ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Effects of fire frequency on oak litter decomposition and nitrogen dynamics

Daniel L. Hernández · Sarah E. Hobbie

Abstract Fire can alter a multitude of ecosystem properties that have the potential to affect rates of litter decomposition and nitrogen dynamics. In this study, we examined the effect of long-term variation in fire frequency in Minnesota oak savanna on rates of litter mass loss of a common tree species (*Quercus ellipsoidalis*) to determine how site and intraspecific litter characteristics impacted by variation in fire frequency affect rates of decomposition, litter N dynamics, and litter microbial biomass. Although an increase in fire frequency resulted in higher litter temperatures, lower litter moisture, and decreased soil N and P availability, site characteristics had no net effect on rates of mass loss. Rather, litter C:N ratio, which increased with increased fire frequency, was the dominant predictor of rates of decomposition and litter N dynamics. Increased litter C:N led to decreased rates of decomposition and N immobilization, regardless of the characteristics of the site of decomposition. Therefore, it is the indirect effects of long-term variation in fire frequency on litter characteristics rather than fire's direct effects on site characteristics that determine fire effects on decomposition and N dynamics in this system. Slower rates of decomposition and increased N immobilization of litter produced in frequently burned sites may enhance fire-induced N losses, further decelerating rates of N cycling in frequently burned sites.

Communicated by Amy Austin.

D. L. Hernández (✉)
Biology Department, Hamline University, Saint Paul, MN, USA
e-mail: dhernandez01@hamline.edu

S. E. Hobbie
Department of Ecology, Evolution and Behavior,
University of Minnesota, Minneapolis, MN, USA

Introduction

Fire plays a major role in the structure and functioning of many ecosystems. It is a disturbance with a high potential to influence decomposition and nutrient cycling, as it affects ecosystems both physically and chemically, impacting site as well as litter characteristics (Neary et al. 1999; Certini 2005). Both the frequency and intensity of fire determine the magnitude of its effects on ecosystem processes (Certini 2005). Studies examining the effects of fire intensity (most commonly measured by fire temperature) on ecosystem processes are relatively common. However, because of the difficulty in experimentally manipulating the frequency of fire (i.e., the number of fires over a given time period), less is known about how changes in fire frequency may influence ecosystems. Recent changes in land management strategies have led to both increases in the use of prescribed fires in some areas and suppression of fire in others (Neary et al. 1999). Therefore understanding the role of fire frequency in influencing ecosystem processes is important to understanding the overall effects of fire in systems where fire is a common phenomenon.

Fire effects on ecosystem properties that are relevant to litter decomposition and nutrient cycling can be grouped into three related and often interdependent categories—effects on physical characteristics of the environment, effects on the plant community (and related effects on litter chemistry), and effects on soil nutrients. Although the magnitude of the effect can vary with fire intensity, ecosystem type, and climate, increased fire frequency in savanna and

grassland systems generally results in increased canopy openness (Reich et al. 2001), increased soil pH (Tester 1989; Certini 2005), decreased litter moisture, and increased litter temperature (Raison et al. 1986). In savanna systems, fire leads to a more grass-dominated plant community (Reich et al. 2001) and encourages the recruitment of species tolerant of fire (Bond and Keeley 2005). Some species respond to increased fire frequency with changes in plant traits such as growth form and biomass allocation (Ojima et al. 1994; Bond and Keeley 2005). Some species also respond to the altered soil N availability resulting from increased fire frequency with declines in leaf and litter N (Reich et al. 2001).

Repeated fire generally reduces soil N availability by decreasing soil N pools (Harden et al. 2003) and rates of N mineralization (Ojima et al. 1994; Turner et al. 1997; Reich et al. 2001; Dijkstra et al. 2006). N volatilizes at relatively low temperatures, similar to that of C ($\sim$200°C), resulting in a decline in organic N stocks immediately following fire (Boerner 1982; Certini 2005). Fire can cause organic N to change chemical form to NH_4^+, resulting in a "pulse" of biologically available N immediately following fire (Christensen and Muller 1975). However, if nitrified, NH_4^+ may be lost from the system through leaching, creating another pathway of N loss (Certini 2005). In a meta-analysis examining the fates of N following fire, Wan et al. (2001) showed that soil NH_4^+ concentrations generally increase immediately following fire, then slowly return to pre-fire levels over the year following fire, while soil NO_3^- reaches its peak 6–12 months following fire and then declines.

These biological and chemical effects of fire can impact litter decomposition through changes in both the environment for decomposition and in litter characteristics. Rates of decomposition are influenced by site characteristics (i.e., climate, soil nutrient availability, characteristics of the microbial community) (Meetenmeyer 1978; McClaugherty et al. 1985; Wardle 2002) as well as litter characteristics such as the chemical composition of the decomposing litter (Melillo et al. 1982; Hobbie 1992; Enriquez et al. 1993). Studies to determine the relative importance of site versus litter characteristics in determining rates of decomposition are common (McClaugherty et al. 1985; Ashton et al. 2005; Hobbie 2005). However, it is unknown how the relative importance of site and litter characteristics changes with fire frequency.

