Fire, N Availability, and Plant Response in Grasslands: A Test of the Transient Maxima Hypothesis

John M. Blair

Ecology, Vol. 78, No. 8 (Dec., 1997), 2359-2368.

Ecology, 78(8), 1997, pp. 2359–2368

FIRE, N AVAILABILITY, AND PLANT RESPONSE IN GRASSLANDS: A TEST OF THE TRANSIENT MAXIMA HYPOTHESIS

JOHN M. BLAIR

Division of Biology, Kansas State University, Manhattan, Kansas 66506 USA

Abstract. In tallgrass prairie, periodic spring fires often result in enhanced aboveground net primary productivity (ANPP) that exceeds the productivity of either annually burned or unburned sites. This study evaluated two alternate hypotheses for the "pulse" in productivity following an infrequent fire: (1) enhanced ANPP results from increased net N mineralization rates due to the removal of surface litter and elevated soil temperatures following fire (the enhanced mineralization hypothesis) or (2) enhanced ANPP results from a transient release from both light and N limitation during a nonequilibrium period as a switch from energy to N limitation occurs (the transient maxima hypothesis). The former hypothesis predicts greater N availability following an infrequent fire, relative to either annually burned or unburned prairie. The latter predicts that N availability following an infrequent fire will decline to intermediate levels, relative to unburned and annually burned prairie, and continue to decline with successive annual fires.

To test these hypotheses, I measured inorganic soil N, net N mineralization rates, and plant productivity and N content at Konza Prairie in sites with several different burn histories (unburned, annually burned, infrequently burned). Inorganic soil N and cumulative net N mineralization rates were greatest on the unburned sites, lowest in annually burned sites, and intermediate in infrequently burned sites. Net N mineralization rates and plant tissue N content both declined with successive spring burning. These results did not support the enhanced mineralization hypothesis but indicated that enhanced ANPP following an infrequent fire resulted from an accumulation of inorganic and mineralizable N in the absence of fire which, under conditions of adequate light availability, was utilized following a spring fire. This is consistent with the transient maxima hypothesis and suggests that nonequilibrium responses to multiple, variable resources (light, energy, N) are an important aspect of tallgrass prairie ecosystem dynamics.

Key words: fire; Kansas; Konza Prairie; LTER; N cycling; nitrogen availability; nitrogen mineralization; nonequilibrium dynamics; tallgrass prairie; transient maxima hypothesis.

INTRODUCTION

Periodic fire is essential for the development and maintenance of tallgrass prairie ecosystems (Collins and Wallace 1990), and affects many key characteristics of tallgrass prairie including plant species composition (Collins et al. 1995), productivity (Hulbert 1969, Abrams et al. 1986, Briggs and Knapp 1995), and ecosystem nutrient cycles (Seastedt and Ramundo 1990, Ojima et al. 1994). The cycling of N is affected greatly by fire frequency, since volatilization of N during combustion of aboveground biomass and detritus is the major pathway of N loss in tallgrass prairie ecosystems (Ojima et al. 1990, Seastedt and Ramundo 1990). Therefore, the degree to which plant productivity is limited by N availability in these grasslands varies substantially with fire frequency. Plants growing in annually burned prairie exhibit many characteristics associated with N limitation (Knapp and Gilliam 1985), including lower tissue N concentrations (Schimel et al. 1991), higher nitrogen use efficiency (NUE) (Ojima et al. 1990), and greater increases in productivity in response to N additions (Seastedt et al. 1991), compared to unburned tallgrass prairie. In contrast, plant productivity in unburned prairie is constrained more by energy limitations than by N availability, due to the shading effects of accumulated detritus (Knapp and Seastedt 1986), and plant responses to fertilizer N in these sites are minimal (Seastedt et al. 1991, Turner et al., *in press*). A third factor that can limit productivity in these grasslands is soil water content, which is typically lower in burned sites relative to unburned sites, and which varies with topographic position. Thus, patterns of productivity in tallgrass prairie are best explained within the context of a nonequilibrium system where the relative limitations of N, energy, and water vary across multiple scales in both space and time (Seastedt and Knapp 1993).

An analysis of 19 yr of data from the Konza Prairie Long-Term Ecological Research (LTER) program indicates that, in spite of considerable interannual variability, aboveground net primary productivity (ANPP) is typically greater in annually burned sites, compared to long-term unburned sites, provided that soil moisture

Manuscript received 16 October 1996; revised 12 January 1997; accepted 24 January 1997.

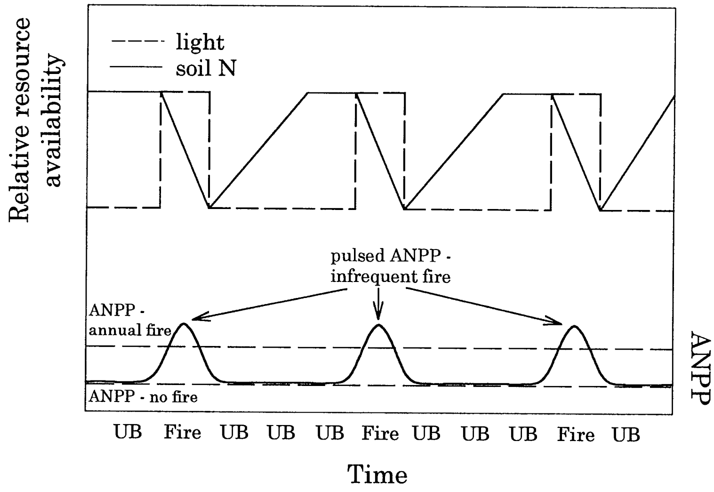

FIG. 1. A graphical illustration of the transient maxima hypothesis, which predicts transient "pulses" of plant productivity (———) greater than average productivity in tallgrass prairie either annually burned or unburned (– – –), as a result of increased light availability and gradually declining N availability following infrequent fires in generally unburned (UB) prairie (modified from Seastedt and Knapp 1993). Note that the figure illustrates patterns of change in resource supply rates; the specific temporal dynamics of these changes may vary.

