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FIRE AND TOPOGRAPHIC EFFECTS ON DECOMPOSITION RATES AND N DYNAMICS OF BURIED WOOD IN TALLGRASS PRAIRIE

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Summary—Decay rates and N dynamics of wood in soils of annually burned and unburned tallgrass prairie were measured over a 3-y period. Wooden dowels were placed at upland, mid-slope and lowland sites in two annually burned and two unburned watersheds. After 3 y, an average of only 15% of initial wood mass remained in burned watersheds, while 34% remained in unburned watersheds. Topographic position also significantly affected decay rates, with dowels decaying faster in the shallow-soil, upland sites and slope sites than in the deep-soil, lowland sites. This pattern is opposite of that generally observed for plant productivity (i.e. greater at lowland sites compared to uplands), and suggests that the controls of belowground decomposition and plant productivity are dissimilar. Dowels in both burned and unburned watersheds showed significant increases in N concentration over 3 y. Topographic position did not affect N concentration in the residual dowel material. Burn treatment, however, did affect N concentration, with dowels decomposing in burned watersheds having a higher average N concentration (0.5% after 3 y exposure) than dowels in unburned watersheds (0.43%). Relatively rapid decay rates resulted in net release of N, despite increased N concentration in the residual material. Faster net N release on the annually burned watershed was due to faster mass loss, since there were no differences in the rate of increase in N concentration per unit mass lost. Surface soil temperatures on burned prairie following spring fire usually exceed those on unburned prairie. However, average monthly summer soil temperatures (May–August) at a 10 cm depth in burned and unburned plots during the study were not statistically different and could not explain decay rate differences. Additionally, one of our unburned watersheds was accidentally burned during the first year of the study. Surprisingly, there were no significant differences in rates of wood decay between that watershed and the other unburned watershed. This suggests that indirect effects of annual fire (i.e. changes in the composition of soil flora and fauna) may override the short-term effects of fire (i.e. changes in soil temperature and moisture) on belowground decomposition in tallgrass prairie.

INTRODUCTION

Studies of the effects of fire on soil processes in the tallgrass prairie are few. A review by Seastedt and Ramundo (1990) reported that, with very few exceptions, most of the belowground work had been conducted on plant growth responses. Since then, new information on the effects of fire on soil physical (Seastedt and Briggs, 1991) and microbial dynamics (Garcia and Rice, 1994) has become available. Fire affects both the temperature and moisture content of prairie soils (Hulbert, 1969; Seastedt and Briggs, 1991; Knapp *et al.*, 1993). After a fire, surface to 10 cm deep soil temperatures in burned sites are usually substantially greater (ca. $\geqslant$ 10°C) than those of unburned soils. However, after re-establishment of the vegetation canopy, soil temperatures of burned sites may approximate, or drop below, those in unburned sites, depending upon soil moisture (Seastedt and Briggs, 1991). Higher soil temperatures in burned soils generally result in enhanced microbial respiration (Raich and Schlesinger, 1992) and, in years with sufficient moisture, higher microbial biomass (Garcia and Rice, 1994), which should translate into faster rates of organic matter decomposition. Seastedt *et al.* (1991) showed that buried root litter in unburned tallgrass prairie decayed more rapidly than surface litter, but comparisons were not made between rates of decay in the soils of burned and unburned prairie. Fire frequency also affects N availability in the tallgrass prairie (Seastedt, 1988; Seastedt *et al.*, 1991; Ojima *et al.*, 1994). N content of litter and exogenous N supply affect N immobilization and mineralization in soil and may also influence decomposition rates of litter (Pastor *et al.*, 1987).

More recent studies of the Konza prairie have evaluated the significance of topographic constraints on water, nutrient and energy dynamics of this system

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(Schimel *et al.*, 1991; Knapp *et al.*, 1993; Benning and Seastedt, 1995). Uplands in the Flint Hills region tend to have shallow, rocky soils and often are more water stressed than the deep-soil, lowlands. Hillslopes usually have intermediate soil resource characteristics. Differences in plant productivity attributed to topography usually are more evident on burned watersheds, due to the interactive effects of fire and topography on soil moisture (Knapp *et al.*, 1993).