In this study, we took advantage of a long-term prescribed burning experiment in a Minnesota oak savanna to determine the role of fire in influencing rates of intraspecific litter decomposition and nutrient dynamics. A gradient in both soil N availability and *Quercus ellipsoidalis* litter N concentrations has developed as a result of variation in fire frequency at this site, with both factors declining with increased frequency of fire (Reich et al. 2001). Higher fire

frequency has led to increased soil pH (Tester 1989), increased canopy openness (Reich et al. 2001), and lowered N mineralization rates below trees in frequently burned sites compared to unburned sites (Reich et al. 2001; Dijkstra et al. 2006). We hypothesized that increased fire frequency would reduce rates of decomposition through effects on both site and litter characteristics. As a result of decreased litter moisture and decreased soil N availability (site characteristics), we expected increased fire frequency would result in lower rates of decomposition regardless of litter characteristics. In addition, because of decreased litter N concentrations (a litter characteristic), we expected increased fire frequency to slow rates of decomposition regardless of site characteristics. We hypothesized that litter decomposition is N-limited, and expected low-N litter to show high rates of N immobilization, especially when decomposed in sites with high N availability. Finally, we expected litter microbial biomass to be positively related to rates of decomposition, but not necessarily N immobilization. Both processes are microbially mediated; however, the conditions that favor rates of decomposition and microbial growth are similar (Paul and Clark 1996), while N immobilization is more likely to be dependent on initial litter chemistry rather than microbial biomass.

Materials and methods

Study area

We conducted a leaf litter decomposition experiment at Cedar Creek Ecosystem Science Reserve (formerly Cedar Creek Natural History Area), a National Science Foundation Long-Term Ecological Research site in Anoka County, Minnesota (45°25′N, 93°10′W). Soils at this site are sandy, infertile and excessively drained (Typic and Alfic Udipsamments). Mean annual precipitation is 79 cm, with mean daily temperatures ranging from 22°C in July to −11.5°C in January.

A prescribed burning experiment was initiated at this site in 1964 to examine the response of the plant community to varying fire frequency and to maintain oak savanna vegetation (Peterson and Reich 2001). Aerial photographs reveal that woodlands with scattered grass patches dominated vegetation in the area prior to the initiation of the burning experiment. A total of 19 burn units ranging from 2.4 to 30 ha have received burn treatments ranging in frequency between 0 and 0.84 fires per year. Prescribed burns are conducted in the spring and are of relatively low intensity, typically not hot enough to completely burn the litter layer (Dijkstra et al. 2006). Units that have remained unburned are characterized by closed canopy oak forest (primarily northern pin oak, *Quercus ellipsoidalis* E.J. Hill) while

frequently burned sites are open savanna dominated by C4 and C3 grasses and sedges [*Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Sorghastrum nutans* (L.) Nash, *Poa pratensis* L. and *Carex* spp.] with interspersed oak stands (*Q. ellipsoidalis*, and bur oak, *Quercus macrocarpa* Michx.).

Experimental design

Our goal for this experiment was to investigate the effects of fire frequency on oak litter decomposition and N dynamics. We selected litter of pin oak because it is the dominant tree species across the entire gradient. Bur oak is common in the frequently burned units; however, it is rare in the unburned units. In addition, pin oak litter N concentrations decrease significantly with increasing fire frequency (Reich et al. 2001). Because soil N availability also declines with increasing fire frequency even within oak-dominated patches (Dijkstra et al. 2006), we focused on those patches, comparing the relative importance of site and litter characteristics on decomposition simultaneously. We acknowledge that increased fire frequency changes plant community composition from tree to grass-dominated vegetation (Peterson and Reich 2001), affecting the composition of litter (and possibly the environment) at the larger scale of a burn unit. However, beneath trees, oak litter makes up the dominant litter type regardless of burn frequency (personal observation). Additional research at this site is currently underway to study the effects of the shift in vegetation on litter composition in burned and unburned units and how this shift influences rates of root and litter decomposition (M. Norris, personal communication).

For this study, we classified burn units into three categories—high burn (burn frequency >0.80), medium burn (burn frequency between 0.33 and 0.50), and control (unburned since 1964). We selected three units (hereafter, "sites") in each category for a total of nine sites. We selected three replicate plots in each site that were similar in plant community composition and structure. Replicate plots were nested within each site for analyses (see "Data analysis," below), so our level of replication for all analyses is three (i.e., three sites at each level of fire frequency). In order to isolate the influence of site N availability, we aimed to minimize the microclimate variation caused by differences in canopy openness across the burn frequency gradient by selecting plots in control sites that were characterized by forest gaps—openings in the canopy near a mature pin oak tree, while plots in the more frequently burned sites were located in stands of one or several mature pin oak trees surrounded by grassland.

In October 2001, fresh *Q. ellipsoidalis* leaf litter was collected from the ground in three sites representing each of the three burn frequencies—high, medium, and control.