is adequate (Briggs and Knapp 1995). The sustained high ANPP of annually burned sites occurs in spite of greater N limitation, relative to unburned prairie, and appears to be due, in part, to a more favorable energy environment that results in an increased NUE by the dominant warm-season grasses (Ojima et al. 1994). Interestingly, the greatest rates of ANPP in tallgrass prairie often occur during the growing season following a spring fire in an infrequently burned prairie—that is, prairie that is burned after an extended period without fire (Hulbert and Wilson 1983, Seastedt et al. 1991, Briggs et al. 1994). These "pulses" of high ANPP, which also can occur following periodic droughts, are not sustainable but may play an important role in the long-term accrual of organic matter in these ecosystems. Fertilization experiments have demonstrated lower plant production responses to added N following an infrequent fire, relative to annually burned prairie (Seastedt et al. 1991), leading to the hypothesis that the pulse in ANPP following an infrequent fire is related to increased N availability. One potential explanation is that soil organic N accumulates in the absence of fire, and that warmer soil temperatures following removal of accumulated litter and standing dead vegetation (Knapp and Seastedt 1986) stimulate mineralization of soil N (Risser and Parton 1982, Hulbert 1988, Ojima et al. 1994). A prediction of this "enhanced N mineralization hypothesis" is that N availability should be elevated following an infrequent fire, relative to either annually burned sites or unburned sites. An alternate explanation is that the pulse in ANPP occurs in response to a simultaneous and temporary release from multiple resource constraints (an example of the "transient maxima hypothesis"; Seastedt and Knapp 1993). According to this hypothesis, enhanced ANPP following an infrequent fire is due to relatively high availability of both light and N, as the ecosystem switches from one limited primarily by energy (light and temperature) to one limited by soil N availability (Fig. 1). During this transition phase, the relative availability of both light and N are greater than the availability of one or the other of these potentially limiting resources when tallgrass prairie ecosystems are either left unburned or are burned annually. A prediction of the transient maxima hypothesis is that relative N availability should be lowest in the N-limited annually burned sites, and greatest in the energy-limited, unburned sites. N availability in sites that are burned for the first time following a prolonged absence of fire is expected to decline over time, and thus become intermediate between annually burned and unburned sites. A corollary is that continued spring fires should reduce N availability to levels characteristic of annually burned sites. To date, there have been few studies that have directly quantified soil N dynamics under annually burned, infrequently burned, and unburned prairie, and there have been no tests of the transient maxima hypothesis as a mechanism to explain pulsed patterns of productivity in tallgrass prairie ecosystems.

The main objective of this study was to determine if the pulse in tallgrass prairie ANPP in response to infrequent fire was due to greater net N mineralization following a fire, relative to unburned and annually burned sites (the enhanced mineralization hypothesis), or due to a combination of adequate N availability and a favorable energy environment (the transient maxima hypothesis). A second objective was to determine how N availability and plant responses were affected by two consecutive years of burning, as a means of assessing the potential sustainability of the response to infrequent fires. To address these objectives I compared soil N availability, plant productivity, and plant tissue chemistry on adjacent replicate plots on uplands and lowlands that were either annually burned, unburned, or infrequently burned (burned once or for two consecutive years during the course of the study). The study was done in both upland and lowland areas since previous studies have indicated that N availability and responses to fire can vary with topographic position (Schimel et al. 1991, Knapp et al. 1993, Benning and Seastedt 1995, Turner et al., *in press*).

METHODS

Site description

This research was conducted between May 1994 and October 1995 on the Konza Prairie Research Natural Area (KPRNA), a 3487-ha tallgrass prairie located in the Flint Hills of eastern Kansas (39°05′ N, 96°35′ W). The region was characterized by relatively steep topography, with elevations from 320 to 444 m. Soils varied considerably with topography. Uplands typically had shallow rocky soils, while lowlands were characterized by deeper soils formed by thick colluvial and alluvial deposits. Vegetation at Konza was representative of unplowed native tallgrass prairie and was dominated by the C_4 grasses big bluestem (*Andropogon gerardii*), Indian grass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Andropogon scoparius*). Mean precipitation is 835 mm/yr (30-yr average), with 75% of this occurring during the April to September growing season (Bark 1987). Mean monthly air temperature varies from −3°C in January to 27°C in July. Mean monthly soil temperature at 5 cm depth varies from 1.6°C in January to a high of 29.3°C in July.

Experimental design

Replicate 10 × 10 m plots of each fire treatment were established on an upland area of adjacent watersheds (watersheds 1D and 10D) that either were annually burned or were on a scheduled 10-year burn cycle, and on a lowland area of two adjacent watersheds (watersheds 1C and 10C) with the same scheduled burn cycles ($n = 2$ plots per fire treatment per topographic location). All plots at a given topographic position were located in close proximity and on similar soils. Three fire treatments were included in 1994: "annually burned" (spring fires for >17 consecutive years), "unburned" (burned only twice in the past 18 yr; 1986 and 1991 for the upland site, 1973 and 1991 for the lowland site), and "burned 1×" (previously "unburned," but burned in the spring of 1994). The treatments "unburned" and "burned 1×" were assigned randomly to plots located within unburned watersheds. Although both "unburned" plots were burned during a wildfire in spring of 1991, accumulations of surface detritus (average 580 g/m^2) had recovered to levels characteristic of unburned prairie (Seastedt 1985) by 1994. Experimental plots were burned on 4 May 1994. In 1995, the burned 1× plots were burned a second time, creating an additional fire treatment ("burned 2×"), and the unburned plots were split so that half remained unburned and half was burned for the first time ("burned 1×"). Plots were burned between 6 and 14 April 1995. Soil temperature probes were installed (7 cm deep) in burned and unburned plots at both locations.