In 1990, an intersite decomposition experiment was initiated to measure effects of climatic variation, and other factors, on surface and buried litter decomposition (the LIDET project; Harmon *et al.*, 1996). A variety of litter types, including wood, was placed in representative sites of selected North and Central American biomes. Due to the need for long-term "undisturbed" sites, unburned prairie sites were chosen at Konza prairie for that study. Our concern was that the study would misrepresent decay rates of litter on frequently burned prairie sites, which is (or was) the norm for this region (e.g. Collins and Wallace, 1990). Obviously, fire overrides decomposition processes of surface litter, but buried substrates also are subjected to different physical, chemical and biological microclimates created by the fires. Given the size of the soil organic matter pool, the potential error in using decomposition values from unburned sites as averages for the tallgrass prairie biome needed to be evaluated.

Here, we quantified the effects of fire and topographic position on belowground decomposition rates and N dynamics of woody substrates. Buried wooden dowels were used as a common substrate in these experiments for several reasons. Buried litter studies employing litterbags are difficult to conduct over extended periods because of root growth into the bags. The use of wooden dowels eliminated this problem, and also avoided the problem of artificial microclimates created by fine-mesh litterbags. Additionally, the dowels provided a uniform, recalcitrant substrate that allowed comparisons of decay rates between or among years, which allowed for an evaluation of the effects of climatic variation on decay rates. Finally, the use of dowels allowed direct comparisons with data from the LIDET study.

MATERIALS AND METHODS

Studies took place in the Konza Prairie Research Natural Area, about 15 km south of Manhattan, KS. This tallgrass prairie is a Long-Term Ecological Research (LTER) site. Descriptions of the vegetation and soils of this area are referenced in Seastedt and Ramundo (1990). Fire effects on this system have been discussed in detail in a number of chapters found in Collins and Wallace (1990).

A multi-year decomposition study was initiated in the fall of 1990 as part of an intersite comparison of decay rates conducted by the Long-Term Intersite Decomposition Experiment Team (LIDET; Harmon *et al.*, 1996). Wooden dowels made from untreated *Gonystylus bancannus*, a tropical hardwood tree species, were used in these studies. Dowels for the multi-year LIDET study were 1.25 cm dia and 61 cm in length. Initial %C of the dowels was about 50% and initial %N was about 0.32%. Dowels were placed at four lowland unburned sites, with one-half of the dowel (30 cm) buried vertically in the soil and the other half exposed aboveground. Dowels were collected annually in the fall, and then oven-dried at 55°C to constant weight. Only results from the belowground portion of the dowels are reported here.

In September 1990, we initiated a similar 3-y study to evaluate the effects of fire and topographic position on decomposition rates and N dynamics of buried woody substrates. For this second study, 10 dowels (*G. bancannus*; 1.25 cm dia and 15 cm in length) were buried vertically (0–15 cm) at lowland, upland and slope positions on each of two annually burned and two long-term unburned watersheds. The long-term unburned sites were last burned was in 1980. A 20 cm piece of rebar was used to create holes for each dowel. The shorter length of these dowels, compared to the LIDET study, was to accommodate the shallower upland soils. Harvests were made using a 2.54 or 5.08 cm coring tool driven around each dowel, and carefully separating the dowel from the surrounding soil. Collections ($n = 6$ six dowels per watershed) were made twice during each of the first 2 y, and at the end of the third year. Dowels were oven-dried at 80°C to constant weight. Percent of initial mass remaining was determined and annual decay rates were calculated using a single negative exponential decay model (Olson, 1963). N and C analyses also were done on ground dowels using a Carlo Erba C/N analyzer.

Soil temperature data (10 cm depth) were obtained for the growing seasons (May through August) of the years 1991–1993, from burned and unburned plots adjacent to the Konza Prairie main climatic station. These data were analyzed in an attempt to make correlations among fire treatments, soil temperatures, decay rates and N dynamics. Mean annual air temperature and cumulative precipitation data also were obtained from the main Konza Prairie climatic station for the September–August periods corresponding to study years 1, 2 and 3.

