REGULAR ARTICLE

Positive feedbacks between decomposition and soil nitrogen availability along fertility gradients

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Abstract

Background and aims We determined the relationship between site N supply and decomposition rates with respect to controls exerted by environment, litter chemistry, and fungal colonization.

Methods Two reciprocal transplant decomposition experiments were established, one in each of two long-term experiments in oak woodlands in Minnesota, USA: a fire frequency/vegetation gradient, along which soil N availability varies markedly, and a long-term N fertilization experiment. Both experiments used native *Quercus ellipsoidalis* E.J. Hill and *Andropogon gerardii* Vitman leaf litter and either root litter or wooden dowels.

Results Leaf litter decay rates generally increased with soil N availability in both experiments while belowground litter decayed more slowly with increasing soil N. Litter chemistry differed among litter types, and

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these differences had significant effects on below-ground (but not aboveground) decay rates and on aboveground litter N dynamics during decomposition. Fungal colonization of detritus was positively correlated with soil fertility and decay rates.

Conclusions Higher soil fertility associated with low fire frequency was associated with greater leaf litter production, higher rates of fungal colonization of detritus, more rapid leaf litter decomposition rates, and greater N release in the root litter, all of which likely enhance soil fertility. During decomposition, both greater mass loss and litter N release provide mechanisms through which the plant and decomposer communities provide positive feedbacks to soil fertility as ultimately driven by decreasing fire frequency in N-limited soils and vice versa.

Introduction

The effect of plant species on soil processes such as nutrient cycling and storage has been well documented through previous studies and reviews (e.g. Chen and Stark 2000; Cornelissen 1996; Elgersma et al. 2011; Fornara and Tilman 2008; Gower and Son 1992; Hobbie 1992; Hobbie et al. 2006; Lovett et al. 2004; Reich et al. 1997; Rothstein et al. 2004; Scott and Binkley 1997; Turner et al. 2011; Wedin and Tilman 1990). Decomposition is a critical ecosystem process that mediates plant-soil relationships through regulation of nutrient turnover and the formation and accumulation of soil organic matter. In fact, recycling of nutrients through decomposition is the primary source of plant-available nutrients in most unmanaged terrestrial ecosystems, far outweighing supply from external inputs including atmospheric deposition or fixation on an annual basis (Whittaker et al. 1979). Factors such as climate, litter quality (chemistry), and the decomposer community have been shown to be important controls of decomposition rates (Berg and McClaugherty 2007; Staaf and Berg 1981; Swift et al. 1979). For example, Meentemeyer (1978) found that on the continental scale, the environment (climate) was the predominant control of decay while on the regional or local scale, litter (plant substrate) quality, and lignin content in particular, was

more closely related to decay rates. A more recent analysis (Cornwell et al. 2008) found similar results, but as strong a role for litter chemistry as for climate on the global scale.

Additional studies have evaluated the local influence of soil N availability on decay but consensus has yet to be reached (Sariyildiz and Anderson 2003). Knorr et al. (2005) reviewed relevant literature and concluded that on average across all studies, N additions did not have a significant nor consistent effect on decay. They suggested that this result was due to strong interactions between N supply, litter quality, and atmospheric N deposition such that the decomposition of detritus with relatively high lignin concentrations was inhibited by high rates of N fertilization as was the decay of litter in areas with high background N deposition rates (Knorr et al. 2005). Hobbie (2005, 2008) and Hobbie et al. (2012) directly investigated the effects of external N supply and litter N on decomposition, finding inconsistent effects of the two sources of N. Results generally supported the frequently held assumption that N limits decomposition in its early stages, particularly in sites with low soil N availability (Hobbie 2005; Hobbie et al. 2012).

Given the inconsistent relationships between decomposition and soil N fertility, the objectives of this study were to examine plant species and habitat effects on decomposition across two different soil N fertility gradients, each established by a different long-term manipulation in oak woodlands in Minnesota, USA. First, we determined the relative importance of substrate and habitat in controlling decomposition across a gradient of N availability resulting from variation in fire frequency and associated vegetation (Grigal et al. 1974; Peterson and Reich 2001; Reich et al. 2001) to determine whether N effects on decomposition and litter N dynamics along this gradient act to reinforce the gradient in soil N availability that arises from variation in fire frequency. Second, to more narrowly isolate the effects of N on decomposition, we established a complementary decomposition experiment in a nearby N fertilization manipulation. Additionally, we related patterns of decomposition to fungal colonization. We hypothesized that (i) decay rates would be related to substrate chemistry (e.g. would be faster for high N substrates and slower for substrates with high C:N, % lignin, or lignin:N) and (ii) decay rates would be higher in sites of greater soil N status, litter production, and soil moisture through positive effects on

the decomposer community. These hypotheses reflected our belief that decomposition at this site is N-limited and would be positively correlated to both litter N content and soil N supply. Lastly, we hypothesized that (iii) higher rates of decomposition would be related to higher abundances of decomposer organisms, specifically litter fungi.

In both the fire frequency and fertilization experiments, we established a reciprocal transplant decomposition study using dominant litter types from the two extremes of the savanna gradient, oak (*Quercus ellipsoidalis* E.J. Hill) litter from the oak woodlands that dominate at the low fire frequency (and relatively N-rich) end of the fire frequency gradient and C₄ grass (*Andropogon gerardii* Vitman) litter from the open savannas that dominate the high fire frequency (and relatively N-poor) end of the fire frequency gradient (Peterson and Reich 2001; Reich et al. 2001). Such an approach enabled us to separate effects of habitat (e.g. fire, microclimate, or fertilization) and litter type on decomposition rates and consequently on patterns of soil N cycling. This study complements a previous decomposition study across the same fire frequency gradient that focused on variation in substrate quality within oaks (Hernández and Hobbie 2008).

Methods

Site description

Cedar Creek Ecosystem Science Reserve (Cedar Creek hereafter), is a 2,300 ha reserve located on the Anoka sandplain in east central Minnesota, USA (45° 25′N, 93°10′W) in the historical transition zone between tallgrass prairie and northern hardwoods. Upland soils are Entisols derived from a glacial outwash sandplain and are excessively drained, very uniform fine sands (>90 % sand) of the Sartell and Zimmerman series (Grigal et al. 1974). These soils have low capacity for retaining soil N and are thus N-poor. Numerous nutrient addition experiments performed in both old fields and native savanna have shown that N is the major soil resource limiting plant growth (Tilman 1984, 1987). Previous work at Cedar Creek has shown evidence for strong plant species influences on nutrient dynamics (Dijkstra et al. 2006; Knops et al. 2001; Wedin and Tilman 1990); however, much of this work did not

directly address decomposition patterns of both aboveground and belowground litter with respect to fertility gradients. Cedar Creek has a continental climate with cold winters, hot summers, and precipitation (66 cm/year) spread fairly evenly throughout the year. The mean July temperature is 22.2 °C while the mean January temperature is −10°C.