Soil N measurements

In situ net N mineralization was measured monthly from 10 May through 30 November 1994, and from 25 April through 10 October 1995, using an intact buried soil core technique (modified from Raison et al. 1987). Six sharpened PVC [polyvinyl chloride plastic] cores (5 cm diameter × 15 cm long) per plot were driven 14 cm into the ground, and covered with lids to prevent leaching losses. In unburned sites surface litter was moved to the side prior to inserting the cores, and then replaced to provide natural shading over the cores. Small holes in the exposed upper 1 cm of the tubes allowed for gas exchange. Cores were incubated in the field for ~30-d intervals. At the time PVC cores were placed, six similar soil cores were taken in adjacent locations to measure initial soil inorganic N content. Subsamples of field-moist soil, sieved through a 4-mm screen, were extracted with 2 mol/L KCl solution, and concentrations of inorganic N (NH_4-N and [NO_2 + NO_3]-N) were determined colorimetrically using an Alpkem FlowSolution analyzer. Additional subsamples of soil were dried at 60°C to determine gravimetric soil water content, and to calculate extractable soil N concentrations as N mass per unit mass of dry soil. Concentrations of extractable soil N were converted to mass per unit area using an average soil bulk density of 1 g/cm^3 (Seastedt and Ramundo 1990). Daily net N mineralization rates for specific incubation periods were calculated as ($N_F - N_I$)/(incubation time in days), where N_F is the final concentration of total extractable N (NH_4-N + NO_3-N) in postincubation PVC cores and N_I is the initial concentration of total extractable N in the adjacent core taken at the start of the incubation period. Cumulative N mineralized over the growing season was calculated by summing net N mineralization rates from specific incubation periods, and extrapolating values for the short periods between incubations.

Plant responses

Aboveground net primary productivity (ANPP) was estimated by clipping all vegetation within 0.1-m^2 quadrats ($n = 6$ quadrats per plot) to ground level at the end of the growing season. Biomass clipping was done on 1 October 1994 and on 26 August 1995. The earlier clipping date in 1995 was selected to allow analysis of grass tissue N content near the time of peak aboveground biomass accumulation. Clipped vegetation was sorted into grass and forb biomass produced during the current growing season and previous dead (unburned watersheds only), dried (at 60°C), and weighed. Individual grass and forb samples from 1995 were ground and analyzed for total C and N content using a Carlo–Erba C/N analyzer. Roots and rhizomes were sampled on 25 September 1995. Soil cores (5 cm diameter × 15 cm deep, $n = 6$ cores per plot) were

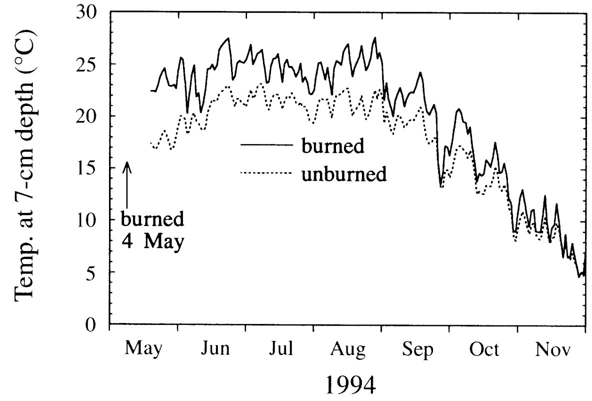

FIG. 2. Mean daily soil temperatures at a depth of 7 cm in burned and unburned upland plots ($n = 3$ probes per treatment) in 1994.

collected and washed to remove soil. Plant tissue was sorted into live roots, dead roots, and rhizomes. Individual samples were ground and analyzed for C and N content.

Data analysis

Data from each year were analyzed separately, first by two- or three-way ANOVA using fire treatment, topographic position, and date of sampling (where appropriate) as main factors. If there was no significant effect of topographic position, upland and lowland plots were combined to evaluate fire effects. Log transformations were used to normalize data where appropriate. An arcsine transformation was used to normalize tissue C and N concentrations. Tukey's mean separation test was used to determine where significant differences occurred. All analyses were done using SAS (SAS Institute 1989), and the level of significance for all tests was $P < 0.05$ unless otherwise noted.

RESULTS

Climatic conditions

Soil moisture and temperature are important driving variables for nitrogen mineralization in grassland ecosystems, and the results presented here should be considered in the context of climatic conditions during the time of the study. Annual precipitation in 1994 (636 mm total) was 24% lower than the long-term average for Konza Prairie (835 mm/yr), although it was well within the range of extremes that characterize climate at the site (Bark 1987). Precipitation during January–March 1994 was 28 mm (71% below average) and growing season precipitation (April–October) was 478 mm (24% below average). In contrast, annual precipitation in 1995 was 990 mm, or 18% above the long-term average. Precipitation during January–March 1995 was 128 mm (32% above average), while growing season precipitation was 818 mm (30% above average).

Soil temperature measurements from 1994 are presented to illustrate differences between burned and unburned plots (Fig. 2). Mean daily soil temperatures were up to 6°C higher in burned upland plots, relative to unburned upland plots, throughout much of the growing season. Results from the lowland plots (not shown) were similar, although differences between burned and unburned plots did not remain as great later in the growing season.

An ANOVA of gravimetric soil water content (0–14 cm depth) across all dates in 1994 indicated no significant differences in soil moisture between upland and lowland sites, which were pooled for subsequent analyses. However, across all dates in 1994 soil water content was significantly greater on unburned plots relative to either annually burned or burned 1× plots ($P = 0.0001$; Fig. 3). In 1995, differences among fire treatments were not significant across all dates ($P = 0.09$). However, fire effects were significant on each of the first three sample dates in 1995, with annually and 2× burned sites typically drier than the other sites (Fig. 3). As with soil temperature, treatment effects on soil water content diminished from early to late in the growing season in both years.

Soil N responses

Seasonal patterns in the concentrations of inorganic soil N (NH_4-N + NO_3-N) are presented for both 1994

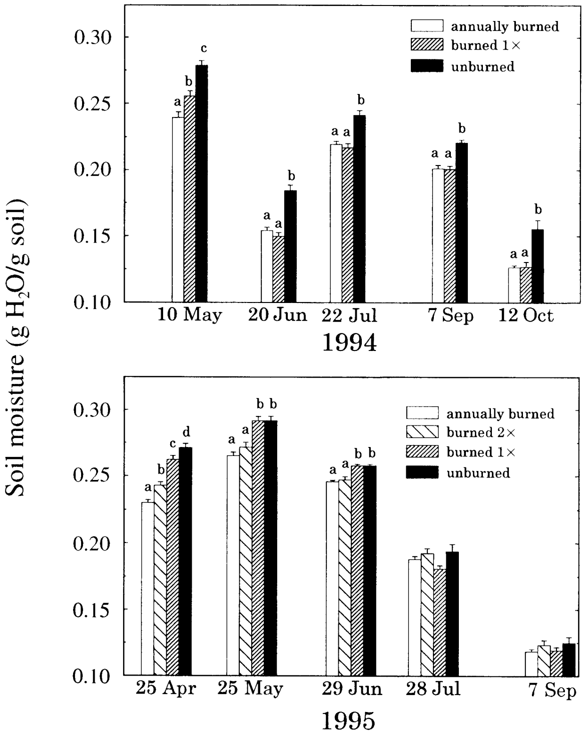

FIG. 3. Gravimetric soil moisture (mean and 1 SE) at the start of in situ N mineralization assays in plots subjected to different fire treatments in 1994 and 1995. Values are averages of plots located at upland and lowland positions. Significant differences among fire treatments on specific sample dates are indicated by different letters above the bars.

