechanisms for linkages between plant community composition and tissue quality on the one hand, and soil nutrient dynamics on the other, run the gamut from positive feedbacks (Wedin 1995; Wedin 1996), to negative feedbacks (Tateno and Chapin 1997), to feedbacks whose direction is scale-dependent (de Mazancourt and Loreau 2000a; de Mazancourt and Loreau 2000b; Knops et al. 2002), to predominance of climatic effects (Burke et al. 1998; Hooper and Johnson 1999).

Many of the discrepancies in results between studies of disturbance effects on grassland C and N cycles may stem from the modulating influence of climate, and from the staggered phenologies of different plant functional types within that climatic context (Biondini and Manske 1996; Derner et al. 1997; Biondini et al. 1998; Derner et al. in preparation). Seasonality of climatic variation may be as significant as annual means for grassland plant-soil C and N dynamics (Ojima et al. 1993; Epstein et al. 1999). One approach to assess the relative roles of these different factors is to monitor seasonal shifts in the concentration and isotopic composition of C and N in plant materials at various stages of incorporation into the soil (e.g. surface litter, soil density fractions, bulk soil). In particular, $\delta^{13}C$ of surface litter and soil organic matter density fractions serves as an index of the relative inputs from C_3 and C_4 plants (Boutton et al. 1998; Staddon 2004). Similarly, $\delta^{15}N$ of these pools offers a gauge of the balance between inputs and exports of N to and from the system (Peterson and Fry 1987; Cook 2001). Such measurements may be especially informative in grasslands of the southern Great Plains, where the balance between C_3 and C_4 grasses is more mixed than in other North American grasslands.

This study examines effects of fire and clipping on soil C and N storage and dynamics in a mixed-grass prairie of the southern Great Plains. The study site is climatically distinct relative to tallgrass prairie and shortgrass steppe sites where more intensive research has been carried out on the relative influences of climate and disturbance on plant-soil nutrient dynamics (Burke et al. 1998). In such a system, spring fire might be anticipated to favor a shift in aboveground community composition, in favor of C_4 perennial grasses, as well as an increase in the C:N ratio of live tissue of individual plants. Thus, we hypothesized that spring fire would increase soil C pools and decrease soil inorganic and total N, with increases in C:N ratios of litter, SOM, and SOC reflecting the volatilization losses of N from aboveground biomass. The hypothesized effect of clipping was a moderation of fire effects via reduced fuel loads and thus fire intensity.

METHODS

Study site

Research was conducted on a 1 ha grazing exclosure on the W.T. Waggoner Ranch in Wilbarger County, Texas (33° 51'N, 99° 26' W, elevation 381 m). Mean annual precipitation for the site is 665 mm, bimodally distributed, with peaks in May (18% of annual total) and September (12% of annual total). Mean annual temperature is 16.1° C, with monthly average extremes ranging from 36° C in July to -2.5° C in January. Soils are classified as fine, mixed, thermic Typic Paleustolls of the Tillman series.

Dominant cool season (C_3) grasses include Texas wintergrass (*Nasella leucotricha* (Trin & Rupr) Pohl), a native perennial bunchgrass, and Japanese brome (*Bromus japonicus* Thunb. ex Murr.), an exotic annual grass. Dominant warm season (C_4) grasses include the perennial bunchgrass sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), and the stoloniferous, sod-forming buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.). The study site was root-plowed and seeded with sideoats grama in 1974. It has not been burned since that time. The site was grazed by cattle at a moderate stocking rate (1 cow 12 ha^{-1}) from the late 1800s to 1988, when livestock were removed.

Experimental design

Vegetation and nutrient dynamics were evaluated on experimental plots in a 2 x 3 factorial design (fire x clipping). Treatments were randomly assigned to thirty, 6x6-m plots (n = 5 replicates/treatment combination). The following treatments were implemented annually beginning in 1999: 1) control (no fire, no clipping), 2) continuous clipping, 3) spring clipping, 4) spring fire, 5) spring fire + spring clipping, and 6) spring fire + continuous clipping. Plots in the spring clipping treatment were mown to 5 cm height once per year in late April, and those in the continuous clipping treatment were mown monthly (except during drought). Clipped plant material was transported offsite. Plots in the fire treatment were subjected to prescribed fires in March 1999, 2000, and 2002, and February 2001. Fire plots were treated using a ring-fire prescribed burn technique (Pyne et al. 1996). Intensity was classified as low to moderate for all fires, with flame height not exceeding 1.5 m in any fire. Rainfall was measured at the site.

Sampling and analysis

Sampling was carried out at approximately monthly intervals. Vegetation and soils were sampled from June 2000 through May 2002, while litter was sampled from July 2001 through May 2002. During each sampling period, a 1x1 m subplot was randomly chosen from each of the 30 6x6 m treatment plots. Since sampling was destructive, no subplots were resampled. The following sampling procedures were performed on each 1x1 m subplot.

Surface litter, defined as all detached plant material above mineral soil, was collected from a square 0.125 m^2 quadrat at the center of each subplot, dried for 5 d at 60 °C, and weighed.

A composite soil sample consisting of 8, 2.5-cm diameter cores sampled 10 cm deep was taken from each subplot. Sampling to this depth has been estimated to account for

70 % of root biomass and 40 % of SOM (Gill et al. 1999), as well as the greatest amount of available N in the profile (Dodd et al. 2000); it is also the depth increment most likely to experience changes in soil C and N storage in response to land management practices (Conant et al. 2001). Soil samples were immediately placed on ice for transport to the laboratory and subsequently stored at 4 °C until analysis. Samples within each treatment replicate were pooled, mixed thoroughly, passed through a 2-mm screen to remove large organic fragments, and pulverized prior to laboratory analysis.

For the June and September 2001 sampling dates, a 30 g, field moist soil subsample from each replicate was brought to 50 % water holding capacity, and incubated in a sealed 1 L jar containing a vial with 10 ml of 1.0 M NaOH to trap respired CO_2. Soils were incubated at 26 °C for 180 d. The NaOH trap was removed and replaced at 1, 3, 5, 7, 10, 17, 24, 38, 59, 88, 128, and 181 d. At each time point, the NaOH was titrated with 0.25 M HCl to determine the amount of CO_2 evolved during each interval (Robertson et al. 1999).

Also for the June and September 2001 sampling dates, a 130 g, field moist subsample from each replicate was removed for density fractionation of soil organic matter according to the methods outlined in (Hassink 1995) and (Meijboom et al. 1995). The density fractionation procedure used a stable silica suspension (Ludox™-TM 50, Rhizosphere Research Products, Wageningen, The Netherlands), with density ranges of $d < 1.13$ g/ml ("light" fraction), 1.13 g/ml $< d <$ 1.37 g/ml ("medium" fraction), and $d >$ 1.37 g/ml ("heavy" fraction).

Plant leaf tissue (June 2000), bulk soil (June 2000, May 2002), soil density fractions (June and September 2001), and litter (July 2001 – May 2002) were analyzed for concentration and isotopic composition of C and N. Samples were dried for 5 d at 60 °C, then ground to pass a 0.5-mm screen. Elemental and isotopic analyses were performed using a Carlo-Erba EA-1108 elemental analyzer (CE Elantech, Lakewood, NJ) interfaced with an isotope ratio mass spectrometer (Delta Plus, ThermoFinnigan, San Jose, CA). Plant leaf tissue samples were from individuals of *B. curtipendula* and *N. leucotricha* in June 2000. Soil samples were subsamples from June 2000 and May 2002. Density fractions were from June and September 2001. Litter samples were from all sampling dates from May 2001 through May 2002. Isotopic composition of C and N was expressed according to the following formulae:

$\delta^{13}C, \delta^{15}N = 1000$ _ $([R_{sample} - R_{standard}] - 1)$

where R is the abundance ratio (13C/12C and 15N/14N, respectively). The standard employed for $\delta^{13}C$ was "Vienna"-PeeDee belemnite; that for $\delta^{15}N$ is atmospheric dinitrogen (Dawson et al. 2002). The precision of these analyses is ± 0.5 for C concentration, ± 0.02 for N concentration, and ± 0.2 for $\delta^{13}C$ and $\delta^{15}N$.

Data analysis

Data were analyzed using SAS Version 9.0 (SAS Institute 2002). Each monthly response variable (litter C and N concentration; soil NO_3^-, NH_4^+, and total N concentration) was separately analyzed using a three-way ANOVA with sampling date, fire, and clipping as factors. Plant leaf tissue C and N concentrations were analyzed using a three-way ANOVA with species, fire, and clipping as factors. C and N concentrations of soil, and mass of SOM density fractions, were analyzed using a three-way ANOVA with sampling date, clipping, and fire as factors. C and N concentrations of SOM density fractions were analyzed using a four-way ANOVA with sampling date, fraction, fire, and clipping as factors. For all variables where treatment effects and treatment-by-sampling date interactions were significant, the analysis was also carried out within each sampling date, excluding sampling date as a factor.

Potential C mineralization data were used to estimate sizes and mean residence times of 'active' and 'passive' SOC pools via fitting to a four-parameter exponential decay model, of the form $y = a^{-bx} + c^{-dx}$, in SigmaPlot (Inc. 1997). In this expression, commonly used to model dynamics of soil organic C, a and c represent the sizes of the active and slow pools, respectively, while b and d represent the respective partial rate constants for those pools. Mean residence time (MRT) is calculated for each pool by taking the reciprocal of the associated rate constant (Robertson et al. 1999).

RESULTS

Plant leaf tissue

There were no significant treatment effects on % C, % N, C:N ratio, δ^{13}C, or δ^{15}N of plant leaf tissue collected in June 2000 (Table 13). *N. leucotricha* had significantly higher mean C:N ratio (40.2 vs. 32.7, F = 9.30, $p = 0.0093$), and more negative mean δ^{13}C (-27.15 vs. –15.00 ‰, F = 1646.66, $p = < 0.0001$) than *B. curtipendula*. The former difference is likely due to differing stages of phenological development between the two species, which possess different photosynthetic pathways, at the time of sampling. The latter occurs as a result of differing C isotope discrimination by the C_3 and C_4 photosynthetic pathways.

TABLE 13. ANOVA results for the effects of fire and clipping on plant tissue concentrations and isotopic ratios of C and N, once species effects are considered.

	Fire	Clipping	Fire x clipping	Fire x species	Clipping x species
Response	*P*	*P*	*P*	*P*	*P*
% C	0.8874	0.2552	0.8072	0.9902	0.5372
% N	0.0970	0.9168	0.9588	0.5918	0.1586
C:N ratio	0.0510	0.8739	0.7382	0.9238	0.1429
δ^{13}C	0.1267	0.2948	0.0405	0.2146	0.1572
δ^{15}N	0.3114	0.7902	0.7452	0.3687	0.7290

TABLE 14. ANOVA results for the effects of fire and clipping on concentration and isotopic ratios of litter C and N, once sampling date effects are considered.

	Fire	Clipping	Fire x clipping	Fire x date	Clipping x date
Response	*P*	*P*	*P*	*P*	*P*
% C	< 0.0001	0.4044	0.5101	0.0587	0.4693
% N	0.0310	0.7067	0.6100	0.0044	0.5841
C:N ratio	0.0019	0.8299	0.6044	0.0152	0.7526
δ^{13}C	0.0010	0.4607	0.1439	0.0457	0.8062
δ^{15}N	0.0235	0.9481	0.9008	0.0055	0.7338

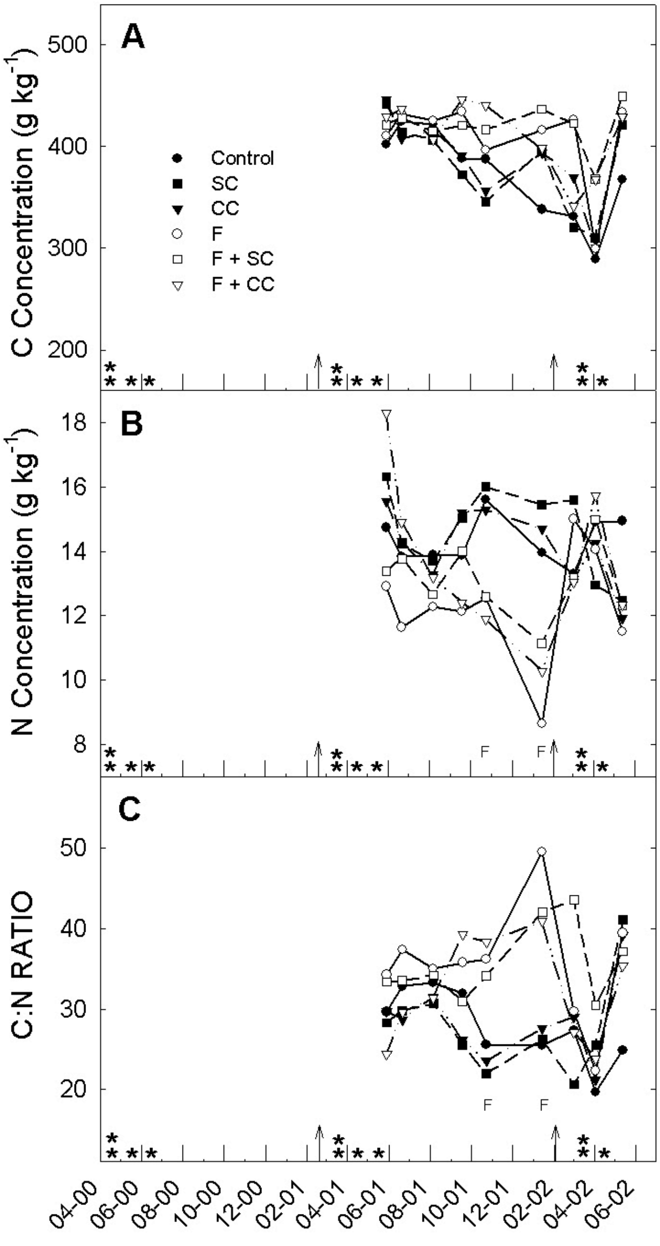

Figure 12. C and N concentrations and C:N ratio of surface litter, May 2001-May 2002. Values are means of five replicates. Significant ($p \leq 0.05$) treatment effects within individual sampling dates are indicated by C (clipping), F (fire), and C/F (fire x clipping interaction) along the x-axis. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis. Treatments are control (no fire, no clipping), SC (spring clipping), CC (continuous clipping), F (fire only), F + SC (fire and spring clipping), and F + CC (fire and continuous clipping).

TABLE 15. Elemental (C,N) and isotopic ($\delta^{13}C$, $\delta^{15}N$) composition of surface litter. Values are means of five replicates ± 1 SE.

A) Litter C (g kg^{-1})

	No clipping	Spring clipping	Continuous clipping
No fire[b]	37.2 ± 0.8	38.1 ± 0.8	39.0 ± 0.8
Spring fire[a]	40.9 ± 0.8	42.0 ± 0.8	41.1 ± 0.8

B) Litter N (g kg^{-1})

	No clipping	Spring clipping	Continuous clipping
No fire[a]	1.44 ± 0.07	1.46 ± 0.07	1.42 ± 0.07
Spring fire[b]	1.23 ± 0.08	1.31 ± 0.07	1.36 ± 0.07

C) Litter C:N ratio

	No clipping	Spring clipping	Continuous clipping
No fire[b]	27.7 ± 2.3	27.8 ± 2.3	28.5 ± 2.3
Fire[a]	35.7 ± 2.3	35.4 ± 2.3	32.3 ± 2.3

D) Litter $\delta^{13}C$ (‰)

	No clipping	Spring clipping	Continuous clipping
No fire[a]	-24.04 ± 0.72	-23.05 ± 0.70	-24.53 ± 0.70
Spring fire[b]	-26.98 ± 0.72	-26.14 ± 0.70	-25.02 ± 0.72

E) Litter $\delta^{15}N$ (‰)

	No clipping	Spring clipping	Continuous clipping
No fire[b]	0.71 ± 0.46	0.88 ± 0.44	0.83 ± 0.44
Spring fire[a]	1.71 ± 0.46	1.53 ± 0.44	1.84 ± 0.46

Note: Different superscript lowercase letters within treatment headings indicate significantly different means ($P < 0.05$).

Litter

Both sampling date and fire treatment significantly affected the C and N concentration, as well as the C:N ratio, of surface litter. For litter N concentration and C:N ratio, sampling date and fire effects also interacted significantly (Table 14). This interaction was due to a sharp decline in litter N, and a corresponding rise in C:N ratio, in fire treatments during October 2001 and January 2002, which did not occur in unburned treatments (Figure 12). Fire increased C concentration, decreased N concentration, and increased C:N ratios of litter relative to those in unburned treatments (Table 15). No significant effects of clipping were observed on litter C and N content.

Isotopic ratios of litter C and N displayed different responses than the concentrations of these elements, however. Fire significantly decreased litter δ^{13}C, with a significant interaction effect present between fire and sampling date (Figure 13; Table 14). Fire was also the only factor that significantly affected litter δ^{15}N, causing an increase relative to no fire treatments (Table 15). Fire also interacted significantly with sampling date in its effect on litter δ^{15}N (Table 14).

Bulk soil

Concentrations of soil organic C (1.94 ± 0.11 vs 1.41 ± 0.11 %, $p < 0.0001$) and total N (0.18 ± 0.01 vs 0.14 ± 0.01, $p =$ < 0.0001), C:N ratio (10.9 ± 0.2 vs 9.8 ± 0.2, $p < 0.0001$), and _^{15}N values (5.66 ± 0.19 vs 5.97 ± 0.19 ‰, $p = 0.0200$) were all significantly lower in May 2002 than in June 2000. Neither fire nor clipping significantly affected overall mean concentrations of soil organic C, total N, C:N ratios, or _^{13}C and _^{15}N values in bulk soils sampled at those times (Tables 16,17).

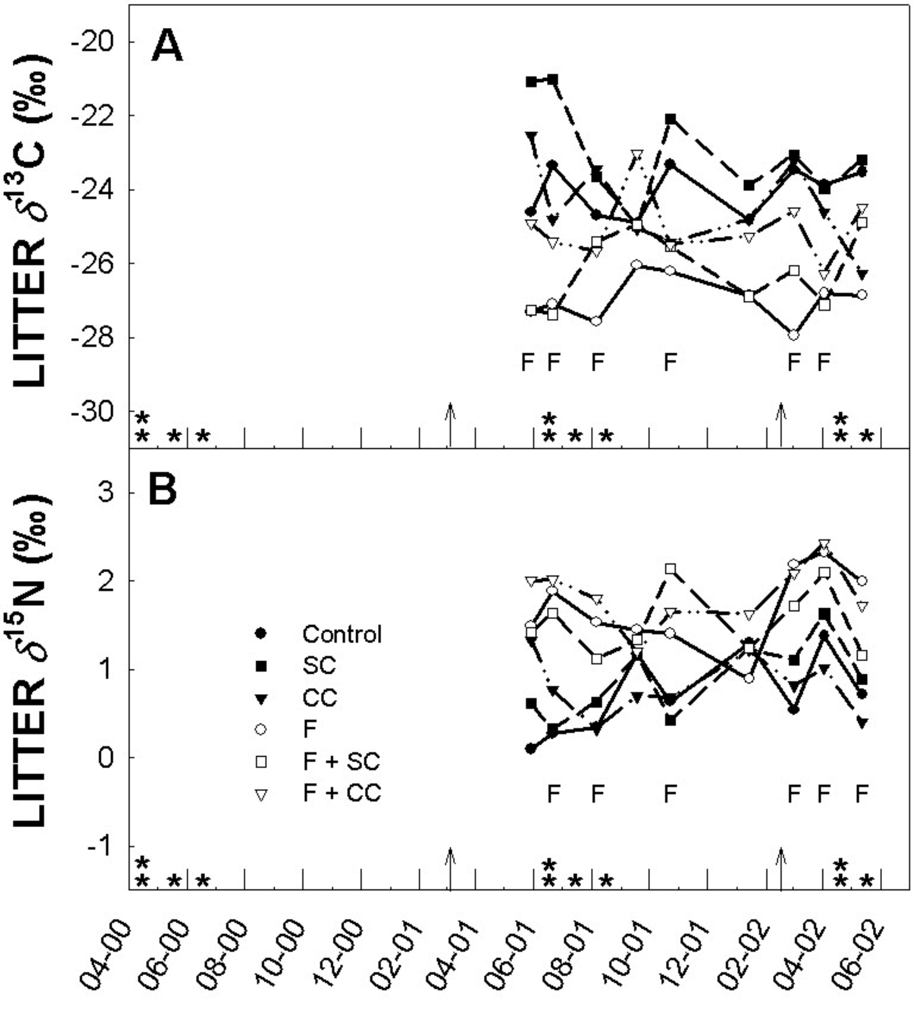

Figure 13. δ^{13}C vs. V-PDB and δ^{15}N vs. AIR of surface litter, May 2001-May 2002. Values are means of 5 replicates. Significant ($p \leq 0.05$) treatment effects within individual sampling dates are indicated by C (clipping), F (fire), and C/F (fire x clipping interaction) along the x-axis. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis.

TABLE 16. ANOVA results for the effects of fire and clipping on concentration and isotopic ratios of bulk soil C and N, once sampling date effects are considered.