Subsamples of collected litter were ground and analyzed for initial chemistry using the methods described below ($n = 5$ per burn frequency). Litter was dried at 65°C and stored in plastic bags in the laboratory until the following spring when it was placed in 20 cm × 20 cm litterbags made from 1-mm-mesh fiberglass window screen. Approximately 1.5 g dry weight was added to each litterbag and initial litter mass was recorded for each litterbag. Litterbags were deployed in May 2002 and all litterbags were placed below the canopy of a mature *Q. ellipsoidalis* tree.

We employed a reciprocal transplant experimental design in which litterbags containing litter from each of the three burn frequencies was placed in every plot. Therefore, with each litterbag we controlled the fire frequency at location of litter origin ("litter type") as well as the fire frequency at the site of decomposition. We placed nine litterbags of each litter type in each plot so that three litterbags of each litter type could be collected at each of three collection dates (243 total litterbags): October 2002, May 2003, and October 2003. In March 2003, in the middle of the experiment, all litterbags were collected from the field and stored at 10°C for 2 weeks to avoid combustion by the prescribed burns conducted in some sites.

Data collection and analysis

Site characteristics

We characterized plots for N and P availability, litter layer moisture content, and litter layer temperature. We used ion-exchange resin (IER) bags to measure nutrient availability in the soil (Giblin et al. 1994). A total of 15 ml of resin [Dowex Marathon MR-3 mixed bead resins (R-100835), Superlco Parke, Bellefonte, Pa.] was placed in nylon stocking bags. Bags were acid-washed in 10% HCl for 2 h and rinsed with deionized water. In May 2002 and 2003, three resin bags were placed at 10 cm soil depth in close proximity to the litterbags. Resin bags were collected and replaced in July and September with a final collection in November. Collected resin bags were rinsed with deionized water, air-dried in aluminum tins and weighed. We extracted the resins using 100 ml of acidified 2 M NaCl. We analyzed extracts for NO_3^-, NH_4^+, and PO_4^{3-} concentrations using an Alpkem autoanalyzer (OI Analytical, College Station, TX, USA) and express inorganic N and P accumulations on a resin mass basis.

In 2003, the second year of the study, we characterized the litter layer in all plots for temperature and moisture content (we assume that relative differences among sites were the same for 2002 and 2003). We placed temperature data loggers (Optic StowAway temperature logger; Onset Computer, Bourne, Mass.) in each plot to measure temperature in the litter layer. Data loggers were placed in a litterbag

along with approximately 2–3 g oak litter to approximate the conditions of the litterbags used in the experiment. Temperature was recorded hourly during the 6-month growing season. Gravimetric moisture (65°C) was measured in the litter layer 3 times over the growing season by collecting litter from a 0.5-m^2 area in each plot.

Litter characteristics

Subsamples of initial litter ($n = 6$) from each fire frequency were analyzed for nutrients (N and P) and C chemistry. Initial litter C fractions were determined using an Ankom fiber analyzer (Ankom Technology, Fairport, N.Y.). Litter was extracted for soluble cell contents, cellulose, hemicellulose and bound proteins, and lignin (plus other recalcitrant) fractions. To measure litter C, N, and P content, litter was ground with a Wiley mill and a subsample finely ground with a mixer mill (CertiPrep 8000-D). Samples were analyzed for total C and N content by combustion on an ECS 4010 element analyzer (Costech Analytical, Valencia, Calif.) at the University of Nebraska, Lincoln. Total litter P content was measured using a persulfate digestion of ground litter. We quantified P content colorimetrically on an Alpkem autoanalyzer (OI Analytical, College Station, Tex.).

We measured litter mass loss at each collection date by comparing final to initial dry mass of each litterbag. Care was taken to include only material that was in the litterbag initially, and we removed soil and other material before weighing. We measured C, N, and P content at each collection date using the methods described above. To determine the change in litter N and P content we compared nutrient content at each collection to initial litter nutrient content.

At the second and third collection date we analyzed litter for microbial biomass using the chloroform fumigation-extraction technique (Robertson et al. 1999). This technique has been used previously to measure soil microbial biomass; however, we found that it is also effective in estimating litter microbial biomass. First, we weighed the litter in each litterbag to determine the total fresh weight. Second, litter was divided into two samples. One sample was dried at 65°C to determine moisture content and this value was used to calculate the dry weight of the litter in each litterbag. Finally, the rest of the litter was homogenized by hand (the small amount of litter remaining at collection made mechanically grinding the litter impossible) while wearing latex gloves. Remaining litter was then divided into two subsamples—fumigated and non-fumigated. Non-fumigated samples were extracted with 0.5 M K_2SO_4 and filtered. Fumigated samples were placed in a vacuum desiccator with boiled chloroform for 2 days and then extracted using the methods above. Extracts of fumigated and non-fumigated samples were analyzed on a total organic C

analyzer with an N measuring unit attached (Shimadzu TOC-V$_{CPN}$). In our analyses we used the difference in labile C in fumigated and non-fumigated litter (measured in milligram per gram liter) as an estimate of microbial biomass.