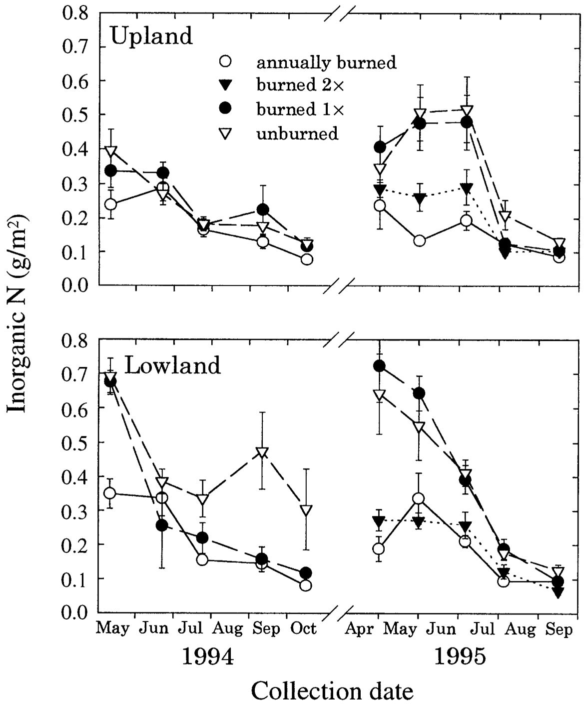

FIG. 4. Concentrations (mean ± 1 SE) of KCl-extractable inorganic N (NO_3-N + NH_4-N) in soils of upland and lowland plots subjected to different fire treatments.

and 1995 (Fig. 4). An ANOVA across all dates in 1994, indicated significant effects of fire treatment (unburned > burned 1× > annually burned, $P = 0.0001$) and topography (lowlands > uplands, $P = 0.0001$), as well as a significant fire treatment × topography interaction ($P = 0.0003$). In 1994, fire generally had a greater effect on extractable N at the lowland site. An ANOVA across all dates in 1995 indicated significant effects of fire treatment only (burned 1× ≈ unburned > burned 2× ≈ annually burned, $P = 0.0001$). ANOVAs were also done by date to examine the effects of fire treatments and topography in more detail. In 1994, concentrations of extractable soil N were significantly greater in the unburned treatment, compared to the annually burned treatment, and were significantly greater in the lowland plots, on all dates except 20 June. The burned 1× treatment was not significantly different from the unburned treatment on 10 May and 22 July. There were significant fire treatment × topography interactions on the 22 July, 7 September, and 12 October sample dates, with differences between fire treatments being most evident in the lowland plots. In 1995, there were significant effects of fire treatments on all dates, with the unburned and burned 1× treatments generally having greater concentrations of extractable N, relative to the annually burned and burned 2× treatments, which were not significantly different from one another (Fig. 4). Topography had a significant effect only on the 25 May date (lowland > upland). In addition, there was a fire × topography interaction on the 25 April date, when the effects of fire treatment were most pronounced at the lowland site.

There also were significant differences in the form of extractable inorganic N among fire treatments (data not shown). Across all dates, NO_3-N comprised a significantly smaller percentage of extractable inorganic N ($P = 0.0001$) on the annually burned plots (average of 13% in 1994 and 15% in 1995), relative to the other fire treatments, which were not significantly different from one another (averages ranged from 24 to 29%). There also was a significant effect of topography in both years ($P = 0.0001$) with NO_3-N generally comprising a greater proportion of extractable inorganic N on lowland sites (average of 27% among treatments), relative to uplands (average of 18% among treatments).

A preliminary ANOVA of daily net N mineralization rates across all dates in 1994 indicated a significant effect of fire treatment (unburned > burned 1× > annually burned; $P = 0.0001$), but no significant effect of topography. When data were pooled by topographic position, net N mineralization on most dates was significantly greater in the unburned treatment, relative to either fire treatment ($P = 0.0005$), although soils of the burned 1× treatment appeared to have intermediate mineralization rates during the first two measurement periods following spring burning (Fig. 5). Separate ANOVAs by date indicated a significant fire × topography interaction for the June–July and September–October incubation periods. Patterns of net nitrification were similar (data not shown). An ANOVA of daily net N mineralization data, across all dates in 1995, indicated significant effects of fire treatment (unburned > annually burned only; $P = 0.007$) and a significant effect of topography (uplands > lowlands; $P = 0.046$). Separate ANOVAs done by date in 1995 indicated a significant effect of topography (upland > lowland; $P = 0.002$) only during the May–June incubation period. Effects of fire treatments were significant only for July–August and September–October incubation periods (Fig. 5).