Response	Fire	Clipping	Fire x clipping	Fire x date	Clipping x date
	P	*P*	*P*	*P*	*P*
% C	0.7826	0.0884	0.9970	0.2559	0.0269
% N	0.6902	0.0799	0.9844	0.0996	0.0519
C:N ratio	0.6010	0.5796	0.8663	0.4448	0.0375
δ^{13}C	0.3241	0.2850	0.0821	0.1646	0.1592
δ^{15}N	0.3450	0.5196	0.9528	0.9632	0.4005

TABLE 17. Elemental (C,N) and isotopic ($\delta^{13}C$, $\delta^{15}N$) composition of bulk soil. Values are means of five replicates ± 1 SE.

A) Soil C (%)

	No clipping	Spring clipping	Continuous clipping
No fire	1.87 ± 0.19	1.64 ± 0.19	1.45 ± 0.19
Spring fire	1.93 ± 0.19	1.67 ± 0.19	1.48 ± 0.19

B) Soil N (%)

	No clipping	Spring clipping	Continuous clipping
No fire	0.17 ± 0.01	0.16 ± 0.01	0.14 ± 0.01
Spring fire	0.18 ± 0.02	0.16 ± 0.02	0.14 ± 0.01

C) Soil C:N ratio

	No clipping	Spring clipping	Continuous clipping
No fire	10.6 ± 0.3	10.5 ± 0.3	10.2 ± 0.3
Fire	10.4 ± 0.3	10.2 ± 0.3	10.2 ± 0.3

D) Soil $\delta^{13}C$ (‰)

	No clipping	Spring clipping	Continuous clipping
No fire	-20.50 ± 0.72	-20.71 ± 0.72	-21.03 ± 0.72
Spring fire	-22.52 ± 0.72	-21.77 ± 0.72	-19.73 ± 0.72

E) Soil $\delta^{15}N$ (‰)

	No clipping	Spring clipping	Continuous clipping
No fire	5.47 ± 0.33	5.71 ± 0.33	5.88 ± 0.33
Spring fire	5.73 ± 0.33	6.07 ± 0.33	6.04 ± 0.33

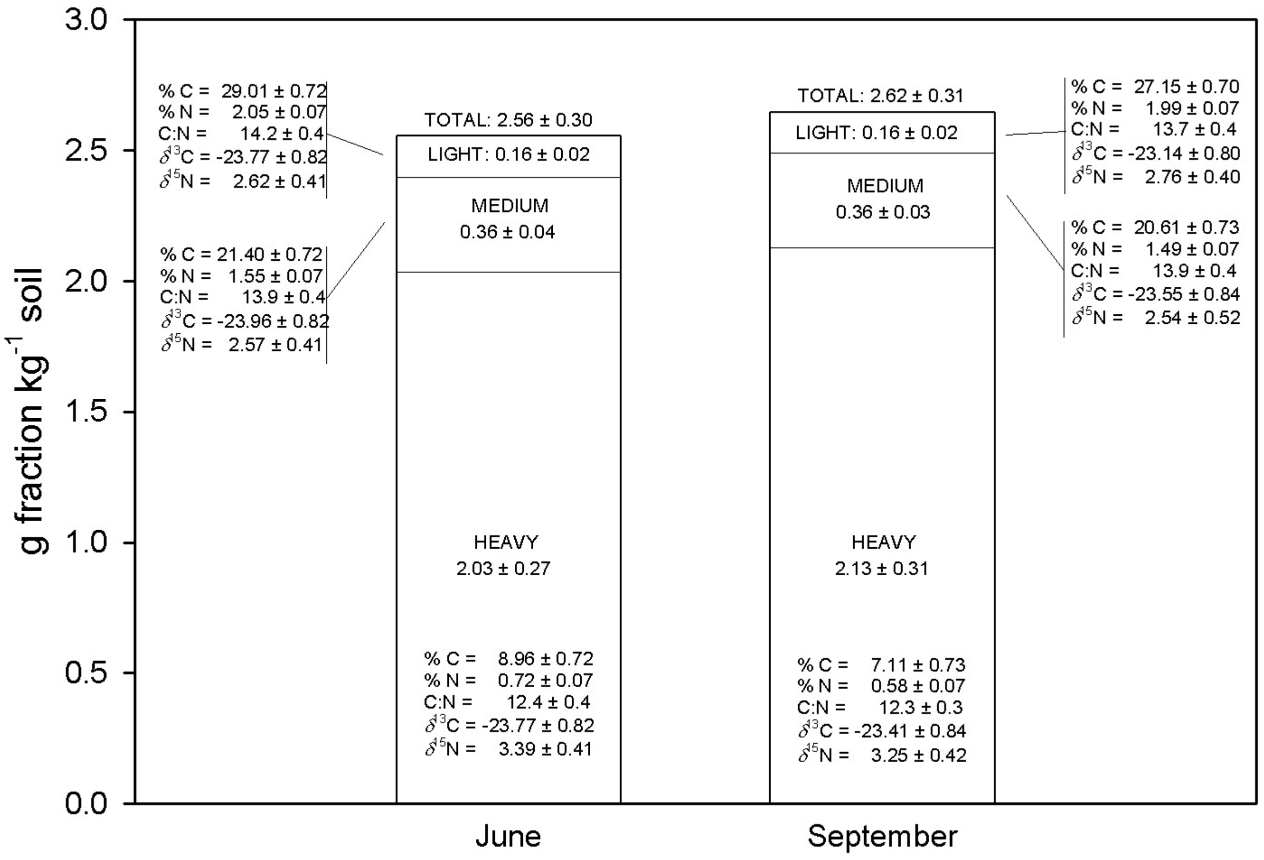

Figure 14. Concentration of soil density fractions, June and September 2001. Shown for each fraction are concentration and isotopic ratios of C and N, and C:N ratio. Values are pooled means of pooled data from all treatments (30 replicates) ± 1 SE.

Soil density fractions

Fire significantly (p = 0.0043) reduced the concentration of the light soil density fraction (0.127 ± 0.014 g fraction kg^{-1} soil) relative to that in no fire treatments (0.187 ± 0.014 g fraction kg^{-1} soil). There was no effect of clipping on concentration of soil density fractions. The total concentration of soil density fractions, or that of each individual fraction, did not vary significantly between sampling dates in June and September 2001 (Figure 14).

The concentration of C and N, and C:N ratio, varied significantly (p < 0.0001) between different soil density fractions. All three variables declined in the order light > medium > heavy (Figure 14). However, across fractions, C (p = 0.0006) and N (p = 0.0084) concentrations also varied significantly between June and September 2001. In June, C concentration of soil density fractions was 19.79 ± 0.42 %, while that of N was 1.44 ± 0.04 %. In September, C and N concentrations of soil density fractions were 18.29 ± 0.42 % and 1.35 ± 0.04 %, respectively. However, these decreases were proportional, so that there was no significant effect of sampling date on the C:N ratio of soil density fractions, either overall or within individual fractions. Neither fire nor clipping significantly affected C or N content of soil density fractions.

In contrast to the results for mass and elemental concentration of soil density fractions, sampling date had no effect on _^{13}C and _^{15}N values. The _^{13}C of soil density fractions did not vary significantly between fractions, nor was it affected by fire or clipping. However, δ^{15}N did vary significantly (p = <0.0001) between fractions (Figure 14).

Concentration of C in the light soil density fraction (Figure 15A) was significantly greater (*p* = 0.0059) in June (291 ± 5 g C kg fraction^{-1}) than September (272 ± 5 g C kg fraction^{-1}). C concentration in medium and heavy soil density fractions was not significantly affected by treatment or sampling date. However, the concentration of light-fraction C in bulk soil (Figure 15B) was significantly lower (*p* = 0.0036) in fire treatments (0.035 ± 0.004 g C in fraction kg soil^{-1}) than in no fire treatments (0.054 ± 0.004 g C in fraction kg soil^{-1}). With density fraction C expressed on a per-area basis (Figure 15C), the same pattern was observed, with light-fraction C significantly lower (*p* = 0.0018) in fire treatments (4.2 ± 0.6 g C in fraction m^{-2}) than in no fire treatments (6.9 ± 0.5 g C in fraction m^{-2}).

Concentration of N (Figure 15D) was not significantly affected by treatment or sampling date in any soil density fraction. The concentration of light-fraction N in bulk soil (Figure 15E), however, was significantly lower (*p* = 0.0042) in fire treatments (0.0025 ± 0.0003 g N in fraction kg soil^{-1}) than in no fire treatments (0.0038 ± 0.0003 g N in fraction kg soil^{-1}). The mass of light-fraction N per unit area (Figure 15F) was also significantly lower (*p* = 0.0018) in fire treatments (0.30 ± 0.04 g N in fraction m^{-2}) than in no fire treatments (0.49 ± 0.04 g N in fraction m^{-2}).

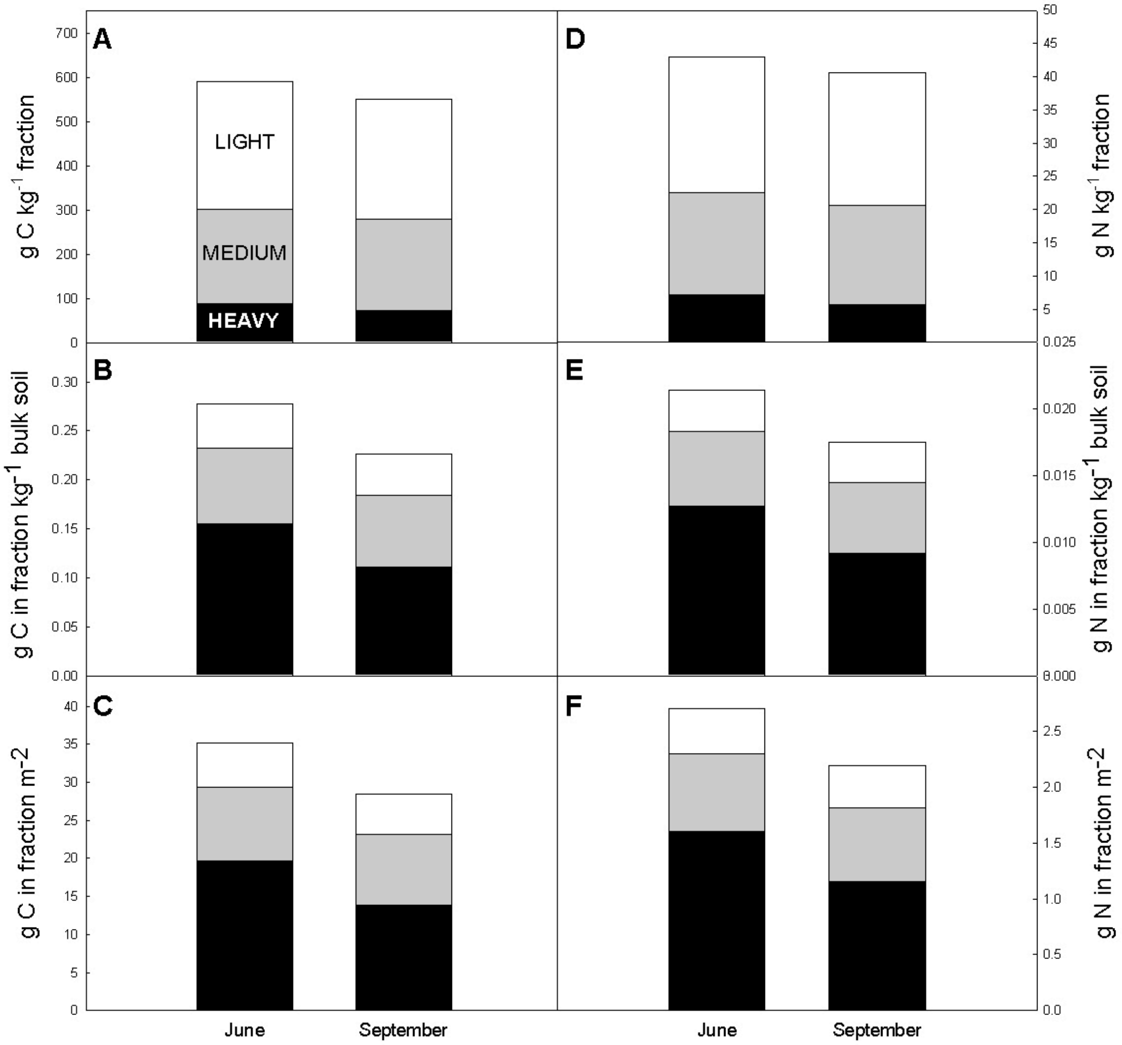

Figure 15. Organic carbon and total nitrogen in soil density fractions, June and September 2001. Values are expressed as concentration of fraction (A: carbon, D: nitrogen), content of fraction in bulk soil (B: carbon, E: nitrogen), and C density of each fraction (C: carbon, F: nitrogen). Values are pooled means of pooled data from all treatments (30 replicates) ± 1 SE.

TABLE 18. ANOVA results for the effects of fire and clipping on pool sizes, rate constants, and mean residence times of active and slow C pools, once sampling date effects are considered.

	Fire	Clipping	Fire x clipping	Fire x date	Clipping x date
Response	*P*	*P*	*P*	*P*	*P*
Active pool	0.5597	0.5153	0.9306	0.7241	0.6830
Active k	0.1632	0.2423	0.4077	0.3554	0.8074
Active MRT	0.2759	0.2855	0.7263	0.8644	0.4914
Slow pool	0.6086	0.1102	0.9203	0.5605	0.7387
Slow k	0.2450	0.2399	0.7462	0.7789	0.5130
Slow MRT	0.2871	0.6808	0.7999	0.3633	0.3975

Potential C mineralization

Neither fire nor clipping significantly affected the estimated size, rate constant, or mean residence time (MRT) of the active C pool (Table 18; Figure 16). The light soil density fraction was about one-third the estimated size of the active pool, while the light and medium density fractions together were approximately equal to that pool (Table 19).

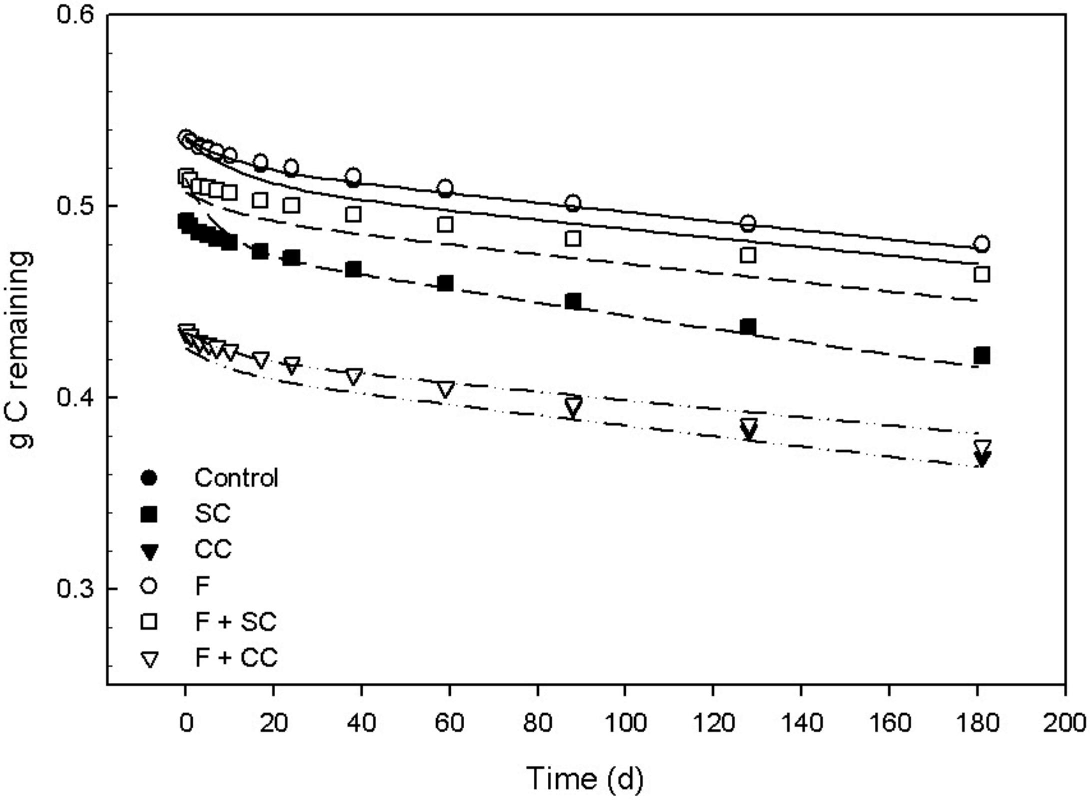

Figure 16. Potential C mineralization during a 180 d incubation. Values are means of five replicates (pooled samples from June and September 2001). Treatments are control (no fire, no clipping), SC (spring clipping), CC (continuous clipping), F (fire only), F + SC (fire and spring clipping), and F + CC (fire and continuous clipping).

TABLE 19. Pool sizes, rate constants, and mean residence times of active and slow C pools as determined by 180 d laboratory incubation. Values are means ± 1 SE.

A) Active pool (g C kg^{-1} soil)

	No clipping	Spring clipping	Continuous clipping
No fire	0.47 ± 0.05	0.39 ± 0.05	0.43 ± 0.05
Spring fire	0.43 ± 0.06	0.39 ± 0.05	0.40 ± 0.05

B) Active k

	No clipping	Spring clipping	Continuous clipping
No fire	0.089 ± 0.020	0.153 ± 0.024	0.104 ± 0.020
Spring fire	0.080 ± 0.025	0.093 ± 0.020	0.097 ± 0.020

C) Active MRT (d)

	No clipping	Spring clipping	Continuous clipping
No fire	14.6 ± 2.6	9.9 ± 3.0	14.4 ± 2.6
Fire	18.3 ± 3.2	13.8 ± 2.6	14.5 ± 2.6

D) Slow pool (g C kg^{-1} soil)

	No clipping	Spring clipping	Continuous clipping
No fire	17.37 ± 1.73	15.98 ± 1.99	14.00 ± 1.73
Spring fire	19.06 ± 2.11	16.30 ± 1.72	14.37 ± 1.73

E) Slow k

	No clipping	Spring clipping	Continuous clipping
No fire	0.0005 ± 0.0001	0.0007 ± 0.0001	0.0007 ± 0.0001
Spring fire	0.0005 ± 0.0001	0.0005 ± 0.0001	0.0006 ± 0.0001

F) Slow MRT (y)

	No clipping	Spring clipping	Continuous clipping
No fire	6.1 ± 1.3	4.8 ± 1.5	4.0 ± 1.3
Spring fire	6.4 ± 1.6	6.2 ± 1.3	6.1 ± 1.3

DISCUSSION

The effects of fire and clipping in this study appear strongly contingent on climatic variation, and vary in accord climatic variation's interactions with plant phenology and with the nature and timing of disturbance. The effects of disturbance on the balance of existing pools versus current inputs of litter appear to be of particular importance for plant and soil C and N pools.

Two years after the initiation of experimental treatments, aboveground live plant tissue showed no changes in concentration or isotopic composition of C or N. This is not consistent with the hypothesis that fire causes intraspecific alterations of tissue chemistry, suggesting instead that the effects of fire and clipping on plant-soil nutrient dynamics in this ecosystem stem instead from shifts in species composition (Van de Vijver et al. 1999; de Mazancourt and Loreau 2000a). The two species analyzed were at different phenological stages at the time of sampling, precluding a direct comparison of tissue chemistry between species. However, the lack of treatment effects on plant tissue nutrient concentrations at two different stages of seasonal plant growth suggests that those effects may have been minor throughout the growth period. Although Hamilton and Frank (2001) found higher shoot concentrations of N in clipped plants in pot experiments, similar results from field-scale studies have also been more variable (Coughenour 1991). In other work, decreases in N concentration of aboveground plant tissue N have resulted from reallocation to roots (Chaneton et al. 1996), and increases have been attributed to distribution of a similar amount of N over lower total live biomass (Van de Vijver et al. 1999).

Indirect support for the hypothesis of altered nutrient-cycling regimes via shifts in the contributions of plant functional types to total system productivity is found in the response of litter C and N content and isotopic ratios to fire and clipping treatments. Given the lack of response of live plant tissue chemistry to treatments, significant increases in litter C content and C:N ratio, and decreases in N content, at first seem paradoxical. However, fire removed the bulk of existing litter (see Chapter II), which consisted of a mixed-age pool in various stages of decomposition with progressively lower C:N ratios. Thus, in fire treatments, only undecomposed inputs from the current season's production, with higher C:N ratios, entered the litter pool (Fynn et al. 2003). The fire-by-date interactions seen in litter N and C:N responses are due to seasonal effects stemming from the same process. Inputs to bare ground in a single season are small relative to the pool removed by fire, and what little N they contain is quickly removed by decomposers and/or leaching. Since clipping reduced current litter inputs, but not the standing litter pool, this rationale also accounts for its lack of effect on litter C and N content.

