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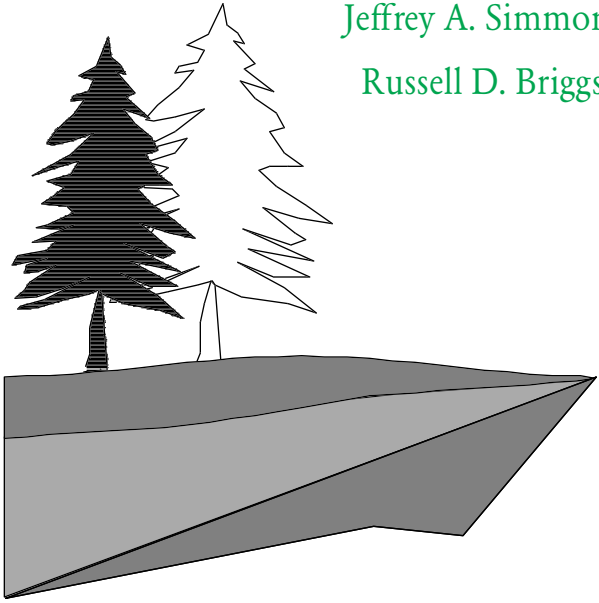

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Red Maple and White Pine Litter Quality: Initial Changes with Decomposition

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INTRODUCTION

Organic matter decomposition is a key process governing the cycling of nutrients in forested ecosystems. The rate of decomposition is affected by litter quality, decomposer populations, and climate (Swift *et al*. 1979). Although climatic variables may govern rates and patterns of decomposition, they generally best describe decomposition at regional and global scales (Dyer et al. 1990). Litter quality characteristics are more important criteria governing decomposition at local scales.

Decomposer populations derive their energy from organic compounds that range from simple monomeric sugars to complex lignins. Simple sugars such as glucose and sucrose are excellent substrates for microbial growth, yielding high energy returns (Aber and Melillo 1991). In contrast, lignin is one of the slowest decaying molecules in nature (Alexander 1977) because of its complex chemical structure. Several enzymes are required for complete lignin breakdown, and energy from the breakdown of more labile compounds is required before lignin decomposition can begin (Tate 1987; Aber and Melillo 1991). Studies that have examined how the organic complexity of forest litter influences litter decomposition include Berg et al. (1982a), Melillo et al. (1982), McClaugherty and Berg (1987), and Taylor et al. (1989a). The inorganic chemistry of litter also affects decomposition since nutrient mineralization rates govern nutrient availability to heterotrophic microorganisms. Studies on nutrient dynamics during forest litter decomposition have been conducted for N (e.g., Lousier and Parkinson 1978; Berg and Staaf 1981; Blair 1988a), P (e.g., Berg and Staaf 1987; Rustad and Cronan 1988), K (e.g., Blair 1988b; Bockheim et al. 1991), Ca (e.g., Staaf and Berg 1982; Rustad and Cronan 1988), Mn (Edmonds 1984; Berg and Staaf 1987); Mg (Lousier and Parkinson 1978; Bockheim et al. 1991), Fe and Al (Rustad and Cronan 1988; Bockheim et al. 1991), Cu and Zn (Gosz et al. 1973; Bockheim et al. 1991), and B (Bockheim et al. 1991).

The specific objectives of this study were (a) to define the organic and inorganic composition of foliar litter from red maple (*Acer rubrum* L.) and white pine (*Pinus strobus* L.), and (b) to determine the shifts in the organic and inorganic composition of these two litter types during the initial stages of decomposition. These two species were chosen because of their prominence in the northeastern U.S. and the contrast they afforded in litter quality characteristics which have a strong influence on litter decomposition.

MATERIALS AND METHODS

This study was part of the "Maine Gradient Study" (MEGS), a comprehensive research program designed to evaluate the relationship between spatial gradients in climate and forest ecosystem function. Briggs and Lemin (1992) identified four major climate regions in Maine. Within each of these regions, four sites containing three randomly located 0.025-ha plots were established along transect lines (Simmons et al. 1996), for a total of 48 plots in the study.