Cumulative net N mineralization calculated for the 1994 growing season (Fig. 6) was significantly affected by fire treatments ($P = 0.004$), but was not significantly different in upland and lowland sites. Soils in unburned plots mineralized ~3× more total N over the growing season (3.1 ± 0.3 g/m^2) than soils in annually burned plots (1.0 ± 0.2 g/m^2). Net mineralization in plots burned 1× was intermediate (1.7 ± 0.2 g N/m^2). In 1995, cumulative net N mineralization was affected by both fire treatment ($P = 0.001$) and topography ($P = 0.04$). As in the previous year, soils in unburned plots mineralized the most N (2.7 ± 0.3 g/m^2), while annually burned plots mineralized the least N (1.5 ± 0.2 g/m^2). The less frequently burned treatments were intermediate, with net mineralization in the plots burned 1× (2.4 ± 0.3 g N/m^2) being more similar to the unburned treatment, and net mineralization in the plots

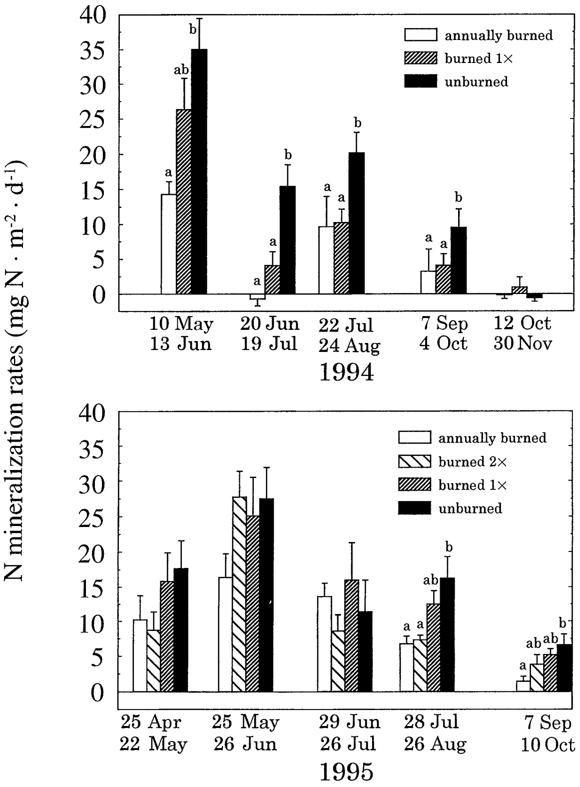

FIG. 5. Daily net N mineralization rates (mean and 1 SE) for the incubation periods specified beneath each set of histogram bars, in 1994 and 1995. Different letters above histogram bars indicate significant differences among fire treatments on individual sample dates.

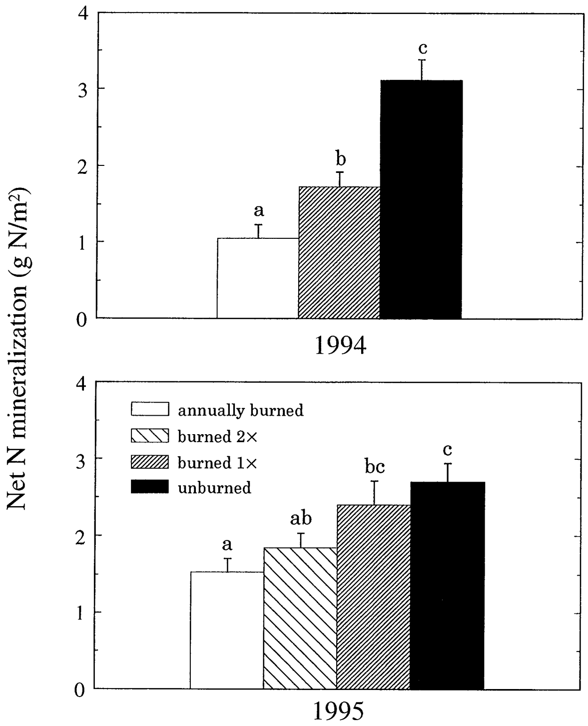

FIG. 6. Cumulative net N mineralization (mean and 1 SE) for different fire treatments, averaged across topographic position, during the growing seasons of 1994 and 1995. Different letters above histogram bars indicate significant differences among fire treatments.

burned 2× (1.8 ± 0.2 g N/m^2) being more like the annually burned treatment.

Plant responses

Aboveground net primary productivity (ANPP) across all sites and treatments was 451 ± 18 g/m^2 in 1994 (mean ± 1 SE), and was 518 ± 16 g/m^2 in 1995, reflecting differences in precipitation between these two years. In 1994, ANPP was affected by fire treatment ($P = 0.03$), topographic position ($P = 0.04$), and a fire × topography interaction ($P = 0.009$). As expected, ANPP was generally greater in the lowland plots relative to uplands. Across topographic positions, ANPP was significantly greatest in the burned 1× plots (Fig. 7). The fire × topography interaction was due to differences in the relative productivity of annually burned and unburned plots at upland and lowland sites. Annually burned plots were more productive than unburned plots in the lowland sites, while annually burned plots had the lowest productivity in the upland sites, presumably due to increased water limitation in shallow upland soils during a relative dry year. In 1995, there was a significant effect of fire treatment ($P = 0.003$) and a significant effect of topographic position ($P = 0.03$), but no significant interaction. Averaged across topographic positions, mean ANPP of the burned 1× treatment (589 g/m^2) was 37% greater than that of the unburned treatment (431 g/m^2), while both annually burned and burned 2× plots were intermediate and not significantly different from one another (mean of 526 g/m^2; Fig. 7).

There also were significant effects of fire treatment ($P = 0.02$), but not topography, on live root biomass, with the greatest live root biomass in the most frequently burned treatments (annually burned and burned 2×) and the lowest live root biomass in the burned 1× treatment. Root biomass in the unburned treatment was intermediate, but not significantly different from the burned 1× treatment (Fig. 8). There were no significant effects of fire treatment on dead root or rhizome mass.

The N content of both grass shoots and live roots was similarly affected by fire treatment and topographic position (Table 1). The tissue N concentrations of both grass shoots and roots near peak biomass (26 August 1995) was significantly greater in unburned and burned 1× treatments, than in either annually burned or burned 2× treatments. Across all fire treatments, tissue N concentrations of grass shoots were greater in upland, relative to lowland, plots. There was no effect of topographic position on N concentrations of grass roots.