Litter C and N isotopic ratios, reflecting an integrated signal of inputs of different plant functional types to the current litter pool, presented a different response pattern stemming from the same mechanisms. Although neither fire nor clipping altered isotopic ratios within plant species, both shifted the relative production of different species and functional types in a given season. As noted, the magnitude of such shifts in the response of the total nutrient content of the surface litter pool to clipping was small; however, the isotopic ratio is a more sensitive indicator, and thus reflects these relatively small changes in inputs. This pattern is reflected by the correspondence between the greater magnitude of litter removal under fire than clipping on the one hand, and the significant effect of fire, but not clipping, on litter C and N isotopic ratios on the other. The increased δ^{15}N of litter in response to fire was consistent with the hypothesis of more "open" N cycling as a consequence of fire's volatilization of aboveground N (Austin and Vitousek 1998), and also with the posited mechanism of large reductions in the standing litter pool.

Given the pronounced effects of fire on the tissue chemistry of litter, the lack of treatment effects on bulk soil organic C and total N is somewhat puzzling. Nonsignificant decreases in SOC and total N were observed in response to both fire and spring clipping. In contrast to the present finding, Hamilton and Frank (2001) found that clipping increased SOC in greenhouse experiments. This result was attributed to increased release of root exudates from defoliated plants, a pattern unlikely to occur in the C_3 annual grasses most heavily impacted by this study's clipping treatments (see Chapter II). In northern short and mixed-grass prairie ecosystems, SOC and N in the upper profile were higher in long-term grazing treatments than in ungrazed controls (Manley et al. 1995; Derner et al. 1997; Schuman et al. 1999a; Schuman et al. 1999b; Reeder and Schuman 2002; Schuman et al. 2002; Derner et al. in preparation). However, other studies in these regions have reported no change following grazing (Frank et al. 1995; Augustine and Frank 2001). In midgrass and tallgrass prairie ecosystems, reductions in SOC and total N in response to grazing have been reported (Derner et al. 1997; Derner et al., unpublished manuscript). The lack of treatment-caused shifts in isotopic composition of SOC and total N in this study reflect the large sizes of those pools relative to the flows altered by experimental manipulations.

Fire's reduction of light-fraction SOM is likely a consequence of its removal of the accumulated surface litter pool. The lack of similar clipping effects is attributable to the fact that the current-season litter inputs intercepted by clipping are smaller than the accumulated surface pool (Chapter II). Taken together, these results suggest that the light fraction isolated by the methodology used in this study corresponds well to the portion of the litter pool that occupies a transitional point between surface litter and soil organic matter. That fraction is susceptible to loss via combustion, but is not affected by interception of current-season inputs by clipping. Heavier SOM fractions were unaffected by fire or clipping. However, other sources of C than litter may be important components of the total soil C pool. Little information on root biomass, or its response to fire and clipping, is available for this system. However, seasonal peaks in root production do correspond to maxima in aboveground live biomass of C_3 annual grasses and soil C efflux (Hubbard 2003; see Chapter VI). This suggests that root dynamics of C_3 annual grasses, and the large influence of clipping on those plants, may have a substantial influence on soil C stocks in the study system. Epstein et al. (2002) assumed root:shoot ratios of approximately 1:1 across the full extent of Great Plains grasslands, though values as high as 7:1 have been reported for other grassland ecosystems (Distel and Fernandez 1986).

The light SOM density fraction isolated in this research was smaller than the estimated active pool of SOC, while the medium fraction was similar in size. Assuming that all C mineralized in laboratory incubations derived from these sources, the active pool would correspond to the total SOM with a density less than or equal to 1.25 g cm^{-3}. Though fire reduced the amount of light-fraction SOM, no treatment effects were observed on rates of C mineralization during laboratory incubations. Rate differences in those incubations occurred, instead, only between samples from different sampling dates (June and September 2001). These differences were observed only during the first 3 days of incubation, suggesting, along with the observation of significant treatment effects in the light fraction only, that labile SOM is the more responsive pool (Frank and Groffman 1998). Higher potential C mineralization rates in June are intuitively compatible with the large amounts of C_3 annual grass-derived litter entering litter/SOM pools at that time. Seasonal shifts in the makeup of the microbial decomposer community might also account for the observed rate differences in potential C mineralization between sampling dates, but further work is necessary to evaluate this hypothesis and further elucidate the portions of the SOM pool responsible for the observed activity. Responses of soil C and N pools depend on alterations in biomass turnover both below- and aboveground, with the potential for different patterns between plant functional groups and species (Sun et al. 1997; Johnson and Biondini 2001; Levang-Brilz and Biondini 2003).

Overall, these results highlight the importance of idiosyncracies in the responses of individual plant species or functional types to disturbance at different stages in the respective phenologies. Even a single clipping event was sufficient to reduce both current-season inputs and subsequent abundance of C_3 annual grasses. Those inputs were likely high to due above-normal winter precipitation during the study. Fire, occurring earlier than clipping in the phenological stages of this C_3 grass, had less pronounced effects on its development. The lack of summer rainfall may have minimized fire and clipping treatment impacts related to the dynamics of the C_4 grasses which typically increase in response to burning at that time. Continued monitoring during years of more normal rainfall amounts and distribution would help clarify these relationships. Additionally, concurrent assessments of the relative contributions of standing pools and current inputs of litter, as well as those of above- versus belowground biomass turnover, would enhance the understanding of the role of disturbance in plant-soil nutrient dynamics in this ecosystem.

CHAPTER V

SOIL CARBON AND NITROGEN RESPONSES TO SEASONAL FIRE IN A SOUTHERN MIXED GRASSLAND

INTRODUCTION

Fire as an agent of disturbance can affect C and N dynamics of grassland ecosystems. By impacting plant production, standing stocks of vegetation and surface litter, and community composition, fire alters flows of these nutrients between plant and soil compartments of the ecosystem (Woodmansee and Wallach 1981; Hobbie 1992; Wedin 1996). Variation in climatic factors as well as the pool of available plant species and functional types give rise to differing responses to fire both across and within individual ecosystems (McGill et al. 1986; Vinton and Burke 1995; Vinton and Burke 1997; Burke et al. 1998; Burke and Lauenroth 2002). The contrasted effects of fire in different seasons have received relatively little attention in efforts to comprehend these interactions, as both prescribed management burns and ecological studies of fire have focused primarily on fires early in the growing season (Howe 1994; Howe 1995; Howe 2000).

As a consequence of high interannual variability in precipitation coupled with grasses' low proportion of permanent structural tissue, grasslands have the highest variation of any biome in annual ANPP (Fuhlendorf et al. 2001; Knapp and Smith 2001). Within the regional context of the North American Great Plains, gradients in precipitation and temperature give rise to corresponding clines in ANPP (Burke et al. 1991; Burke et al. 1997; Epstein et al. 1997a; Paruelo et al. 1999; Lane et al. 2000), proportional biomass of C_3 and C_4 species (Paruelo and Lauenroth 1996; Epstein et al. 1997b; Tieszen et al. 1997; Epstein et al. 1998), plant tissue chemistry , soil microbial biomass (Wardle 1992; Zak et al. 1994), and decomposition and soil organic matter content (Post et al. 1982; Couteaux et al. 1995; Amelung et al. 1997; Derner et al. 1997; Amelung et al. 1998; Epstein et al. 2002; Derner et al. in preparation). Mean annual precipitation and temperature in the mixed-grass prairie of the southern Great Plains are distinct from those of the tallgrass prairie and shortgrass steppe sites where fire-mediated grassland plant-soil dynamics have been most intensively studied in North America (Burke and Lauenroth 2002).

In the southern Great Plains, the convergence of highly variable and strongly seasonal climatic patterns with the presence of a mixture of C_3 and C_4 grass species with differing phenological and physiological attributes creates the conditions for seasonality of a disturbance such as fire to play a key role in modulating biogeochemical cycles. However, few studies have incorporated season of fire as a discrete, replicated treatment (Engle and Bidwell 2001). Given that the historic fire regime in the southern great Plains consisted predominantly of more intense fires in drier and warmer periods of the year, this emphasis may overlook key elements of native plant species' adaptive responses to fire-induced disturbance (Howe 1994).

Plant responses to aboveground disturbance are tightly coupled to size and flux of soil C and N pools (Hobbie 1992). Certain conceptual models of these relationships in grassland ecosystems predict feedbacks in plant-soil nutrient dynamics (Wedin 1995; Wedin 1996; Tateno and Chapin 1997); others assign such feedbacks a more minor role relative to climatic factors (Burke et al. 1998) or microbial activity (Knops et al. 2002). Monitoring of seasonal shifts in the concentration and isotopic composition of C and N in plant materials at various stages of incorporation into the soil (e.g. surface litter, soil density fractions, bulk soil) provides a means of distinguishing which (or which combinations) of these models are applicable in a given study system. In particular, $\delta^{13}C$ of surface litter and soil organic matter density fractions serves as an index of the relative inputs from C_3 and C_4 plants (Staddon 2004). Similarly, $\delta^{15}N$ of these pools offers a gauge of the balance between inputs and exports of N to and from the system (Peterson and Fry 1987; Cook 2001).

This study compares the effects of spring (typical management fire) and fall (typical wildfire) fire on pools of C and N in plant, litter, soil organic matter, and bulk soil pools in a mixed grassland ecosystem of the southern Great Plains. If a positive-feedback model of nutrient dynamics is operative, an increased proportion of C_4 grasses following spring fire would result in higher concentrations of C, and lower concentrations of N, in all pools along the decompositional sequence. Since warm-season fires often produce a shift toward greater abundance of C_3 species (Whisenant et al. 1984b; Howe 2000; Ansley et al. unpublished manuscript), the opposite pattern of nutrient response would be anticipated. If climatic factors or microbial activity constrain the operation of positive feedbacks in plant-soil C and N cycles, fire-induced shifts in plant tissue chemistry would not be expected to be transferred into bulk soil and soil density fractions.

METHODS

Study site

Research was conducted on a 1 ha grazing exclosure on the W.T. Waggoner Ranch in Wilbarger County, Texas (33^{o} 51'N, 99^{o} 26' W, elevation 381 m). Mean annual precipitation for the site is 665 mm, bimodally distributed, with peaks in May (18% of annual total) and September (12% of annual total). Mean annual temperature is 16.1^{o} C, with monthly average extremes ranging from 36^{o} C in July to -2.5^{o} C in January. Soils are classified as fine, mixed, thermic Typic Paleustolls of the Tillman series.

Dominant cool-season (C_3) grasses include Texas wintergrass (*Nasella leucotricha* (Trin & Rupr) Pohl), a native perennial bunchgrass, and Japanese brome (*Bromus japonicus* Thunb. ex Murr.), an exotic annual grass. Dominant warm-season (C_4) grasses include the perennial bunchgrass sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), and the stoloniferous, sod-forming buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.). The study site was root-plowed and seeded with sideoats grama in 1974. It has not been burned since that time. The site was grazed by livestock from the late 1800s to 1988, when livestock were removed.

Experimental design

Vegetation and nutrient dynamics were evaluated on experimental treatment plots in a single-factor design. Treatments were randomly assigned to fifteen 6x6-m plots (n = 5 replicates/treatment combination/year). The following treatments were implemented annually beginning in 1999: 1) control (no fire), 2) spring fire, and 3) fall fire. Plots in the spring fire treatment (typical management fire) were subjected to prescribed fires in March 1999, 2000, and 2002, and February 2001, while those in the fall fire treatment (typical wildfire) were burned in September 1999, 2000, and 2002, and October 2001. Spring and fall fire plots were treated using a ring-fire prescribed burn technique (Pyne et al. 1996). Intensity was classified as low to moderate for all fires, with flame height not exceeding 1.5 m in any fire.

Sampling and analysis

Sampling was carried out at approximately monthly intervals. Vegetation and soils were sampled from June 2000 through May 2002, while litter was sampled from July 2001 through May 2002. During each sampling period, a 1x1 m subplot was randomly chosen from each of the 15 6x6 m treatment plots. Since sampling was destructive, no subplots were resampled. The following sampling procedures were performed on each 1x1 m subplot.

Surface litter, defined as all detached plant material above mineral soil, was collected from a square 0.125 m^2 quadrat at the center of each subplot, dried for 5 d at 60 °C, and weighed.

A composite soil sample consisting of 8, 2.5-cm diameter cores taken 10 cm deep was taken from each subplot. Sampling to this depth has been estimated to account for 70 % of root biomass and 40 % of SOM (Gill et al. 1999), as well as the greatest amount of available N in the profile (Dodd et al. 2000); it is also the depth increment most likely to experience changes in soil C and N storage in response to land management practices (Conant et al. 2001). Soil samples were immediately placed on ice for transport to the laboratory and subsequently stored at 4 °C until analysis. Samples within each treatment replicate were pooled, mixed thoroughly, passed through a 2-mm screen to remove large organic fragments, and pulverized prior to laboratory analysis.

For the June and September 2001 sampling dates, a 30 g, field moist soil subsample from each replicate was brought to 50 % water holding capacity, and incubated in a sealed 1 L jar containing a vial with 10 ml of 1.0 M NaOH to trap respired CO_2. Soils were incubated at 26 °C for 180 d. The NaOH trap was removed and replaced at 1, 3, 5, 7, 10, 17, 24, 38, 59, 88, 128, and 181 d. At each time point, the NaOH was titrated with 0.25 M HCl to determine the amount of CO_2 evolved during each interval (Robertson et al. 1999).

Also for the June and September 2001 sampling dates, a 130 g, field moist subsample from each experimental unit was removed for density fractionation of soil organic matter according to the procedure described in (Hassink 1995) and (Meijboom et al. 1995). The density fractionation procedure used a stable silica suspension (Ludox™-TM 50, Rhizosphere Research Products, Wageningen, The Netherlands), with density

(ρ) ranges of $\rho < 1.13$ g/ml ("light" fraction), 1.13 g/ml $< \rho < 1.37$ g/ml ("medium" fraction), and $\rho > 1.37$ g/ml ("heavy" fraction).

Plant leaf tissue, bulk soil, soil density fractions, and litter were analyzed for concentration and isotopic composition of C and N. Samples were dried for 5 d at 60 °C, then ground to pass a 0.5-mm screen. Elemental and isotopic analyses were performed using a Carlo-Erba EA-1108 elemental analyzer (CE Elantech, Lakewood, NJ) interfaced with an isotope ratio mass spectrometer (Delta Plus, ThermoFinnigan, San Jose, CA). Plant leaf tissue samples were from individuals of *B. curtipendula* and *N. leucotricha* in June 2000. Soil samples were subsamples from June 2000 and May 2002. Density fractions were from June and September 2001. Litter samples were from all sampling dates from May 2001 through May 2002. Isotopic composition of C and N was expressed according to the following formulae:

$$\delta^{13}C, \delta^{15}N = 1000 \_ ([R_{sample} - R_{standard}] - 1)$$

where R is the abundance ratio ($^{13}C/^{12}C$ and $^{15}N/^{14}N$, respectively). The standard employed for $\delta^{13}C$ was "Vienna"-PeeDee belemnite; that for $\delta^{15}N$ is atmospheric dinitrogen (Dawson et al. 2002). The precision of these analyses is ± 0.5 for C concentration, ± 0.02 for N concentration, and ± 0.2 for $\delta^{13}C$ and $\delta^{15}N$.

Data analysis

Data were analyzed using SAS Version 9.0 (SAS Institute 2002). Each monthly response variable (litter C and N concentrations and isotopic compositions) was separately analyzed using a two-way ANOVA with sampling date and fire as factors.

Plant leaf tissue C and N concentrations and isotopic compositions were analyzed using a two-way ANOVA with species and fire as factors. C and N concentrations and isotopic compositions of bulk soil, and mass of soil density fractions, were analyzed using a two-way ANOVA with sampling date and fire as factors. C and N concentrations and isotopic compositions of soil density fractions were analyzed using a three-way ANOVA with sampling date, fraction, and fire as factors. For all variables where treatment effects and treatment-by-sampling date interactions were significant, the analysis was also carried out within each sampling date, excluding sampling date as a factor. Significant differences between treatment effects were evaluated via pairwise comparisons of least squares means.

Potential C mineralization data were used to estimate sizes and mean residence times of ‘active’ and ‘passive’ SOC pools via fitting to a four-parameter exponential decay model, of the form $y = a^{-bx} + c^{-dx}$, in SigmaPlot (Inc. 1997). In this expression, commonly used to model dynamics of soil organic C, a and c represent the sizes of the active and slow pools, respectively, while b and d represent the respective partial rate constants for those pools. Mean residence time (MRT) is calculated for each pool by taking the reciprocal of the associated rate constant (Robertson et al. 1999).

RESULTS

Plant leaf tissue

There were no significant treatment effects on C and N concentrations, C:N ratio, or δ^{15}N of plant leaf tissue collected in June 2000 (Table 20). *N. leucotricha* had significantly more negative mean δ^{13}C (-27.16 ± 0.33 vs. –15.60 ± 0.36 ‰) than *B. curtipendula*, due to differing C isotope discrimination by the C_3 and C_4 photosynthetic pathways.

Litter

There were no significant effects of fire on C and N concentration, or C:N ratio of surface litter (Table 21; Figure 17). Fire in either season decreased litter δ^{13}C values, with the decline being significantly different from the no fire treatment in the case of spring fire only. Litter C concentration and δ^{13}C and δ^{15}N values varied significantly with sampling date (Table 21; Figure 18). C concentration declined markedly during late spring, and δ^{15}N values increased over the course of the study period, while δ^{13}C values displayed single annual peaks whose timing varied between fire treatments.

Fire also significantly affected C and N isotopic ratios of surface litter, but with different patterns than those observed for elemental concentrations. C isotopic values were lower (more negative) in both fire treatments relative to the no fire control, while N isotope ratios were significantly higher in spring fire than no fire treatments, with values in fall fire treatments being intermediate between, and not significantly different from, spring fire and no fire treatments (Table 22; Figure 18).

TABLE 20. ANOVA results for the effects of plant species and seasonal fire on plant tissue concentrations and isotopic ratios of C and N.

	Fire	Species	Fire x species
Response	*P*	*P*	*P*
% C	0.4438	0.4335	0.2247
% N	0.2512	0.9857	0.4692
C:N ratio	0.1260	0.8561	0.5710
δ^{13}C	0.8052	< 0.0001	0.3162
δ^{15}N	0.2470	0.7280	0.6933

TABLE 21. ANOVA results for the effects of fire season and sampling date on concentration and isotopic ratios of litter C and N.

	Fire	Date	Fire x date
Response	*P*	*P*	*P*
% C	0.1405	< 0.0001	0.0989
% N	0.1831	0.2779	0.8776
C:N ratio	0.2183	0.0986	0.1753
δ^{13}C (‰)	0.0461	0.5511	0.3468
δ^{15}N (‰)	0.3335	0.0003	0.0012

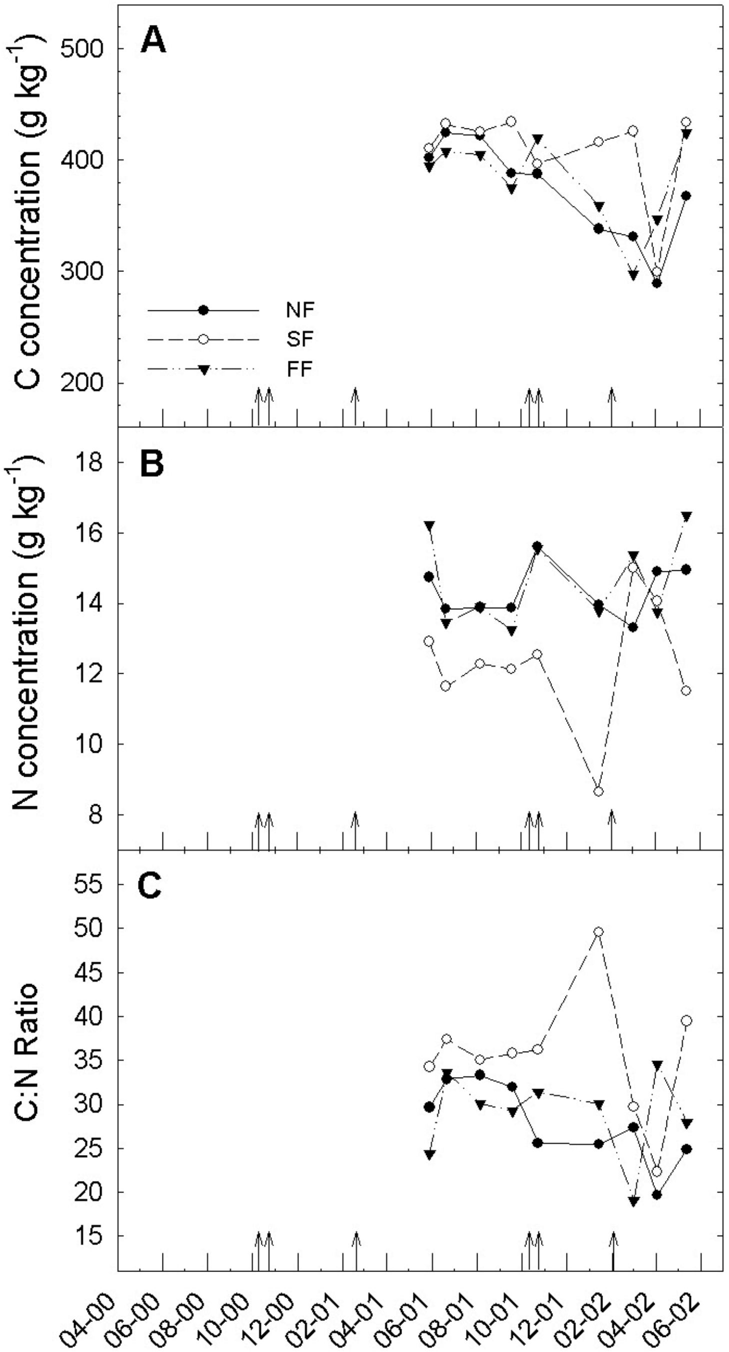

Figure 17. C and N concentrations and C:N ratio of surface litter, May 2001-May 2002. Values are means of five replicates ± 1 SE. Dates of spring (arrows) and fall (double arrows) fires are shown on the x-axis. Treatments are no fire (NF), spring fire (SF), and fall fire (FF).