Fire frequency/vegetation gradient

A 210 ha portion of Cedar Creek that was historically oak savanna has been subject to a prescribed burning experiment since 1964 to investigate the effects of fire frequency on species composition and ecosystem functioning. The sites (3–27 ha in size, mean = 14 ha) within this savanna framework cover a gradient of vegetation types spanning the range found at the prairie-forest border including open savanna (prairie with sparse oak canopy cover) to closed canopy oak forest. Sites were delineated and randomly assigned to a burning regime at the inception of the program. Prescribed (spring burning) fire frequencies range from 0 to 0.8 fires per year. Within these stands, permanent plots (75×50 m) were established between 1984 and 1995 for which there is an existing data set of species composition, above- and belowground production, soil net N mineralization, and litterfall, among other variables. In general, the fire frequency gradient is simultaneously a compositional gradient from oak-dominated (low fire frequency) to C₄-grass-dominated (high fire frequency), a productivity gradient, and a soil N availability fertility gradient, the latter two gradients negatively associated with fire frequency (Table 1, Norris 2008; Reich et al. 2001); for brevity hereafter we will refer to this as a fire frequency gradient. The experimental design has been previously described by Peterson and Reich (2001) and Reich et al. (2001).

We conducted two decomposition experiments. The first experiment was to discern litter type versus habitat effects across the fire frequency gradient. We conducted a reciprocal transplant consisting of four litter types across nine plots covering the range of fire frequency plots: three each of high (0.66–0.82 fires per year), intermediate (0.37–0.47), and low (0–0.11) fire frequency. The four litter types were leaf litter and roots of *Andropogon gerardii* and *Quercus ellipsoidalis*, which are dominant species at the high and low ends of the fire frequency gradient, respectively.

Table 1 Summary table of site characteristics by habitat for each of the fire frequency and fertilization gradients during relevant study years (Norris 2008). Soil measurements (0–20 cm) include mineral N (extractable ammonium + nitrate) and gravimetric soil water content averaged from 5 measurements each growing season and the cumulative net N mineralized over the entire season (April–October). Total soil C and N (0–20 cm) were measured once each season

Fire frequency/vegetation gradient						
Fire frequency category	Average actual fire frequency (fires/year)	Mineral N (kg/ha)	Net N min. (kg/ha/year)	Total soil N (Mg/ha)	Total soil C (Mg/ha)	Soil H$_2$O (%)
High	0.75	3.3	9.4	1.9	32.5	7.0
Intermediate	0.41	3.6	19.4	2.3	36.8	7.5
Low	0.04	5.7	47.5	2.7	44.9	7.9
Fertilization experiment						
Fertilization treatment	N fertilization rate (g N/m^2/year)	Mineral N (kg/ha)	Net N min. (kg/ha/year)	Total soil N (Mg/ha)	Total soil C (Mg/ha)	Soil H$_2$O (%)
Control	0	4.1	22.8	2.0	32.8	7.3
Low N	5.4	8.4	21.3	4.2	43.9	8.6
High N	17	14.9	45.6	3.6	41.1	8.1

Quercus leaf litter was collected weekly in the fall of 2000 in a single plot of low fire frequency using shade cloth spread beneath oak woodland ensuring collection of recently senesced leaves. *Quercus* roots (≤ 2 mm diameter) were dug (0–25 cm) from an area with very little understory vegetation. *Andropogon* litter (including leaves and stems) and roots (approximately 1 mm diameter, collected at 0–25 cm depth) were harvested from clones of *Andropogon gerardii* in a single area of high fire frequency. Roots of both species were washed to remove soil. All leaf and root material was air-dried at room temperature prior to placement in litterbags. Litterbags were constructed of 1 mm fiberglass mesh, 15×15 cm for the foliar litter and 10×10 cm for the root litter, and filled with 4.5 g and 3.0 g of air-dried leaf and root litter, respectively. These bags contained substrates at densities similar to the average natural density of those substrates (*unpublished data*) across the savanna gradient. In May 2001, we established 5 subplots in each of the 9 fire frequency plots, located regularly in the four corners and center of permanent plots. These five subplots enabled sampling of 5 replicate samples for each litter type at each harvest. Each subplot contained 5 samples of each of the 4 substrates so that one sample of each substrate could be collected during each of 5 harvesting times at approximately 5, 12, 17, 24, and 29 months. At the time of field placement, foliar litterbags were tacked to the soil surface and the root litterbags were buried in the top 10 cm of soil. At this time, 10 samples of each litter type were carried to the field

and returned to the laboratory for immediate processing for determination of initial substrate chemistry and to create conversion factors for mass lost during handling and to relate oven-dried mass (60 °C for 48 h) to air-dried mass. Initial litter chemistry included total C and N (Carlo Erba NA 1500 analyzer, Carlo Erba, Milano, Italy) and C fractions (including soluble C, hemicelluloses, cellulose, and lignin) determined by sequential acid extraction (neutral detergent fiber, acid detergent fiber) (ANKOM 220, ANKOM Technology, Macedon, NY). Upon litterbag collection, samples were cleaned of soil, oven-dried (60 °C for 48 h), and weighed. Samples were then ground for C and N analysis to calculate N immobilization or release by determining the product of percent N and the mass of the residual sample and dividing by the N content of the original sample. Litterbags were briefly removed immediately prior to and replaced following prescribed burning to allow for the continuation of decay while maintaining the local environmental effects of fire frequency.

Fertilization gradient

Within one burn unit (high fire frequency=0.65 fires per year), an artificial N gradient, ongoing since 1983, was established over 9 plots. Plots (20×50 m) were randomly assigned one of three fertilization treatments (*n*=3 for each treatment): unfertilized control, 5.4 gN/m^2/year, and 17 gN/m^2/year in the form of granular NH$_4$NO$_3$ applied twice each growing season. In

addition to N, the two fertilized treatments also receive supplemental micronutrients to maintain soil nutrient (i.e. cation) and chemical (e.g. pH) status in spite of N fertilization. Although there was a shift in herbaceous vegetation along this fertilization gradient, the tree canopy cover was fairly consistent and both *Andropogon gerardii* and *Quercus ellipsoidalis* were abundant.