RESULTS

General climatic conditions for the study period are presented in Table 1. Mean annual air temperature generally decreased from 1990 to 1993, with mean air temperature values of 14.4, 13.1 and 11.4°C for study years (September–August) 1, 2 and 3, respectively. Mean summer soil temperatures (May–August) in burned plots were slightly higher than those in unburned plots, although the differences were not statistically significant. The mean summer soil temperature (May–August) at a 10 cm

Table 1. Mean annual air temperatures and mean summer soil temperatures (10 cm depth) for unburned and burned sites for the period September–August of 1990–1993; total annual precipitation also is presented for these years

Variable	Collection year 1 (1990–1991)	2 (1991–1992)	3 (1992–1993)
Mean annual air temperature (°C)	14.4	13.1	11.4
Mean summer soil temperature (°C)*			
Unburned	23.3	20.2	21.1
Burned	24.4	22.0	22.0
Total annual precipitation (mm)	609	998	1530

* For summers of 1991, 1992 and 1993.

depth in unburned plots was 21.2, while the average was 22.8°C in burned plots. There was an increase in annual precipitation from 1990 to 1993, with total precipitation values of 609, 998 and 1530 mm for study years 1, 2 and 3, respectively. The long-term annual average for Konza Prairie is about 830 mm. Mean monthly soil temperatures (May–August) for burned and unburned plots are provided in Table 2. Again, soil temperatures usually were higher in burned plots than in unburned plots, but the differences were not statistically significant.

Both fire history and topographic position significantly affected decomposition rates of buried wooden dowels. ANOVA of the mass loss data indicated significant effects of fire treatment (faster decomposition on the annually burned watersheds, $P = 0.004$) and topographic position (faster decomposition on the upland and slope sites, compared to the lowland sites, $P = 0.014$). There were no interaction effects between fire treatment and topographic position. Patterns of mass loss for dowels in burned and unburned watersheds (averaged across all topographic positions) are presented in Fig. 1. Rates of mass loss on the burned watersheds are markedly faster rate than on the unburned watersheds. Dowels from the burned watersheds had 71, 28 and 14% of initial mass remaining after 1, 2 and 3 y in the field, respectively, while the dowels from unburned watersheds had 82, 55 and 34% of initial mass remaining for those same exposure periods.

One of the unburned watersheds used in this study was accidentally burned in a wildfire in 1991. The accidental burning of this watershed potentially complicated what was initially a long-term unburned vs annually burned comparison, but did allow us to make comparisons of decomposition on annually burned, unburned and infrequently burned watersheds. Comparison of the patterns of mass loss of dowels on the two previously unburned watersheds, one of which was accidentally burned, indicated no significant differences between the two sites (Fig. 2).

Figure 3 compares the patterns of mass loss for dowels buried at each of the three topographic positions (lowland, upland and mid-slope), averaged across both fire treatments. The fastest decay rates occurred in the upland sites and the slowest decay rates occurred in the lowland sites. Mid-slope sites appeared to exhibit intermediate decay rates, but these were not statistically different from the upland sites (Duncan's multiple range test, $P > 0.05$).

Decay rates of the 30 cm deep wood dowels used in the intersite LIDET study were markedly slower than the decay rates obtained in our study (Fig. 4; Table 3). During the first year of the LIDET study, there was a relatively large loss of mass of the dowels (16%), which was similar to the dowels in our unburned sites (18.4%). Mass loss in the LIDET study was much less in the second year, and increased only slightly in the third year. The proportions of initial mass remaining were 84, 83 and 75% after 1, 2 and 3 y in the field, respectively. These mass loss rates were much lower than for our 15 cm deep dowels.