TABLE 22. Concentrations and stable isotopic ratios (± 1 SE) of surface litter, May 2001 - May 2002.

	No fire	Spring fire	Fall fire
C (g kg^{-1})	372 ± 13	409 ± 13	381 ± 12
N (g kg^{-1})	14 ± 1	12 ± 1	15 ± 1
C:N ratio	27.6 ± 3.3	35.7 ± 3.3	28.9 ± 3.2
$\delta^{13}C$ (‰)	-24.04 ± 0.77^{a}	-26.98 ± 0.77^{b}	-26.37 ± 0.77^{ab}
$\delta^{15}N$ (‰)	0.71 ± 0.46	1.71 ± 0.46	1.22 ± 0.44

Note: Different superscript lowercase letters within rows indicate significantly different means ($P < 0.05$).

TABLE 23. ANOVA results for the effects of fire season and sampling date on concentration and isotopic ratios of bulk soil C and N.

	Fire	Date	Fire x date
Response	*P*	*P*	*P*
% C	0.4144	0.0202	0.2196
% N	0.3677	0.0013	0.0798
C:N ratio	0.7433	0.0009	0.9722
$\delta^{13}C$	0.1752	0.4510	0.4144
$\delta^{15}N$	0.6367	0.038	0.9332

TABLE 24. Concentrations and stable isotopic ratios (± 1 SE) of bulk soil.

	No fire	Spring fire	Fall fire
C (g kg^{-1})	18.7 ± 2.2	19.3 ± 2.2	15.3 ± 2.2
N (g kg^{-1})	1.7 ± 0.2	1.8 ± 0.2	1.5 ± 0.2
C:N ratio	10.6 ± 0.3	10.4 ± 0.3	10.3 ± 0.3
$\delta^{13}C$ (‰)	-20.50 ± 0.72	-22.52 ± 0.72	-21.76 ± 0.72
$\delta^{15}N$ (‰)	5.47 ± 0.33	5.73 ± 0.33	5.28 ± 0.33

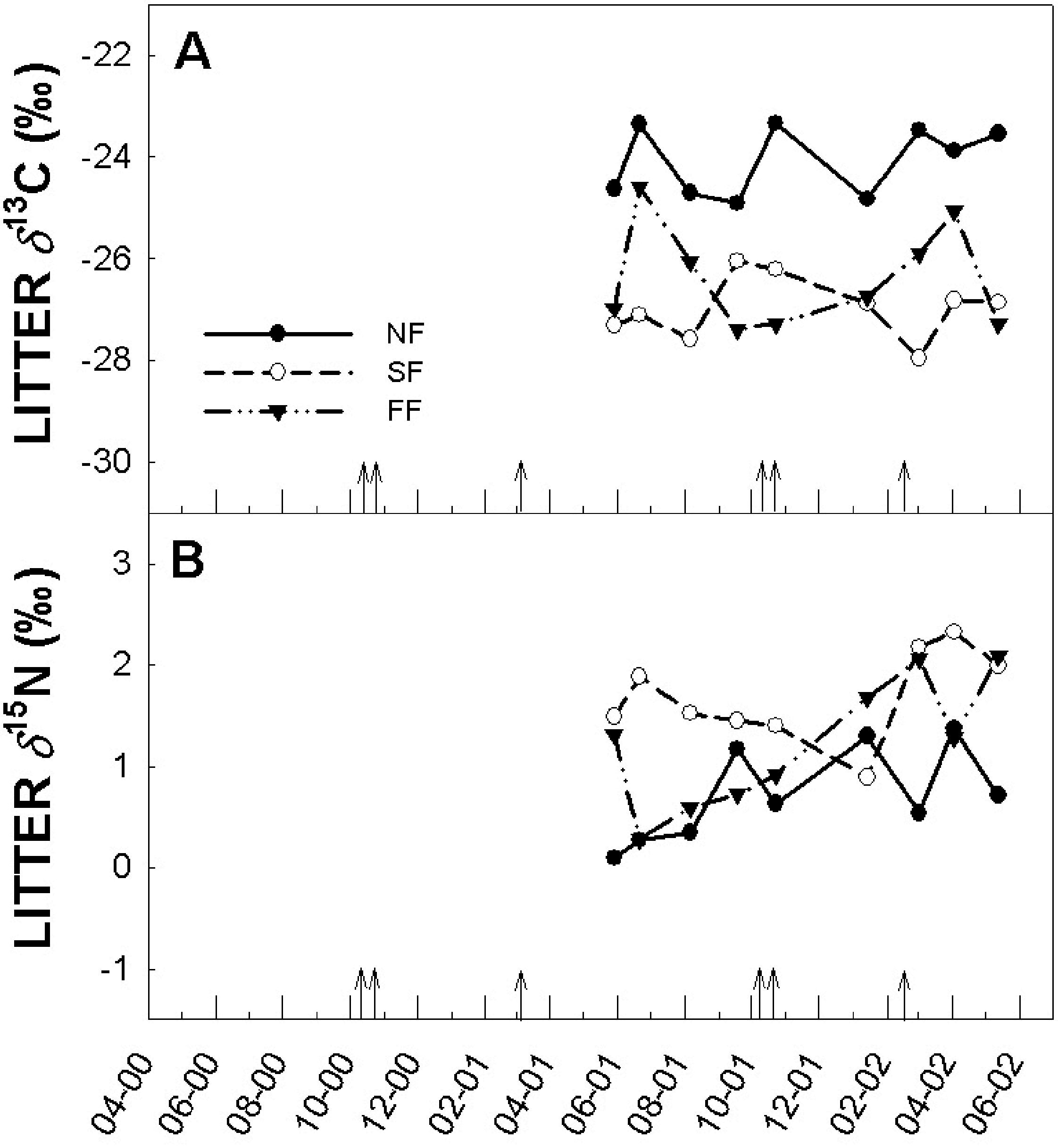

Figure 18. δ^{13}C vs. V-PDB and δ^{15}N vs. AIR of surface litter under seasonal fire, May 2001-May 2002. Values are means of five replicates ± 1 SE. Dates of spring (arrows) and fall (double arrows) fires are shown on the x-axis. Treatments are no fire (NF), spring fire (SF), and fall fire (FF).

Bulk soil

Concentrations of soil organic C (20.7 ± 1.8 vs 14.8 ± 1.8 g kg^{-1}) and total N (1.8 ± 0.1 vs 1.5 ± 0.1 g kg^{-1}), and C:N ratio (11.1 ± 0.2 vs 9.8 ± 0.2) were all significantly higher in June 2000 than in May 2002. However, there was no significant effect of seasonal fire on these variables (Table 23).

Bulk soil $\delta^{13}C$ and $\delta^{15}N$ values were not significantly affected by fire treatments (Table 24). Bulk soil $\delta^{13}C$ values did not change significantly between June 2000 and May 2002; however, bulk soil $\delta^{15}N$ values increased significantly (from 5.28 ± 0.27 to 5.50 ± 0.27) over the course of the study (Table 23).

Soil density fractions

There was no significant effect of fire or sampling date on the total concentration of soil density fractions, nor on that of any individual soil density fraction, in bulk soil (Figure 19).

There was no significant effect of seasonal fire on C and N concentration or C:N ratio of soil organic matter in any soil density fraction. C and N concentration and C:N ratio all varied significantly between soil density fractions, decreasing in the order light > medium > heavy (Figure 19). There was no significant effect of sampling date on C and N content of soil density fractions.

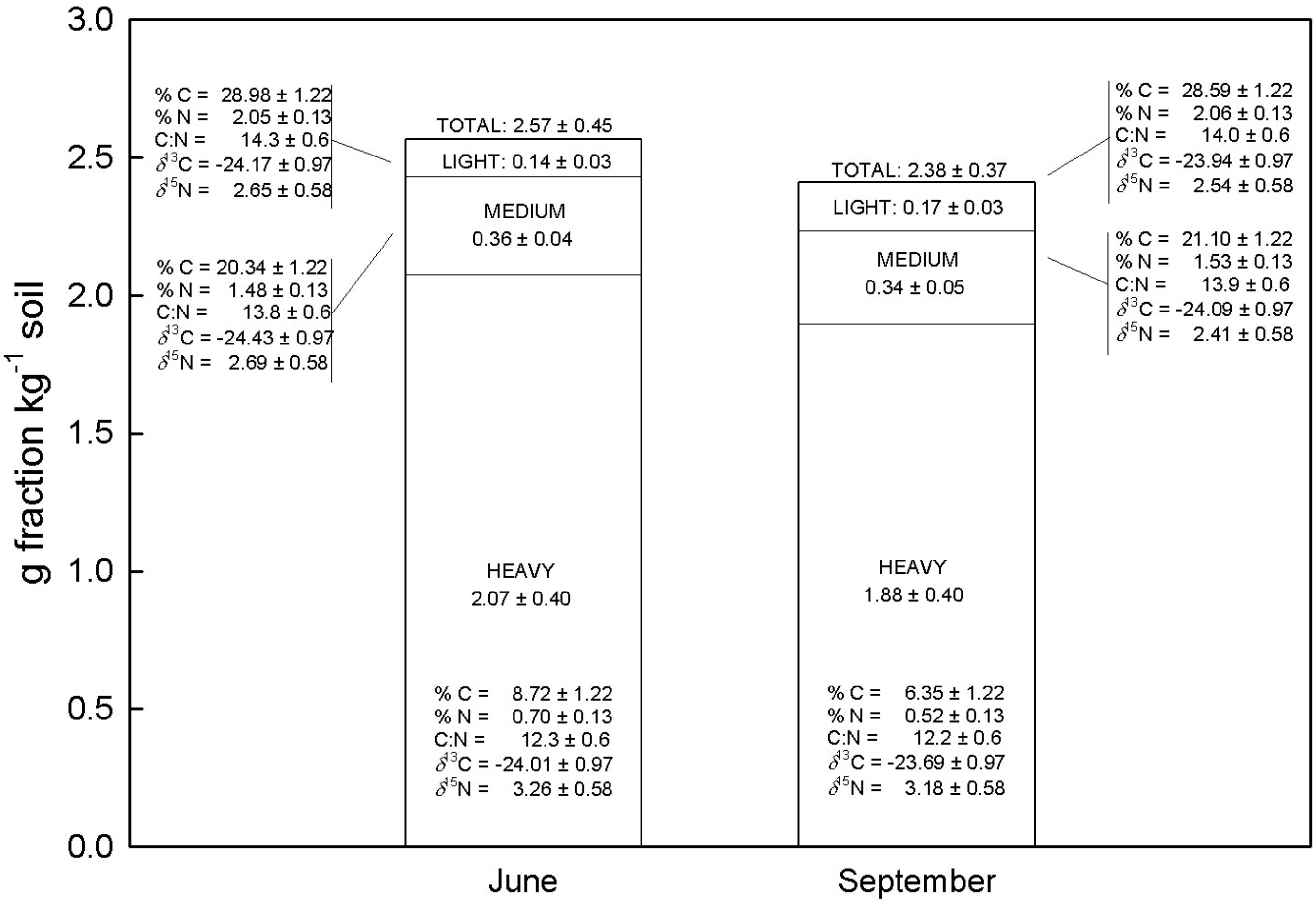

Figure 19. Concentration of soil density fractions under seasonal fire, June and September 2001. Shown for each fraction are concentration and isotopic ratios of C and N, and C:N ratio. Values are pooled means of pooled data from all treatments (15 replicates) ± 1 SE.

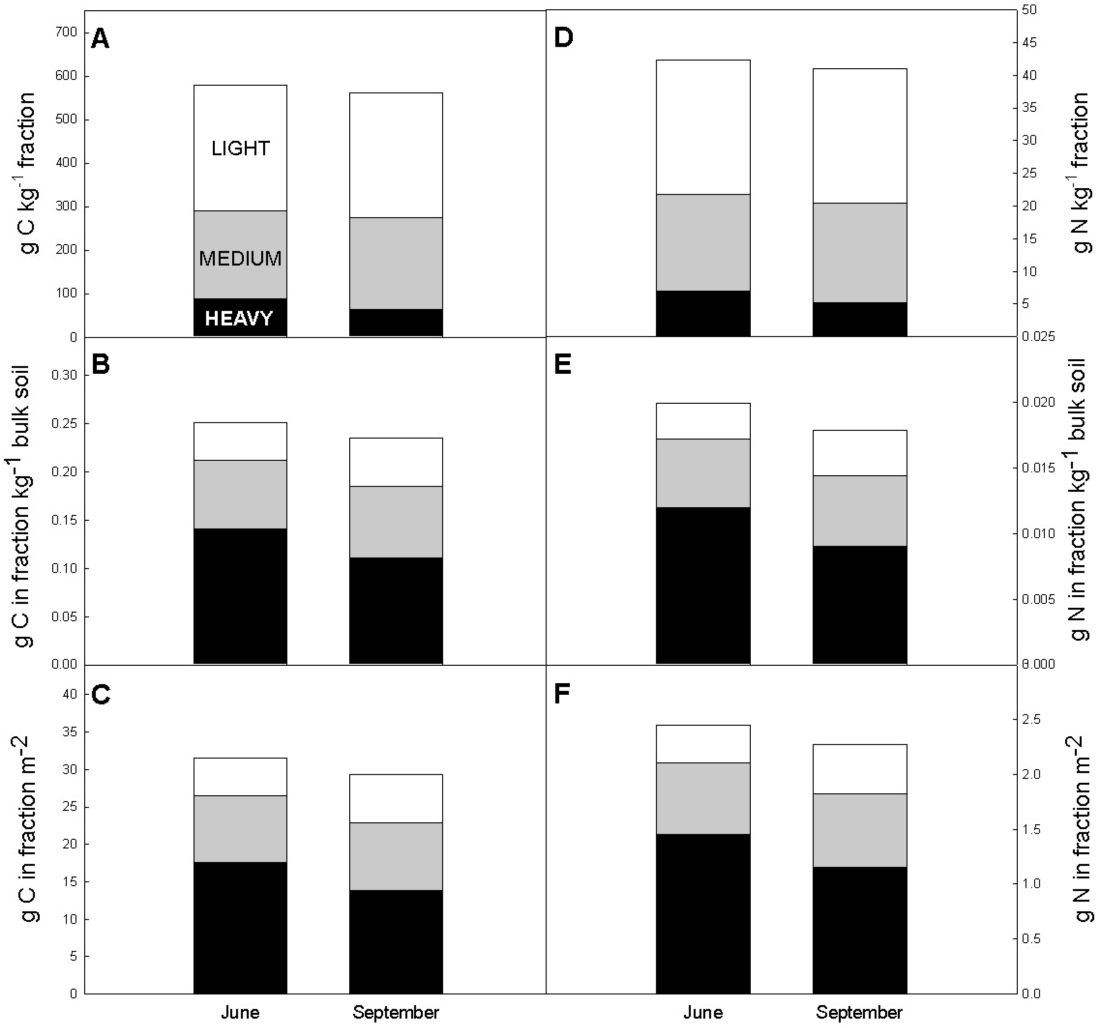

Figure 20. Organic carbon and total nitrogen in soil density fractions under seasonal fire, June and September 2001. Values are expressed as carbon (A) and nitrogen (D) concentration of fraction, carbon (B) and nitrogen (E) content of fraction in bulk soil, and carbon (C) and nitrogen (F) density of each fraction. Values are pooled means of pooled data from all treatments (15 replicates) ± 1 SE.

There were no significant effects of fire treatment, density fraction, or sampling date on soil δ^{13}C and δ^{15}N values of soil density fractions (Figure 19).

The C content of soil density fractions, the concentration of soil density fraction C in bulk soil, and the mass of soil fraction C per unit area, were unaffected by fire or sampling date (Figure 20).

There were no significant effects of fire or sampling date on N concentrations in soil density fractions, on the concentration of soil density fraction N in bulk soil, or the mass of soil density fraction N per unit area (Figure 20).

Potential C mineralization

Neither sampling date nor fire significantly affected amounts of C mineralized during 180 d of laboratory incubation, nor the pool sizes and turnover rates estimated from the incubation. Fitting of the two-pool model of soil C kinetics to pooled long-term incubation data yielded an estimated active pool size of 0.48 ± 0.04 g C kg $^{-1}$ soil with a rate constant of 0.08 ± 0.01, for a mean residence time (MRT) of 12.3 days. The size and rate constant of the slow SOC pool were estimated at 17.24 ± 1.10 g C kg $^{-1}$ soil and 0.00050 ± 0.00035, respectively, for an MRT of 5.5 years (Figure 21). The estimated size of the active SOM pool was roughly half that of the light density fraction, and about equal to that of the medium density fraction.

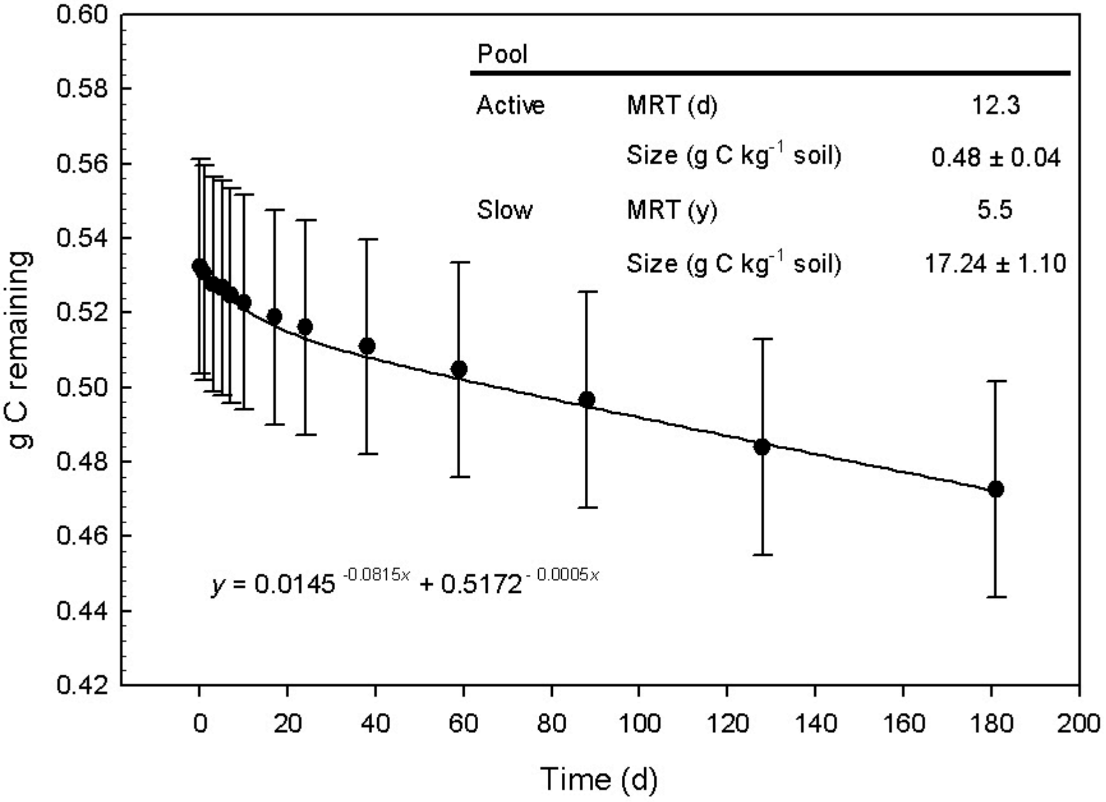

Figure 21. Potential C mineralization under seasonal fire during a 180 d incubation. Values are means of 30 replicates (pooled samples from June and September 2001) ± 1 SE. The solid line represents the fitted two-pool exponential decay model, of the general form $y = a^{-bx} + c^{-dx}$. Mean residence times are given in units of d for the active pool, and y for the slow pool.

DISCUSSION

Observed effects of seasonal fires were not always in the expected direction. Seasonal variation in temperature and moisture is one factor responsible for these discrepancies between hypothesized and observed responses. Operating within that climatic context, the role of the timing of fire, and its differing modes of action on litter pools and standing biomass of different plant functional types, are other such factors. All three together conditioned plant and soil C and N responses to disturbance in this study.

Based on the lack of fire effects on C and N concentration and isotopic ratios of aboveground live plant tissue, feedback mechanisms of positive (Wedin 1995; Wedin 1996) or negative (Tateno and Chapin 1997) nature do not appear to be active in this ecosystem to the same degree as in others (Johnson and Matchett 2001). A process more akin to that predicted by the indeterminate dominance model for more arid grasslands (Vinton and Burke 1997; Burke et al. 1998) seems to more closely approximate the observed behavior of the system . Fire-induced shifts in C and N composition of litter and soil pools, if observed, might not then be due to intraspecific alterations of plant tissue chemistry, and could stem instead from other factors, such as changes in the composition of the plant community (Van de Vijver et al. 1999; de Mazancourt and Loreau 2000a).