The second decomposition experiment took place in this artificial fertility experiment. Leaf litterbags were constructed and filled in the same manner as above. The effect of the shifts in the belowground environment on decay patterns were examined using a common substrate of untreated birch wooden dowels (3 per bag, 14.6×0.2 cm long, commercially available as Cotton Tail Medical Products quality wood applicators, CITMED, Citronelle, AL), emphasizing habitat (fertilization) effects on belowground decay rather than in addition to species effects. This experiment utilized 4 subplots located randomly in each plot (four replicate samples per plot at each harvest). Litterbags were placed in the field in May 2002, and collected 4 times at approximately 2, 5, 12, and 17 months after field placement. Collection and handling of litterbags was identical to the previous experiment.

Decomposer community

Fungal colonization on litterbag samples was analyzed as one component of the decomposer community. Both morphological and molecular approaches were taken to describe the fungal colonization on samples collected from both decomposition experiments throughout the course of the experiment. As the first step of litter bag processing, fungal colonization on the surface of the litter was noted as the extent of fungal mycelia coverage in terms of a cover class 0–5 where 0 = no fungi present and 5 = entire litter bag sample surface colonized. Although we did not directly measure fungal biomass, such estimates of fungal colonization have been shown to correspond to fungal biomass by Nilsson et al. (2007) who found a positive significant correlation between visual estimation of fungal mycelia and the amount of a phospholipid fatty acid commonly used to indicate fungal biomass. This measure was used in addition to a simpler frequency metric of colonization by noting fungal presence or absence in each of the replicate samples per treatment. To ensure that what we considered fungal colonization

was in fact formed by fungi, a small (~2 mm×2 mm) portion of tissue was removed from each unique looking fungal colonization patch on a given litter bag. DNA from this tissue was then extracted and ITS rDNA gene region PCR-amplified from a subset of these samples using a kit based method (Avis et al. 2003). Because this type of sampling equates to environmental sampling and it is likely that such "colonization patches" included more than a single fungus, most of the successful amplicons were subsequently cloned (Avis et al. 2006). For cloned samples, 1–3 clones were picked and then sequenced. Three samples were not cloned, and were sequenced directly after PCR. Sequences were then assigned an identity after BLAST analysis. It is important to note that this approach was not exhaustive (not all tissues collected were analyzed) because there were large amounts of colonization on numerous samples and it was not feasible to analyze all samples. Hence, this molecular approach was used largely to confirm that the colonization we measured was indeed by fungi. A parallel and on-going study is currently examining these tissues and decomposer fungal communities in much greater detail.

Litterfall collection

Tree litterfall was collected in 20 L buckets for the duration of both experiments. In both experiments, 12 replicate buckets were placed systematically in each 75×50 m plot in the fire frequency gradient and randomly in each 20×50 m plot in the fertilization gradient. Buckets were sampled weekly during the fall season and as needed throughout the remainder of the year. Samples were oven-dried (60 °C for 48 h) and weighed. Total litterfall included mostly senesced leaves (61 % on average) but also acorns and small woody debris.

Calculations and analysis

Decomposition rates were calculated using a single exponential decay model $X_t/X_0 = e^{-kt}$, where X_t/X_0 represents the fraction of original mass remaining at time t in years and k is the annual decay constant (Olson 1963). A linear model was fit to the data by regressing the natural logarithm of the proportion of mass remaining over time in years, where k, the annual decomposition rate, is equal to the slope.

Decay rates were calculated by plot and by treatment for all litter types in both experiments (fire frequency or fertilization, $n=3$ in each case). The reciprocal transplant design permitted analysis and comparison of the effects of litter type and habitat on decomposition. A two-way factorial ANOVA was performed to test for treatment (habitat) and litter type effects on decay rates (k), final percent mass remaining, and the final percent of initial N. Analysis was done separately for aboveground and belowground litter types because of presumably differing microclimate and decomposition environments. When treatment effects were found to be at least marginally significant, $p \leq 0.10$, post-hoc Tukey's HSD tests were done to determine differences between individual treatments. Also, we used backward stepwise regressions (with model reduction following AIC) to determine variables best related to decay rates and final % N remaining. Because decay rates (k) and the final % mass remaining were highly correlated ($p<0.0001$, $R^2=0.88$ and $p<0.0001$, $R^2=0.94$ in the fire frequency and fertilization gradients, respectively), only k was used in these secondary analyses. Variables potentially related to treatment effects included soil moisture, annual soil net N mineralized and total soil N (Table 1, Norris 2008), and fungal colonization. Other metrics were considered (mean inorganic N and total soil C) but were found to be highly correlated with other variables (soil net N mineralized and total soil N, respectively). Soil nutrient dynamics (soil C and N dynamics) have been presented in greater detail elsewhere (Reich et al. 2001; Norris 2008) and were only used here as potential explanatory variables; these measurements were made in all permanent plots in both experiments at eight replicate subplots. In situ net N mineralization rates and inorganic N concentrations in the soil (0–20 cm) were determined via monthly 1 M KCl extractions during the growing season (April–October). Subsamples from these soils were analyzed for total soil C and N once each year (Norris 2008). We interpret litter chemistry effects (including initial %N, C:N ratio, % lignin, and lignin:N ratio) qualitatively due to having only four litter types.

Fungal colonization was examined with respect to time (fungal succession), litter type, and treatment. There was no consistent pattern over time with either measure of colonization so time was removed from further analyses and data were averaged for each plot over the duration of the experiment. We used ANOVA to analyze the effects of treatments and litter types separately for aboveground and belowground samples. When a significant effect was found, post-hoc Tukey's HSD tests examined individual differences between levels of treatment. All statistics were performed using JMP (SAS Institute Inc., Cary, NC).

Results

Fire frequency/vegetation gradient

Decomposition rates of aboveground substrates (both *Quercus* and *Andropogon* leaf litter) generally increased with decreasing fire frequency (Fig. 1a and b) resulting in a marginally significant fire frequency effect ($p=0.067$) (Table 2). As increasing fire frequency was also strongly and inversely associated with soil fertility (Table 1), decomposition rates were positively related to both annual soil net N mineralized ($p=0.0187$) and soil moisture ($p=0.0334$) in a multiple regression model (whole model: $p=0.0001$, $R^2=0.70$). In contrast, there was no effect of litter type (or treatment x litter type interaction) on either final mass remaining or the decay rate for leaf litter. Nonsignificant effects of litter type on decomposition were likely due to lower lignin and N concentrations in *Andropogon* compared with *Quercus* such that the two litter types differed little in their lignin:N ratios (Table 3).