Data analysis

All data were analyzed using the statistical package JMP version 5.1 (SAS Institute, Cary, N.C.). The two-way ANOVAs were used to determine the effects of site fire frequency (high, medium, and control) and litter type (high burn, medium burn, and control) on litter mass loss and N dynamics (ANOVA was used instead of regression because there was little to no variation in fire frequency within each of the three categories of fire frequency). Each of the three collection dates was analyzed separately as the data did not fit a negative exponential decomposition model (hence it was not possible to summarize the data using decomposition rate constants). We analyzed our data using a two-way nested ANOVA design with plot as a random effect nested within site. Thus, in our results $n = 3$ for each level of fire frequency. Mean comparisons among burn frequencies and among litter types were done using Tukey's honest significant difference. All mean comparisons are noted in "Results". We used simple linear regression to determine the relationships between litter microbial biomass and litter mass loss and N dynamics.

Results

Initial litter C chemistry was similar among litter types except that litter from control sites had slightly greater percent cellulose than litter from high-burn sites (Table 1). However, there were significant differences in initial litter N and P: both were significantly higher in control litter than in litter from high-burn sites, with litter from unburned control sites having 41% more N than litter from high-burn sites (Table 1).

Similar to the results of previous studies at Cedar Creek (Reich et al. 2001; Dijkstra et al. 2006), we found that soil N availability declined with increased fire frequency (Fig. 1). Soil NH_4^+ and NO_3^- availability measured using IER was significantly higher in control sites than in high-burn sites (Tukey's HSD; Fig. 1). Soil PO_4^{3-} availability was also higher in control sites. Fire frequency also influenced temperature and moisture in the litter layer, with control sites significantly cooler and wetter than burned sites (Tukey's HSD; Table 1).

Despite the significant effect of fire frequency on these site characteristics, litter decomposition was not significantly different among the three burn frequencies at any of the three collection dates (two-way ANOVA; Fig. 2). In

Table 1 Environmental characteristics (litter temperature and moisture) and initial litter nutrient and C fraction concentrations for litter used in decomposition experiment

Site fire frequency	Growing season litter temperature (°C)	Growing season litter moisture	Initial litter nutrients (%)			Initial litter C fractions (%)		
			N	P	Cell solubles	Hemicellulose and proteins	Cellulose	Lignin and recalcitrants
High	18.9 (0.42) a	13.8 (0.8) a	0.631 (0.03) a	0.049 (0.001) a	50.9 (0.52)	14.2 (0.21)	16.6 (0.43) a	18.6 (0.20)
Medium	18.3 (0.38) a	14.1 (1.4) a	0.769 (0.02) ab	0.050 (0.001) a	49.5 (0.36)	14.6 (0.11)	17.4 (0.23) ab	18.7 (0.25)
Control	17.6 (0.36) b	21.6 (2.3) b	0.887 (0.04) b	0.056 (0.002) b	46.8 (1.84)	16.6 (1.78)	17.9 (0.32) b	18.8 (0.23)

Values are means (SEs) of growing season values for environmental characteristics and of subsamples of initial litter. *Different letters* within a column indicate significant differences among fire frequencies ($P < 0.05$, Tukey's HSD)
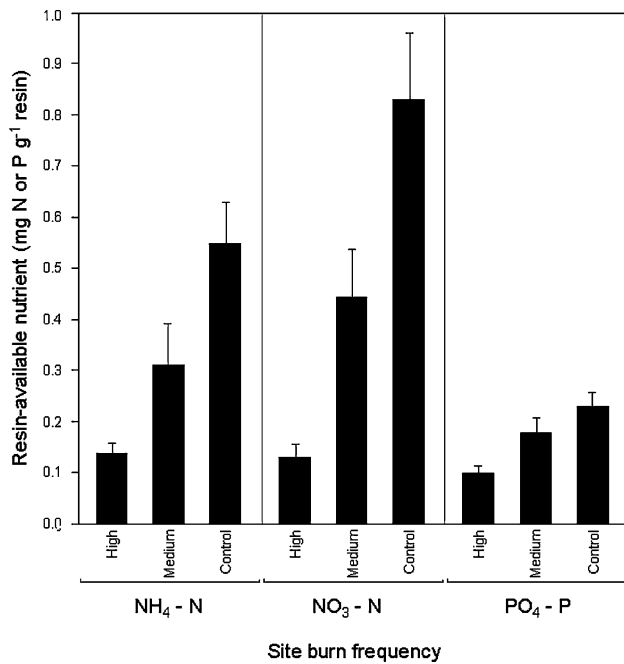

Fig. 1 Fire frequency effects on soil N and P availability measured using ion-exchange resin bags during the 2003 growing season. Data shown represent nutrient availability (mean ± 1 SE) summed over the three sampling dates during the growing season. *Symbols* represent the fire frequency of the site of litter origin

Fig. 2 Mean litter mass loss over two growing seasons (±1 SE) grouped by site of decomposition. *Symbols* represent the fire frequency of the site of litter origin: *open triangle* indicates high burn, *open square* indicates medium burn, *dark filled circle* indicates control

contrast, by the final collection date, litter type (i.e., site of litter origin) significantly influenced rates of litter decomposition (two-way ANOVA, $P = 0.040$; Fig. 2). There was no significant effect of litter type for the first two collection dates. On the final collection date, litter from high-burn sites had decomposed more slowly than litter from control sites, regardless of the location in which the litter was decomposed ($P < 0.05$, Tukey's HSD). Litter from medium-burn sites decomposed at an intermediate rate and did not differ from either the control or high-burn sites. There were no significant site by litter type interactions ($P = 0.94$).