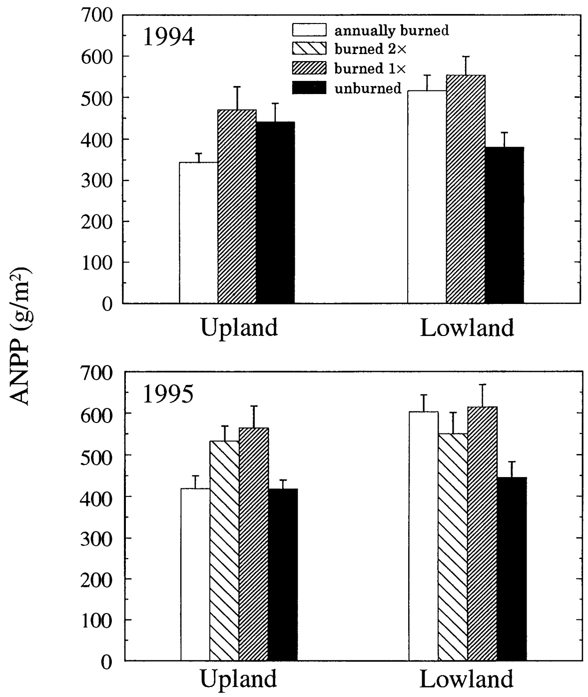

FIG. 7. Annual aboveground net primary productivity (mean and 1 SE) in upland and lowland tallgrass prairie plots subjected to different fire treatments in 1994 and 1995.

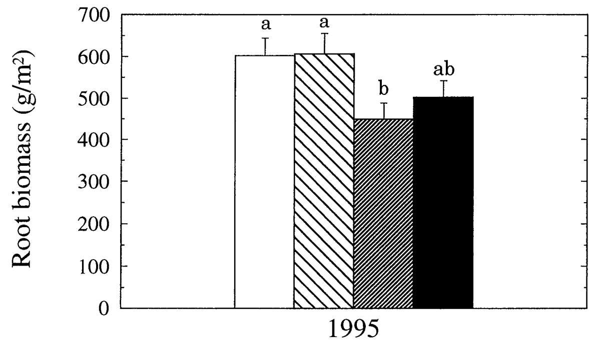

FIG. 8. Live root biomass under different fire treatments at the end of the 1995 growing season (mean and 1 SE). Shading key is the same as in Fig. 7. Different letters above histogram bars indicate significant differences among fire treatments.

DISCUSSION

Fire frequency significantly affects soil N dynamics and the availability of inorganic N in tallgrass prairie ecosystems (Seastedt and Ramundo 1990, Blair et al., *in press*). In this study, annually burned tallgrass prairie exhibited both lower concentrations of extractable inorganic N and lower net N mineralization rates, relative to unburned prairie. Nitrogen concentrations in shoots and roots of grasses from annually burned plots also were significantly lower than in grasses from unburned plots. These results are consistent with other studies that have demonstrated that repeated, frequent burning in tallgrass prairie leads to lower soil nitrogen availability (Risser and Parton 1982, Ojima et al. 1994), and increases the degree to which plant productivity is N limited (Seastedt et al. 1991). However, it is important to note that much of our understanding of the role of fire frequency in tallgrass prairie N cycling comes from studies of plant responses to added N (Seastedt et al. 1991), and to date there have been very few studies that have provided detailed data on available soil N pools or in situ net mineralization rates under different fire regimes (Ojima et al. 1994, Turner et al., *in press*).

Daily net N mineralization rates for specific incubation periods ranged from 35 to -0.5 mg $N \cdot m^{-2} \cdot d^{-1}$, and tended to be highest early and lowest late in the growing season (Fig. 5). These seasonal trends likely resulted, in part, from patterns of soil water availability, which also tended to decline throughout the growing season (Fig. 3). Cumulative net N mineralization rates for the entire growing season ranged from 1 to 3.1 g N/m² in this study, with the highest rates occurring in the unburned treatment. These rates are similar to those reported by Ojima et al. (1994) and Turner et al. (*in press*), and indicate that net mineralization of organic N in the upper 10–15 cm of soil can provide ~1–4 g $N \cdot m^{-2} \cdot yr$ for plant uptake. While net N mineralization across the entire rooting depth is likely to be somewhat greater, this still represents ~1–4× the annual inputs of inorganic N in bulk precipitation at Konza Prairie (Gilliam 1987, Blair et al., *in press*), and 60–250× the

TABLE 1. Grass shoot and root tissue N concentrations in upland and lowland plots of different fire treatments (mean ± 1 SE, $n = 12$ plant samples per fire treatment in each topographic position). Different capital letters indicate significant differences between topographic positions. Different lowercase letters indicate significant differences among fire treatments.

	Annually burned	Burned 2×	Burned 1×	Unburned
Grass shoots (% N)				
	a	a	b	b
Upland A	0.633 ± 0.011	0.612 ± 0.013	0.693 ± 0.021	0.740 ± 0.025
Lowland B	0.637 ± 0.018	0.673 ± 0.013	0.783 ± 0.026	0.808 ± 0.023
Grass roots (% N)				
	a	a	b	b
Upland A	0.695 ± 0.010	0.658 ± 0.033	0.756 ± 0.040	0.769 ± 0.039
Lowland A	0.706 ± 0.064	0.678 ± 0.047	0.842 ± 0.032	0.827 ± 0.046

average hydrologic output of dissolved N (Dodds et al. 1996). Clearly, net N mineralization rates represent a significant flux in the tallgrass prairie N cycle. It also is interesting to note that net nitrification and the relative proportion of inorganic N as NO_3-N were affected by burning treatment, and were lowest in the annually burned treatment. This suggests that fire frequency may affect the potential for N losses from tallgrass prairie by leaching or denitrification. While studies of hydrologic flux at Konza Prairie have not detected any strong effects of fire on watershed-level leaching losses of N, it does appear that denitrification losses are lower in annually burned, relative to unburned, tallgrass prairie (Groffman et al. 1993).

The responses of plant productivity to fire treatments in this study were variable, with some significant interactions of fire treatment and topographic position; these varied across years and complicated interpretation of the data. An analysis of the long-term plant productivity data from Konza Prairie has demonstrated strong interactions among fire frequency, climate, and topographic position that can influence ANPP in tallgrass prairie (Briggs and Knapp 1995). In 1994, for example, drier than normal conditions likely limited productivity in both annually burned and burned 1× treatments at the upland topographic position, resulting in a significant fire × topography interaction. In 1995, infrequently burned upland plots were more productive than either unburned or annually burned upland plots, while all burning treatments appeared to enhance productivity, relative to the unburned plots, at the lowland site. However, when averaged across topographic positions the burned 1× treatment resulted in greater ANPP than either unburned or annually burned treatments in both years. This is consistent with other studies showing a transient increase in productivity of tallgrass prairie in response to an infrequent fire (Seastedt et al. 1991, Hulbert and Wilson 1993).