Such shifts were indeed observed in litter pools, with lower δ^{13}C values in response to spring fire treatments. This would be inconsistent with the increase in C_4 perennial grass production commonly associated with spring burning in tallgrass prairie (Towne and Owensby 1984; Collins 1987; Howe 1994; Howe 1995; Engle and Bidwell 2001). However, probably as a consequence of consecutive summer droughts during the study period, productivity of these species was limited and no increase was observed (see Chapter III). However, an observed shift toward increased total production of C_3 perennial grasses, with a decrease in C_3 annual grasses, may account in part for fire's effect on litter chemistry. Another potential explanation is that fire removed most of the standing litter pool, meaning that litter sampled from fire treatments consisted almost entirely of undecomposed, low-$\delta^{13}C$ inputs from the current season's production. The lack of fire effects on litter chemistry in fall fire treatments, seemingly counterintuitive due to the higher intensity of fires in that season, is likely due to the lower production and standing litter pool in those treatments.

Consistent with the lack of fire effects on the quality of litter inputs to the soil, fire did not affect concentrations of organic C or total N in bulk soil during 4 years of annual treatment. It appears likely that other sources must be responsible for large contributions to soil C and N pools. Roots are likely a significant source of C. Though this study quantified neither their biomass nor their response to treatments, previous work at the site has shown them to be responsive to fire, potentially compensating for any decrease in litter inputs (Hubbard 2003).

The hypothesis that the portion of the litter pool affected by fire is a relatively small portion of the total C input to the soil is not supported by the lack of treatment effects on concentration and isotopic composition of C and N in SOM density fractions. However, the gradual and significant decrease in C and N content and C:N ratio in progressively heavier SOM density fractions is consistent with the hypothesis that the fractions isolated via this methodology represent materials in successive stages of decomposition. Lack of fire effects carried through to potential C mineralization rates and the C pool sizes and mean residence times estimated from those kinetics.

As a disturbance, fire has a demonstrated impact on the litter component of plant-soil C and N dynamics in the study system. That role is subject to modulation by climatic factors, as evidenced by the elimination of the normal contribution of C_4 grasses by repeated summer drought. Disturbances associated with a certain set of aboveground responses may also stimulate complementary and potentially offsetting ones belowground. An assessment of these responses, as well as the behavior of both above- and below-ground system components under conditions of normal- and above-normal precipitation, are needed continuations of this work for a more complete comprehension of plant-soil nutrient dynamics in mixed grasslands of the southern Great Plains.

CHAPTER VI

SOIL RESPIRATION AND N MINERALIZATION RESPONSES TO SPRING FIRE AND CLIPPING IN A SOUTHERN MIXED GRASSLAND

INTRODUCTION

The amount of carbon stored globally in soil organic matter is twice as large as that held in the atmosphere (Eswaran et al. 1993). Soil respiration is an important determinant of the rate of carbon cycling through the soil system. This flux is equal to or greater than global ANPP, and roughly ten times greater than that originating from anthropogenic fossil fuel combustion (Schlesinger 1997). Thus, even relatively small changes in the environmental factors controlling soil respiration and N mineralization could generate increases in atmospheric greenhouse gas inputs larger than current total fossil fuel emissions (Raich and Schlesinger 1992). Grassland soils have respiration rates 20 % higher than those of forests in similar climatic zones, and therefore represent a key element in the understanding and management of these cycles and their consequences (Raich and Tufekcioglu 2000).

Rates of both soil respiration and N mineralization are goverened by temperature and moisture (Kucera and Kirkham 1971; Schimel et al. 1990; Conant et al. 2000; Franzluebbers et al. 2002), at spatial scales ranging from submeter (Bunnell et al. 1977; Robertson et al. 1988; Jackson and Caldwell 1993) to global (Raich and Potter 1995; Trumbore et al. 1996). These abiotic factors, in turn, are subject to modification by disturbances such as fire and clipping. By reducing the amount of aboveground plant cover, both fire and clipping tend to increase soil temperatures (Whisenant et al. 1984a; Blair 1997; Knapp et al. 1998), though the pattern is not universal (Mielnick and Dugas 2000). Soil moisture can either increase (Owensby et al. 1970) or decrease (Whisenant et al. 1984a; Blair 1997), depending on whether the increased evaporation rates from warmer soils is greater than the decrease in evapotranspiration rates from reduced leaf surface area (Bremer et al. 1998).

In addition to modulating abiotic controls of respiration and N mineralization, disturbance can also alter biotic factors that influence these soil processes (Burke et al. 1991; Ojima et al. 1993; Seastedt et al. 1994). Both plant roots and heterotrophic soil microbes contribute to overall soil respiration, and either component may dominate depending on the circumstances (Kucera and Kirkham 1971; Warembourg and Paul 1977; Dugas et al. 1999). By stimulating root growth, fire can increase grassland soil respiration rates, while grazing and clipping can reduce them (Bremer et al. 1998; Knapp et al. 1998; Johnson and Matchett 2001). N mineralization, by contrast, can be inhibited by fire (Turner et al. 1997; Johnson and Matchett 2001) , and is generally (Shariff et al. 1994; Frank and Groffman 1998) but not always (Augustine and Frank 2001) stimulated by grazing. Changes in community composition and the quantity and quality of above- and below-ground plant tissue inputs are other mechanisms by which biologically-mediated effects of fire and clipping may affect soil respiration and N mineralization, independently of temperature and moisture effects (Hobbs 1996).

The relative importance of biotically and abiotically mediated responses of soil respiration and N mineralization to disturbance has been most extensively studied in tallgrass prairie ecosystems. Under other climatic regimes, such as more water-limited ecosystems, they may differ (Hobbs 1996; Burke et al. 1998). However, few measurements have been made of these fluxes, and the consequences for them of disturbance, in semiarid areas (Raich and Schlesinger 1992; Ansley et al. 2002). Interactive effects of different disturbance types have also received relatively little attention despite their potential significance (Hobbs et al. 1991; Johnson and Matchett 2001, Ritchie, 1998 #530). As such, a significant body of knowledge relevant to planning for land use effects on global C and N budgets is underrepresented in the literature.

This study assesses the effects of spring fire, and clipping at two levels of intensity, on soil respiration, net in situ N mineralization, soil inorganic N, soil moisture, and soil temperature in soils of a mixed native grassland in the southern Great Plains. We hypothesized that: (1) both fire and clipping would increase soil surface temperatures and decrease soil moisture content as a result of removal of standing biomass; (2) soil respiration and N-mineralization would increase in clipping and fire treatments in response to increases in soil temperature; (3) rates of both soil respiration and net N mineralization, as well as soil concentrations of inorganic N, would be reduced due to combustion losses of aboveground plant N during fire; and (4) Clipping would reduce the effects of fire on soil respiration and N-mineralization by limiting the intensity of fire.

METHODS

Study site

Research was conducted on a 1 ha grazing exclosure on the W.T. Waggoner Ranch in Wilbarger County, Texas (33^o 51'N, 99^o 26' W, elevation 381 m). Mean annual precipitation for the site is 665 mm, bimodally distributed, with peaks in May (18% of annual total) and September (12% of annual total). Mean annual temperature is 16.1^o C, with monthly average extremes ranging from 36 °C in July to -2.5 °C in January. Soils are classified as fine, mixed, thermic Typic Paleustolls of the Tillman series.

Dominant cool season (C_3) grasses include Texas wintergrass (*Nasella leucotricha* (Trin & Rupr) Pohl), a native perennial bunchgrass, and Japanese brome (*Bromus japonicus* Thunb. ex Murr.), an exotic annual grass. Dominant warm season (C_4) grasses include the perennial bunchgrass sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), and the stoloniferous, sod-forming buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.). The study site was root-plowed and seeded with sideoats grama in 1974. It has not been burned since that time. The site was grazed by cattle at a moderate stocking rate (1 cow 12 ha^{-1}) from the late 1800s to 1988, when livestock were removed.

Experimental design

Dynamics of soil respiration, N mineralization, soil moisture, and soil temperature were evaluated on experimental plots in a 2 x 3 factorial design (fire x clipping). Treatments were assigned randomly to thirty 6x6-m plots (n= 5 replicates/treatment combination). The following treatments were implemented annually beginning in 1999: 1) control (no fire, no clipping), 2) continuous clipping, 3) spring clipping, 4) spring fire, 5) spring fire + spring clipping, and 6) spring fire + continuous clipping. Plots in the spring clipping treatment were mown to 5 cm height once per year in late April, and those in the continuous clipping treatment were mown monthly (except during drought). Clipped plant material was transported offsite. Plots in the fire treatment were subjected to prescribed fires in February/March 1999, 2000, 2001, and 2002. Fire intensity for all fires in all years was classified as low to moderate, with flame heights not exceeding 1.5 m. Rainfall was measured at the site.

Sampling and analysis

Sampling was carried out at approximately monthly intervals from June 2000 through May 2002. During each sampling period, a 1x1 m subplot was randomly chosen from each of the 30 treatment plots. Since sampling was destructive, no subplots were resampled. The following sampling procedures were performed on each 1x1 m subplot.

A composite soil sample consisting of 8 cores 2.5 cm in diameter and 10 cm deep was taken from each subplot. Sampling to this depth has been estimated to account for 70 % of root biomass and 40 % of SOM (Gill et al. 1999), as well as the greatest amount of available N in the profile (Dodd et al. 2000); it is also the depth increment most likely to experience changes in soil C and N storage in response to land management practices (Conant et al. 2001). Soil samples were immediately placed on ice for transport to the laboratory and subsequently stored at 4 °C until analysis. Samples within each treatment replicate were pooled, mixed thoroughly, passed through a 2-mm screen to remove large organic fragments, and pulverized prior to laboratory analysis. Gravimetric soil moisture was measured by drying a 10 g field-moist subsample from each subplot for 5 d at 105 °C and re-weighing (Jarrell et al. 1999). Remaining soil was dried for 5 d at 60 °C. A 7-g subsample of dried soil was ground to pass a 2-mm screen and shaken for 1 h with 28 ml 2 M KCl. The extract was filtered through # 2 filter paper and analyzed for content of NO_3^- and NH_4^+ on a Technicon autoanalyzer (Grasshoff 1969).

A LI-COR 6200 infrared gas analyzer (IRGA) was used to measure *in situ* soil temperature (at 10 cm) and soil respiration (in a chamber formed by a PVC collar 10 cm in diameter and extending 5 cm above, and 1-2 cm below, the soil surface) (Norman et al. 1992; Dugas et al. 1997). This method quantifies total CO_2 flux from the soil, and therefore represents the sum of respiration by roots and the respiration of heterotrophic soil organisms. No effort was made to separate root from heterotrophic respiration. Measurements were made on each subplot at 6-h intervals (0400, 1000, 1600, and 2200 h) during a 24-h period. Each measurement consisted of the average of four instantaneous rates of soil C efflux calculated on the basis of a 5 ppm change in the concentration of CO_2 in the respiration chamber. Some reports exist of significant differences in rates of soil C efflux between day and night measurement periods (Osman 1971; Redman 1978; Grahammer et al. 1991; Bremer et al. 1998), while other authors have found no difference (Knapp et al. 1998; Dugas et al. 1999; Mielnick and Dugas 2000). No significant difference between day and night rates of soil C efflux occurred at any sampling date during the study, so average rates from each of the four intervals during the 24-hour measurement period were averaged to calculate a single rate for each sampling date.

The resin-core incubation technique (DiStefano and Gholz 1986) was used to estimate net N mineralization. A single PVC core (4 cm diam. x 10 cm deep) was removed from each subplot, capped with bags of Rexyn I-300 anion-absorption resin, and returned to the hole from which it was taken to incubate until the following sampling period. At the end of the incubation, concentration of NO_3^- and NH_4^+ in incubated soil samples was determined using the procedure described above. Concentration of total inorganic N in the incubated core was subtracted from that of the composite sample, and added to that of the bottom resin bag, to provide an index of *in situ* N mineralization (DiStefano and Gholz 1986; Hart et al. 1994; Bhogal et al. 1999).

Data analysis

Data were analyzed using SAS Version 9.0 (SAS Institute 2002). Soil temperature and soil C efflux values were averaged across the four measurements per time period, and then across the four time periods per sampling date, prior to statistical analysis of the entire study period. Each response variable was analyzed separately using a three-way ANOVA with sampling date, fire, and clipping as factors. For all variables where significant interactions existed with sampling date, the analysis was also carried out within each sampling date, excluding sampling date as a factor. Where there were no significant treatment effects on soil C efflux or N mineralization, these variables were regressed upon independent variables of soil temperature, soil gravimetric moisture content, temperature by moisture interaction, and live plant cover.

RESULTS

Sampling date was a significant factor for all response variables. Three-way interactions between sampling date, fire treatment, and clipping treatment were not significant for any response. In 2000, precipitation during the summer growth period of C_4 grasses (April – September) was below normal in every month, and the total for the period was 60 % of normal. In 2001, precipitation was below normal in 5 of the 6 months, with only August exceeding the normal amount (Figure 1).

Soil moisture content values displayed similar seasonal patterns across all treatments, reaching their highest levels in late winter, declining through spring and early summer, and remaining near their minimum from midsummer through early fall (Figure 22). Fire also reduced overall mean soil moisture content, but interacted significantly with sampling date (Table 25). Fire-related reductions in soil moisture content occurred in the late spring and early summer of 2000 and 2002, and in late summer 2001 (Figure 22A).

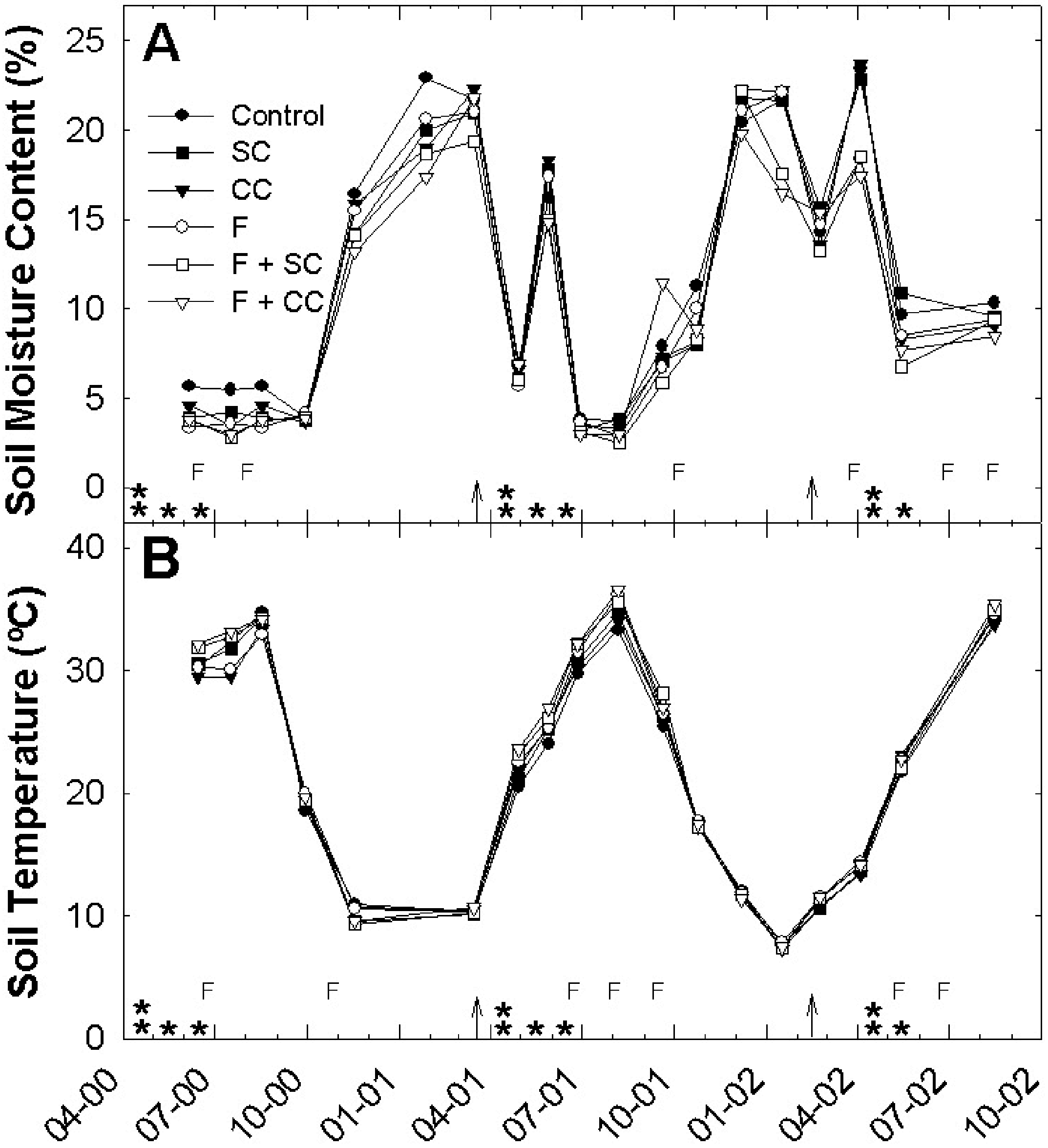

Figure 22. Mean monthly soil gravimetric moisture content (Panel A) and temperature (Panel B) , June 2000-August 2002. Values are means of five replicates. Treatments are control (no fire, no clipping), SC (spring clipping), CC (continuous clipping), F (fire only), F + SC (fire and spring clipping), and F + CC (fire and continuous clipping). Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis. Significant ($p < 0.05$) treatment effects within individual sampling dates are indicated by C (clipping) and F (fire) along the x-axis.

TABLE 25. ANOVA results for the effects of fire and clipping on soil moisture, temperature, respiration, and net N mineralization, once sampling date effects are considered.

	Fire	Clipping	Fire x clipping	Fire x date	Clipping x date
Response	*P*	*P*	*P*	*P*	*P*
Soil moisture content	0.0036	0.0794	0.9860	< 0.0001	0.0398
Soil temperature	0.0009	0.8191	0.1372	0.0044	0.6890
C efflux	0.4674	0.6186	0.1856	0.9696	0.8691
Net N mineralization	0.0174	0.3434	0.8637	0.8738	0.9999

TABLE 26. Mean (± 1 SE) overall temperature (A), moisture content (B), C efflux (C), and net N mineralization of surface 10 cm of soils, June 2000 - May 2002.

A) Soil gravimetric moisture content (%)

	No clipping	Spring clipping	Continuous clipping
No fire	12.19 ± 0.35	11.48 ± 0.35	11.50 ± 0.35
Spring fire	11.30 ± 0.35	10.49 ± 0.35	10.58 ± 0.36

B) Soil temperature (ºC)

	No clipping	Spring clipping	Continuous clipping
No fire	22.33 ± 0.24	22.44 ± 0.24	21.86 ± 0.24
Spring fire	22.79 ± 0.24	22.91 ± 0.24	23.20 ± 0.24

C) Soil respiration (g CO_2 m^{-2} mo^{-1})

	No clipping	Spring clipping	Continuous clipping
No fire	258.4 ± 14.3	254.1 ± 14.3	234.0 ± 14.4
Fire	245.0 ± 14.3	220.8 ± 14.6	254.8 ± 14.4

D) Net N mineralization (g $[NO_3^- + NH_4^+]$-N m^{-2} mo^{-1})

	No clipping	Spring clipping	Continuous clipping
No fire[a]	1.10 ± 0.19	0.87 ± 0.19	0.73 ± 0.19
Spring fire[b]	0.59 ± 0.18	0.55 ± 0.18	0.40 ± 0.18

Note: Different superscript lowercase letters within treatment headings indicate significantly different means (P < 0.05).

TABLE 27. Soil respiration (g CO_2 m^{-2} mo^{-1}) as predicted by soil temperature (ºC), soil gravimetric moisture content (%), and live vegetation cover, June 2000 - August 2002. N = 108; adjusted r2 = 0.5858; root mean square error = 123.30).