In contrast to mass loss, litter N dynamics were dependent on both site and litter characteristics (Fig. 3). Although litter from medium-burn-frequency sites and control sites showed only small changes in N content over time, litter
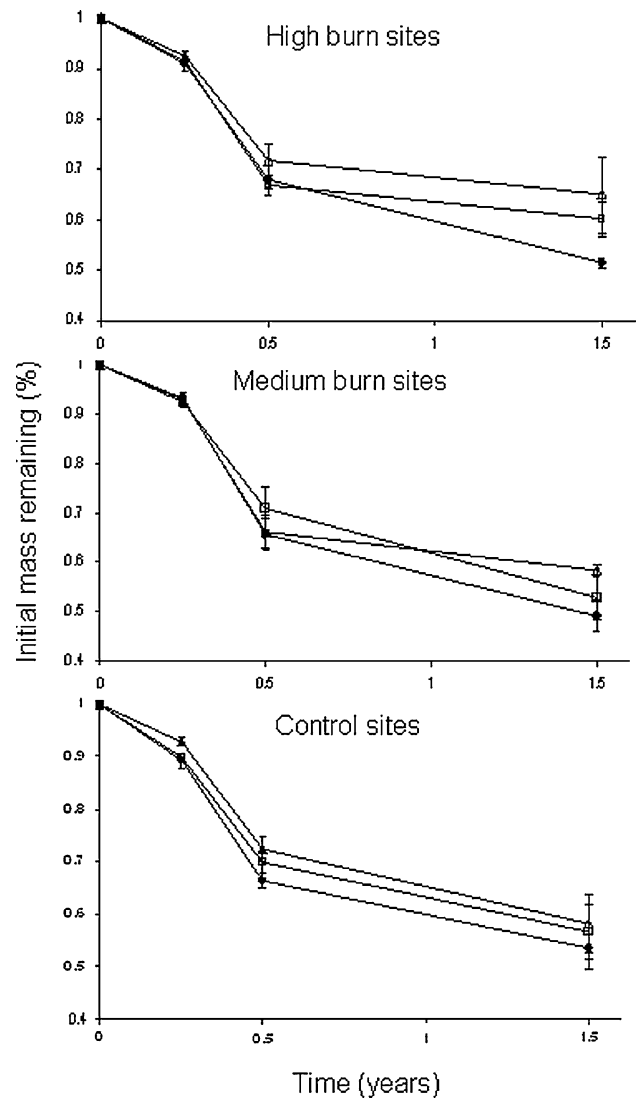
from high-burn sites showed a net immobilization of N over the two growing seasons (Fig. 3). Thus, the effect of litter type was significant on both the second and third
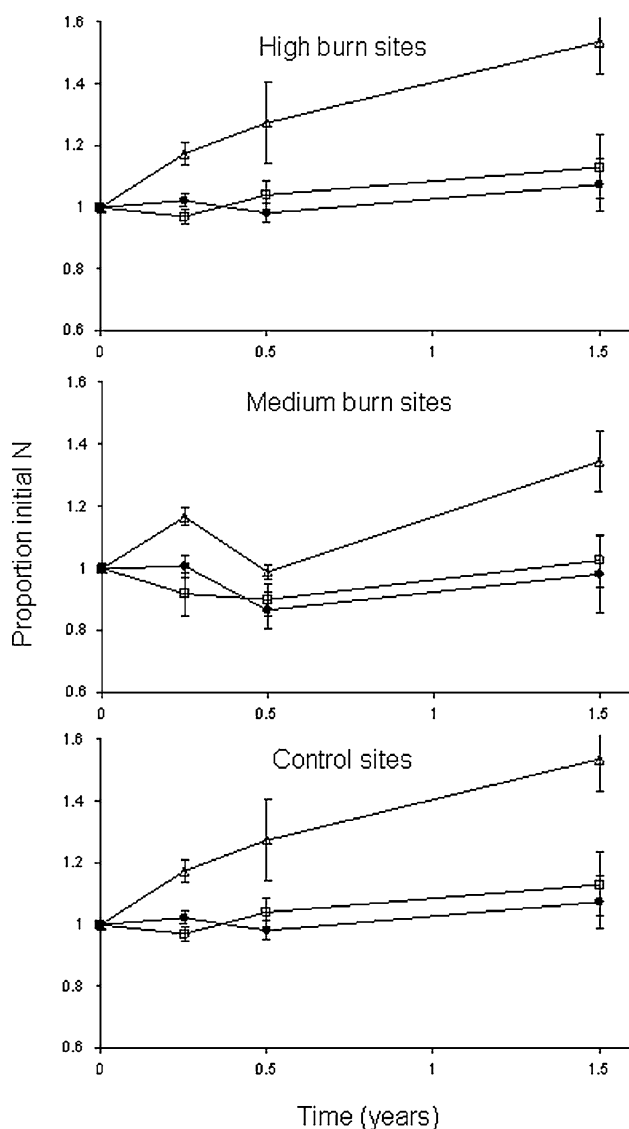
Fig. 3 N dynamics in decomposing litter in sites with high, medium, and control fire frequency. Values over 1.0 indicate the litter N content increased above its initial value. *Symbols* represent the fire frequency of the site of litter origin: *open square* indicates high burn, *open square* indicates medium burn, *dark filled circle* indicates control. Values are mean ± SE