A laboratory incubation microcosm study was also carried out to evaluate the short-term effects of temperature and moisture on litter decomposition using the design of Taylor and Parkinson (1988). Briefly, each microcosm consisted of a 2.84-liter cylindrical container made of polyvinyl chloride, with a mesh bottom to allow for free drainage. Cores from the O horizon of a thoroughly studied coniferous stand (Fernandez et al. 1993) were used in the bottom of the microcosms, overlain by a 1×1-mm nylon mesh and overlain by the litter samples. Microcosms were incubated at three different temperatures (5°C, 15°C, and 25°C), each at four different moisture regimes ranging from air-dried (85%) to field capacity (435%). Each treatment combination was replicated three times.

Litter Bag Methodology

Litter was collected by raking a domestic site in Orono, Maine, dominated by red maple with a minor component of white pine in the fall of 1992. Litter was dried in a drying room at approximately 60°C. The litter was manually sorted by species (red maple and white pine); fine leaf fractions were excluded.

Litter decomposition rates were determined using the litter bag technique of Bocock (1964), modified by Rustad and Cronan (1988). Litter bags were 20×20 cm and made of 1-mm acrylic-coated mesh. This mesh size allows for the movement of most soil fauna into the litter bag (Edwards and Heath 1963) facilitating decomposition and preventing loss of needles. Four to six grams of air-dried litter were placed into each bag. Exact weights were recorded, and the bags were glued shut with Thermogrip™ hot adhesive and tagged with an identifying code.

Three types of litter bags (red maple, white pine, and a 1:1 mixture by mass of red maple and white pine) were placed in a 5×5-m subplot within each plot. Triplicates of each litter type were buried in each subplot in June 1993. The bags were randomly located within the subplots and buried in the middle of the O horizon (approximately in the Oe) for a total of nine bags within each

subplot. The bags were secured in the forest floor with a plastic peg. Flags were laid on the ground beside each buried bag to facilitate recovery following incubation.

The buried bags were recovered in December 1993 after a six-month *in situ* incubation period. Immediately following collection, litterbags were placed in plastic bags and transported to the laboratory. Samples were removed from plastic bags and dried in paper bags in a drying room at approximately 60°C.

Mass Loss Determination

All litter was removed from each of the mesh bags and foreign materials such as roots, mushrooms, and soil were carefully removed by hand. Decomposition was defined as the reduction in mass over the six-month field incubation period. Subsamples of litter before and after incubation were placed in an oven at 70°C for 48 hours to calculate mass on an oven-dry basis.

Considerable care was taken to manually remove mineral soil from litter samples following the field incubation prior to applying a correction calculation. To account for the possibility of mineral soil remaining on the samples following manual cleaning, subsamples were ashed in a muffle furnace at 550°C for five hours to calculate percent organic matter or ash-free dry matter (% AFDM). Samples of mineral soil from each site were ashed and a correction factor was then calculated according to the methods of Blair (1988a) to account for mineral soil contamination. Mass loss of each sample was expressed as % mass remaining (ash-free oven-dry mass).

Chemical Analyses

Following determination of mass loss, samples were ground in a Wiley™ mill to pass a No. 20 stainless steel mesh (i.e., 1-mm mesh size). Samples from each plot were pooled by species and chemical analyses were conducted on triplicate subsamples of each pooled red maple and white pine sample. Triplicate samples of the original (pre-decomposition) red maple leaves and white pine needles were also analyzed for litter quality. Quality control included certified standard pine needles (National Institute of Standards and Technology Standard Reference Material 1575), replicates and blanks. Subsamples of the ground samples were dry-ashed and then digested using 50% HCl and concentrated HNO_3, according to the methods of Robarge and Fernandez (1986). Digested samples were analyzed for total P, K, Ca, Mg, Al, Fe, Zn, Cu, B, and Mn by inductively coupled plasma spectroscopy (ICP) at the Department of

Applied Ecology and Environmental Sciences Analytical Laboratory, University of Maine.

