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Long-term effects of experimental nitrogen additions on foliar litter decay and humus formation in forest ecosystems

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Abstract

Decomposition rates and N dynamics of foliar litter from 4 tree species were measured over a 72 month period on the Chronic Nitrogen Addition plots at the Harvard Forest, Petersham MA, beginning in November 1988. Plots received nitrogen additions of 0, 5 and 15 g N $m^{-2}{\cdot}yr^{-1}$ in two different stand types: red pine and mixed hardwood. Bags were collected in August and November of each year and litter analysed for mass remaining, nitrogen, cellulose and lignin content. Mass remaining was significantly greater for litter in nitrogen treated plots than in control plots after 48 months. Lignin content of litter was significantly higher with nitrogen treatments but there was little effect of treatment on cellulose content. N concentration was similar between treatments, but greater mass remaining in treated plots resulted in a higher total amount of N in humus produced in the high N plot. This mechanism could be a sink for up to 1.5 g $N{\cdot}m^{-2}{\cdot}yr^{-1}$ of the 1.5 g $N{\cdot}m^{-2}{\cdot}yr^{-1}$ added annually to the high N plots. Reduced decomposition rates in conjunction with increased lignin accumulation could impact global carbon sequestration as well.

Introduction

Decomposition of foliar litter has long been recognized as an important process in forest ecosystems, both for nutrient recycling and humus formation (e.g. Berg, 1986; Bocock, 1964; Gosz et al., 1973). Because of the relative ease of access to materials and establishment of experiments, a considerable number of studies have been conducted on litter decay, and relationships between litter characteristics and decomposition dynamics developed. While most of the studies have involved short-term measurements of mass loss only, enough long-term data exist from a smaller number of studies to describe the entire process of transformation from fresh litter to humus (Aber et al., 1990; Berg, 1986; Melillo et al., 1982).

In temperate forests, both rates of mass loss and temporal changes in nitrogen content have been linked to the carbon quality and nitrogen content of the initial material (Berg and Agren, 1984; McClaugherty et al., 1985; Melillo et al., 1982). Predictive relationships have been developed from the larger data sets (Aber et at., 1990; Meentemeyer and Berg, 1986) and several models of decomposition and nutrient cycling in forests include these concepts and relationships as controlling mechanisms (e.g. Aber et al., 1990; Parton et al., 1988; Pastor and Post, 1986).

As human influences on the Earth's biogeochemical cycles increasingly affect ecosystem processes, conditions under which decomposition occurs will also change. One such change is the increase of nitrogen deposition to forested ecosystems, particularly in the Northeastern United States and in Europe (Galloway, 1995; Shannon and Sisterson, 1992; Vitousek et al., 1997; Wright and van Breemen, 1995). Nitrogen is a critical element in the decay of foliar litter in temperate forests. N concentration in the decaying material is altered by immobilization and mineralization processes such that N dynamics during decay do not parallel C losses. Higher N availability to decomposers, either through higher concentrations in litter or elevated mineral N concentrations in throughfall and

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soil solutions, may accelerate the decay process in the early stages (Melillo et al., 1982). In later stages of decay, however, higher N content in organic matter may reduce decay rate of older litter and humus by randomizing bond structures and reducing the efficiency of ligninolytic enzymes (Berg, 1986), while elevated mineral N concentrations in solution may suppress the production of this enzyme systems by microbes (Keyser et al., 1978; Tien and Meyr, 1990). Increased N deposition may result in either faster or slower release of carbon from decaying detritus, and thus affect predicted interactions between N deposition and carbon sequestration in temperate forest ecosystems (Aber et al., in press; Townsend et al., 1996).

To understand the effects of increased N deposition on the entire litter decay process and its eventual effect on humus quantity and chemistry, long-term field experiments under altered conditions are required. In this paper we present the results of a long-term (6 year) field study of the effects of experimentally elevated nitrogen deposition on the carbon (C) and nitrogen (N) dynamics of the decomposition of several types of forest foliar litter.

Materials and methods

The Chronic Nitrogen Addition plots are located at the Harvard Forest in central Massachusetts (42 30′ N, 72 10′ W), a National Science Foundation Long-Term Ecological Research site since 1988. Annual temperatures range from an average of 19 °C in July to an average of −12 °C in January and average annual precipitation is 112 cm (Van Cleve and Martin, 1991). Total N deposition to the forest is approximately 0.8 $g \cdot m^{-2} \cdot yr^{-1}$ (0.6 $g \cdot m^{-2} \cdot yr^{-1}$ wet and 0.2 $g \cdot m^{-2} \cdot yr^{-1}$ dry; Ollinger et al., 1993). The dominant soil types are stony- to sandy-loams formed from glacial till.