Over time, the percent of initial N in these aboveground litter samples demonstrated much greater variability than did the decay rates (Fig. 1a and b). Only the *Quercus* leaves in the high and intermediate fire frequency plots exhibited a net release of N over the 2.5 year experiment (less than 100 % of original N content remained). There was a consistently greater percentage of initial N in *Andropogon* leaves compared to *Quercus*; and in both litter types, proportionally more N was immobilized in low fire frequency (more N-rich) plots. These patterns resulted in significant effects of both litter type and fire frequency treatment on the percent of initial N present at the final collection (Table 2). At that time, *Quercus* had significantly less percent of initial N (98.1 % on average) than *Andropogon* (146.3 %) as did the intermediate (109.6 %) and high (110.3 %) fire frequency plots compared to the low fire frequency plots
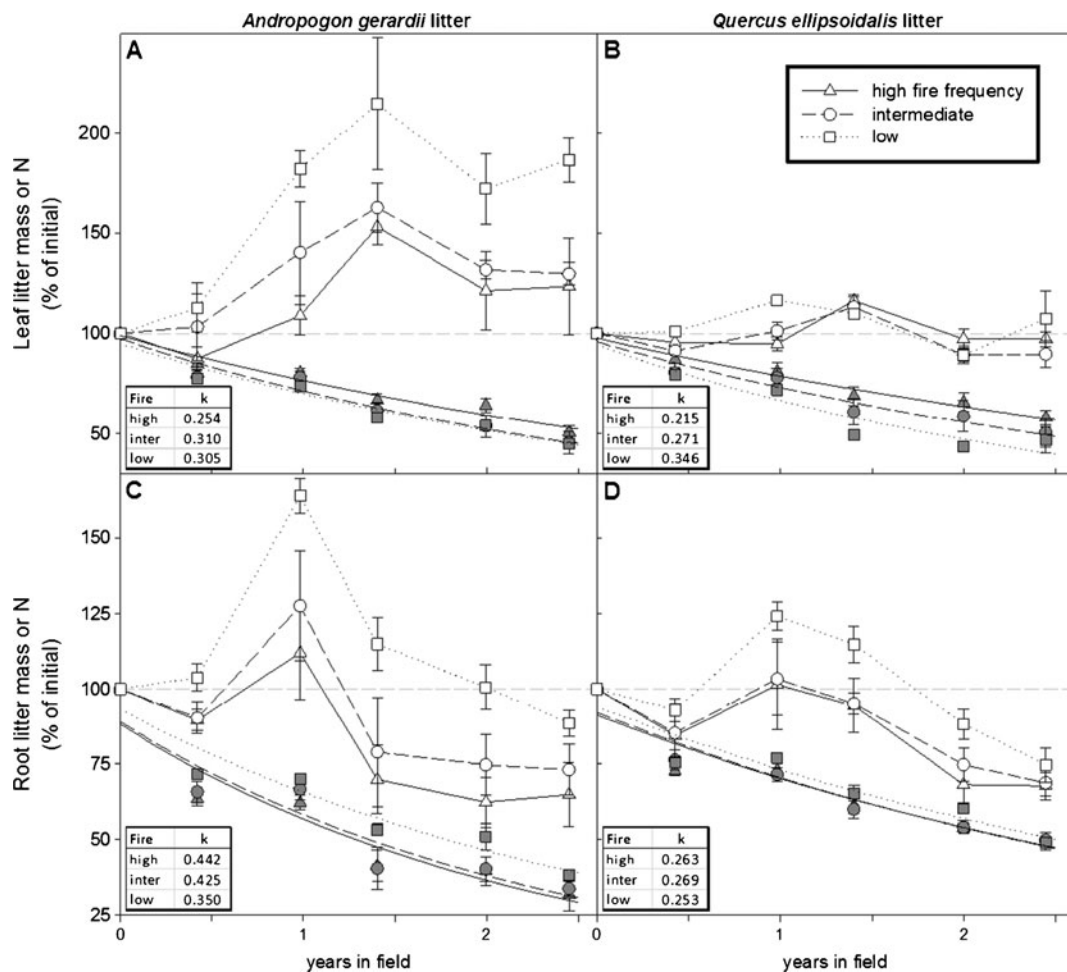
Fig. 1 Litter mass (*grey* symbols) and N (*open* symbols) as the percent of initial for *Andropogon* and *Quercus* leaf litter samples (**a** and **b**, respectively) and root litter samples (**c** and **d**, respectively) placed across a fire frequency/vegetation gradient. *Symbols* represent the mean (±1 SE). *Squares* represent low fire frequency plots, *circles* the intermediate plots, and *triangles* the high fire frequency plots. *Decay curves* are fit to the mass loss data using a single exponential decay model for each species. The *inset* tables present decay constants (k) for each litter type and habitat (R^2 values varied from 0.729 to 0.943, averaged 0.851 while the *p*-value for each model was <0.0001)

(146.7 %) when averaging across both litter types. Higher immobilization by decomposing *Andropogon* litter likely resulted from its relatively low initial N concentration compared to *Quercus* litter (Table 3). Across sites, percent of initial N remaining at the final harvest was best related to fire frequency ($p=0.0752$).

In contrast to leaf litter, roots from the two species differed significantly in decomposition ($p=0.0003$, Table 2) because *Andropogon* roots had much less mass remaining on average (34.6 %) and consequentially, a higher decay rate than the *Quercus* roots (49.3 % mass remaining) (Fig. 1c and d). Also in contrast to leaf litter,

there was no significant effect of fire frequency on decay rates belowground ($p=0.3131$). These differences were potentially due to differences in root diameters (slightly smaller in *Andropogon* roots) or in initial litter chemistry, as *Andropogon* roots had significantly lower lignin content (although they also had lower %N and higher C: N ratios) than did *Quercus* roots (Table 3).