Property	Coefficient	$P > \|t\|$
Intercept	-499.48	< 0.0001
Soil temperature	22.24	< 0.0001
Soil gravimetric moisture content	27.02	< 0.0001
Live vegetation cover	2.29	0.0037
Temperature x moisture	1.96	< 0.0001

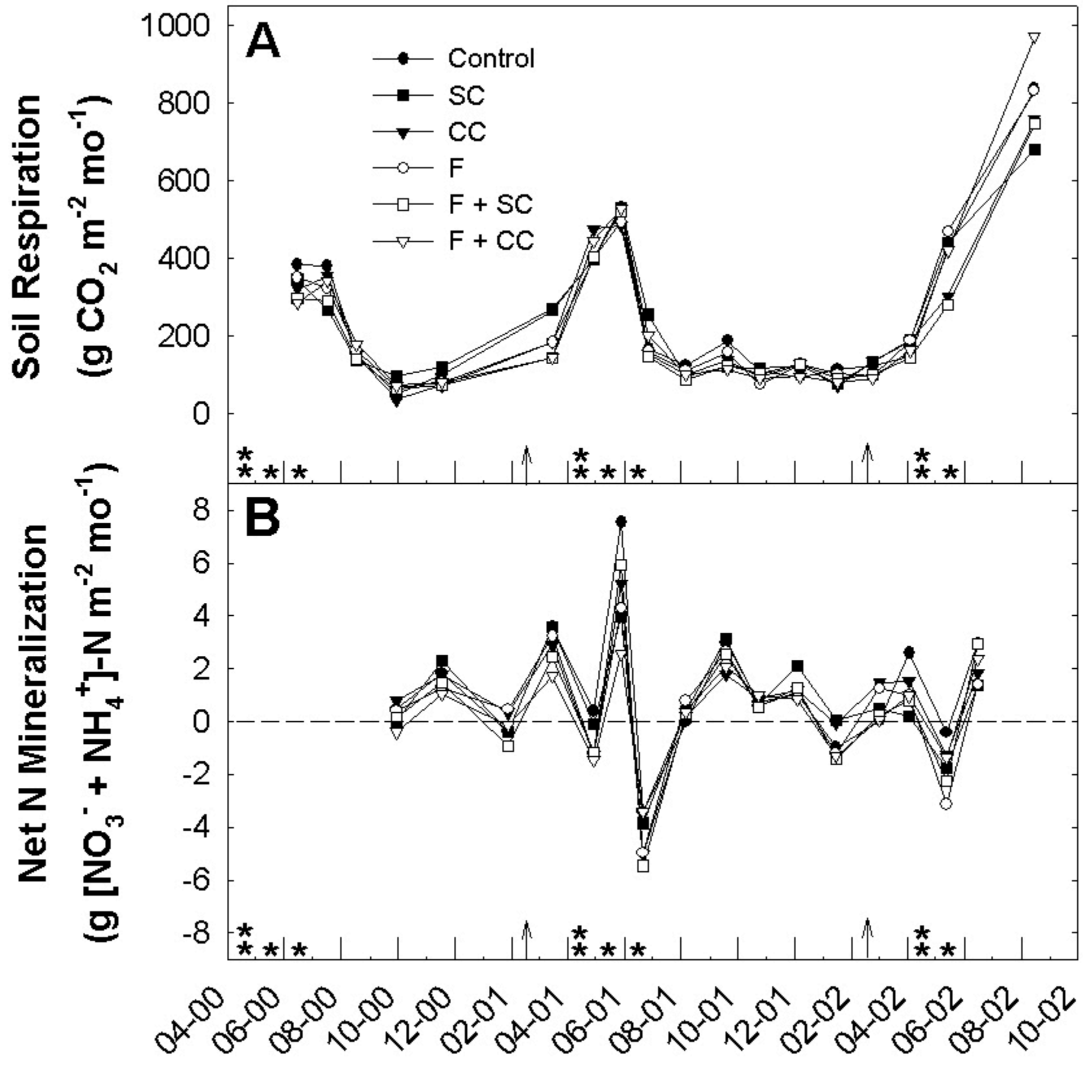

Figure 23. Mean monthly soil respiration (Panel A) and net N mineralization (Panel B), June 2000 - August 2002. Values are means of 5 replicates. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis.

Soil temperatures also followed similar seasonal trends in all treatments (Figure 22B). Soil temperatures were lowest in January and peaked in August. Fire significantly affected mean overall soil temperature, but also interacted significantly with sampling date (Table 25). Fire increased soil temperatures relative to those in no fire treatments from mid-spring to early summer in all study years; in other seasons, temperatures were comparable across all treatments (Figure 22B). There was no significant effect of clipping on soil temperature (Table 26).

Soil respiration rates remained low through most of the year, peaking in late spring to early summer, with a return to low levels by August of all study years except 2002, when abnormally high rains occurred in that month (Figure 23A). There were no significant effects of either fire or clipping on overall mean soil respiration (Table 25). A multiple linear regression model, of the general form RESP = INT + A * TEMP + B * MOIST + C * VEG + D * TEMP * MOIST, revealed significant effects of soil moisture content and soil temperature, as well as live vegetation cover, on monthly soil respiration rates. Soil respiration also responded significantly to a moisture-by-temperature interaction term (Table 27; Figure 24). Cumulative respiration (June-May) was estimated as 680 g C m^{-2} y^{-1} for 2000-1, and 488 g C m^{-2} y^{-1} for 2001-2.

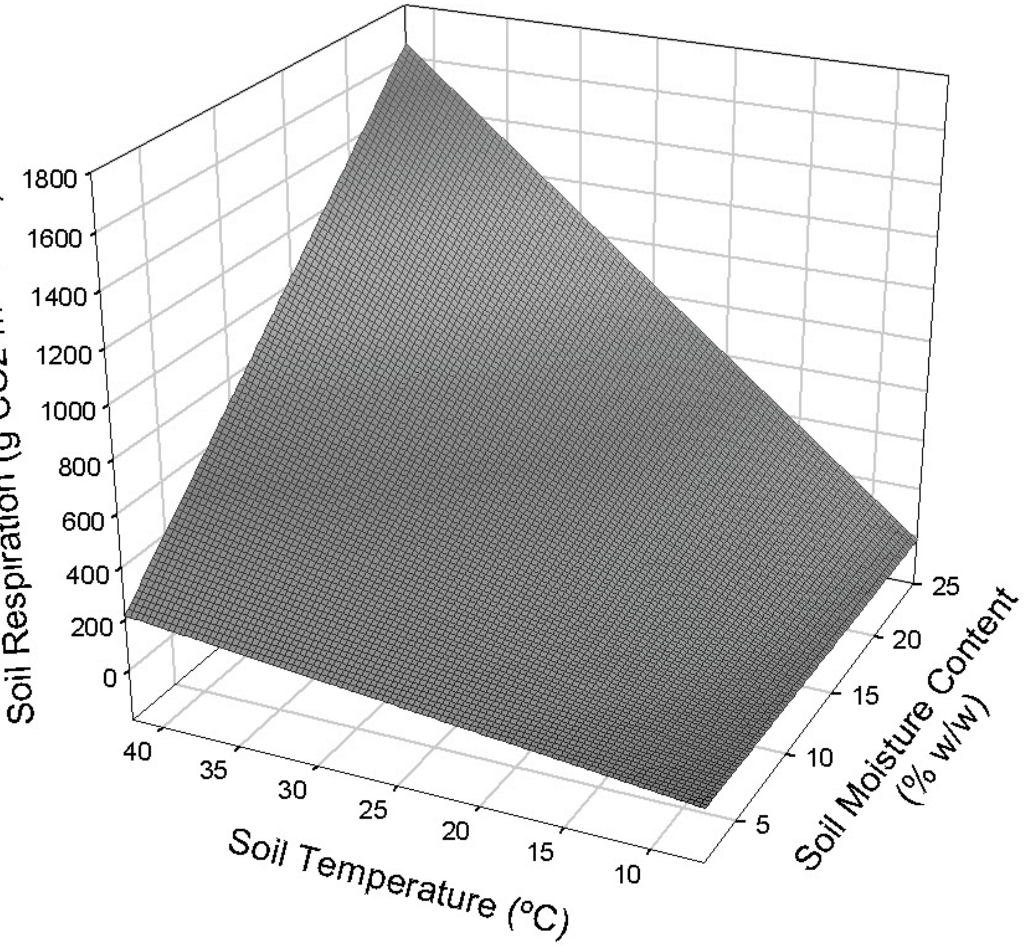

Figure 24. Effect of changes in gravimetric soil moisture content and soil temperature on soil respiration. Regression coefficients for parameters are in Table 27.

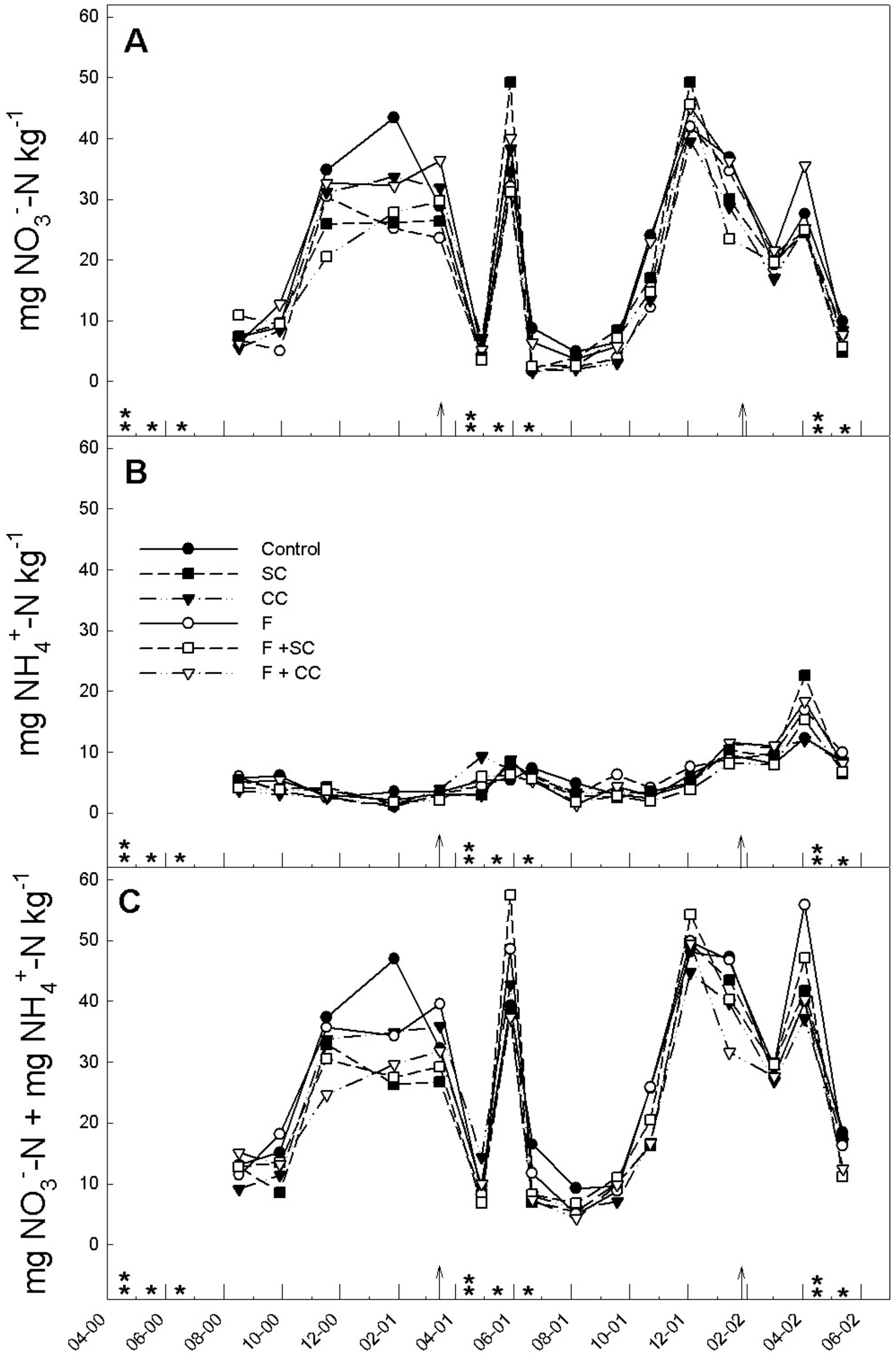

Figure 25. Concentration of soil NO$_3^-$, NH$_4^+$, and NO$_3^-$ + NH$_4^+$, August 2000-May 2002. Values are means of 5 replicates. Significant ($p \leq 0.05$) treatment effects within individual sampling dates are indicated by C (clipping), F (fire), and C/F (fire x clipping interaction) along the x-axis. Dates of spring fire (arrows) and spring (double asterisks) and continuous (all asterisks) clipping treatments are shown on the x-axis.

Seasonal maxima in rates of net N mineralization occurred simultaneously with those in soil respiration; however, the former demonstrated more frequent oscillations between high and low (or negative) values between sequential pairs of sampling dates (Figure 23B). Mean overall net N mineralization rates were reduced by roughly fifty percent in the spring fire treatment (0.51 ± 0.11 g [NO_3^- + NH_4^+]-N m^{-2} mo^{-1}) relative to the no fire treatment (0.90 ± 0.11 g [NO_3^- + NH_4^+]-N m^{-2} mo^{-1}). There was no significant effect of clipping on net N mineralization (Tables 25,26).

Sampling date significantly influenced the levels of bulk soil NO_3^-, NH_4^+, and total inorganic N (Table 28). Total soil inorganic N concentrations were lowest during the summer months and peaked during winter, with a sharp decline and increase in mid-to-late spring 2001 and 2002. NH_4^+ was present at lower concentrations, and was less seasonally variable, while NO_3^- was the dominant form of inorganic N in the soil (Table 29; Figure 25). There were no significant effects of clipping or fire on soil NO_3^-, NH_4^+ or total inorganic N concentrations.

TABLE 28. ANOVA results for the effects of fire and clipping on soil inorganic N, once sampling date effects are considered.

	Fire	Clipping	Fire x clipping	Fire x date	Clipping x date
Response	*P*	*P*	*P*	*P*	*P*
Soil NO_3^-	0.7633	0.2922	0.8375	0.6595	0.7083
Soil NH_4^+	0.4411	0.4518	0.6567	0.8882	1
Soil total inorganic N	0.8817	0.2876	0.8045	0.8934	0.8177

TABLE 29. Mean concentrations (± 1 SE) of nitrate (A), ammonium (B), and total inorganic nitrogen (C) in bulk soil, June 2000 - May 2002.

A) Soil NO_3^- (mg kg^{-1} soil)

	No clipping	Spring clipping	Continuous clipping
No fire	22.4 ± 2.5	17.7 ± 2.5	18.8 ± 2.6
Spring fire	22.2 ± 2.5	20.1 ± 2.5	18.4 ± 2.6

B) Soil NH_4^+ (mg kg^{-1} soil)

	No clipping	Spring clipping	Continuous clipping
No fire	5.2 ± 0.5	5.4 ± 0.5	5.1 ± 0.5
Spring fire	5.3 ± 0.5	5.2 ± 0.5	4.4 ± 0.5

C) Soil total inorganic N (mg NO_3^- + NH_4^+ kg^{-1} soil)

	No clipping	Spring clipping	Continuous clipping
No fire	27.6 ± 2.6	23.0 ± 2.6	24.1 ± 2.7
Fire	27.7 ± 2.7	25.3 ± 2.6	22.9 ± 2.6

DISCUSSION

The results of this study support the general hypothesis that fire and clipping alter microclimatic variables in mixed native grasslands of the southern Great Plains. However, the magnitude of such alterations was apparently not sufficient to cause corresponding changes in the rates of soil C efflux, and observed reductions in soil net N mineralization in fire treatments were likely due to other mechanisms.

The importance of seasonal climatic variation for nutrient cycling in the study system is evident from the strong dependence of all response variables on sampling date. Soil temperature and moisture varied predictably throughout the year, and rates of soil C efflux and net N mineralization tracked these trends, peaking in April and May, when temperatures had begun to climb but soil moisture content was still relatively high.

These broad seasonal patterns in soil moisture content and temperature were subject to slight but significant modulation by disturbance. Fire significantly increased soil temperature and decreased soil moisture content. The significant interaction with sampling date, present in both effects, stems from the fact that fire effects were limited to particular windows during the year, occurring primarily during late spring and early summer. Whisenant et al. (1984a) found that spring burning in *N. leucotricha*-dominated communities caused significant decreases in soil water for 2 to 6 months following burning, with significant temperature increases persisting longer.

Clipping did not significantly affect soil moisture content or temperature, and manifested no significant interaction with sampling date. Varied effects of clipping on soil moisture and temperature have been reported. In contrast to this study, Owensby et al. (1970) found that clipping increased soil water in tallgrass prairie, a difference which might be due to that study's considerably greater sampling depth or to regional temperature differences between the study sites. Following clipping, Bremer et al. (1998) reported a significant decrease in soil moisture content in the surface 10 cm, but only during the dormant season, while an increase in soil temperature was limited to the growing season. Both results were attributed to the presence of a larger mulch layer in unclipped treatments. Blair (1997) found that fire increased soil temperature and decreased moisture content, with differences being most pronounced early in the growing season and diminishing thereafter; significant moisture differences were present only in a year of lower than normal precipitation. Taken together, these similarities and differences from the present findings highlight the importance both of regional differences in climate and of interannual variability in precipitation within a single site for the outcome of fire and clipping effects on soil moisture and temperature.

Rates of soil respiration are governed, among other factors, by soil temperature and moisture content (Kucera and Kirkham 1971; Bunnell et al. 1977; Schimel et al. 1990; Knapp et al. 1998; Dugas et al. 1999; Conant et al. 2000; Franzluebbers et al. 2002). Thus, the finding in this study of significant effects of fire and clipping on temperature and moisture, but not respiration, at first seems paradoxical. However, a comparison of the threefold amplitude of seasonal variation in moisture and temperature versus the magnitude of fire- and clipping-related shifts in these variables (on the order of 1 % and 1ºC, respectively) provides an explanation for this seeming discrepancy (Figure 2). According to the multiple regression model (Table 3), fire-caused changes in soil temperature and moisture content were not adequate to generate a corresponding shift in mean soil respiration rates greater than the standard error. Moreover, soil respiration was relatively insensitive to changes in soil temperature or moisture content if either variable was below some threshold value (Figure 3). This is a common finding in other studies (Redman 1978; Howard and Howard 1993; Knapp et al. 1998). In some cases even the sign of the slope of the regression line between soil C efflux and either temperature or moisture changes depending on the value of the other (Bremer et al. 1998; Franzluebbers et al. 2002). Since seasonal maxima in soil temperature and moisture content were almost precisely out of phase with one another, such combinations of relatively high values of both are unlikely to occur during the windows of time in which significant treatment effects were manifested (Figure 2).

While fire has significantly increased (Knapp et al. 1998; Johnson and Matchett 2001), and clipping reduced (Bremer et al. 1998; Wan and Luo 2003), soil respiration in some studies, the pattern is not ubiquitous (Ross et al. 1997; Mielnick and Dugas 2000; Husta and Litvak 2003). Earlier work at this study site found that fire caused a significant but transient decrease in soil C efflux in one year but not another. Monthly soil moisture and temperature, and net annual C efflux, also differed significantly between years (Hubbard 2003). Thus, interannual variability in climatic factors plays a key role in the effects of fire and clipping on both soil microclimatic variables and their effects on soil C efflux, to the point of determining whether the ecosystem acts as a net C source or sink in a given year (Kim et al. 1992; Frank 2002). The more consistent (and opposite) pattern of increase in soil C efflux following fire in more mesic tallgrass prairie ecosystems may be due to regional climatic differences. In one Kansas study, a between-treatment temperature difference of 6 °C corresponded to a fourfold difference in soil respiration. Also in Kansas, Bremer et al. (1998) reported a minimum 3 °C temperature difference required for a measurable difference in soil C efflux rates. By contrast, Franzluebbers et al. (2002), working at a more southerly prairie, calculated a value of 12 °C, matching a more general pattern of higher Q_{10} values (more pronounced

T responses) at lower temperatures (Kirschbaum 1995; Lomander et al. 1998). These two groups also report threshold temperatures of 14-20 °C (Bremer et al. 1998) and 10 °C (Franzluebbers et al. 2002) below which effects of changes in soil moisture on soil C efflux are negligible, in keeping with the fact that the water limited nature of Great Plains grasslands limits the correlation between temperature and C mineralization (Burke et al. 1998; Epstein et al. 2002).

The importance of biotic factors in determining rates of soil C efflux is highlighted by the significance of live vegetation cover as an independent variable in the multiple regression analysis. Seasonal maxima in C efflux rates were contemporaneous with those in live plant foliar cover (see Chapter II), suggesting that root respiration may contribute substantially to the overall flux, as in other studies (Norman et al. 1992; Bremer et al. 1998; Knapp et al. 1998; Franzluebbers et al. 2002). Further support for this interpretation may be found in the fact that fire caused significant reductions in the mass of surface litter (see Chapter II), but not soil C efflux rates. Published estimates of the contribution of root respiration to total soil C efflux range from 20 to 70 percent or more, with a trend toward higher proportions in more arid ecosystems (Kucera and Kirkham 1971; Wildung et al. 1975; Herman 1977; Klein 1977; Warembourg and Paul 1977; Redman 1978; Anderson 1991; Raich and Schlesinger 1992; Dugas et al. 1999; Hanson et al. 2000; Wan and Luo 2003). Since increased root growth appears to be a fairly generalized response of grasslands to fire, some of the regional differences in the strength and sign of the relationship between fire and soil C efflux in grassland ecosystems may stem from differing proportions and phenological overlap of C_3 and C_4 plants in the community (Klein 1977; Johnson and Matchett 2001; Hubbard 2003).