Two adjacent stands were chosen for the study: a 70-year old red pine plantation (*Pinus resinosa* Ait.) and a 50-year-old mixed hardwood stand dominated by black and red oak (*Quercus velutina* Lam.; *Q. rubra* L.) but also including black birch (*Betula lenta* L.), red maple (*Acer rubrum* L.) and American beech (*Fagus grandifolia* Ehrh.).

Four treated plots were established within each stand: control, low N (5 g $N \cdot m^{-2} \cdot yr^{-1}$), high N (15 g $N \cdot m^{-2} \cdot yr^{-}$) and low N plus sulfur (as Na_2SO_4) which was not used for the litter decomposition portion of the experiment. Each plot measured 30×30 meters (0.09 ha) and was divided into thirty-six 5×5 m subplots. Litterbags were placed in one of the corner 5×5 m subplots. Fertilizer additions of NH_4NO_3 began in 1988 as six equal applications over the growing season. A partial application was made in year one (1988) with full year doses applied in all following years. Total fertilizer applied through 1994 is listed in Table 1.

Table 1. Total NH_4NO_3 fertilizer (as g N m^{-2}) added to plots containing litter bags for the duration of the decomposition experiment

Year	Treatment		
	Control	Low N	High N
1988	0	3.8	11.3
Litter placed in plots, November, 1988			
1989	0	5	15
1990	0	5	15
1991	0	5	15
1992	0	5	15
1993	0	5	15
1994	0	5	15
Total N Added	0	33.8	101.3

Fresh litterfall was collected in the fall of 1988 on nylon mesh screens which were placed in the experimental stands but outside of the treated plots. Litter was air dried and sorted into red pine (RP), red maple (RM), yellow birch (YB) and black oak (BO). One mm mesh nylon window screening was cut and sewn into 20×20 cm bags. Approximately 9.5–10.0 g of air-dried litter was weighed and placed into each bag, along with an aluminum tag bearing a unique number. The bags were sewn closed and 12 bags connected together with a piece of nylon string. Four replicate bags of three species were placed on each string. During the period of time that air-dried litter was weighed and placed in bags, sub-samples of each species were weighed and then dried for 48 h at 70 °C to determine an air-dry to oven-dry conversion factor. Litter bags containing red pine and red maple foliage were placed in plots of both stands, black oak bags were placed in the hardwood plots only and yellow birch bags in the pine plots only. Fourteen strings of litterbags were placed in each plot.

One string of bags was collected from each plot in mid-August and mid-November, beginning in 1989 and continuing through 1993. In 1994, two strings were pulled up on each collection date, completing the

Table 2. Summary of decomposition bag collections

Collection number	Collection date	Months of decomposition	No. of bags collected/plot
1	Aug. 1989	9	12
2	Nov. 1989	12	12
3	Aug. 1990	21	12
4	Nov. 1990	24	12
5	Aug. 1991	33	12
6	Nov. 1991	36	12
7	Aug. 1992	45	12
8	Nov. 1992	48	12
9	Aug. 1993	57	12
10	Nov. 1993	60	12
11	Aug. 1994	69	24
12	Nov. 1994	72	24

Table 3. Initial litter chemistry of the four tree species decomposed. Values are means with one standard deviation in parentheses

Species	*n*	Nitrogen (%)	Lignin (%)	Cellulose (%)
Red Pine	14	0.64	25.5	38.6
		(0.02)	(0.73)	(0.45)
Red Maple	14	0.82	16.9	35.4
		(0.03)	(0.56)	(0.75)
Yellow Birch	7	1.18	16.3	40.3
		(0.05)	(0.70)	(2.1)
Black Oak	7	0.74	25.4	39.6
		(0.06)	(1.04)	(0.61)

experiment in November 1994. Each collection was numbered in succession and is summarized in Table 2. After air drying in the laboratory, each mesh bag was cut open on all 4 sides, the aluminum tag removed, and laid into a tray. Ingrown roots were removed with tweezers and the decomposed litter placed into a paper bag. Samples were dried at 70 °C for 48 h and the dry weight of the decomposed sample (final weight) recorded. Individual samples were ground using a Wiley mill with a 1 mm mesh screen. After grinding, the 4 replicates of each species within a plot and collection, were combined into two replicates in order to increase sample volume for analysis. Ground and combined samples were analyzed for percent nitrogen, lignin, and cellulose using near-infrared spectroscopy (Bolster et al., 1996; McLellan et al., 1991). Initial litter chemistry was determined from subsamples of the original litter collection and are listed in Table 3.