Subsamples of the ground samples were pulverized for C and N analysis in a Spex™ 8000 ball mill, and oven-dried at 70°C for 48 hours before weighing. Three to 4 mg of oven-dry sample were weighed into a tin capsule which was sealed and rolled into a ball using forceps. Tin balls were placed in a labeled assay plate and analyzed on a Carlo Erba™ NA1500 C/N analyzer at the Institute of Ecology, University of Georgia, Athens, Georgia.

The analytical procedures of Van Soest et al. (1991) were used to determine the organic chemistry of litter. The filterbag technique of Komarek et al. (1994) was used instead of the conventional reflux apparatus system of Van Soest et al. (1991), reducing the amount of time required in the filtering stage of the procedure. The analysis was conducted in the Department of Animal, Veterinary and Aquatic Sciences, University of Maine.

This is a sequential analysis that first determines the neutral detergent fiber content of the litter, followed by acid detergent fiber content, and acid detergent lignin content. The neutral detergent fiber procedure removes soluble cell components from the litter, such as simple sugars and amino acids, thus % neutral detergent fiber is the non-soluble fraction remaining. The soluble cell material (to be referred to as soluble C compounds) is calculated by subtracting % neutral detergent fiber from 100. Hemicelluloses are removed during the acid detergent fiber procedure and the difference between % acid detergent fiber and % neutral detergent fiber is the % hemicellulose content. The acid detergent fiber procedure removes cellulose, leaving a residue of lignin and "lignin-like" compounds such as cutin, acid detergent insoluble nitrogen, and acid insoluble ash. This residue will be referred to as % lignin, which is equal to the % acid detergent fiber. Percent cellulose content is calculated as the difference between % acid detergent fiber and % acid detergent lignin.

Two additional variables were calculated from the above results, hemicellulose and lignocellulose. Hemicellulose is defined by McClaugherty and Berg (1987) as all insoluble polymer carbohydrates, i.e., the sum of cellulose and hemicellulose. Lignocellulose is the sum of holocellulose and lignin. These derived parameters can be useful since it has been found that hemicellulose and cellulose are often intimately associated with lignin (McClaugherty and Berg 1987; Tate 1987), so decomposition of these fractions may not occur independently of each other.

Statistical Analysis

The experimental design was a split split plot design. Climatic regions were the main experimental unit, with sites split within each region, and plots split within each site to increase the power of the design to determine differences among sites. Species differences were examined at the between plot level (i.e., within sites).

Differences in mass loss were examined among each of the three litter types (red maple, white pine, and mixed-litter. The effects of litter quality on rates of decomposition were examined using only the pure litter for the two species (i.e., red maple and white pine). An analysis of variance (ANOVA) was conducted using the SAS statistical software (SAS Institute, Inc. 1988). Tukey's means separation test was used to evaluate significant differences among means (alpha=0.05).

RESULTS AND DISCUSSION

Patterns in Mass Loss

Mass loss rates for the six month *in situ* incubation period differed significantly by litter type ($P<0.001$). Mean values for mass remaining ranked as follows: red maple < mixed-litter < white pine, consistent with results reported for other studies (Table 1). Differences in decomposition rates among the three litter types in this study were attributed to differences in litter quality. Berg and Staaf (1981) noted an initial period following litterfall when mass loss is primarily due to leaching of water soluble substances. They noted these leaching losses occurred independent of microorganisms, and referred to some of their results showing that it took up to a year for fungal populations to reach a maximum in coniferous litter. Most of the water soluble substances in litter are decomposed rapidly, and it is likely that differences in the size of the leachable fraction among litter types determine mass loss differences in the initial stages of decomposition.