Roots exhibited different N dynamics than leaf litter in that both root types across all three fire frequency levels exhibited a net release of N (Fig. 1c and d). However, similar to leaf litter, roots exhibited greater N immobilization with decreasing fire frequency,

Table 2 Summary results of 2-way ANOVAs for each experiment with litter type and fire frequency or fertilization as main effects for decay rate (k), final mass remaining, and final percent of initial N. Coefficient of determination (R^2) and p-values are provided for each of the whole models and p-values for each of two main effects. The interaction term was not significant in all cases ($p > 0.10$)

	Dependent variable		
	k	Final % of initial mass remaining	Final % of initial N
Fire frequency/vegetation gradient			
Aboveground litter	$R^2 = 0.42$, $p = 0.198$	$R^2 = 0.28$, $p = 0.487$	$R^2 = 0.75$, $p = 0.0023$
Effect tests (Prob >F)			
Fire frequency	0.0674	0.2546	0.0202
Litter type	0.6699	0.2627	0.0006
Belowground litter	$R^2 = 0.01$, $p = 0.734$	$R^2 = 0.75$, $p = 0.002$	$R^2 = 0.40$, $p = 0.239$
Effect tests (Prob >F)			
Fire frequency	0.3131	0.6587	0.1048
Litter type	0.0003	<0.0001	0.3692
Fertilization experiment			
Aboveground litter	$R^2 = 0.46$, $p = 0.147$	$R^2 = 0.39$, $p = 0.256$	$R^2 = 0.74$, $p = 0.0034$
Effect tests (Prob >F)			
Fertilization	0.0429	0.1059	0.0039
Litter type	0.2969	0.216	0.0092
Belowground litter	$R^2 = 0.02$, $p = 0.929$	$R^2 = 0.05$, $p = 0.865$	$R^2 = 0.61$, $p = 0.0594$
Effect tests (Prob >F)			
Fertilization	0.9287	0.865	0.0594

although the effect of fire frequency on root N was marginal. The final percent of initial N was negatively correlated to annual net N mineralized in the soil ($p = 0.0044$, $R^2 = 0.41$ by stepwise regression).

Table 3 Initial chemistry (mean ± 1 SE) of leaf litter, roots, and wooden dowels used in the decomposition experiments. Statistics refer to comparisons between *Quercus* (sampled from a low fire frequency plot) and *Andropogon* (sampled from a high fire frequency plot) leaf litter or roots for each measure of initial litter chemistry

	%N	C:N	%lignin	lignin:N
Fire frequency/vegetation gradient				
Andropogon leaf litter	0.33±0.098	141.05±2.21	9.24±0.34	29.11±2.59
Quercus leaf litter	0.89±0.054	54.72±0.44	20.83±0.31	23.99±0.81
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p = 0.0657$
Andropogon roots	0.45±0.081	102.29±1.31	19.02±0.45	43.27±2.07
Quercus roots	0.68±0.074	73.40±0.86	29.64±0.54	44.13±1.4
	$p < 0.0001$	$p < 0.0001$	$p < 0.0001$	$p = 0.7264$
Fertilization experiment				
Andropogon leaf litter	0.54±0.045	89.56±2.85		
Quercus leaf litter	0.84±0.015	58.96±1.18		
	$p = 0.0002$	$p < 0.0001$		
Wooden dowels	0.16±0.009	301.88±16.98		

Fertilization gradient

Leaf litter samples decomposed significantly more quickly in N fertilized plots compared to control plots ($p=0.0429$, Table 2) and the stepwise regression indicated that the most important effect on k was fertilization ($p=0.0215$, $R^2=0.29$) and not another factor associated with the treatment (e.g. soil net N mineralization despite strong positive correlation with fertilization). Although *Andropogon* leaves had a greater response to fertilization than *Quercus* leaves, there was no statistical effect of litter type ($p>0.10$) on decay rates or mass remaining in the fertilization experiment, nor was there a significant interaction term.

The final percent of initial N at the last harvest varied significantly among fertilization treatments ($p=0.0039$) and litter types ($p=0.0092$) (Table 2). Both leaf litter types demonstrated net N immobilization with fertilization over the duration of the experiment (134.3 %, 116.8 %, and 98.4 % for high N, low N, and control plots, respectively, averaged between substrates) (Fig. 2). Across the fire frequency gradient, *Quercus* leaves (105.9 %) accumulated significantly less N than the *Andropogon* leaves (127.1 %), perhaps reflecting their higher initial N concentration (Table 3).

The wooden dowels had the highest decay rates in these experiments (<25 % of the original mass remaining by the end of the experiment) (Fig. 2c) but decomposition rates were unaffected by fertilization ($p=0.929$) or any other site characteristic. Wooden dowel N dynamics resembled those of the leaf litter as dowels in the high N plots accumulated more N than in either the low N or control plots ($p=0.059$). Both fungal presence and fertilization were significantly positively related to final N content ($p=0.0165$ and $p=0.0248$, respectively).

Decomposer community

All tissue samples collected for molecular analysis were identified as fungi (Supplemental table 1) and therefore we consider all colonization to be fungal. Notably, an individual sample's "colonization morphotype" was not an ideal surrogate for a single identity as most morphotypes consisted of multiple fungi. Fungi were identified on all litter bag types and were mostly saprobic, although some were mycorrhizal or predatory.

Both fungal abundance and frequency on both above- and belowground litter varied significantly with fire frequency (but not litter type) (Table 4): low fire frequency plots had significantly greater colonization than the intermediate and high frequency plots (Fig. 3).

In contrast to the fire frequency gradient, there were no significant fertilization (treatment) effects on colonization of leaf litter, but leaf litter of *Quercus* had significantly greater fungal colonization than did that of *Andropogon* (Table 4, Fig. 4). Similarly, belowground, there were no significant effects of N fertilization on colonization of wooden dowels, although colonization was greater than it was for leaf litter aboveground.

Discussion

The results of this study highlight the complex interactions in the decomposition process as factors involving substrate chemistry, soil nutrient status, and decomposer community all impacted patterns of decay, ultimately leading to a positive feedback between soil fertility and decomposition despite contrasting mechanisms above- and belowground.

Substrate effects

Patterns of decay rates and N dynamics in decomposing detritus varied by treatments, litter types, and litter placement (leaf litter on soil surface versus buried roots or wooden dowels). Our first hypothesis, that decay rates would differ by species depending on litter chemistry, was supported for root litter but not for foliar litter. *Quercus* and *Andropogon* leaf litter decomposed at similar rates despite different tissue chemistry, perhaps because *Quercus* leaf decay was limited by high lignin concentrations despite high leaf N while decomposition in *Andropogon* leaves was likely limited by low leaf N despite relatively low lignin concentrations. These contrasting and offsetting constraints of initial foliar litter chemistry on decomposition may have precluded clear litter chemistry effects on decay rates. There may be additional important litter chemistry parameters associated with our litter types, e.g. Mn (Davey et al. 2007) or P (Mooshammer et al. 2012), but these were not measured and thus cannot be evaluated.