Mass loss data for each litter and stand type were fit to an exponential decay function:

$$M_\mathrm{i}/M_\mathrm{o} = \mathrm{e}^{-kT_\mathrm{i}}$$

where M_o is the mean initial (time zero) mass for each species-stand combination, M_i is the mean mass remaining at each time interval i, and T_i is the time in years. A k value was computed for each time period, and a mean calculated for each stand and species combination. A least significant difference (LSD) statistic (Miller and Miller, 1988) was calculated using data on percent original mass, N, lignin and cellulose remaining for each stand and species combination as well, allowing determination of statistically significant differences over time. LSD is calculated as follows:

$$s\sqrt{(2/n)} \times t_{h(n-1)}$$

where s in the within-sample estimate of σ and $h(n-1)$ is the number of degrees of freedom of this estimate (Miller and Miller, 1988; Snedecor and Cochran, 1967). All LSD values were calculated at $P = 0.05$.

Results

Long-term, N additions affected both the rates of mass loss and the C and N chemistry of all substrates. There was also a secondary effect of a litter type-forest type interaction.

Mass loss

Both red maple and red pine litter decayed more rapidly in the hardwood stand than in the pine stand. Nitrogen additions depressed decomposition rate in all litter types and stands tested (Figure 1). For both the red pine and red maple litter in the hardwood stand, approximately twice as much mass remained in the high N treatment as in the control plot. By the end of 72 months, differences between control and high N treatments were significant for all litters between plots, although differences were larger in the hardwood stand than in the pine stand. Values for k calculated for each litter type and plot (Table 4) suggest that overall decay rate declined by 20–50% across treatments. Differences in the percentage of original mass remaining between treatments, became larger with time.

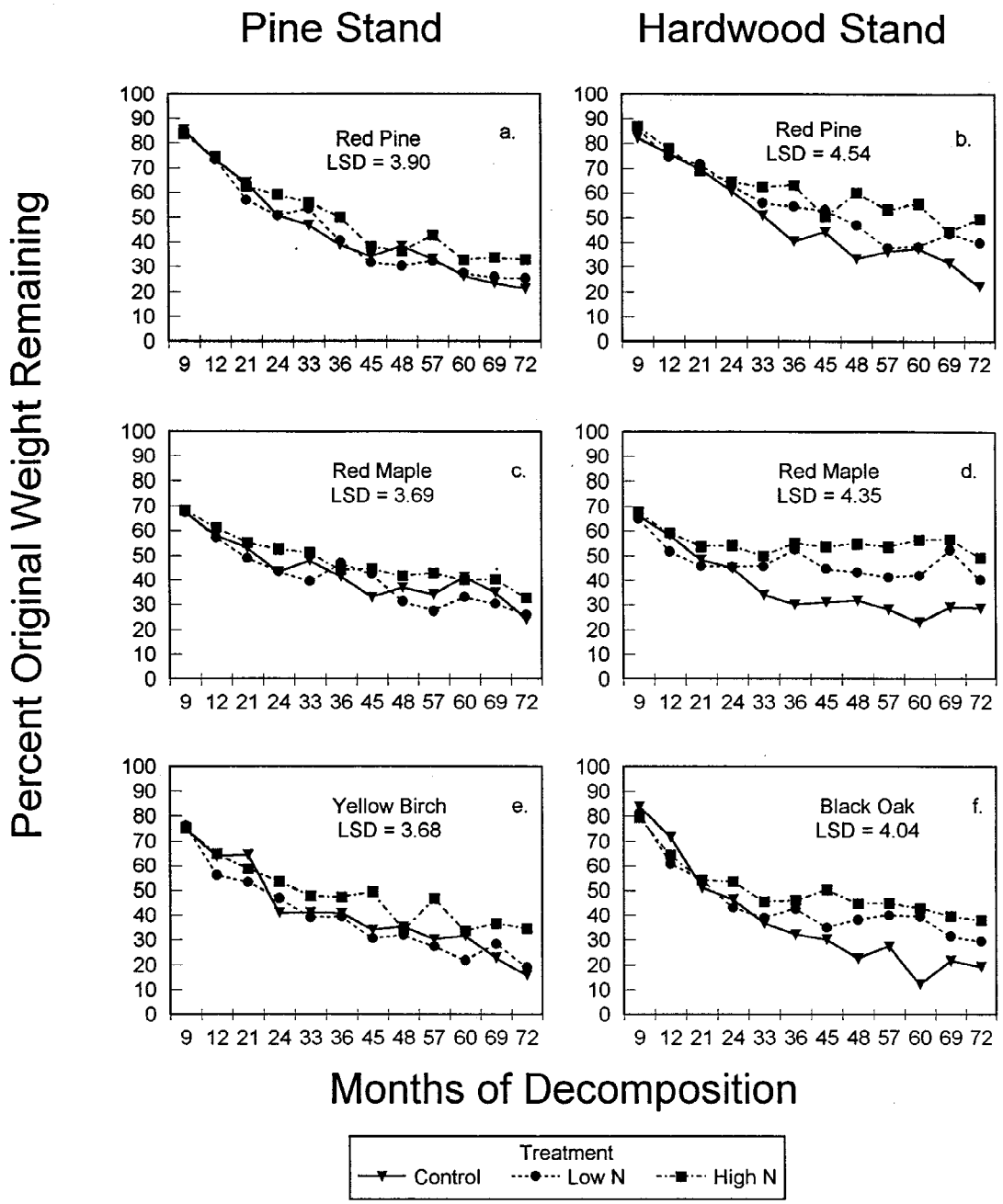

Figure 1. Percent of original weight remaining by stand and treatment for each species: (a) red pine in pine stand; (b) red pine in hardwood stand; (c) red maple in pine stand; (d) red maple in hardwood stand; (e) yellow birch in pine stand and (f) black oak in hardwood stand. LSD values are calculated for each species/stand combination. Each point represents the mean of four litterbags.