Table 2. Mean monthly summer (May–August) soil temperatures (°C) at 10 cm depth in burned and unburned plots

Year + treatment	Month May	June	July	August
1991				
Unburned	20.7	23.2	25.1	24.3
Burned	21.5	24.0	26.4	25.7
1992				
Unburned	17.1	19.3	22.4	21.9
Burned	20.4	21.5	23.7	22.5
1993				
Unburned	16.7	20.8	23.9	23.2
Burned	18.8	22.2	24.1	22.8

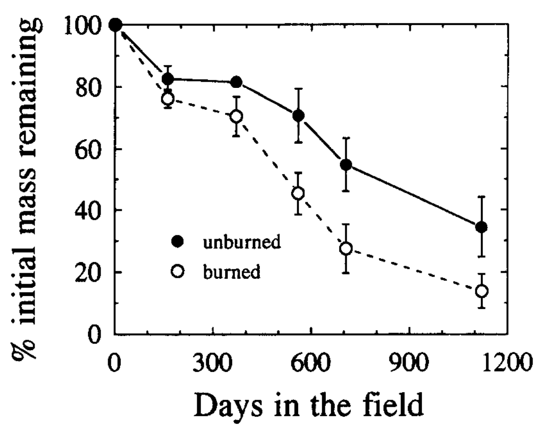

Fig. 1. Percent mass remaining ($\bar{x} \pm$ SE) of wooden dowels decomposing in burned (O- - -O) and unburned (●——●) watersheds, averaged across all topographic positions.

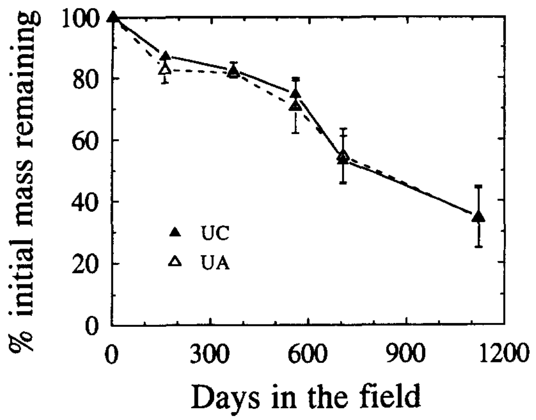

Fig. 2. Percent mass remaining ($\bar{x} \pm$ SE) of wooden dowels in the long-term unburned watershed, UA (△- - -△), and in the accidentally burned long-term unburned watershed, UC (▲——▲), averaged across all topographic positions.

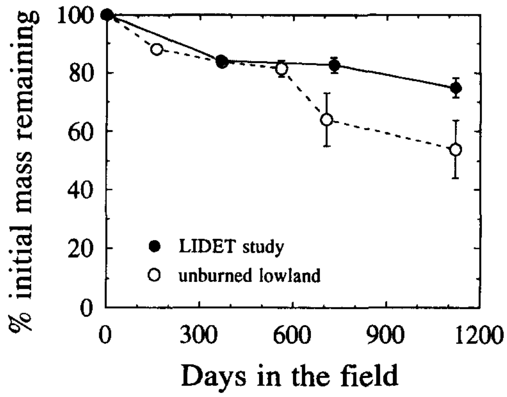

Fig. 4. Percent mass remaining ($\bar{x} \pm$ SE) of wooden dowels from LIDET study (●——●) vs those from the unburned, lowland sites in our study (○- - -○).

Fire frequency significantly affected N concentration in the remaining dowel material ($P = 0.037$), with dowels in burned watersheds having a higher mean percent N content over the 3-y period than dowels in unburned watersheds. There was no significant effect of topographic position on N concentration, and no interaction between fire and topographic position. Changes in N concentration over time in dowels from burned and unburned watersheds, averaged over all topographic positions, are presented in Fig. 5. Net accumulation or release of N was calculated by combining mass loss and N concentration data (Fig. 6). Surprisingly, we did not observe any net accumulation of N in spite of a relatively high initial C-to-N ratio of 156. Net release of N was faster on the annually burned watershed ($P = 0.004$), and there was no effect of topographic position. To determine whether differences in N dynamics on burned and unburned watersheds were due to faster decomposition rates, or a difference in N retention or accumulation during decomposition, percent mass remaining was regressed against N concentration in the residual material (cf. Aber and Melillo, 1980), and presented in Fig. 7. Note that initial N concentration is not included in these regressions due to apparent leaching losses in the first 160 d (Aber and Melillo, 1980). Neither the slopes nor the intercepts of the regressions differed significantly between the burned and unburned watersheds (i.e. the increase in N concentration per unit C lost was the same for dowels in both watersheds).