Mass loss rates reported in this study (Table 1) were in good agreement with others in the literature after only six months of *in situ* incubation, suggesting that a majority of the mass loss occurs during this period of the year. Some decomposition also occurs during the late fall, winter, and early spring and should be considered for comprehensive evaluations of ecosystem cycling. Using an ATP assay technique, Ausmus (1973) reported a flush of microbial activity during May in the forest floor of a deciduous forest stand in Tennessee. Rustad and Cronan (1988) found lower annual mass loss

Table 1. Percent mass remaining * and initial chemistry of decomposing litter for red maple (RM) and white pine (WP) litter. Organic compounds, C and N are in percent dry weight; all other litter quality variables are in mg g^{-1}.

	Mass	SOLC#	CELL	HEMI	LIGN	HOLO	LIGNO	C/N	C	N	Ca	Mg	K	P	Al	Fe	Mn	Cu	B	Zn	Location
RM	60	61.7	17.4	10.3	10.6	27.7	38.3	70	50.4	0.72	10.0	1.6	3.2	0.62	0.22	0.28	0.37	0.010	0.02	0.051	This study
	46	-	17.3	-	12.7	-	-	-	-	1.2	-	-	-	0.14	-	-	-	-	-	-	Coweeta, NC[a]
	53	-	-	-	9.6	-	-	86	48.2	0.56	11.2	2.8	2.9	0.42	-	-	-	-	-	-	Coweeta, NC[b]
	50	-	-	-	17.2	38.9	-	-	-	0.68	-	-	-	-	-	-	-	-	-	-	Harvard Forest, MA[c]
	68	-	-	-	-	-	-	53	52.9	1.00	7.83	1.8	-	1.69	0.03	0.085	0.24	-	-	-	Tunk Mountain, ME[d]
WP	75	35.8	22.7	16.4	25.0	39.1	64.2	83	51.9	0.63	9.4	1.1	1.8	0.57	0.61	0.44	0.25	0.005	0.014	0.047	This study
	69	-	-	-	22.5	44.7	-	-	-	0.44	-	-	-	-	-	-	-	-	-	-	Blackhawk Is., WI[c]
	63	-	23.3	-	31.0	-	-	-	-	0.90	-	-	-	0.11	-	-	-	-	-	-	Coweeta, NC[a]
	79	-	-	-	-	-	-	86	55.1	0.64	4.61	1.2	-	0.75	0.24	0.095	0.2	-	-	-	Tunk Mountain, ME[d]

* % mass remaining in this study is for a six-month decomposition period; % mass remaining in the other studies reported here is for a 1-year decomposition period.

Litter quality abbreviations: CELL, cellulose (%); LIGN, lignin (%); HOLO, holocellulose (%); SOLC, soluble or labile carbon compounds (%); HEMI, hemicellulose (%); LIGNO, lignocellulose (%).

[a]Cromack & Monk 1975

[b]Blair 1988 a,b

[c]Aber *et al.* 1990

[d]Rustad & Cronan 1988

than the values reported here for composition of both red maple and white pine litter in a softwood site in Maine, and attributed their unexpectedly low rates to a dry summer in the first year of their incubation. Differences in the microbial community between our mixed hardwood-dominated sites and the softwood site of Rustad and Cronan (1988) may also have contributed to lower decomposition rates in their study.

There was no evidence for a synergistic effect of mixing species on rates of mass loss, because the mean % mass remaining of the two single species (67.5%) was not significantly different from the observed rate for the mixed-litter (68.5%). Although red maple litter decomposes more rapidly than white pine, it did not enhance decomposition of the more recalcitrant white pine needle litter when the two were mixed. Similar results were reported by Klemmedson (1992) in decomposition studies that used mixtures of gambel oak (*Quercus gambilii* Nutt.) and ponderosa pine (*Pinus ponderosa* Laws.) and by Blair et al. (1990) for mixtures of red maple, dogwood (*Cornus florida* L.), and chestnut oak (*Quercus prinus* L.). In contrast, Taylor et al. (1989b) found that alder (*Alnus crispa* (Ait.) Pursh) accelerated the decomposition of trembling aspen (*Populus tremuloides* Michx.), and Rustad and Cronan (1988) reported a higher decomposition rate for white pine litter when mixed with red spruce (*Picea rubens* Sarg.) and red maple. Rustad and Cronan (1988) attributed enhanced rates of decomposition to the heterogenous microbial environment created by litter mixing, whereas Taylor et al. (1989b) suggested that the higher litter quality of alder may have accelerated decomposition in aspen.