Table 4. Calculated k values for each species and plot combination. A dash indicates a combination that was not measured

Plot	Species			
	Red Pine	Red Maple	Yellow Birch	Black Oak
Pine control	0.26	0.24	0.27	–
Pine low	0.23	0.23	0.20	–
Pine high	0.18	0.19	0.16	–
Hardwood control	0.25	0.21	–	0.31
Hardwood low	0.15	0.15	–	0.28
Hardwood high	0.12	0.12	–	0.18

Nitrogen content

Nitrogen dynamics differed between species in the control plots (Figure 2). Red pine showed a significant decrease in total N content between the initial material and the 9 month collection in both stands. This was followed by a 1 year period of net immobilization after which net mineralization occurred. Red maple litter in the two control plots showed little change between initial and 9 month values, no significant net immobilization, and slow but continuous net mineralization. Yellow birch and black oak both showed net immobilization at 9 months, followed by net mineralization.

Total N content of all litter types increased with N additions in the hardwood stand, but not the pine stand (Figure 2). For the two litter types present in both stands, total N content was higher in the hardwood stand than in the pine stand, and differences between treatments were also larger in the hardwood stand. In the high N addition plots, significant net mineralization did not occur. Total N content remained high as decay rates were reduced in the later stages of decomposition.

In previous studies, we have been able to express the interaction between C and N dynamics in decaying litter with fractional mass remaining as a function of N concentration in the remaining material (Aber et al., 1990). This same relationship holds for litters decaying in the control plots (Figure 3) but breaks down in the later stages of decay under N treatments, where litters accumulate more N for a given increment in mass loss. Between plots, litters tend to have similar N concentration across treatments and stands, but have higher fractional mass remaining at any given time in plots with added N. This effect tends to be greater under the high N treatment compared with the low N treatment, and in the hardwood stand compared with the pine stand.

Carbon constituents

Total lignin content increased significantly between initial materials and the 9 month materials in all species-stand combinations (Figure 4). Net disappearance of lignin then followed in all cases. Nitrogen additions depressed lignin decay significantly in all combinations. Cellulose content declined immediately and continuously throughout the decay sequence for all species-stand combinations (Figure 5). Cellulose decay was also depressed by N amendments. Analyses of the relative rates of mass loss and the loss of cellulose and lignin do not suggest preferential removal of either constituent under the different N addition regimes.

Discussion

Total nitrogen content of litter often increases during the first months of decomposition due to immobilization of nitrogen from the soil solution (Anderson, 1973; McClaugherty et al., 1985; Melillo et al., 1982). It has therefore been assumed that the earliest stage of litter decomposition by microbes is limited by nitrogen availability, and that increases in available nitrogen will increase decay rates. Results from this study contradict this assumption. Nitrogen additions did not increase decay rates consistently in the first year, and actually reduced them over the long term.

Berg and Staaf (1980) recognized three phases of nitrogen dynamics in decomposing litter: (i) (an initial leaching phase; (ii) a period of accumulation (net immobilization) and (iii) a final release phase (net mineralization). Most field litter decay studies in temperate forests are of short duration, but many investigators report that net nitrogen release occurs by the end of year two (Aber et al., 1990; Blair, 1988; Gosz, 1973; McClaugherty et al., 1985). In the high N plots, N accumulation continued for 36 to 48 months, and there was no consistent indication of net N mineralization even by the end of 72 months for several species-stand combinations. This is expressed in the inverse-linear relationship between mass loss and N concentration in the remaining material (Figure 3), which demonstrates an increase in N immobilization per unit mass loss in the later stages of decay in the N