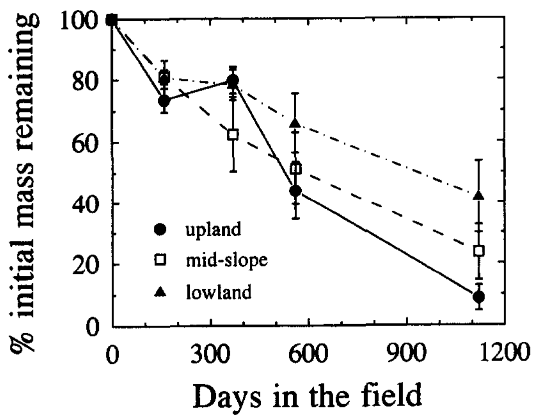

Fig. 3. Comparison of wooden dowel decay rates at different topographic positions. Mean percent mass remaining ($\pm$ SE), averaged across fire treatments, is presented.

DISCUSSION

Data from buried wooden dowels indicate substantially faster belowground decomposition in soils of annually burned watersheds, compared to comparable soils on unburned watersheds (Fig. 1, Table 3). Faster belowground decomposition in annually burned watersheds could be the result of a combination of direct and indirect factors resulting from repeated, frequent fires. Changes in the soil surface energy budget, caused by removal of surface detritus (Knapp and Seastedt, 1986) can substantially alter soil temperature and moisture, affecting microbes and soil fauna directly via changes in activity rates, and indirectly by changes in species composition of the decomposer biota. The accidental burn of one of our previously unburned watersheds in 1991 resulted in an unintentional "experiment" that provided insights into the relative importance of short-term direct vs long-term indirect effects of fire. In spite of the accidental fire and, presumably, the

Table 3. Wood decay rates. Mean mass loss expressed as cumulative % of initial mass lost over the 3-y period and as annual mass lost (% of mass at beginning of year lost that year)

	Cumulative % mass lost			Annual % mass lost		
	1991	1992	1993	1991	1992	1993
LIDET	16.0	17.4	25.1	16.0	1.7	9.3
Burned	29.5	72.5	86.2	29.5	61.0	49.8
Unburned	18.4	45.2	65.6	18.4	32.8	37.2

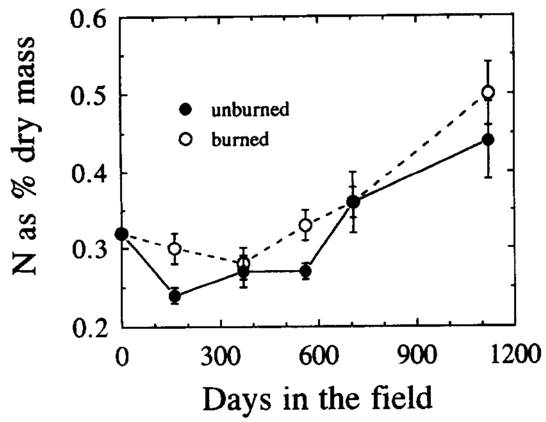

Fig. 5. N concentration ($\bar{x} \pm$ SE) in wood dowels, as percent dry mass, over time in unburned (●——●) and burned (○- - -○) watersheds.

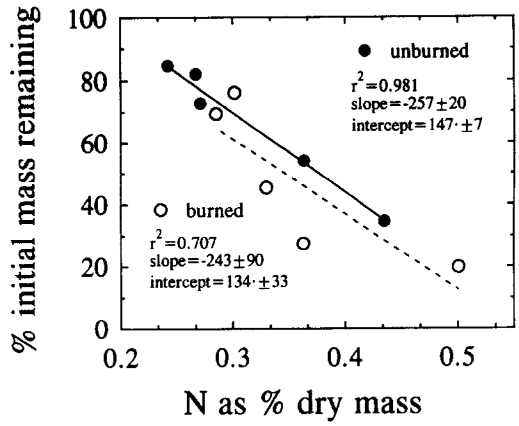

Fig. 7. Regression of percent initial mass remaining versus N concentration in the residual material for dowels in unburned (●——●) and burned (○- - -○) watersheds.