No significant differences in total mass loss were detected among the four climate regions for any litter type within the six-month time frame of the experiment. In addition, no significant correlations between either climate or site variables and decomposition were detected (Delaney 1994), and therefore only absolute changes are reported here in Table 1. Three factors may have contributed to our failure to detect any significant relationship between mass loss and climate or site: (a) the relatively short incubation period, (b) high variability, and (c) the relatively small magnitude of regional climatic differences across our gradient. However, the effects of temperature on mass loss were readily apparent in the microcosm experiment, in which the range of temperatures was considerably wider than that found across the state (Table 2). Mass loss of red maple litter incubated at 25°C was significantly greater than that at either 5°C or 15°C. Varying the

Table 2. Percent mass of red maple leaf litter remaining following two month decomposition period in microcosm chambers at three temperatures, four moisture levels # (wet=W, intermediate wet=IW, intermediate dry=ID, and dry=D). Coefficients of variation (%) are in parentheses; (n=3).

Temp	Moisture	% Mass remaining
5	W	95.1Aa* (4)
	IW	96.9Aa (2)
	ID	95.9Aa (2)
	D	95.2Aa (1)
15	W	94.2Aa (1)
	IW	96.1Aa (4)
	ID	95.1Aa (1)
	D	97.5Aa (2)
25	W	84.7Ba (3)
	IW	85.2Ba (2)
	ID	84.7Ba (2)
	D	87.4Ba (3)

• Means followed by the same upper case letter are not significantly different among temperatures. Means followed by lower case letters are not significantly different among moisture treatments within temperatures.

Moisture treatments: wet (W) (4.35g H_20/g soil), intermediate wet (IW) (3.2g H_20/g soil), intermediate dry (ID) (2.09g H_20/g soil), dry (D) (0.85g H_20 water/g soil).

soil moisture content from air dry to field capacity in the microcosm study did not have any significant effect on mass loss.

Simmons et al. (1996) reported on two years of data from this gradient project and showed a significant correlation with decomposition and carbon cycling variables. The lack of a response to temperature in the study reported here might imply that the initial phase of decomposition is less dependent on temperature than longer term decay functions. Perhaps the leaching phase is not temperature sensitive, but more affected by nutrient limitations. This would be supported by the lack of a significant difference between the 5°C and 15°C treatments in the incubation study. Mass loss rates reported here were not affected by site variables, despite the range of conditions included in the gradient study. We might conclude from this that soil properties, initial microbial communities, or climate were of minor importance in affecting decomposition compared with litter quality for the initial decay phase.

The microcosm study, however, did show an influence of temperature and moisture on decomposition of red maple in a highly controlled environment (Table 2). Mass loss was significantly greater ($P<0.0001$) at 25°C than at 5°C or 15°C, but there were no significant differences in mass loss among moisture treatments. Apparently only large differences in temperature (>10°C) have a significant effect on litter decomposition. This may explain why mass loss rates in the field study were not correlated with climatic variables. During the six month *in situ* incubation period temperature differences among sites were of a smaller magnitude, and moisture appears to play an even lesser role than temperature.

Effects of Substrate Quality

Litter quality characteristics before decomposition are shown in Table 1. Carbon accounted for greater than half the total mass of each litter type. Of the organic compounds in both litters, soluble C accounted for the largest proportion, and hemicellulose the smallest. Calcium and K were the dominant macronutrients in both species. The variables soluble C, lignin, K, Al, and C/N ratio showed the greatest differences between species. Red maple litter had higher concentrations of all nutrient elements when compared with white pine litter, with the exception of Fe and B. Initial lignin, N, and P concentrations in red maple and white pine are within the range of values reported by other studies listed in Table 1. Other litter quality variables are not as widely reported in the literature, but data available suggest that values in the current study are comparable.