Previous studies have demonstrated that plant productivity in tallgrass prairie burned for the first time after a prolonged absence of fire is relatively unresponsive to N additions (Old 1969, Seastedt et al. 1991), leading to the hypothesis that enhanced productivity of those prairies is due to increased N availability (e.g., Kucera and Ehrenreich 1962, Hulbert 1988, Seastedt et al. 1991). In the present study, however, comparisons of net N mineralization rates in plots burned for the first time, vs. those from plots left unburned and those burned annually, did not support the enhanced N mineralization hypothesis. That is, although soil temperatures were clearly elevated in the growing season following a fire, relative to unburned plots, the increased temperatures did not result in greater net N mineralization rates. Since both the unburned and burned 1× plots were presumed to have similar mineralizable soil organic N pools initially, it appears that decreased soil water availability following the removal of surface detritus (Knapp 1985) may be important in reducing net N mineralization rates following an infrequent fire. Therefore, high rates of ANPP in plots burned for the first time cannot be explained solely on the basis of N availability. These results appear to contradict those reported by Ojima et al. (1994) regarding the short- and long-term effects of fire. Ojima et al. (1994) compared long-term annually burned and unburned plots at the Aldous site (Manhattan, Kansas), to unburned and newly burned (1 and 2 yr) plots at Konza Prairie, and concluded that the short-term effect of fire was to increase N availability, while the long-term effect of annual burning was to reduce N availability. One reason for the apparent discrepancy between the results of these two studies may be methodological. Ojima et al. (1994) used a buried bag method, which maintains soil water content at the level it had when the soil was initially collected. In contrast, the buried tube method used in this study allowed soils to dry over the course of the 30-d incubations. Therefore, the lower soil water content characteristic of burned sites likely played a more important role in limiting net N mineralization rates, even in infrequently burned plots. While reductions in soil water availability may be important in affecting short-term N mineralization responses to burning, other factors, including changes in quantity and quality organic N pools (Ojima et al. 1994), are likely to be important in the longer term.

Comparisons of N mineralization rates and extractable soil N pools generally were consistent with the predictions of the transient maxima hypothesis. That is, soil N availability was greatest in unburned plots, where other factors, such as energy inputs to plants and the soil surface, are thought to limit plant productivity (Knapp 1984, Knapp and Seastedt 1986). When these unburned plots were burned after 3 yr without burning, soil N availability generally began to decline but remained significantly greater than in the annually burned plots. Although the decline in N availability was not always immediate, N decline is the predicted response if the system were in transition from a state of energy limitation to a state of N limitation (Fig. 1). The lack of increased plant productivity in response to N additions in newly burned prairie (Seastedt et al. 1991) would suggest that, although N mineralization rates are reduced relative to unburned prairie, N availability remains adequate to support high plant productivity. An additional factor may be the ability of the dominant grasses to draw on internal N reserves accumulated in the absence of fire, as suggested by the relatively high N tissue concentrations observed in the unburned plots, and the decline in tissue N content with repeated burning (Table 1). In either case, the production response to an infrequent fire is nonsustainable, since as energy limitations are removed, other factors such as N or water availability will begin to limit productivity. Based on the annual decrease in seasonal net N mineralization rates (Fig. 6), it appears that N availability approaches levels characteristic of annually burned grasslands in ~3 yr. These relatively rapid changes suggest either that mineralization of N in tallgrass prairie soils involves a dynamic pool of organic N that is reduced by repeated frequent burning, or that inputs of new C alter the potential for immobilization of N in these soils. Belowground plant tissues were sensitive to the effects of burning, with fire appearing to increase live root mass and lower root tissue N content. In fact, live root mass and N content of roots reached levels comparable to those of annually burned prairie with only two successive years of burning. Other studies also have indicated increases in the quantity and decreases in the quality (higher C/N ratios) of roots in response to burning in tallgrass prairie (Benning 1993, Ojima et al. 1994). Because root production and turnover represent major inputs of new soil organic matter in these ecosystems, these changes are likely to alter mineralization/immobilization relationships in tallgrass prairie soils. While the decline in net N mineralization rates appeared to occur relatively quickly as previously unburned prairie was burned, there are no data available regarding the temporal dynamics by which N mineralization rates increase when fire is excluded from previously burned tallgrass prairie. A planned fire treatment reversal experiment at Konza Prairie will allow the question of biological hysteresis in the decline and recovery dynamics of mineralization rates to be addressed.

The large degree of variability in the availability and relative importance of light, N, and water as limiting resources in tallgrass prairie (Schimel et al. 1991, Knapp et al. 1993, Turner et al., *in press*) appears to make these ecosystems very responsive to changing environmental conditions or changing management practices. With respect to altered fire frequencies, an important point is that soil and plant responses to fire in tallgrass prairie depend on fire history. Soil N dynamics and plant responses in prairies burned for the first time, or burned twice following an extended period without fire, are likely to be quite different from those in prairies that are burned more or less frequently. Therefore, predicting or interpreting the responses of grassland ecosystems to fire depends on knowledge of the fire history of the site. The results of this study, and others (Hulbert and Wilson 1983, Seastedt et al. 1991, Briggs et al. 1994) indicate that shifts in resource limitation associated with intermittent fires can temporarily increase aboveground productivity in these grasslands. Given that intermittent fires historically were an important component of tallgrass prairie, these periods of enhanced productivity may have played an important role in the large accumulations of organic matter characteristic of these ecosystems. Similar shifts in relative resource availability can occur in response to intermittent grazing or periodic drought (Seastedt and Knapp 1993), which also may allow for transient increases in productivity. These transient responses to nonequilibrium conditions appear to play a significant role in affecting the dynamics of tallgrass prairie ecosystems, and may be important in other terrestrial ecosystems.

ACKNOWLEDGMENTS

Thanks to Dee Coulson, Mitch Emig, Krista Mobley, and Michelle Ross for assistance with both field sampling and laboratory analyses. Thanks to Tim Seastedt and Alan Knapp for contributing to the development of these ideas, and to Loretta Johnson for critiquing the manuscript. Funding for this research was provided by a grant from the NSF Long-Term Ecological Research (LTER) program to Kansas State University (DEB-9011662). Kansas Agricultural Experiment Station Contribution No. 97-406-J.