In contrast to soil C efflux, net N mineralization responded significantly to fire, and in a manner more consistent with results from other locations. The observed 50 % reduction in rates of in situ net N mineralization in fire treatments corresponds closely to findings from tallgrass prairie ecosystems (Turner et al. 1997; Johnson and Matchett 2001; Reich et al. 2001). These differing patterns of response of C and N mineralization suggest that the two processes may be controlled by different factors (Turner et al. 1997). Even if fire-induced treatment differences in soil temperature and moisture were large enough to create significant differences in N mineralization, they were only significant during certain periods of the year, while fire effects on mineralization manifested no significant interaction with sampling date. The change in N mineralization rates was also proportionally much larger than that in temperature and moisture, and in any event an increase in temperature would be expected to increase, rather than decrease, mineralization rates.

Soil inorganic N, in the form of both NO_3^- and NH_4^+, displayed strong seasonal variation. Consistent with other studies of soil inorganic N in Great Plains grasslands, NO_3^- was the more abundant form of nitrogen throughout the year (Wienhold et al. 2001). NO_3^- concentration increased gradually from fall through early spring, with a subsequent sharp decline and immediate rebound in late spring corresponding to the peak growth and sharp dieback of C_3 annual grasses (Chapter II). NH_4^+ was relatively less abundant, with a less pronounced amplitude of seasonal variation, and tended to increase in concentration throughout the period of the study, perhaps as a consequence of consecutive summer droughts (Woodmansee et al. 1981). The lack of fire effects on inorganic N stands in contrast to many studies in tallgrass prairie (Towne and Owensby 1984; Hobbs et al. 1991; Ojima et al. 1994; Blair 1997; Ajwa et al. 1999). However, other researchers have found a similar lack of response in that ecosystem (Turner et al. 1997; Wan et al. 2001). Repeated summer drought at the study site may have been the dominant factor in determining soil N dynamics.

The hypothesis that loss of aboveground N via volatilization during combustion is responsible for the reduction in N mineralization rates appears plausible (Turner et al. 1997); however, the majority of the N loss in this case seems likelier to come from senesced litter rather than standing vegetation (see Chapter II). This suggestion permits explanation of fire effects on soil temperature, moisture, and N mineralization via a single mechanism – litter removal – that is also consistent with the lack of significant effects on soil C efflux and the absence of significant interactions between fire and clipping in any response. It is also compatible with the idea that above- and belowground controls differ in their importance for C and N cycles in grassland ecosystems (Burke et al. 1997; Frank and Groffman 1998; Knops et al. 2002). The elucidation of the relative importance of these controls in years with normal summer precipitation and C_4 grass productivity, and the role of root dynamics in overall soil C efflux, remain as areas for further investigation.

CHAPTER VII

SOIL RESPIRATION AND N MINERALIZATION RESPONSES TO SEASONAL FIRE IN A SOUTHERN MIXED GRASSLAND

INTRODUCTION

The global soil C pool is twice the magnitude of atmospheric stocks (Eswaran et al. 1993). The rate of carbon cycling through this terrestrial pool is controlled by soil respiration. The total amount of C transferred to the atmosphere annually via soil respiration is equal to or greater than global ANPP, and roughly ten times greater than the anthropogenic contribution via combustion of fossil fuels (Schlesinger 1997). Thus, increases in atmospheric greenhouse gas inputs greater than current fossil fuel emissions could result from relatively minor changes in the abiotic factors (particularly temperature and soil moisture) that govern soil respiration (Raich and Schlesinger 1992). Respiration rates of grassland soils average 20 % higher than those of forests in similar climatic zones; therefore, soil respiration and the environmental parameters that control it in grasslands must be well-quantified in order to understand and manage regional and global C cycles (Raich and Tufekcioglu 2000).

Fire's potential to alter microclimatic variables, and thus the size of C and N fluxes from grassland soils, is well documented (Burke et al. 1991; Ojima et al. 1993; Seastedt et al. 1994). In tallgrass prairie ecosystems, increases in soil respiration rates and decreases in rates of N mineralization typically follow fire (Blair 1997; Turner et al.

1997; Knapp et al. 1998; Johnson and Matchett 2001). The mechanisms responsible for these responses may be abiotic, biotic, or both. Burned areas typically have higher soil surface temperatures and lower soil moisture for a period of weeks to months following fire (Whisenant et al. 1984a; Knapp et al. 1998). These variables, in turn, have a strong influence on rates of both soil respiration and N mineralization (Kucera and Kirkham 1971; Schimel et al. 1990; Conant et al. 2000; Franzluebbers et al. 2002). Biotically mediated mechanisms of fire influence on grassland C and N fluxes can include changes in plant community composition, with potential cascading effects on the quantity and quality of production and hence soil litter inputs, as well as shifts in the relative allocation of resources and growth to above- vs. belowground plant tissues (Burke et al. 1991; Ojima et al. 1993; Seastedt et al. 1994; Hobbs 1996).

Relatively few measurements have been made of these fluxes, and the consequences for them of disturbance, in more arid grasslands (Raich and Schlesinger 1992; Ansley et al. 2002). The role of fire season in modulating grassland C and N dynamics has received even less study. There is a growing awareness of the importance of fire season on aboveground vegetation dynamics. A common, though not universal, pattern is that the relative abundance of C_3 grass species increases following fall fires, while that of C_4 grasses increases after burns in the spring (Whisenant et al. 1984a; Hulbert 1988; Howe 1994; Howe 1995; Howe 2000; Engle and Bidwell 2001). This shift in community composition between plant functional types of relatively lower (C_3) and higher (C_4) tissue C:N may have marked consequences for biotically mediated fire effects on grassland C and N cycles (Wedin 1995; Wedin 1996). However, in more arid grasslands, abiotic factors (particularly moisture limitation) may predominate (Hobbs 1996; Burke et al. 1998).

This study evaluates the impacts of seasonal fire on soil respiration, N mineralization, soil moisture content, and soil temperature in a native mixed grassland of the southern Great Plains. We hypothesized that spring fire would promote increased productivity of C_4 grasses in a mixed C_3/C_4 grass community, thus reducing soil temperatures and increasing soil moisture content via increased shade from a more complete canopy. Increased soil respiration and decreased N mineralization were expected as consequences of increased root growth and higher litter C:N ratios, respectively. More intense fall fires were hypothesized to reverse these response patterns by fostering an increased ratio of C_3 to C_4 grass production.

METHODS

Study site

Research was conducted on a 1 ha grazing exclosure on the W.T. Waggoner Ranch in Wilbarger County, Texas (33^o 51'N, 99^o 26' W, elevation 381 m). Mean annual precipitation for the site is 665 mm, bimodally distributed, with peaks in May (18% of annual total) and September (12% of annual total). Mean annual temperature is 16.1^o C, with monthly average extremes ranging from 36 °C in July to -2.5 °C in January. Soils are classified as fine, mixed, thermic Typic Paleustolls of the Tillman series.

Dominant cool season (C_3) grasses include Texas wintergrass (*Nasella leucotricha* (Trin & Rupr) Pohl), a native perennial bunchgrass, and Japanese brome (*Bromus japonicus* Thunb. ex Murr.), an exotic annual grass. Dominant warm season (C_4) grasses include the perennial bunchgrass sideoats grama (*Bouteloua curtipendula* (Michx.) Torr.), and the stoloniferous, sod-forming buffalograss (*Buchloë dactyloides* (Nutt.) Engelm.). The study site was root-plowed and seeded with sideoats grama in 1974. It has not been burned since that time. The site was grazed by cattle at a moderate stocking rate (1 cow 12 ha^{-1}) from the late 1800s to 1988, when livestock were removed.

Experimental design

Dynamics of soil moisture, temperature, C efflux, and N mineralization were evaluated on experimental plots in a single-factor design. Treatments were randomly assigned to fifteen 6x6-m plots (n = 5 replicates/treatment combination/year). The following treatments were implemented annually beginning in 1999: 1) control (no fire), 2) spring fire, and 3) fall fire. Plots in the spring fire treatment (typical management fire) were subjected to prescribed fires in in February/March, while those in the fall fire treatment (typical wildfire) were burned in September/October, of 1999, 2000, 2001, and 2002. Fire intensity for all fires in all years was classified as low to moderate, with flame heights not exceeding 1.5 m. Rainfall was measured at the site.

Sampling and analysis

Sampling was carried out at approximately monthly intervals from June 2000 through May 2002. During each sampling period, a 1x1 m subplot was randomly chosen from each of the 30 treatment plots. Since sampling was destructive, no subplots were resampled. The following sampling procedures were performed on each 1x1 m subplot.

A composite soil sample consisting of 8, 2.5-cm diameter cores taken 10 cm deep was taken from each subplot. Sampling to this depth has been estimated to account for 70 % of root biomass and 40 % of SOM (Gill et al. 1999), as well as the greatest amount of available N in the profile (Dodd et al. 2000); it is also the depth increment most likely to experience changes in soil C and N storage in response to land management practices (Conant et al. 2001). Soil samples were immediately placed on ice for transport to the laboratory and subsequently stored at 4 °C until analysis. Samples within each treatment replicate were pooled, mixed thoroughly, passed through a 2-mm screen to remove large organic fragments, and pulverized prior to laboratory analysis. Gravimetric soil moisture was measured by drying a 10-g field-moist subsample from each subplot for 5 d at 105 °C and re-weighing (Jarrell et al. 1999). Remaining soil was dried for 5 d at 60 °C. A 7-g subsample of dried soil was ground to pass a 2-mm screen and shaken for 1 h with 28 ml 2 M KCl. The extract was filtered through # 2 filter paper and analyzed for concentration of NO_3^- and NH_4^+ on a Technicon autoanalyzer (Grasshoff 1969).

A LI-COR 6200 infrared gas analyzer (IRGA) was used to measure *in situ* soil temperature (at 10 cm) and soil respiration (in a chamber formed by a PVC collar 10 cm in diameter and extending 5 cm above, and 1-2 cm below, the soil surface) (Norman et al. 1992; Dugas et al. 1997). This method quantifies total CO_2 flux from the soil, and therefore represents the sum of respiration by roots and the respiration of heterotrophic soil organisms. No effort was made to separate root from heterotrophic respiration. Measurements were made on each subplot at 6-h intervals (0400, 1000, 1600, and 2200 h) during a 24-h period. Each measurement consisted of the average of four instantaneous rates of soil C efflux calculated on the basis of a 5 ppm change in the concentration of CO_2 in the respiration chamber. Some reports exist of significant differences in rates of soil C efflux between day and night measurement periods (Osman 1971; Redman 1978; Grahammer et al. 1991; Bremer et al. 1998), while other authors have found no difference (Knapp et al. 1998; Dugas et al. 1999; Mielnick and Dugas 2000). No significant difference between day and night rates of soil C efflux occurred at any sampling date during the study, so average rates from each of the four intervals during the 24-hour measurement period were averaged to calculate a single rate for each sampling date.

The resin-core incubation technique (DiStefano and Gholz 1986) was used to estimate net N mineralization. A single PVC core (4 cm diam. x 10 cm deep) was removed from each subplot, capped with bags of Rexyn I-300 anion-absorption resin, and returned to the hole from which it was taken to incubate until the following sampling period. At the end of the incubation, concentration of NO_3^- and NH_4^+ in incubated soil samples was determined using the procedure described above. Concentration of total inorganic N in the incubated core was subtracted from that of the composite sample, and added to that of the bottom resin bag, to provide an index of *in situ* N mineralization (DiStefano and Gholz 1986; Hart et al. 1994; Bhogal et al. 1999).

Data analysis

Data were analyzed using SAS Version 9.0 (SAS Institute 2002). Soil temperature and soil C efflux values were averaged across the four measurements per time period, and then across the four time periods per sampling date, prior to statistical analysis of the entire study period. Each response variable was separately analyzed using a two-way factorial ANOVA with sampling date and fire as factors. For all variables where significant interactions existed with sampling date, the analysis was also carried out within each sampling date, excluding sampling date as a factor. Where there were no significant treatment effects on soil C efflux or N mineralization, these variables were regressed upon independent variables of soil temperature, soil gravimetric moisture content, temperature by moisture interaction, and live plant cover.

RESULTS

Sampling date was a significant factor for all response variables (Table 30). In 2000, precipitation during the summer growth period of C_4 grasses (April – September) was below normal in every month, and the total for the period was 60 % of normal. In 2001, precipitation was below normal in 5 of the 6 months, with only August exceeding the normal amount (Figure 1).

Soil moisture content values displayed similar seasonal patterns across all treatments. Soil moisture was highest in late winter, declined through spring and early summer, and remained near its yearly minimum from midsummer through early fall (Figure 26A). There were no significant effects of fire on overall mean soil moisture (Tables 30, 31).

Soil temperature followed similar seasonal trends in all treatments (Figure 26B). Soil temperatures were lowest in January and peaked in August. Overall mean soil temperatures were not significantly affected by fire treatments (Tables 30, 31) .

Soil respiration rates remained low (< 100 g CO_2 m^{-2} mo^{-1}) through most of the year, peaking in late spring to early summer, with a return to low levels by August of all study years except 2002, when abnormally high rains occurred in that month (Figure 27A). Overall mean monthly rates of soil C efflux were not significantly affected by fire in either season (Tables 30, 31).

Seasonal maxima in rates of net N mineralization occurred simultaneously with those in soil C efflux; however, the former demonstrated more frequent oscillations between high and low (or negative) values between sequential pairs of sampling dates (Figure 27B). Net N mineralization did not respond significantly to fire in either season (Table 30). A multiple linear regression model revealed significant effects of soil moisture content and soil temperature, as well as live vegetation cover, on monthly rates of net N mineralization. N mineralization did not respond significantly to a moisture-by-temperature interaction term (Table 32).

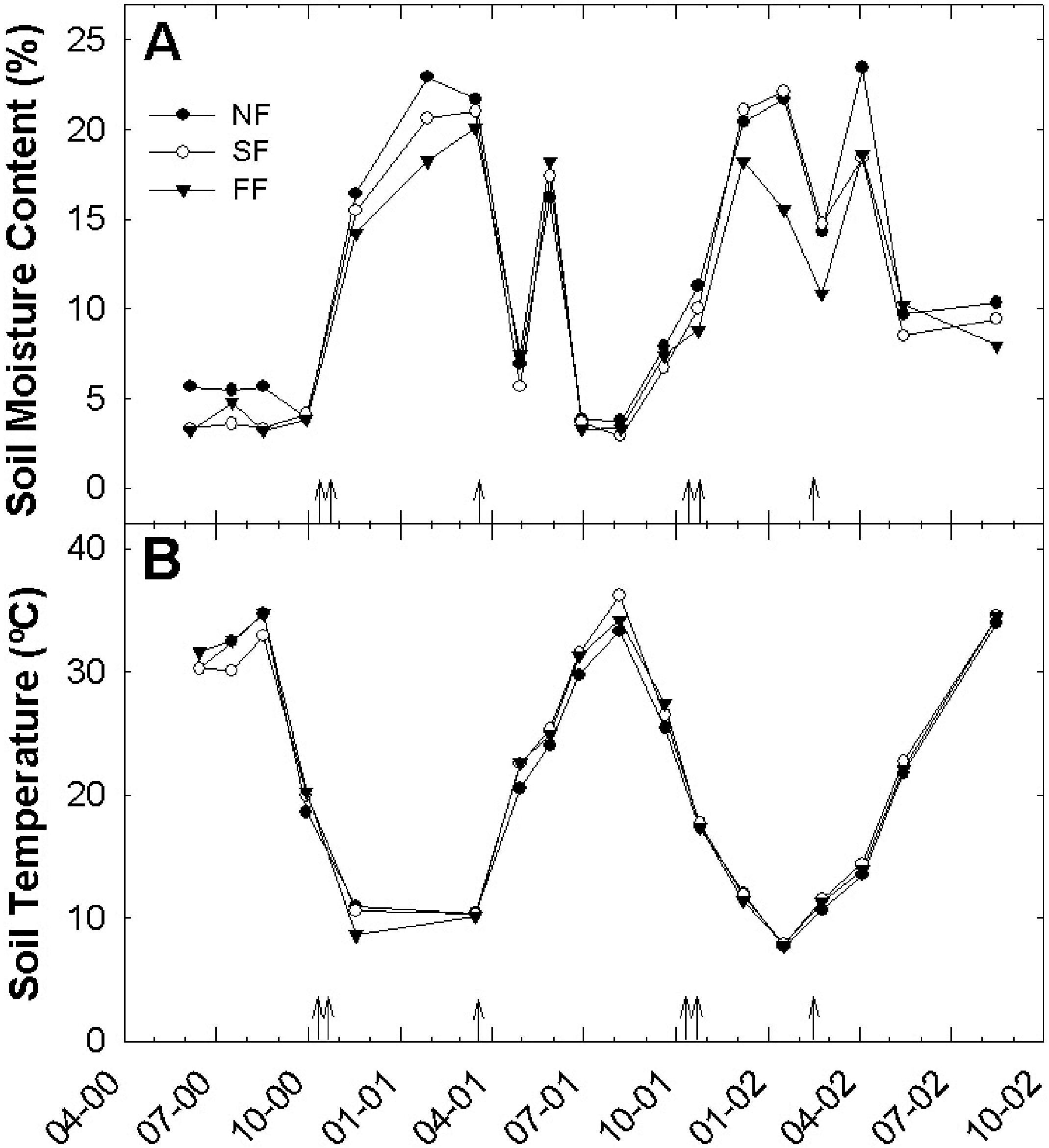

Figure 26. Mean monthly soil gravimetric moisture content (Panel A) and temperature (Panel B) under seasonal fire, June 2000-August 2002. Values are means of five replicates. Significant ($p \geq 0.05$) treatment effects within individual sampling dates are indicated by different lowercase letters. Dates of spring (single arrows) and fall (double arrows) fire are shown on the x-axis. Treatments are control (NF, no fire), SF (spring fire), and FF (fall fire).

TABLE 30. ANOVA results for the effects of fire season and sampling date on soil moisture, temperature, respiration, and net N mineralization.

	Fire	Date	Fire x date
Response	*P*	*P*	*P*
Soil moisture content	0.0605	< 0.0001	0.0003
Soil temperature	0.1255	< 0.0001	0.0026
C efflux	0.1423	< 0.0001	0.689
Net N mineralization	0.2068	< 0.0001	0.4371

TABLE 31. Mean (± 1 SE) overall temperature, moisture content, C efflux, and net N mineralization of surface 10 cm of soils, under seasonal fire, June 2000 - Aug 2002.

	No fire	Spring fire	Fall fire
Soil moisture content (%)	12.19 ± 0.47	11.30 ± 0.47	10.41 ± 0.47
Soil temperature (°C)	22.33 ± 0.19	22.79 ± 0.19	22.90 ± 0.19
C efflux (g CO_2 m^{-2} mo^{-1})	258.39 ± 13.37	244.96 ± 13.37	218.50 ± 13.37
Net N mineralization (g [NO_3^- + NH_4^+]-N m^{-2} mo^{-1})	1.10 ± 0.21	0.59 ± 0.21	0.62 ± 0.21

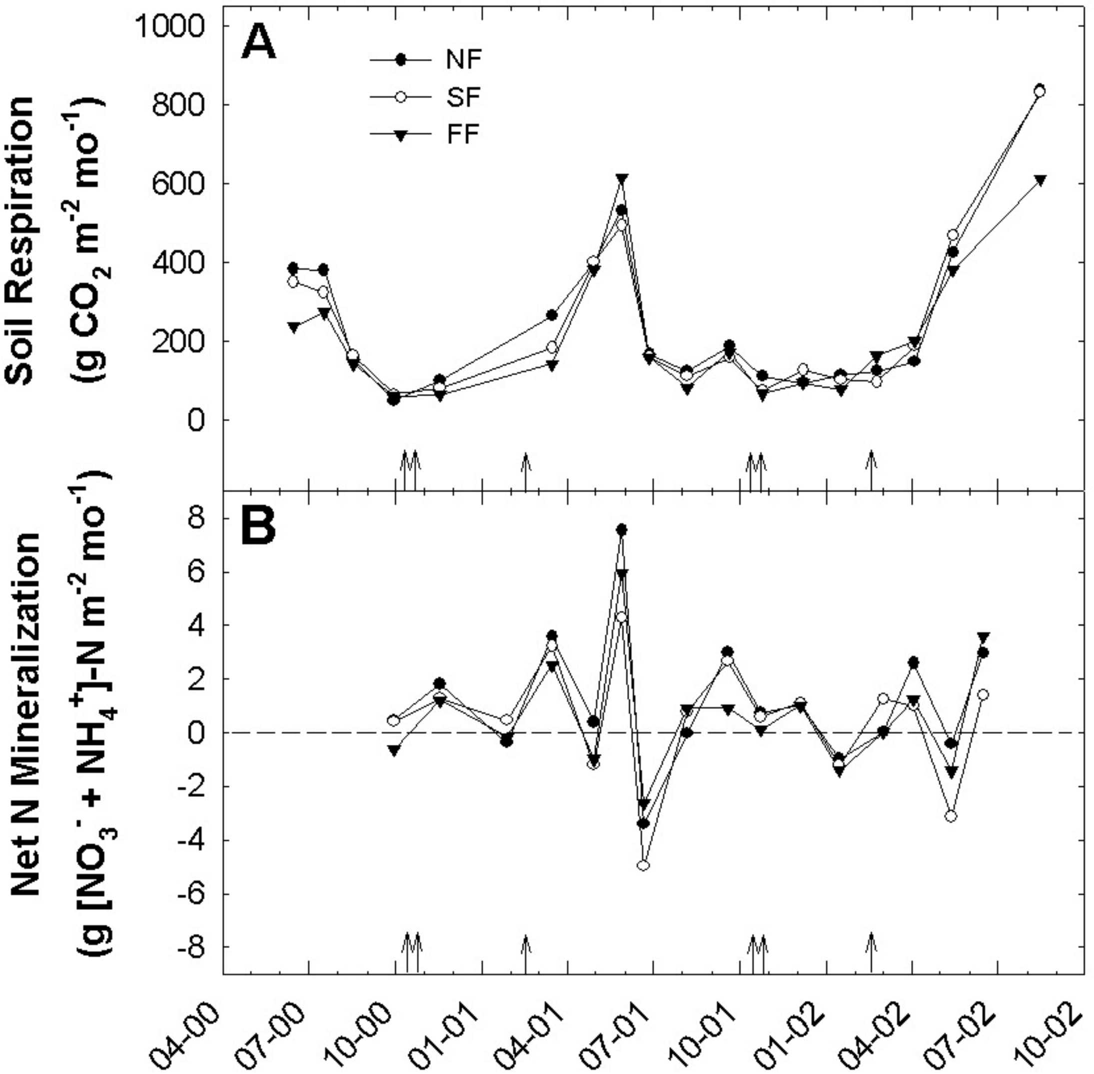

Figure 27. Mean monthly soil respiration (Panel A) and net N mineralization (Panel B) under seasonal fire, June 2000 - August 2002. Values are means of 5 replicates. Dates of spring (single arrows) and fall (double arrows) fire are shown on the x-axis.