springtime soil warming that occurred following that fire, wooden dowels on this watershed exhibited patterns of mass loss that were identical to those on the remaining unburned watershed. This indicates that infrequent burning does not have the same effect on decomposition processes as does annual burning. Although this "experiment" in infrequent burning was not replicated, it does suggest that the indirect effects of frequent fire, rather than immediate direct effects, may be largely responsible for the differences in the decay rates observed on the annually burned and unburned watersheds. These indirect effects may include changes in soil biota and quality or quantity of belowground organic inputs (Ojima *et al.*, 1994).

If simple biophysical (temperature and moisture) constraints dominated the controls on decomposition, then we would expect to see (1) a correlation among temperature, moisture and decay rates or (2) a relationship between year-to-year changes in physical variables and decomposition. Although elevated soil temperatures are common immediately

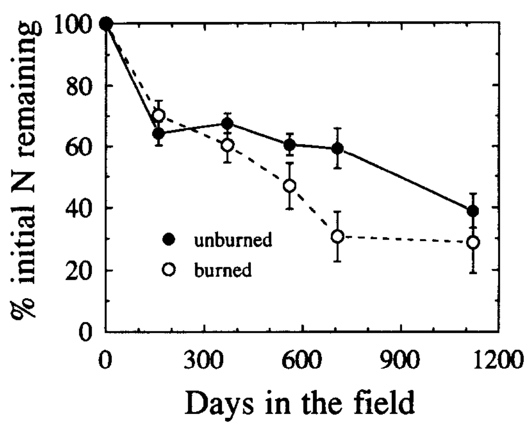

Fig. 6. Changes in total N content ($\bar{x} \pm$ SE) of wooden dowels, expressed relative to the amount of total N origianlly present (net N release) in unburned (●——●) and burned (○- - -○) watersheds.

following fire, soil temperature data from burned and unburned plots suggest that these temperature differences did not persist for long following spring fires and did not play a major role in the enhanced decay rates in burned watersheds (Table 2). Burned plots had slightly warmer soil temperatures, which was expected (Ehrenreich, 1959; Hulbert, 1969; Old, 1969). Hensel (1923) found that burned prairie soil will reach higher temperatures than unburned soil early in the season because the aboveground plant material has been removed. However, once vegetation regrowth occurs, a more vigorous canopy on burned areas may generate a cooling effect on soils. Soil moisture also plays a role in determining the soil temperature, since water in the soil acts as a thermal buffer; moist soils have lower maximum temperatures than drier soils (Seastedt and Briggs, 1991). Unburned soils tend to remain moister (Knapp *et al.*, 1993), which also contributes to cooler temperatures on those sites. However, since our data suggest only modest, statistically non-significant differences in average monthly soil temperatures between burned and unburned watersheds, the doubling of the rate of wood decay in the burned watersheds cannot be explained solely by the higher soil temperatures found there. Even if soils on burned watersheds averaged 2–3°C higher temperatures, this difference should not cause a doubling of mass loss (e.g. Raich and Schlesinger, 1992).

Fauna, especially termites (*Reticulitermes* sp.), may be an important determining factor in the rate of wood decay. Observations of dowels in our study suggests that termites may be more prevalent in annually burned sites. However, further investigation into the pattern of termites abundance in relation to wood decomposition needs to be done. In terms of fauna in general, we speculate that the unburned watershed which was accidentally burned once did not show the enhanced decay rate associated with burned watersheds because the flora and fauna present there did not exhibit the long-term responses to the changes in temperature and moisture initiated by more frequent fire. The role of annual fire, then, may be to increase the activities and densities of certain biota, which are then responsible for the faster rate of wood decay in burned watersheds, although this remains to be examined. These indirect effects of fire also may amplify the effects of changes in temperature and moisture on biotic decomposition processes. Regardless of the specific roles of the biota, the fact that the decay rates of wood on both burned and unburned watersheds increased after the first year in the field suggests that there was some type of "conditioning" of the wood which subsequently stimulated decomposition. Microbial colonization of the material may have been followed by enhanced grazing by generalist fauna detritivores regardless of fire treatment.