In contrast to mass loss, the leaf litter of the two species differed in their N dynamics. Low initial litter N concentration in *Andropogon* leaf litter likely contributed to the observed much greater N immobilization than in *Quercus* leaf litter. The same pattern was evident in a much broader study of continental decomposition
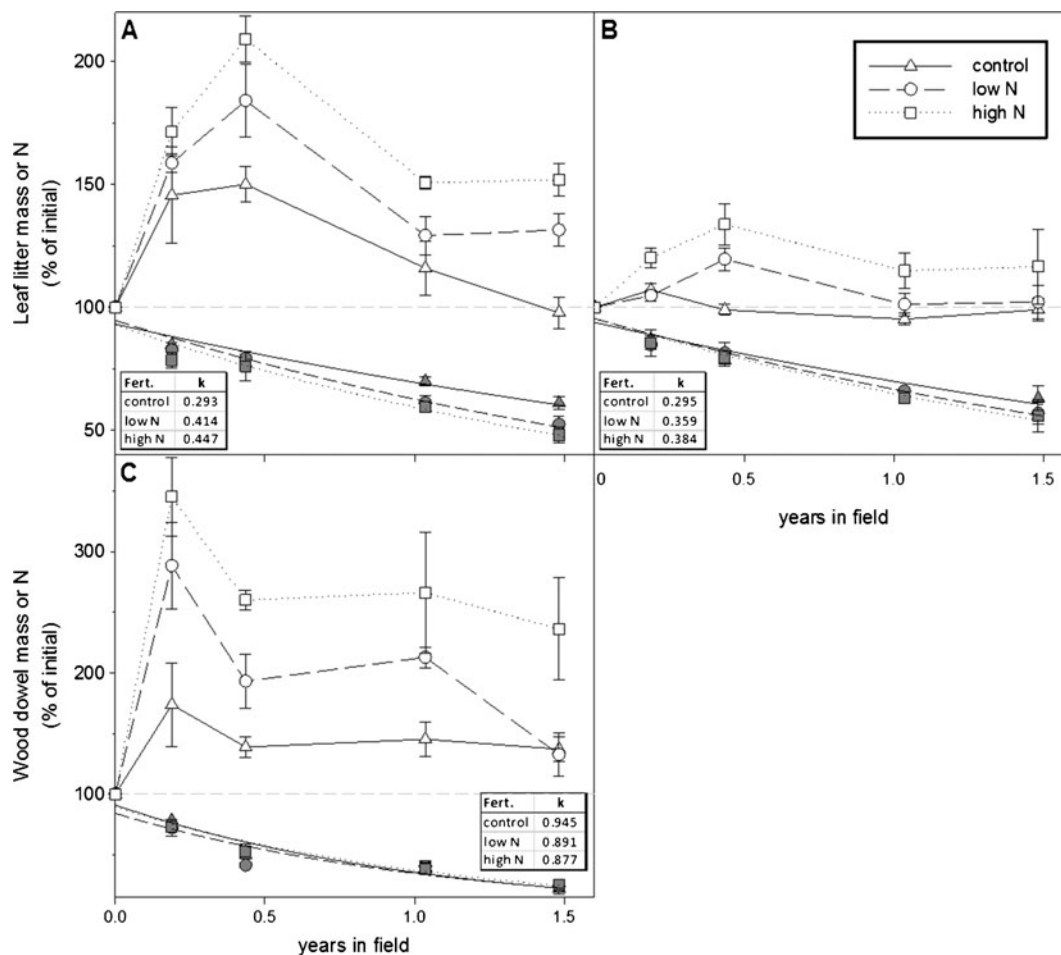
Fig. 2 Litter mass (*grey* symbols) and N (*open* symbols) as the percent of initial for *Andropogon* (**a**) and *Quercus* (**b**) leaf litter samples and wooden dowels (**c**) placed across a fertilization gradient. *Symbols* represent the mean (±1 SE). *Triangles* represent control (no added N) plots, *circles* the low N plots, and squares the high N fertilized plots. *Decay curves* are fit to the mass loss data using a single exponential decay model. The *inset* tables present decay constants (*k*) for each litter type and habitat (R^2 values varied from 0.778 to 0.923, averaged 0.866 while the *p*-value for each model was <0.0001)

patterns that found that initial leaf litter N controlled litter N dynamics, regardless of climate or other litter properties (Parton et al. 2007).

Decay rates belowground differed from those aboveground in that root decay differed between species. While patterns of initial litter chemistry were the same above- and belowground (Table 3) (*Quercus* leaf litter and roots had higher lignin while *Andropogon* leaf litter and roots had lower N), roots of the two species differed in diameter, potentially contributing to differences in decomposition rates. The greater surface area:volume of the smaller *Andropogon* roots (~1 mm vs. 2 mm diameter in *Quercus* roots) may have enabled greater microbial colonization; however, this speculation is in contrast to recent studies that have found slower decay

in lower order roots (Fan and Guo 2010; Goebel et al. 2011). Thus, the differences in belowground decay estimates by bulk fine roots may obscure finer patterns of decay and explanatory mechanisms linking plant traits to soil nutrient dynamics (Hobbie et al. 2010).

Habitat effects

As we hypothesized, across both fertility gradients, patterns of foliar litter decomposition were best explained by treatment (habitat), with decay more rapid in relatively N-rich conditions. In the fire frequency gradient, annual soil net N mineralization rates were 5-fold higher in the high than in the low fire frequency plots and these elevated N cycling rates corresponded with a 20 % and