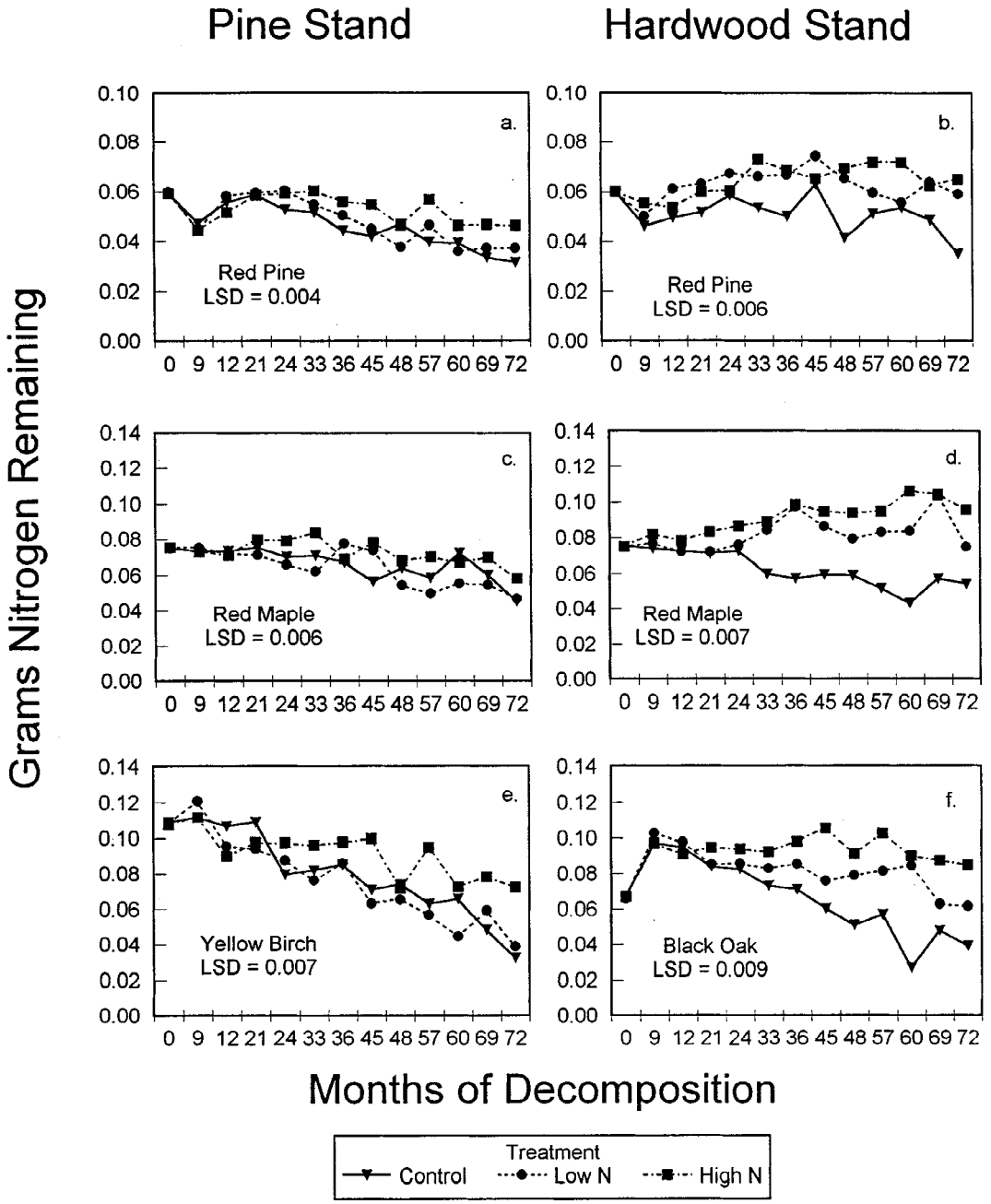

Figure 2. Grams of nitrogen remaining by stand and treatment for each species: (a) red pine in pine stand; (b) red pine in hardwood stand; (c) red maple in pine stand; (d) red maple in hardwood stand; (e) yellow birch in pine stand and (f) black oak in hardwood stand. LSD values are calculated for each species/stand combination. Samples combined for chemical analysis, n = 2, samples/collection date.