The relative changes in litter quality during the six-month *in situ* incubation period were computed as follows: [(value at six months - initial value) / initial value] × 100 (Figures 1 and 2) soluble C decreased in both species, and hemicellulose decreased only in white pine (Figure 2). With the exception of soluble C, changes in the proportional distribution of organic constituents differed significantly between white pine and red maple (Figure 1).

Decreases in soluble C might be expected as it represents the most labile fraction of the organic compounds. Hemicellulose decreased in white pine but not in red maple, indicating that hemicellulose decomposes more rapidly than overall mass loss rates in white pine, but the opposite is true in red maple. Different organic fractions decompose at different rates (Berg and Agren 1984), and it sometimes requires a certain proportion of the faster decomposing fractions to already be decomposed before it is possible to detect a decline in the concentration of slower decomposing compounds. The

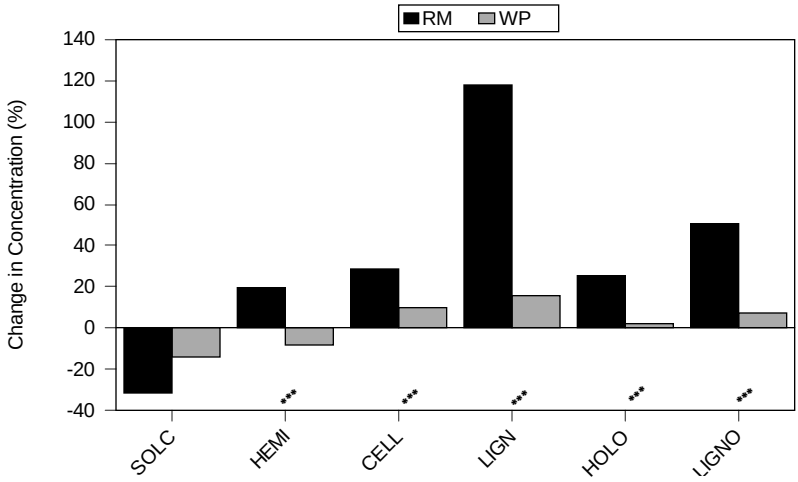

Figure 1.

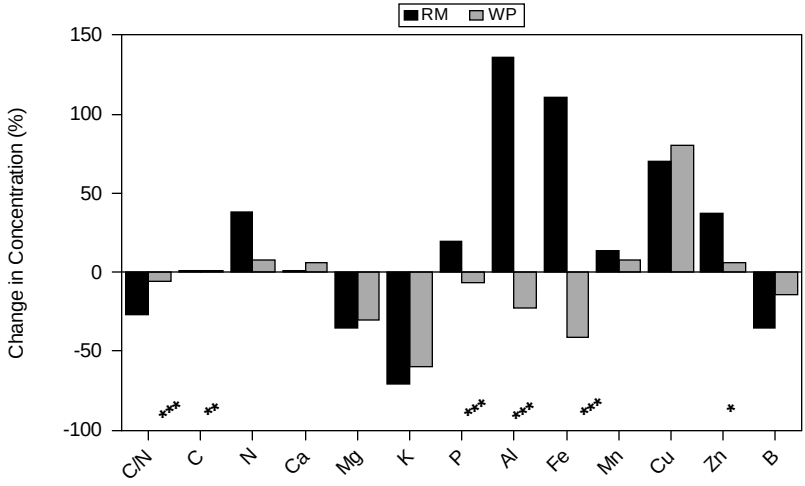

Figure 2.

larger initial concentration of soluble C in red maple (Table 1) suggests that a larger proportion of soluble C must first decompose before relative decreases in hemicellulose can occur. In contrast, white pine hemicellulose concentration had already begun to decline in this study, because of the relatively small initial soluble C concentration in this litter type. These data also suggest that in white pine hemicellulose decomposes faster than cellulose, which contradicts Berg et al. (1982b) who reported that cellulose decomposed faster than hemicellulose. Hemicellulose may also decompose faster than cellulose in red maple (Figure 1) because the increase in cellulose concentration is greater than the increase in hemicellulose after six months of decomposition, suggesting that the onset of a decrease in hemicellulose concentration may occur earlier than the onset of a decrease in cellulose concentration. Lignin concentrations increased in both species as expected, given its reputation for being the most recalcitrant among organic compounds in litter (Aber and Melillo 1991).