collection dates as high-burn litter exhibited greater N immobilization than medium burn or control litter ($P < 0.001$ in both years; Tukey's HSD). The effect of site of decomposition was significant for litter N dynamics on the second collection date (two-way ANOVA, $P < 0.001$; Fig. 3). Between the first and second collection dates litter in high- and medium-burn sites showed a period of N release while litter in the control sites did not exhibit the same trend (Fig. 3). However, site was no longer significant after 1.5 years ($P = 0.215$) and there was no site by litter type interaction for any of the collection dates. Litter P content increased over time; however, final litter P content

measured in the litterbags showed no differences among litter types or sites (data not shown).

Microbial biomass was a significant predictor of rates of mass loss in the litter; however, there was no relationship between microbial biomass and N dynamics. Total litter mass loss measured at the end of two growing seasons was positively related to microbial biomass ($P < 0.001$, $r^2 = 0.20$, data not shown), with greater mass loss occurring in litterbags in which we measured higher microbial biomass. A similar relationship was observed after only the first year of decomposition as well ($P < 0.001$; data not shown). There was no relationship between litter microbial biomass and N content in the litter in the first or second year of the study ($P = 0.352$ and 0.298, respectively; data not shown). There was no significant difference in microbial C:N among litter types or among sites in either year (data not shown).

Discussion

Even though fires consume much of the aboveground litter before it completely decomposes, fires only occur with a maximum frequency of 4 out of 5 years and are of low intensity, resulting in incomplete combustion of the litter layer. Thus, examining the early stages of leaf litter decomposition remains important to understanding ecosystem C and nutrient dynamics, even in frequently burned sites. Indeed, previous research at this site found that fires in frequently burned sites consume 73% of aboveground litter on average in plots beneath trees (Dijkstra et al. 2006). Among the different fire frequency treatments imposed by this experiment, burned sites range from having a minimum of a 2-year respite from fire once every 5 years to a 10-year respite from each fire. Therefore, rates of decomposition and nutrient dynamics in the early stages of litter decay play a role in determining the overall effect of fire on C and nutrient cycling in burned as well as unburned oak ecosystems at this site, even in the most frequently burned sites.

We found that litter characteristics were more important in determining rates of decomposition than site characteristics, with litter from high-burn sites decomposing more slowly than litter from medium or control sites, regardless of the site in which the litter was decomposed. Research at Cedar Creek has shown primary production to be N limited (Tilman 1984), and the faster rates of decomposition of high-N litter (from high-burn sites) along with the high rates of N immobilization in decomposing litter suggest that decomposition of fresh litter in some N-poor sites is N limited as well. Therefore we expected that fire would influence decomposition by way of a decline in soil N availability resulting in a decrease in N supply to decomposers. In contrast, the primary effect of soil N availability on decom-

position appears to be through its indirect effect on litter chemistry, rather than through direct supply of exogenous N to decomposers. We hypothesize that this litter chemistry effect is primarily caused by differences in initial litter N content, as other aspects of initial litter chemistry did not vary significantly among litter types. Along this fire frequency gradient, oak trees in more frequently burned sites respond to decreased soil N availability by producing high C:N litter—initial litter N concentrations were 41% higher in control sites compared to high-burn sites. This low-quality litter of frequently burned sites then decomposes more slowly than litter from trees in unburned sites.

Our results indicate that the differences in site characteristics due to fire had little direct effect on decomposition. Higher litter temperatures and lower litter moisture in frequently burned relative to unburned sites may have had opposing effects on decomposition, with little net effect. However, relative soil N availability was 5–10 times higher in control sites than high-burn sites (Reich et al. 2001; also see Fig. 1), so the lack of site effects on rates of decomposition was surprising. Previous studies investigating the role of exogenous and litter N on decomposition also have found a lack of an effect of exogenous N supply on decomposition (McClaugherty et al. 1985; Prescott 1995; Knorr et al. 2005) including previous studies at Cedar Creek (Pastor et al. 1987; Hobbie 2005). However, some studies investigating the effect of N fertilization on decomposition have shown results ranging from positive (O'Connell 1994; Hobbie 2005) to negative (Fog 1988; Prescott 1995) effects of exogenous N on rates of mass loss. In a recent meta-analysis of studies on N-enrichment effects on decomposition, Knorr et al. (2005) found that on average, increasing exogenous N availability had slightly negative effects on average on litter decay.