Fire did not significantly affect overall mean concentrations of soil NO_3^-, NH_4^+, or total inorganic N (Table 33). There was a trend toward lower concentrations of soil NO_3^- in fire treatments, more pronounced in fall fire, but these differences were not significant (Table 34). Sampling date significantly affected overall mean concentrations of both soil NO_3^- and NH_4^+ as well as total inorganic N, as reflected in the pronounced seasonal variation of these values (Table 33). Concentrations of soil ammonium varied less, and were lower than, those of NO_3^- (Figure 28).

TABLE 32. Net N mineralization (g $[NO_3^- + NH_4^+]$-N m^{-2} mo^{-1}) as predicted by soil temperature (ºC), soil gravimetric moisture content (%), and live vegetation cover, September 2000 - June 2002. N = 45; adjusted $r^2 = 0.5402$; root mean square error = 1.33).

Property	Coefficient	$P > \|t\|$
Intercept	6.53	< 0.0001
Soil temperature	-0.17	< 0.0001
Soil gravimetric moisture content	-0.35	< 0.0001
Live vegetation cover	0.05	0.0037
Temperature x moisture	-0.01	0.0583

TABLE 33. ANOVA results for the effects of fire season and sampling date on soil inorganic N.

Response	Fire	Date	Fire x date
	P	*P*	*P*
NO_3^-	0.4355	< 0.0001	0.9230
NH_4^+	0.9734	< 0.0001	0.9522
Total inorganic N	0.0894	< 0.0001	0.9448

TABLE 34. Mean concentrations (± 1 SE) of nitrate, ammonium, and total inorganic nitrogen in bulk soil under seasonal fire, June 2000-May 2002.

	No fire	Spring fire	Fall fire
NO_3^- (mg NO_3^--N kg $^{-1}$ soil)	22.4 ± 2.7	22.2 ± 2.7	17.8 ± 2.7
NH_4^+ (mg NH_4^+-N kg^{-1} soil)	5.2 ± 0.4	5.3 ± 0.4	5.2 ± 0.4
Total inorganic N (mg NO_3^-- + NH_4^+-N kg^{-1} soil)	27.6 ± 2.7	27.4 ± 2.7	23.1 ± 2.7

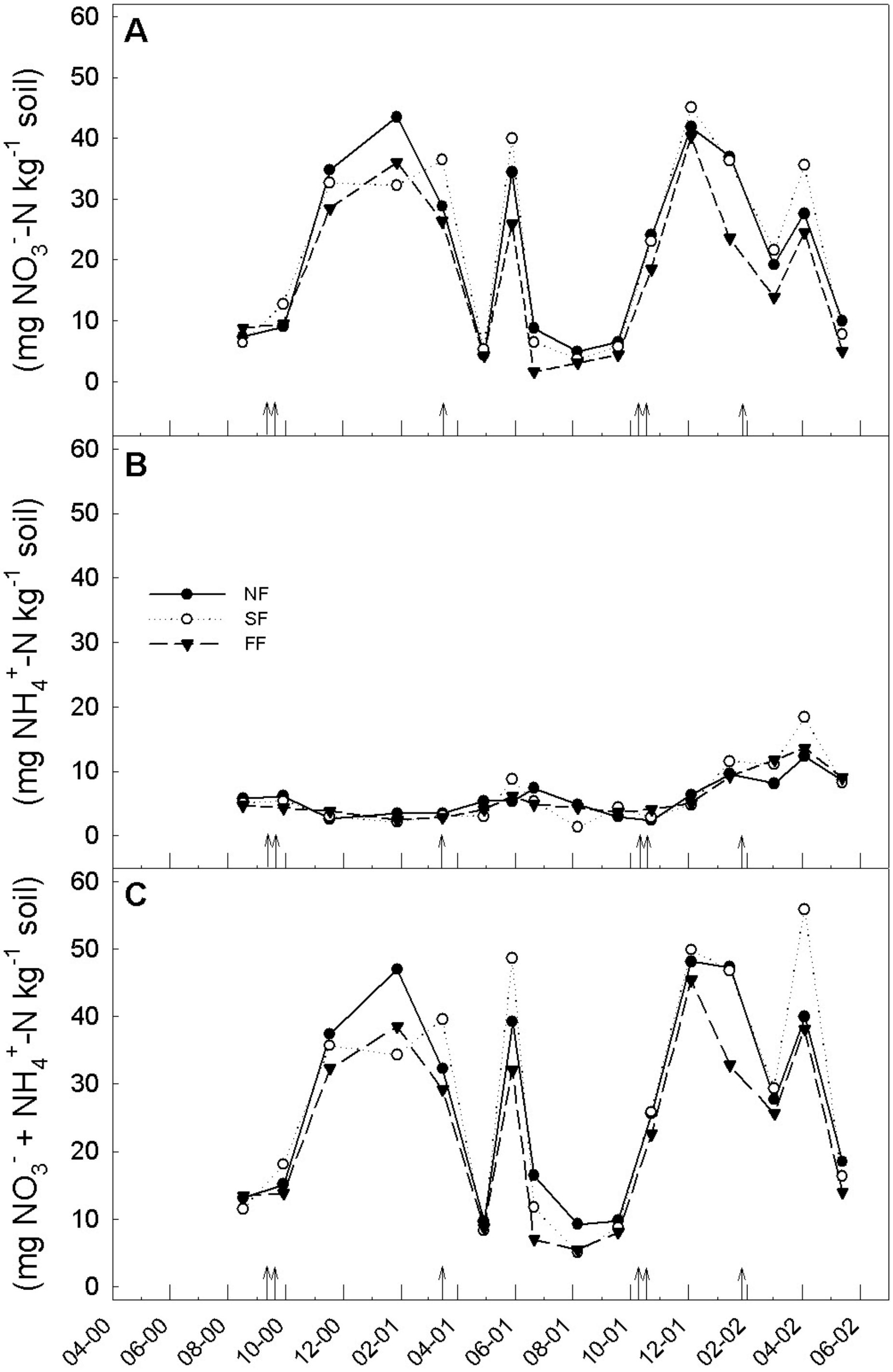

Figure 28. Concentration of soil NO$_3^-$, NH$_4^+$, and NO$_3^-$ + NH$_4^+$ under seasonal fire, May 2001-May 2002. Values are means of five replicates. Dates of spring (arrows) and fall (double arrows) fires are shown on the x-axis.

DISCUSSION

The results of this study support the hypothesis that season of fire alters microclimatic variables in mixed native grasslands of the southern Great Plains. A reduction in the rate of soil C efflux also accompanied fall fire; however, small contemporaneous treatment differences in soil temperature and moisture suggest that biotic factors were largely responsible. Reductions in soil net N mineralization in fire treatments were statistically nonsignificant, and likely also due to other mechanisms.

All response variables showed highly significant response to sampling date, indicating the importance of seasonal climatic variation as a contextual control on nutrient cycling in this ecosystem. Soil temperature and moisture followed predictable seasonal patterns, as did rates of soil C efflux and net N mineralization. Peaks in rates of C and N cycling occurred in April and May, when soil moisture content remained relatively high and temperatures had begun to rise. Seasonal fire did not significantly modify these general seasonal patterns in soil moisture content and temperature. Fire in both seasons significantly increased soil temperature and decreased soil moisture content. A significant interaction with sampling date was present in both effects, due to the fact that fire effects were limited to particular seasonal periods, occurring primarily within the first few months following burning. Increased soil temperature and decreased soil moisture followed spring burning in *N. leucotricha*-dominated communities elsewhere in the southern Plains (Whisenant et al. 1984a), as well as in C_4-dominated tallgrass prairie (Blair 1997; Knapp et al. 1998), although a more southerly tallgrass site showed no response of soil temperature to fire (Mielnick and Dugas 2000). These comparisons illustrate the significance of both regional climatic gradients and site-specific variation in precipitation, both within and between years, for the outcome of fire on soil moisture and temperature.

Soil temperature and moisture content, among other factors, control rates of soil C efflux (Kucera and Kirkham 1971; Bunnell et al. 1977; Schimel et al. 1990; Knapp et al. 1998; Dugas et al. 1999; Conant et al. 2000; Franzluebbers et al. 2002). Fire has led to significant increases in soil C efflux in some studies (Knapp et al. 1998; Johnson and Matchett 2001), but the finding is not generalized (Ross et al. 1997; Mielnick and Dugas 2000; Husta and Litvak 2003). At this study site, earlier work found a brief but significant decrease in soil C efflux following spring fire. This difference, along with monthly soil moisture and temperature, and net annual C efflux, varied significantly between years (Hubbard 2003). Interannual climatic variability thus helps to regulate the effects of fire on both soil microclimatic variables and their modulation of soil C efflux, even determining whether the net system C balance is positive or negative from one year to the next (Kim et al. 1992; Frank 2002). The more commonly reported pattern of increase in soil C efflux following fire in more mesic tallgrass prairie ecosystems may be due to regional climatic differences. In general, decreasing mean annual temperature corresponds to increasing sensitivity of soil respiration to temperature changes (Kirschbaum 1995; Bremer et al. 1998; Lomander et al. 1998; Franzluebbers et al. 2002). Additionally, water limitation is a regional feature of Great Plains grasslands that complicates the interpretation of relationships between temperature and C mineralization (Burke et al. 1998; Epstein et al. 2002). The severity of the summer drought during the period of this study, and its likely reduction of soil respiration rates, is of key importance in interpreting these results.

Mean overall rates of net N mineralization varied nearly twofold between the no fire treatment and those burned in either season; however, this difference was not statistically significant. This outcome is likely due to the combination of limited sample size and high micro-scale spatial variability in *in situ* measurements of net N mineralization (Jackson and Caldwell 1993). Research in tallgrass prairie has found a similar reduction in net N mineralization rates following fire (Turner et al. 1997; Johnson and Matchett 2001; Reich et al. 2001), attributed primarily to volatilization losses from the pool of aboveground N (Hobbs et al. 1991); see Chapter III. Multiple regression analysis revealed a slight but significant influence of both temperature and moisture content on net N mineralization rates. However, these differences are likely of insufficient magnitude and duration to cause a significant difference in rates of nutrient flux. Measurement of N mineralization was terminated prior to above-normal precipitation at a time of elevated soil temperatures in August 2002. It is expected that continued measurements during that period would have substantially increased the magnitude, and perhaps altered the sign, of temperature and moisture parameters in the regression analysis, as well as rendering significant the interaction between the two factors, as observed in an analysis of soil respiration rates from a separate experiment at the same site (see Chapter VI).

In contrast to the bulk of the literature on fire N effects in tallgrass prairie, fire did not reduce available soil N during any sampling period (Towne and Owensby 1984; Hobbs et al. 1991; Ojima et al. 1994; Blair 1997). It is conceivable that the number of replicates sampled in this design was inadequate to reveal such differences against the background of high variability at small spatial scales. However, other work in tallgrass prairie ecosystems has showed a similar lack of response of inorganic N to fire (Turner et al. 1997). In either case, other sources are likely responsible for large contributions to soil C and N pools. Roots are likely a significant source of C. Though this study quantified neither their biomass nor its response to treatments, previous work at the site has shown them to be responsive to fire, potentially compensating for any decrease in litter inputs (Hubbard 2003). The lack of N response may be due to a relatively larger pool of soil N present in microbial biomass (see Chapter III). By controlling the release of this microbial nitrogen in mineral form, soil microbes would have relatively greater influence on N inputs than those of C, which are governed primarily by plant production (Knops et al. 2002).

The different responses of soil respiration and net N mineralization rates suggest that the two processes may be controlled by different factors (Turner et al. 1997), and that treatment differences in soil microclimatic variables may play a relatively minor role in regulating both. The importance of biotic factors in determining rates of net N mineralization is highlighted by the significance of live vegetation cover as an independent variable in the multiple regression analysis. Some role for vegetation in regulating soil C efflux also seems likely based upon the contemporaneous occurrence of peaks in that response with those in live vegetation cover (see Chapter III). However, while reductions in the surface litter pool, like those in N mineralization, are of similar magnitude in both spring and fall fire treatments (see Chapter III), soil C efflux did not decline significantly only following fall fire. Fall fire also reduced the biomass of perennial grasses (virtually eradicating those posessing the C_4 photosynthetic pathway, which were already in decline in response to repeated summer drought), resulting in increased cover and biomass of forbs and C_3 annual grasses with less extensive and/or less continuously active root systems (see Chapter III). At the study site, root growth responds significantly to fire (Hubbard 2003), and root respiration likely represents a substantial contribution to total soil C efflux (Norman et al. 1992; Bremer et al. 1998; Knapp et al. 1998; Franzluebbers et al. 2002); see Chapter II. Thus, above- and belowground controls differ in their importance and mode of action for C and N cycles in this as well as other grassland ecosystems (Burke et al. 1997; Frank and Groffman 1998; Knops et al. 2002). An understanding of the interplay between these mechanism in years with normal summer precipitation and C_4 grass productivity remain as questions for future research.

CHAPTER VIII

CONCLUSIONS

In a community where both C_3 and C_4 grass functional types are strongly represented, repeated summer drought during the C_4 growing season, together with normal or above-normal precipitation during the C_3 growing season, almost certainly influenced dynamics of both above- and belowground production and decomposition. Interpretations of the data reported here must acknowledge the climatic circumstances in which they were recorded as a qualifier to any general assessment of the effects of seasonal fire and clipping in the study system.

Fire alone, in either season, decreased the aboveground cover of live vegetation and increased the amount of bare ground. Fire reduced live vegetation cover for a temporary period following fire, while its increase in the area of bare ground was of longer duration and tended to increase with repeated fires. These findings stand in contrast to reports from tallgrass prairie, where an increase in ANPP is the consistent response to annual spring fire in the absence of grazing (Seastedt and Ramundo 1990; Seastedt and Knapp 1993; Blair 1997; Briggs and Knapp 2001). This discrepancy may reflect moisture limitations on C_4 grass production during the period of the study, or perhaps a more general lack of responsiveness to fire in mixed-grass prairie. Similarly, though decreased abundance of C_4 grasses is a common response to summer or fall fire (Towne and Owensby 1984; Collins 1987; Howe 1994; Howe 1995; Howe 2000; Engle and Bidwell 2001), no such effect was observed in the present study.

In the presence of clipping, spring fire had no effect on live vegetation cover, though it increased the area of bare ground. Both a single spring clipping and continuous monthly clipping during periods of active growth decreased live vegetation cover while increasing the area of bare ground. Responses of live vegetation cover to both fire and clipping appear to have been dominated by the dynamics of C_3 annual grasses. Clipping, both once in spring and at monthly intervals during active growth, significantly reduced the cover of C_3 annual grasses. Continuous clipping also increased the cover of C_3 perennial grasses. Clipping, primarily on the April dates common to both spring and continuous clipping treatments, appears to have occurred at a time during the phenological development of of C_3 annual grasses that reduced their seed production. Both clipping and fire, by reducing the mass of surface litter, may have further reduced C_3 annual grass cover by reducing the number of suitable sites for germination (Whisenant 1990). C_3 perennial grass cover increased under clipping, though not enough to compensate for the reduction by clipping of total live vegetation cover. However, given the bunch-type growth form of *N. leucotricha*, the positive effect of clipping on its live cover suggests that corresponding increases in its biomass could account for the lack of clipping effects on total live biomass of C_3 grasses overall.

Increases in the area of bare ground, however, whether in response to fire or clipping, were a result of decreases in surface litter mass rather than of live vegetation cover. Clipping likely interrupted inputs of current-season plant biomass to surface litter pools, while fire consumed those pools directly.

Litter, rather than live vegetation, also appears to have been the primary conduit for effects of fire and clipping on belowground C and N dynamics in this ecosystem. Fire (in either season) reduced surface litter to a greater extent than clipping, and fire, but not clipping, reduced soil microbial C. Neither fire nor clipping significantly affected microbial N, reflecting a relatively greater decline in aboveground inputs of C relative to N as a result of disturbance. This is consistent with a hypothetical framework in which soil microbial biomass represents the greatest pool of potentially available soil N, and microbes govern the rate of release of mineral N to plants, though their activity is governed by inputs of plant C (Knops et al. 2002). Circumstantial support for this interpretation is available in the observation that peaks in microbial N content were almost exactly out of phase with those in soil inorganic N (compare, for example, Figure 6B, Chapter III, with Figure 4C, Chapter VII).

The conception of litter as the primary conduit for effects of aboveground disturbance on soil C and N cycling was consistent with two other significant fire effects. First, fire reduced the δ^{13}C value of surface litter, suggesting a shift toward greater dominance of C_3 plant material in the litter pool. Since fire consumed a greater volume of surface litter than clipping, and C_4 grass production was low relative to that of C_3 grasses during the study period, such a shift is readily explicable even absent an absolute increase in C_3 grass biomass. Second, fire reduced the amount of light-fraction soil organic matter, assumed to be the next stage after surface litter in the decompositional sequence. The pool size of active soil C estimated from potential C mineralization assays corresponded in magnitude to that of light-fraction organic matter.

Bulk soil C and N concentrations declined over the course of the study period independent of treatment effects. These changes may be due in part to decreased C_4 grass production either as a consequence of repeated summer precipitation deficits, or of increasing dominance by C_3 grasses (both annual and perennial) in response to changes in fire and grazing regimes from those that prevailed historically (Ansley et al. 2004). They also suggest that factors other than aboveground litter inputs may play a substantial role in determining the absolute sizes of soil C and N pools.

Data on soil respiration and net N mineralization provide insight into the potential identity of these other factors. Changes in soil temperature and moisture in response to fire were significant but temporary, and likely too small to account for observed between-treatment differences in C and N flux. This finding provides additional support for the suggestion that both changes in soil moisture and temperature, and the response of soil C and N flux to those changes, may be of greater magnitude in grasslands with lower MAT (Kirschbaum 1995; Lomander et al. 1998). In accord with findings from tallgrass prairie, net N mineralization decreased in response to fire (Turner et al. 1997; Johnson and Matchett 2001; Reich et al. 2001), though it was unaffected by clipping. Again, since fire reduced surface litter, light soil density fractions, and microbial C, it may have reduced the supply of labile organic C that drives microbial N mineralization, thus reducing net N mineralization rates while clipping did not.

In contrast to other reports (Bremer et al. 1998; Wan and Luo 2003), neither fire nor clipping affected soil respiration rates. The contribution of roots as well as microbes to soil respiration may explain why N mineralization responded significantly to fire while soil respiration did not. Soil respiration did show a significant positive relationship with live vegetation cover, suggesting the potential for treatment-induced shifts in root dynamics as one link between disturbance and soil respiration (Norman et al. 1992; Knapp et al. 1998; Franzluebbers et al. 2002). Root production has previously been found to increase in response to fire and clipping at the study site (Hubbard 2003), but was not quantified in the present study.

In summary, disturbance in the form of fire and clipping acted to limit flows of C from aboveground plant production to soil microbial decomposition, with the primary interruption occuring either by prevention of plant material from entering the litter pool (clipping) or by combustion of litter (fire). The resulting effects on soil microbial C content, as well as light-fraction soil organic matter, point toward a dynamic in which microbes conserve soil N, while plant inputs drive the C cycle. Lack of treatment effects on bulk soil C and N pools, coupled with treatment-independent change in those pools during the period of study, suggest that fire and clipping may have a) modified plant-soil C and N cycles via mechanisms not quantified, such as root dynamics, or b) shared a regulatory role with other factors, including those, such as interannual variability in precipitation and directional equilibration of community composition in response to alteration in fire and grazing regimes, that are manifested on longer temporal scales. Further evaluation of these possibilities remains necessary for a more complete understanding of disturbance effects on plant-soil C and N cycles in mixed grassland ecosystems of the southern Great Plains.

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