Absolute amounts of almost all of the organic compounds decreased over the decomposition period, with the exception of lignin in red maple litter. Thus, only the relative changes are presented in Figures 1 and 2 based on the mass loss and concentration data of Table 1. An increase of approximately 30% lignin mass occurred in red maple, being 0.01 g lignin per g fresh litter and 0.14 g lignin per g litter following six months of decomposition. The absolute increase in lignin during decomposition could be the result of polymerization of labile compounds into more complex humic materials (Tate 1987), which are analyzed as part of the lignin fraction. The larger initial concentration of soluble C in red maple provides a greater pool of labile compounds for the microbial community to re-polymerize into a more recalcitrant fraction, which may explain the increase in absolute mass of lignin in red maple as compared to white pine. For white pine litter, absolute concentrations of lignin declined from 0.25 to 0.22 g lignin per g of litter following six months of decomposition.

Figure 2 shows the change in concentrations of nutrients and Al over the decomposition period. Changes in N, Ca, K, and Mg after six months of decomposition generally agreed with changes reported in the literature for a variety of forest litter types (Edmonds 1984; Rustad and Cronan 1988; Bockheim et al. 1991). This effect is more pronounced in red maple litter, compared to white pine. Presumably the larger soluble C pool in red maple creates a more intense demand for N during this early decomposition period. This is reflected in the greater relative increase in red maple litter N

concentrations, and the significantly greater declines in C/N. Nitrogen is conserved as C is utilized by the microbial community. Both K and Mg are not considered limiting nutrients for these ecosystems and are relatively labile, leading to significant decreases in concentrations. The small changes in concentration of C and Ca during the decomposition period indicate that rates of loss for these elements were similar to biomass loss in both species. This suggests that these elements were neither immobilized by microbial communities nor leached from the litter at rates significantly different from overall mass loss.

In this study, P concentration increased slightly in red maple and decreased in white pine. Increases in P concentration after six months decomposition have been noted in longer-term studies that examined decomposition in red maple leaves (Blair 1988a), white pine needles (Rustad and Cronan 1988), Pacific fir (*Abies amabilis* (Dougl.) Forb.) needles (Edmonds 1984), and balsam fir (*Abies balsamea* (L.) Mill.) needles (Lousier and Parkinson 1978). Decreases have also been noted in P concentration after six months for red maple (Rustad and Cronan 1988), aspen (Lousier and Parkinson 1978), and chestnut oak leaves (Blair 1988a). Both species in the study reported here conserved most of the P, resulting in relatively small changes in these concentrations after six months attributable to microbial immobilization through the decomposition period. However, the increase in P concentration in red maple and not in white pine may reflect the same effects of litter decomposition rates as was seen with N concentrations. Namely, the higher soluble C concentrations in red maple litter compared to white pine resulted in more rapid initial rates of red maple decomposition and a more intense demand for and efficient retention of P.

For the microelement concentrations, longer-term studies have reported concentration increases in Fe, Al, Cu, Mn, and Zn after the first six months of decomposition (Lousier and Parkinson 1978; Rustad and Cronan 1988; Bockheim et al. 1991). This was generally the trend found in this study, with the exception of a decrease in the relative Fe and Al concentration in white pine (Figure 2). The increase in Fe and Al concentrations in red maple and their decreases in white pine are attributable to differences in decomposition rates between the two species and metal complexation processes. Unlike P, Al and Fe are not conserved by the microbial community. Gosz et al. (1973) noted that Fe may be complexed with labile organic compounds, resulting in the leaching of some Fe in the early stages of decomposition. If organic compounds released during the decomposition of white pine litter were