Contrary to our hypotheses we also found no interaction between soil N availability and litter chemistry. It has been suggested that when N availability is high, the importance of litter N content in influencing rates of decomposition is reduced (Melillo et al. 1982); however, despite large differences in soil N availability across sites in our study, we found litter N content to be the most significant predictor of rates of decomposition of all the variables we investigated across all sites. Interactions between litter quality and exogenous N have been reported in previous studies (Hobbie 2000; Knorr et al. 2005) where differences in litter quality were due to variation in lignin concentrations rather than N, although the direction of the effect is variable among studies.

Previous studies on the effects of fire on decomposition have found results ranging from no effect (Stark 1977; Grigal and McColl 1977; Monleon and Cromak 1996) to significant reductions in decay rates following fire (Springett 1976; Raison et al. 1986; Monleon and Cromak 1996).

Most of these studies have reported the effects of a single fire event on decomposition, either in the year immediately following the fire or in a chronosequence of sites varying in time since last burning. Our results suggest that the major influence of fire on decomposition is through its effect on litter quality that occurs as a result of repeated burning over time. Although changes in litter quality have been shown to occur fairly rapidly (Ojima et al. 1994), it is possible that these effects are not being captured in studies on infrequently burned sites or that do not take long-term fire history into account.

Results of litter N dynamics suggest that the decomposer community is limited by low substrate N when it is decomposing litter from high-burn sites, but not when decomposing the other litter types (Fig. 3). Litter from high-burn sites that had lower initial N content showed the highest amounts of N immobilized over the 2-year study. Litter from medium-burn and control sites immobilized less N, presumably because initial litter N content was sufficient to meet the demand for N of the decomposer community.

The combined effects of slower rates of decomposition and increased N immobilization associated with increased fire frequency could result in a positive feedback, reinforcing low N availability in frequently burned sites (Fig. 4). Fire promotes N losses through volatilization decreasing soil N availability in frequently burned sites. Sites with low N availability have decreased oak litter N content which results in decreased rates of decomposition and increased rates of N immobilization. N that is immobilized into litter is taken up by microbes from the soil N pool, further decreasing soil N availability and creating a positive feedback (Fig. 4a). When a fire does occur, the litter burned has a relatively higher N content than it did initially, potentially causing even greater declines in soil N over time (Fig. 4b). Although we do not know the relative importance of this effect of intraspecific variation in litter N chemistry on N dynamics compared to the effect of changes in plant community composition that occur as a result of fire, this phenomenon certainly represents a pathway of N loss beneath trees across the fire frequency gradient.
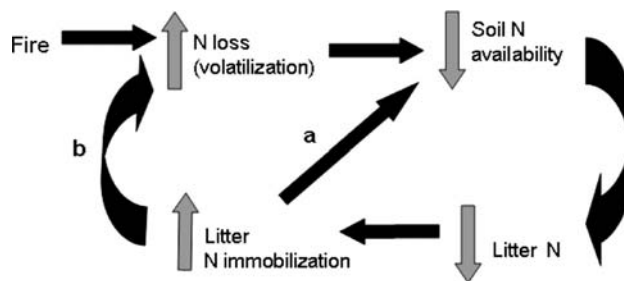

Fig. 4 A positive feedback of decreased soil N availability due to fire is caused by the immobilization of soil N into low-N litter by microbes (*a*), and increased N losses when fire burns litter that has increased N content due to immobilization (*b*)

Microbial biomass was positively related to rates of decomposition. However, microbial biomass showed no correlation with litter N dynamics. Litter N dynamics are certainly microbially mediated, but it is not necessarily the biomass of community that determines these dynamics. More likely it is the discrepancy between the C:N ratio of the litter (that increased with fire frequency) and the C:N ratio of microbial biomass (which was constant across fire frequencies). Changes in microbial community composition could have had further effects on litter N dynamics. For example, in a related study at this site, we found that excluding fungi from litterbags through the use of fungicide resulted in a significant decline in N immobilization (unpublished data). In addition, other studies have found that across the fire frequency gradient fungal abundance is a significant predictor of rates of both root and litter N dynamics (M. Norris, personal communication). Therefore it is possible that shifts in microbial community composition could play a larger role in N dynamics than differences in biomass. Additional research is needed to determine how shifts in microbial community composition affect rates of decomposition and N dynamics in litter.

We acknowledge that this study focuses only on one species of litter and that a major effect of fire at this site is that of changing plant community composition from oak-dominated forest to a C4 grass-dominated oak savanna. The change in community composition has significant effects on nutrient cycling, rates of root and litter decomposition, and other ecosystem properties (Dijkstra et al. 2006). However, long-term differences in fire frequency also have caused significant differences in intraspecific litter chemistry (Reich et al. 2001), likely due to reduced soil N availability, further influencing rates of litter decomposition (this study) and net N mineralization (this study; Dijkstra et al. 2006). Thus, indirect and direct intraspecific responses to burning can be a significant pathway by which fire influences C and N cycling.