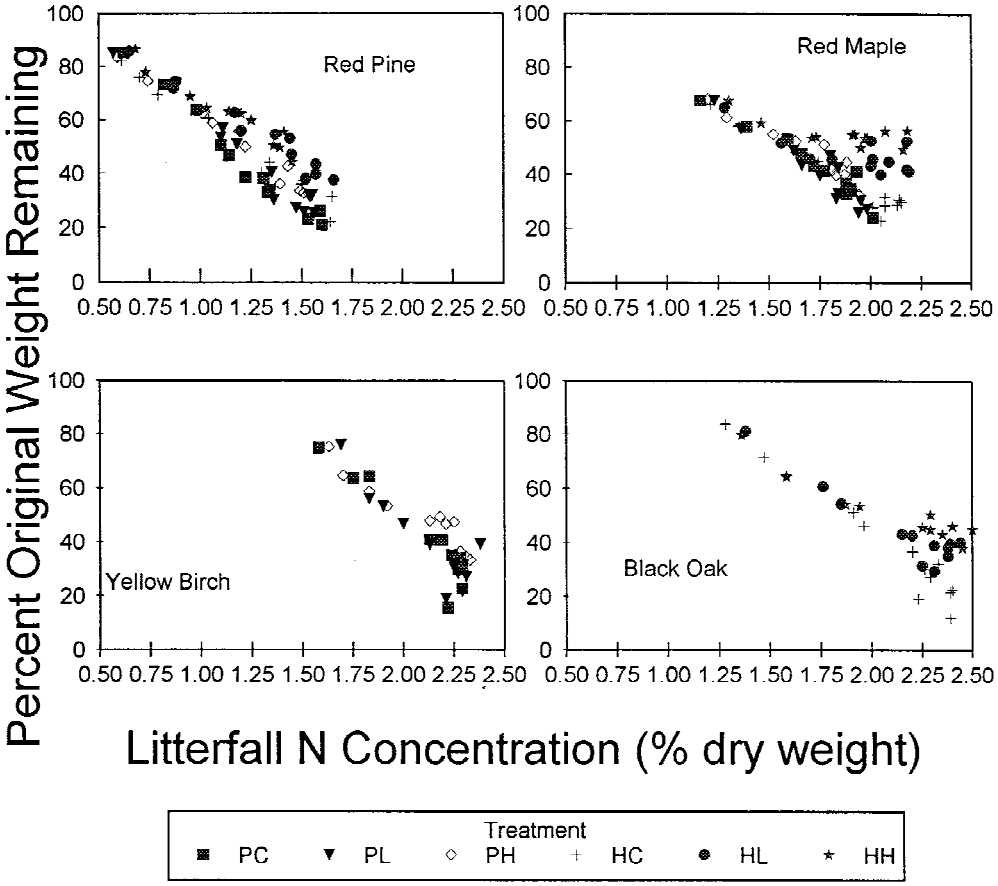

Figure 3. Litter nitrogen concentration as a percent of dry weight versus percent original weight remaining, all treatments included, by species. Each point represents the mean value for one collection.

treated plots. A reduction of net mineralization from older litter classes is in agreement with lower measured rates of net mineralization from whole forest floors in the high N pine stand (Magill et al., 1997).

Berg (1986) also proposed a theory of litter decay and humus formation in which nutrient content, and particularly nitrogen content, stimulates decomposition in nutrient poor litter types in the earliest stages of decay. Higher N concentrations in older litter and humus inhibit decomposition at later stages however, by increasing the randomness of bond structures and so reducing the efficiency of extracellular enzymes. Our results are in agreement with the latter part of this theory, in that large differences in decay rates were induced by N additions (Figure 1). Only black oak litter showed an apparent initial increase in decay rate with higher N additions.

An alternative hypothesis for the depression of decay rates in N amended stands is that the presence of mineral nitrogen in the soil solution inhibits ligninolytic enzyme production by soil microbes, particularly fungi, and that this results in lower rates of humus degradation (Keyser et al., 1978; Tien and Myer, 1990). It was initially thought that we could distinguish between the 'ligninolytic enzyme suppression hypothesis' and the 'Berg hypothesis' by examining the relative decomposition rates of cellulose and lignin under the different N treatments, with a preferential reduction in cellulose supporting the former. Although there was no significant difference in the decay rates of cellulose and lignin across treatments, these results do not necessarily exclude the 'ligninolytic enzyme suppression hypothesis', in that much of the cellulose in foliar litter is 'shielded' by lignin polymers such that the suppression of lignin decay alone would also reduce cellulose disappearance.

Regardless of the mechanism involved, our results suggest that long-term N additions to forest ecosys-