Topographic position also played an important role in belowground decomposition processes. Decay rates of buried wooden dowels were fastest in upland soils and slowest in lowland soils. This pattern is opposite that commonly observed for plant productivity (Schimel *et al.*, 1991; Knapp *et al.*, 1993) and indicates that factors limiting belowground decomposition are not the same as those limiting plant production. Shading effects by the canopy on soil temperatures at lowland sites may explain some of this pattern. Higher soil water and greater clay content in the lowland sites also may have contributed to reduced decay rates by favoring anaerobic conditions, which could slow decomposition. The implications of different patterns and controls of productivity and decomposition for soil organic matter dynamics and C storage across topographic gradients remain to be investigated in these grasslands.

The calculated, annual decomposition rate constants (k-values from the single negative exponential model: %mass remaining at $t = e^{-kt}$) for dowels in the unburned watersheds for days 370, 706 and 1120 were 0.19, 0.27 and 0.34, respectively. The calculated k-values for dowels in the annually burned watersheds for the same days were 0.33, 0.62 and 0.66, respectively. The values from the annually burned watersheds were not only higher, but also showed a greater increase with time. Decay rates from all watersheds, however, seemed to indicate that decay takes place more rapidly after the first year in the field. Seastedt *et al.* (1991) reported a k-value for belowground roots located in unburned watersheds on Konza prairie of 0.66. In all probability, then, roots in soils of burned sites should experience rates of decay substantially higher than the rate reported in the Seastedt *et al.* (1991) study.

Annual decomposition rate constants (k-values) for the LIDET wood dowels in unburned, lowland soils for years 1991, 1992 and 1993 were 0.17, 0.10 and 0.09, respectively. Decay rates of the 30 cm deep LIDET dowels study were much lower than decay rates of the 15 cm deep dowels from our study (Table 3). Depth of dowel rather than treatment appears to dictate this difference since dowels on both burned and unburned watersheds showed similar between-year trends. The slower decay of the LIDET dowels hints at temperature as the reason for some of the differences. The deeper buried LIDET dowels likely experienced lower temperatures, contributing to slower decay rates. Other factors which may have contributed to slower decay rates at deeper depths include a greater clay content, lower microbial biomass, and lower faunal abundance with increasing soil depth.

N concentration of the remaining dowel material increased over the study period, as expected for a high C-to-N ratio substrate (Berg and Staff, 1981). However, the relatively rapid decomposition rates in our study resulted in a net release of N (no net accumulation) throughout the study (Fig. 6). This is generally consistent with results presented in Seastedt *et al.* (1992), indicating that buried substrates with high C-to-N ratios do not immobilize substantial amounts of N in the N-limited soil environments characteristic of these grasslands. The remaining dowel material from annually burned watersheds had a higher N concentration after 3 y than dowels from unburned watersheds, even though annually burned sites tend to be more N limited (Seastedt *et al.*, 1991; Ojima *et al.*, 1994). The greater increase in N concentration could reflect differences in N dynamics during decomposition, or could simply reflect the faster decomposition rates on the annually burned watershed. The plots of mass loss as a function of change in N concentration (Fig. 7) suggest that there are no differences in the rate at which N concentration increases per unit mass lost during decomposition. This suggests that differences in N concentration and net N release are simply due to faster decomposition in the annually burned watersheds (i.e. faster decomposition = more rapid increases in N concentration). The similar rates of increase in N concentration per unit C lost in the two fire treatments also suggests that the faster decomposition in the burned watersheds is accomplished by enhanced microflora and microfauna activities. This would account for the greater N concentration found there, as opposed to a loss of dowel substrate by simple fragmentation caused by macroinvertebrates or physical processes which reduce the amount of mass remaining without substantially altering N concentration in the residual material.

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