Table 4 ANOVA tables from the fire frequency gradient and the N fertilization experiment showing results of 2-way ANOVA (habitat and litter type) on fungal colonization (as fungal abundance and frequency, see text for definition of terms). Coefficient of determination (R^2) and *p*-values are provided for each of the whole models and *p*-values for each of the main effects. The interaction term was not significant in all cases (*p*>0.10)
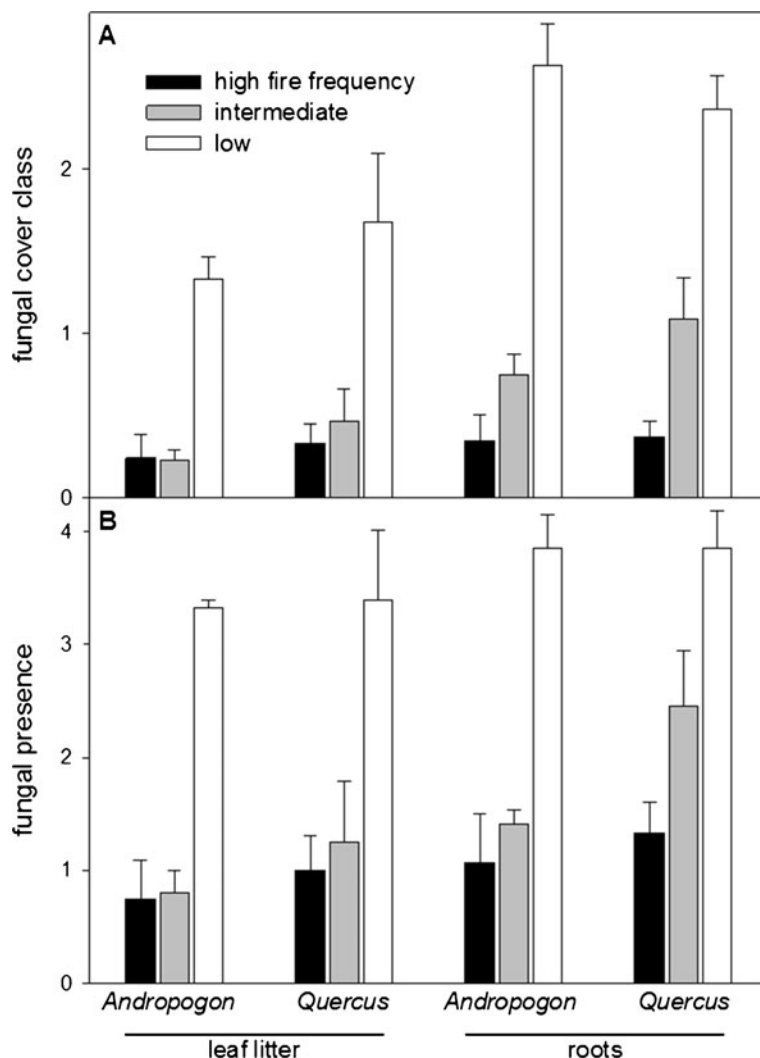
	Dependent variable	
	Abundance	Frequency
Fire frequency/vegetation gradient		
Aboveground litter	R^2=0.52, *p*=0.0003	R^2=0.60, *p*=0.0003
Effect tests (Prob >F)		
Habitat: fire frequency	<0.0001	<0.0001
Litter type	0.2476	0.5047
Belowground litter	R^2=0.82, *p*<0.0001	R^2=0.68, *p*<0.0001
Effect tests (Prob >F)		
Habitat: fire frequency	<0.0001	<0.0001
Litter type	0.8660	0.1957
Fertilization experiment		
Aboveground litter	R^2=0.27, *p*=0.2871	R^2=0.27, *p*=0.291
Effect tests (Prob >F)		
Habitat: fertilization	0.9410	0.9415
Litter type	0.0211	0.0246
Belowground litter	R^2=027, *p*=0.250	R^2=0.35, *p*=0.141
Effect tests (Prob >F)		
Habitat: fertilization	0.2495	0.1414

61 % increase in decay rates of *Andropogon* and *Quercus* leaf litter, respectively. Soil fertility was also correlated with litter N dynamics as sites with greater fertility generally had greater N immobilization or less N release. Therefore, as found elsewhere (Hunt et al. 1988), the controls of litter mass loss (soil fertility) differed from those of litter N dynamics (litter chemistry and fire frequency). This is also consistent with other findings demonstrating contrasting effects of soil N supply on decay depending on interactions with background soil fertility, litter chemistry, and/or atmospheric N deposition (Hobbie 2005; Knorr et al. 2005; Sariyildiz and Anderson 2003). We emphasize the role of soil N fertility in this analysis but it is possible that the availability of other nutrients also impact patterns of decay. For example, the fire frequency gradient does not only produce a gradient in soil N but also in soil P availability (Hernández and Hobbie 2008), cation exchange capacity, and total soil C (Norris 2008); thus we cannot rule out treatment effects by other soil nutrients confounded with the N gradient.

Results from the fertilization experiment largely support those from the fire frequency/vegetation gradient, collectively suggesting that decomposition in these savanna sites varies with external N supply. As soil N availability increased (as indicated by a four-fold increase in extractable inorganic N), leaf litter decay also increased on average 42 %. This pattern in foliar litter is in contrast to Hobbie's (2005) study performed at Cedar Creek which involved comparisons of variation in substrate N and external N supply (fertilization) among a broad range of substrates and over a wider range of habitat types than in our study. In Hobbie (2005), fertilization did not impact first year decay at most (6 of 8) sites; however, fertilization positively affected decay in sites of lower N availability. It is likely that the frequently burned sites studied here were similar in N availability to the old field sites at the lower end of the soil N gradient studied by Hobbie (2005). Regardless, the conflicting effects of external N supply between these two studies are interesting and highlight the complex nature of N effects on decomposition. In a meta-analysis of 500 observations from 24 different studies, Knorr et al. (2005) concluded that N additions do not consistently affect decay rates because the effect could be positive or negative depending on background rates of N deposition (negative effects of added N where background N deposition is high) and litter chemistry (positive effects of added N when litter lignin is low). Our data largely support their conclusion as our foliar

Fig. 3 Fungal colonization of litter substrates in the fire frequency/vegetation gradient by (a) abundance (cover class: 0–5), and (b) frequency (number of plots colonized of 5 possible). *Bars* represent means of treatments (n=3) ($\pm$1 SE)

litters had relatively high quality based on both lignin and N content and demonstrated decay stimulation with increasing N supply. Conversely, roots were of poorer quality and their decay was inhibited by increasing N availability. This pattern belowground suggests that soil fertility had a minimal effect on root decay which may be linked to shifts in the decomposer community composition (Fierer and Schimel 2002) and activity (Keeler et al. 2009) that likely corresponds to the change in vegetation across the fire frequency gradient.