References

Ashton IW, Hyatt LA, Howe KM, Gurevitch J, Lerdau MT (2005) Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. Ecol Appl 15:126–1272

Boerner REJ (1982) Fire and nutrient cycling in temperate ecosystems. Bioscience 32: 187-192

Bond WJ, Keeley JE (2005) Fire as a global herbivore: the ecology and evolution of flammable systems. Trends Ecol Evol 20:387–394

Certini G (2005) Effects of fire on properties of forest soils: a review. Oecologia 143:1–10

Christensen NL, Muller CH (1975) Effects of fire on factors controlling plant growth in *Adenostoma* chaparral. Ecol Monogr 45: 29-55

Dijkstra FA, Wrage K, Hobbie SE, Reich PB (2006) Tree patches show greater N losses but maintain higher soil N availability than grassland patches in a frequently burned oak savanna. Ecosystems 9:441–452

Enriquez S, Duarte CM, Sandjensen K (1993) Patterns in decomposition rates among photosynthetic organisms—the importance of detritus C-N-P content. Oecologia 94:457–471

Fog K (1988) The effect of added nitrogen on the rate of decomposition of organic matter. Biol Rev 63:433–462

Giblin AE, Laundre JA, Nadelhoffer KJ, Shaver GR (1994) Measuring nutrient availability in arctic soils using ion-exchange resins—a field test. Soil Sci Soc Am J 58:1154–1162

Grigal DF, McColl JG (1977) Litter decomposition following forest fire in northeastern Minnesota. J Appl Ecol 14:531–538

Harden JW, Mack M, Veldhuis H, Gower ST (2003) Fire dynamics and implications for nitrogen cycling in boreal forests. J Geophys Res 108:1–8

Hobbie SE (1992) Plant species effects on nutrient cycling. Trends Ecol Evol 7:336–339

Hobbie SE (2000) Interactions between litter lignin and soil nitrogen availability during leaf litter decomposition in Hawaiian montane forest. Ecosystems 3:484–494

Hobbie SE (2005) Contrasting effects of substrate and fertilizer nitrogen on the early stages of decomposition. Ecosystems 8:644–656

Knorr M, Frey SD, Curtis PS (2005) Nitrogen additions and litter decomposition: a meta-analysis. Ecology 86:3252–3257

McClaugherty CA, Pastor J, Aber JD, Melillo JM (1985) Forest litter decomposition in relation to soil-nitrogen dynamics and litter quality. Ecology 66:266–275

Meetenmeyer V (1978) Microclimate and lignin control of litter decomposition rates. Ecology 59:465–472

Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. Ecology 63:621–626

Monleon VJ, Cromak K (1996) Long-term effects of prescribed underburning on litter decomposition and nutrient release in ponderosa pine stands in central Oregon. For Ecol Manage 81:143–152

Neary DG, Klopatek CC, Debano LF, Ffolliott PF (1999) Fire effects on belowground sustainability: a review and synthesis. For Ecol Manage 122:51–71

O'Connell AM (1994) Decomposition and nutrient content of litter in a fertilized eucalypt forest. Biol Fertil Soils 17:159–166

Ojima DS, Schimel DS, Parton WJ, Owensby CE (1994) Long-term and short-term effects of fire on nitrogen cycling in tallgrass prairie. Biogeochemistry 24:67–84

Pastor J, Stillwell MA, Tilman D (1987) Litter bluestem litter dynamics in Minnesota old fields. Oecologia 72:327–330

Paul EA, Clark FE (1996) Soil biology and biochemistry, 2nd edn. Academic, London

Peterson DW, Reich PB (2001) Prescribed fire in oak savanna: fire frequency effects on stand structure and dynamics. Ecol Appl 11:914–927

Prescott CE (1995) Does nitrogen availability control rates of litter decomposition in forests? Plant Soil 169:83–88

Raison RJ, Woods PV, Khanna PK (1986) Decomposition and accumulation of litter after fire in sub-alpine eucalypt forests. Aust J Ecol 11:9–19

Reich PB, Peterson DW, Wedin DA, Wrage K (2001) Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. Ecology 82:1703–1719

Robertson GP, Bledsoe CS, Coleman DC, Sollins P (eds) (1999) Standard soil methods for long-term ecological research. Oxford University Press, New York

Springett JA (1976) Effect of prescribed burning on soil fauna and on litter decomposition in Western Australia forests. Aust J Ecol 1:77–82

Stark NM (1977) Fire and nutrient cycling in a Douglas fir-Larch forest. Ecology 58:16–30

Tester JR (1989) Effects of fire frequency on oak savanna in east-central Minnesota. Bull Torrey Bot Club 116:134–144

Tilman GD (1984) Plant dominance along an experimental nutrient gradient. Ecology 65:1445–1453

Turner CL, Blair JM, Schartz RJ, Neel JC (1997) Soil N and plant responses to fire, topography, and supplemental N in tallgrass prairie. Ecology 78:1832–1843

Wan S, Hui D, Luo Y (2001) Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol Appl 11:1349–1365

Wardle DA (2002) Communities and ecosystems: linking the aboveground and belowground components. Princeton University Press, Princeton