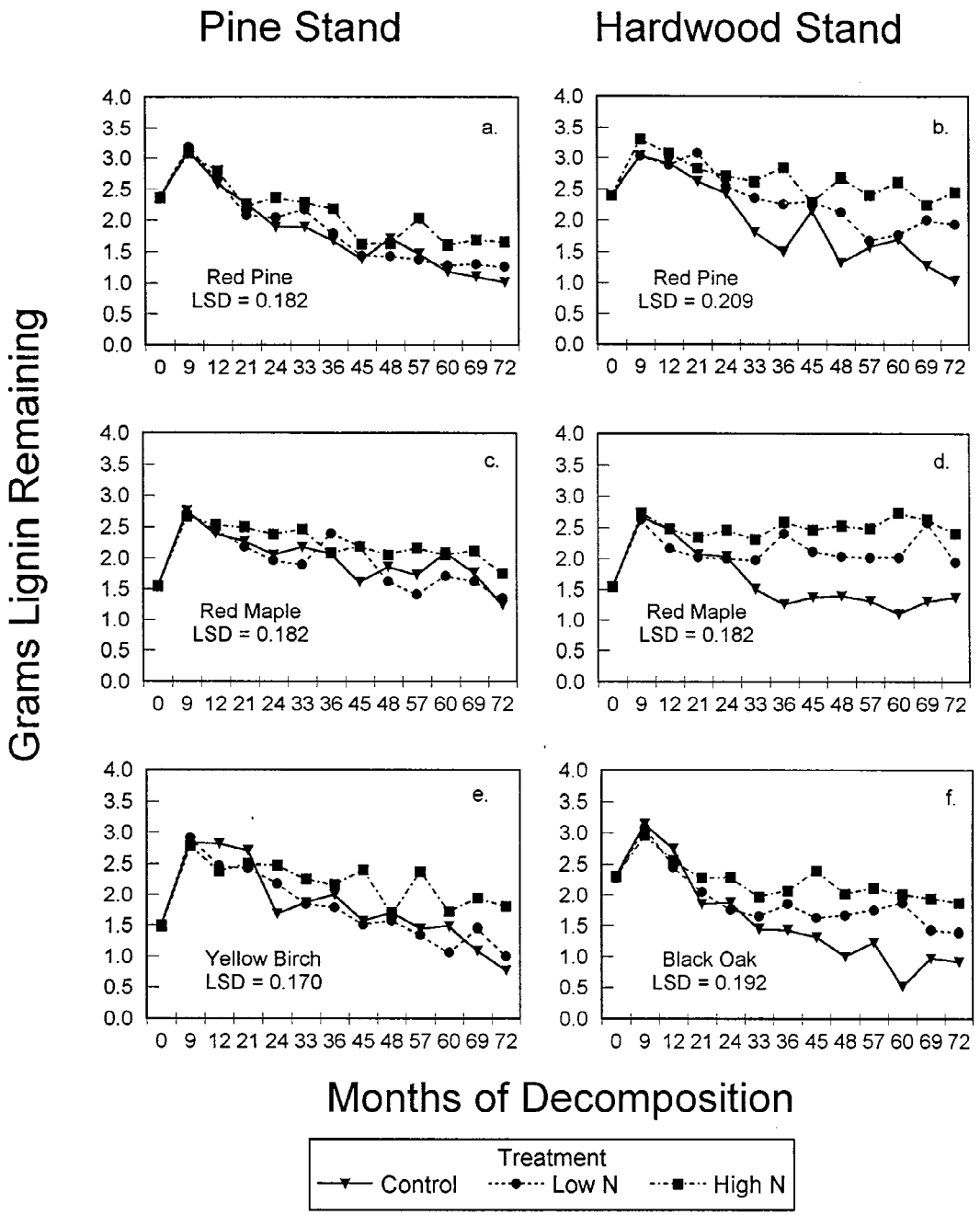

Figure 4. Grams of lignin remaining by stand and treatment for each species: (a) red pine in pine stand; (b) red pine in hardwood stand; (c) red maple in pine stand; (d) red maple in hardwood stand; (e) yellow birch in pine stand and (f) black oak in hardwood stand. LSD values are calculated for each species/stand combination. Samples combined for chemical analysis, $n = 2$, samples/collection date.