Decomposer effects

The final hypothesis, that decay rates would be positively related to abundance of decomposer organisms, was supported by the fungal colonization data from

the fire frequency gradient. Although soil fertility provided a stronger statistical correlation, there was a significant positive correlation between fungal colonization and decomposition rates. In fact, across all litter types, fungal abundance and frequency were strongly, positively correlated with annual soil net N mineralization rate (p<0.0001, R^2=0.74, and p<0.0001, R^2= 0.72, respectively). Therefore, the mechanism by which decay rates were positively related to soil fertility may be through both a larger and more efficient decomposer community (Högberg et al. 2003; Ågren et al. 2001). Through related studies at Cedar Creek, we have found that 1) with decreasing fire frequency and the corresponding increase in soil N availability, that soil microbial biomass also increased (Norris 2008), 2) soil microbial biomass was strongly and
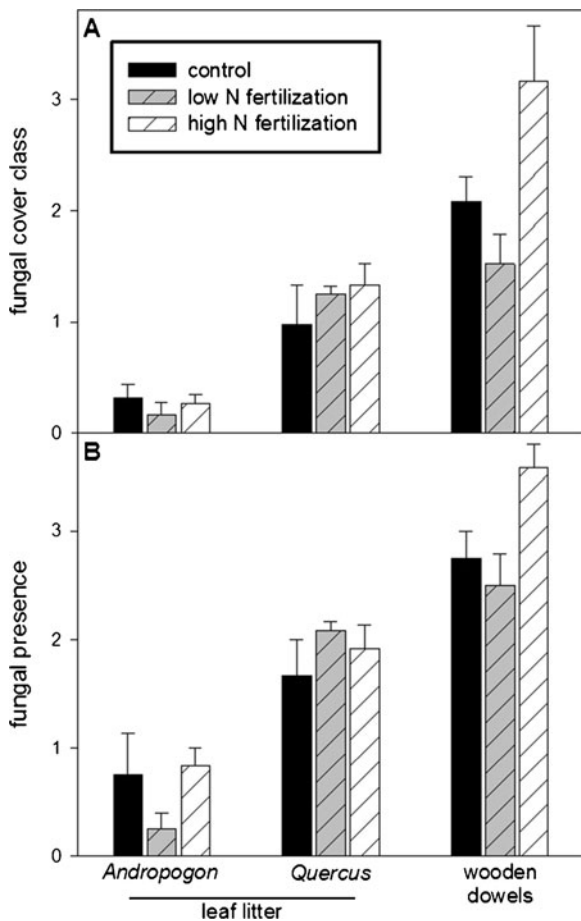
Fig. 4 Fungal colonization of litter substrates in fertilization gradient by (a) abundance (cover class: 0–5), and (b) frequency (number of plots colonized of 4 possible). *Bars* represent mean of treatment ($n=3$) (±1 SE)

positively correlated with soil enzyme activity (Keeler et al. 2009), and that 3) microarthropod abundance was similarly negatively related to fire frequency ($p=0.0032$, $R^2=0.24$) and positively to forest floor mass ($p=0.026$, $R^2=0.18$) (Bolton and Norris *unpublished data*), further evidence of soil fertility enhancing decay as mediated by the decomposer community.

The fungal colonization results from our fertilization experiment contrast those from the fire frequency gradient. Increasing N fertilization did not significantly increase fungal colonization, thereby suggesting that a different mechanism was at work. A number of studies investigating long term fertilization have found reduced fungal biomass and lignin degrading enzymes with fertilization resulting in reduced decay rates (Carreiro et al.

2000; Frey et al. 2004; Saiya-Cork et al. 2002; Sinsabaugh et al. 2002). We hypothesize that the variable effects of increasing soil fertility on fungal colonization in the two experimental gradients may be due to the magnitude of the soil N gradients. In the relatively N-poor Cedar Creek soils, N gradients associated with vegetation shifts tend to be more subtle than fertilization gradients that increase mineral N to a much greater extent. Even sites with low rates of N fertilization exceed inorganic N concentrations in the soils of the high fertility, low fire frequency sites (Table 1). Thus, fertilization seemingly crossed some threshold in soil N availability that altered microbial community composition and may have reduced decomposer efficiency. For example, Keeler et al. (2009) found that although total microbial biomass did not change with fertilization, the community likely shifted to more bacteria-dominated in litter or a fungal-dominated community in the soil based on microbial C:N ratios.

Implications for site fertility

Nitrogen dynamics in the decomposing litter may have important consequences for soil N pools. In the high fire frequency plots, the time until net release (100 % remaining of initial) of litter N exceeds the fire return interval. Therefore if plots are burned at a frequency of 2 years or more often, surface detritus will be a net N sink and further contribute to soil nutrient impoverishment as demonstrated at Cedar Creek (Dijkstra et al. 2006; Reich et al. 2001). Belowground, roots of both species did show net release of N but a more thorough analysis of root production and turnover is needed to determine to what extent this litter contributes to soil N pools and site fertility. Our results corroborate those of Seastedt (1988) who found that grass leaves and stems are a net N sink during the first 2 years of decay while roots are only a temporary sink, suggesting that this enhances N limitation in frequently burned ecosystems (Hernández and Hobbie 2008; Seastedt et al. 1991).

In conclusion, decomposition is a complex ecosystem-level process known to depend on effects of the environment, decomposer organisms, and litter chemistry (Berg and McClaugherty 2007; Cornwell et al. 2008; Swift et al. 1979) and we have evidence that all three influence decay across a diverse range of local habitats. Our results suggest a positive feedback between litter dynamics

and nutrient cycling in this savanna ecosystem that reinforces the N supply patterns established by variation in fire frequency. In the fire frequency gradient, as burning decreases, foliar litter production increases (Norris 2008; Reich et al. 2001), a larger abundance of decomposer organisms is supported, and the decay rate of that litter increases, likely contributing to the greater soil fertility (e.g. net N mineralization) that results from lack of fire (Norris 2008; Dijkstra et al. 2006; Reich et al. 2001). By contrast, litter in the high fire frequency plots is an N sink because of higher N immobilization and combustion of the *Andropogon* leaf litter, and thus contributes to the nutrient poor status that results from frequent fire. There is also a positive feedback on soil fertility likely operating belowground since *Quercus* roots were more abundant in the low fire frequency, high fertility sites and have a higher turnover rate (Reich et al. 2001) and greater N release than *Andropogon* roots common in the high fire frequency plots. In short, prescribed burning controls plant species composition which is strongly related to ecosystem processes including detritus dynamics. Soil fertility, species-specific litter production and chemistry, and the abundance of decomposer organisms are all positively correlated and control the decay rate and patterns of detrital N dynamics, both of which provide a positive feedback to soil fertility status.

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