LITERATURE CITED

Abrams, M. D., A. K. Knapp, and L. C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. American Journal of Botany **73**:1509–1515.

Bark, D. 1987. Konza prairie research natural area, Kansas. Pages 45–50 *in* D. Greenland, editor. The Climates of the Long-Term Ecological Research Sites. Occasional Paper No. 44, Institute of Arctic and Alpine Research, University of Colorado, Boulder, Colorado, USA.

Benning, T. L. 1993. Fire frequency and topoedaphic controls of net primary productivity in the tallgrass prairie. Dissertation. University of Colorado, Boulder, Colorado, USA.

Benning, T. L., and T. R. Seastedt. 1995. Landscape-level interactions between topoedaphic features and nitrogen limitation in tallgrass prairie. Landscape Ecology **10**:337–348.

Blair, J. M., T. R. Seastedt, and C. W. Rice. *In press.* Terrestrial nutrient cycling in tallgrass prairie. *In* A. K. Knapp, J. M. Briggs, D. C. Hartnett, and S. C. Collins, editors. Grassland dynamics: long-term ecological research in tallgrass prairie. Oxford University Press, New York, New York, USA.

Briggs, J. M., J. T. Fahnestock, L. Ward, and A. K. Knapp. 1994. Aboveground biomass in tallgrass prairie: effect of time since last fire. Pages 165–170 *in* R. G. Wickett, P. D. Lewis, A. Woodliffe, and P. Pratt, editors. Proceedings of the Thirteenth North America Prairie Conference (Windsor, Ontario, Canada, 6–9 August 1992).

Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie: climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. American Journal of Botany **82**: 1024–1030.

Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. Ecology **76**:486–492.

Collins, S. L., and L. L. Wallace. 1990. Fire in North American tallgrass prairie. University of Oklahoma Press, Norman, Oklahoma, USA.

Dodds, W. K., J. M. Blair, G. M. Henebry, J. K. Koelliker, R. Ramundo, and C. M. Tate. 1996. Nitrogen transport from tallgrass prairie by streams. Journal of Environmental Quality **25**:973–987.

Gilliam, F. S. 1987. The chemistry of wet deposition for a tallgrass prairie ecosystem: inputs and interactions with plant canopies. Biogeochemistry **4**:203–217.

Groffman, P. M., C. W. Rice, and J. M. Tiedje. 1993. Denitrification in a tallgrass prairie landscape. Ecology **74**: 855–862.

Hulbert, L. C. 1969. Fire and litter effects in undisturbed bluestem prairie in Kansas. Ecology **50**:874–877.

———. 1988. Cause of fire effects in tallgrass prairie. Ecology **69**:46–58.

Hulbert, L. C., and J. K. Wilson. 1983. Fire interval effects on flowering of grasses in Kansas bluestem prairie. Pages 255–257 *in* C. L. Kucera, editor. Proceedings of the Seventh North American Prairie Conference. Southwest Missouri State University, Springfield, Missouri, USA.

Knapp, A. K. 1984. Post-burn differences in solar radiation, leaf temperature and water stress influencing production in a lowland tallgrass prairie. American Journal of Botany **71**: 220–227.

———. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. Ecology **66**:1309–1320.

Knapp, A. K., J. T. Fahnestock, S. P. Hamburg, L. B. Statland, T. R. Seastedt, and D. S. Schimel. 1993. Landscape patterns in soil–plant water relations and primary production in tallgrass prairie. Ecology **74**:549–560.

Knapp, A. K., and F. S. Gilliam. 1985. Response of *Andropogon gerardii* (Poaceae) to fire-induced high vs. low irradiance environments in tallgrass prairie: leaf structure and photosynthetic pigments. American Journal of Botany **72**:1668–1671.

Knapp, A. K., and T. R. Seastedt. 1986. Detritus accumulation limits productivity of tallgrass prairie. BioScience **36**:662–668.

Kucera, C. L., and J. H. Ehrenreich. 1962. Some effects of annual burning on central Missouri prairie. Ecology **43**: 334–346.

Ojima, D. S., W. J. Parton, D. S. Schimel, and C. E. Owensby. 1990. Simulated impacts of annual burning on prairie ecosystems. Pages 118–132 *in* S. L. Collins and L. L. Wallace, editors. Fire in North American grasslands, University of Oklahoma Press, Norman, Oklahoma, USA.

Ojima, D. S., D. S. Schimel, W. J. Parton, and C. E. Owensby. 1994. Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry **24**:67–84.

Old, S. M. 1969. Microclimates, fire, and plant production in an Illinois prairie. Ecological Monographs **39**:355–384.

Raison, R., M. Connell, and P. Khanna. 1987. Methodology for studying fluxes of soil mineral-N in situ. Soil Biology and Biochemistry **19**:521–530.

Risser, P., and W. J. Parton. 1982. Ecological analysis of a tallgrass prairie: nitrogen cycle. Ecology **63**:1342–1351.

SAS Institute. 1989. SAS/SYSTAT user's guide. Version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

Schimel, D. S., T. G. F. Kittel, A. K. Knapp, T. R. Seastedt, W. J. Parton, and V. B. Brown. 1991. Physiological interactions along resource gradients in a tallgrass prairie. Ecology **72**:672–684.

Seastedt, T. R. 1985. Canopy interception of nitrogen in bulk precipitation by annually burned and unburned tallgrass prairie. Oecologia **66**:88–92.

Seastedt, T. R., J. M. Briggs, and D. J. Gibson. 1991. Controls of nitrogen limitation in tallgrass prairie. Oecologia **87**:72–79.

Seastedt, T. R., and A. K. Knapp. 1993. Consequences of nonequilibrium resource availability across multiple time scales: the transient maxima hypothesis. American Naturalist **141**:621–633.

Seastedt, T. R., and R. A. Ramundo. 1990. The influence of fire on below-ground processes of tallgrass prairie. Pages 99–177 *in* S. L. Collins and L. L. Wallace, editors. Fire in North American grasslands. University of Oklahoma Press, Norman, Oklahoma, USA.

Turner, C. L., J. M. Blair, R. J. Schartz, and J. C. Neel. 1997. Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology **78**:1832–1843.