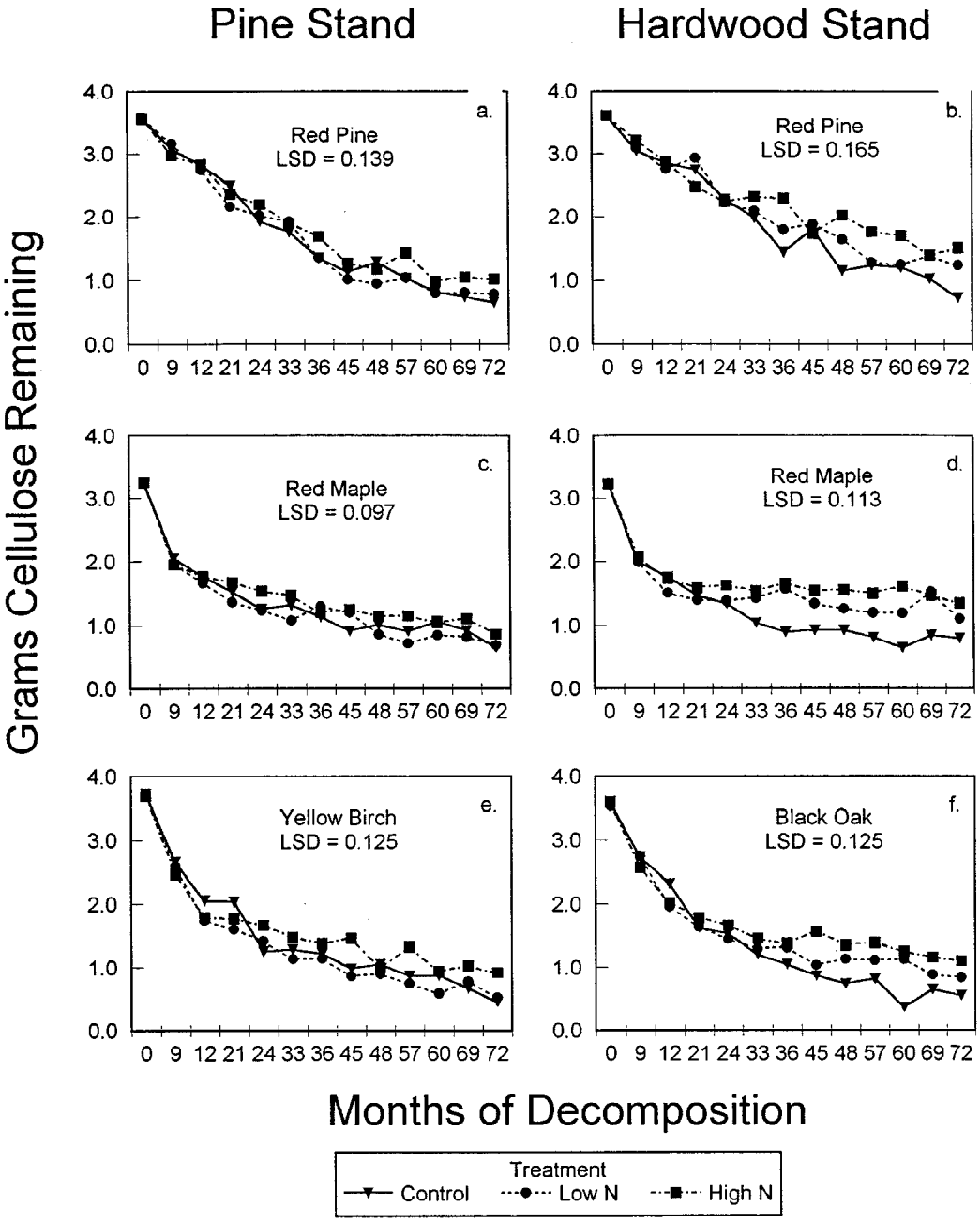

Figure 5. Grams of cellulose remaining by stand and treatment for each species: (a) red pine in pine stand; (b) red pine in hardwood stand; (c) red maple in pine stand; (d) red maple in hardwood stand; (e) yellow birch in pine stand and (f) black oak in hardwood stand. LSD values are calculated for each species/stand combination. Samples combined for chemical analysis, $n = 2$, samples/collection date.

tems will result in significant changes in the chemistry and decomposition of humus. An earlier paper (Aber et al., 1990) described the process of humus formation from litter based on long-term decomposition studies. We determined that the humus formed from a wide variety of litter types consisted of organic matter with a relatively constant lignin:cellulose ratio but a variable N concentration depending on initial N concentration of the litter. External N availability can now be included as a factor affecting N concentration in the humus produced. The earlier study (Aber et al., 1990) suggested that all litter types transferred about 20% of initial litter mass to humus, which was based on the amount of material remaining at the time where decomposition rate declined markedly. The data presented here suggest that the reduction in decay rates associated with the 'humus' designation, occurs in the high N treated plots at the point where 30–50% of initial biomass remains. Thus, stands receiving substantial inputs of N deposition may accumulate higher total soil organic matter with a higher N concentration.

The most surprising result from the Chronic Nitrogen Addition experiment at the Harvard Forest has been the very high, long-term N retention efficiency of both stands (Magill et al., 1997). Since the bulk of added N is retained in soil organic matter (Magill et al., 1997), we have examined various mechanisms by which added mineral N is converted to soil organic N (Aber et al., in press) and determined that incorporation through aboveground biomass production is minimal (Magill et al., 1997). Combining changes in annual input of foliar litter across treatments with changes in the N content of newly formed humus, we calculate that as much as 1.5 g $N \cdot m^{-2} \cdot yr^{-1}$ can be incorporated by altered dynamics of aboveground litter decay. It is unknown if a similar change occurs in decomposition of belowground litter.

Such alterations in humus formation have implications for global carbon budget calculations and models as well. The northern temperate forest region has been suggested as the missing sink for atmospheric CO_2, with this extra sink strength being driven by the fertilization effects of N deposition. Models of this process suggest that C:N ratios of added organic matter are on the order of 120:1 to 150:1 (Aber and Driscoll, 1997; Townsend et al., 1996). Neither of the models referenced include an algorithm by which C:N ratios in soils will narrow due to increased N sequestration during litter decay, or by which rates of soil organic matter decay will be reduced. To the extent that N is tied up in more slowly decaying organic matter with narrow C:N ratios (the humus formed as a result of the processes measured here averages 25:1), the models may overestimate the role of N deposition in fertilization and C sequestration. To the extent that humus decay is suppressed and CO_2 emission from soils is reduced, these models could underestimate the fertilization effect.

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