more acidic and thus more able to transport metals, then leaching of Fe and Al may explain the greater concentration decrease of these elements in white pine, as compared to red maple litter. The greater increase that occurred in Fe and Al concentration in red maple may also be an artifact of extraneous additions of mineral soil Fe and Al to red maple during decomposition. Boron concentrations decreased in both species, which is consistent with the results of Bockheim et al. (1991) who concluded that B is easily leached from plant tissues and is not likely a limiting nutrient in this type of soil environment. This study suggests that the forest floor acts as a sink for certain micronutrients, causing a net accumulation during the first six months of decomposition.

Absolute masses of macro- and micronutrients generally decreased, with the exception of highly significant increases ($P<0.0001$) in Fe (31%) and nonessential Al (40%) in red maple, and Cu (35%) in white pine. The increase in absolute amounts of these elements may be due in part to soil contamination. Differences in the dynamics of these elements between species may also be the result of differences in the litter quality properties of the species. Gosz et al. (1973) found dynamics of Fe in decomposing litter to be highly variable and concluded that Fe accumulation was mostly dependent on microbial activity. They found that Fe accumulation began sooner in faster decomposing leaf litter, which is consistent with the results of this study. It should follow from this that Fe accumulation should occur in white pine as decomposition proceeds, as was noted by Rustad and Cronan (1988). Aluminum dynamics have been reported to be similar to Fe (Rustad and Cronan 1988; Bockheim et al. 1991), and the differences in decomposition rates between the two litter types may also explain Al accumulation in red maple and not in white pine. These two litter types may also differ not just in rates of mass loss, but also in the rates of formation of organic exchange sites and thus the rate of metal complexation. Although most metals form chelation complexes with organic matter, Cu is particularly retained by organic chelators. It is stronger than most other bivalent metal cations (Northmore 1959), particularly in chelating with humic and fulvic acids (Flemming and Trevors 1989). It is possible that strong complexation with solid phase organics resulted in greater Cu retention relative to the proportion of other metals retained.

A decrease of 17% and 19% in the absolute mass of N occurred in red maple and white pine, respectively. Blair (1988a) and Rustad and Cronan (1988) also reported decreases in the absolute mass of N in red maple after six months of decomposition, but Rustad and

Cronan (1988) reported increases in the absolute mass of N in white pine. The results of this study are consistent with the pattern of N dynamics described by Berg and Staaf (1981). They reported three stages in the litter decomposition dynamics of N for a variety of litter types: leaching, accumulation, and release. In the early stages of decay, rapid N loss occurs independently of microbial decomposition in a process known as leaching. Following leaching, accumulation or immobilization of N occurs until a C/N ratio of approximately 30:1 is reached, below which N is mineralized and released. The C/N ratios of red maple and white pine at the end of the decomposition period for this study were approximately 51:1 and 78:1, respectively, suggesting that N remains tightly bound in the decaying litter complex at this early stage of the decay continuum.

CONCLUSIONS

Mass loss differed significantly among litter types, as did the changes in concentration of greater than half of the litter quality variables examined. Changes in concentration of different organic fractions were a function of their rates of decomposition relative to overall mass loss. Changes in element concentrations were generally related to rates of overall biomass loss and microbial requirements for these elements. Decreases in absolute amounts of soluble C, cellulose, hemicellulose, C, N, Ca, Mg, K, P, Mn, Zn, and B occurred in both species after six months of decomposition, suggesting that rates of decomposition and mineralization were greater than immobilization or repolymerization. Absolute mass of lignin, Al, Fe, and Cu increased or decreased depending on species.

These findings define critical changes that occur in the initial phases of the litter decay continuum, typically a process occurring on the surface of the forest floor. Clearly the proportion of soluble organic compounds in fresh litter has a strong influence on patterns of both organic and inorganic chemical losses. Red maple litter shows a relatively rapid mass loss compared to white pine litter with a subsequent rapid increase in the more recalcitrant compounds, particularly those operationally defined as lignin.

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