THE FATE OF NITROGEN MINERALIZED FROM LEAF LITTER – INITIAL EVIDENCE FROM ^{15}N-LABELED LITTER

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Abstract.—Decomposition of leaf litter includes microbial immobilization of nitrogen (N), followed by N mineralization. The fate of N mineralized from leaf litter is unknown. I hypothesized that N mineralized from leaf litter will be re-immobilized into other forms of organic matter, including downed wood. This mechanism may retain N in some forests. To test this hypothesis, oak leaves were enriched with a naturally occurring, stable isotope of N (^{15}N), collected as litter, and allowed to decompose with and without wood (10 cm long, in 3 diameter classes of < 2 cm, 2-4 cm, and 4-6 cm) in litter bags in the forest floor of a central hardwood forest near Morgantown, WV. As oak litter immobilized exogenous N, ^{15}N in litter decreased due to dilution, and then did not change significantly. Nitrogen mineralization in leaf litter did not start for at least 24 months. By the 11th month of decomposition, wood N reached between 140 and 274 percent of the initial N mass, depending on wood diameter. By the 24th month, ^{15}N was detected in wood, supporting the hypothesis. Nitrogen-label was not detected in fresh litter above litter bags, or below litter bags in partly decomposed forest floor or soil. It appears that N mineralized from leaf litter may be transferred to and immobilized in small-diameter downed wood. If these results are confirmed in a larger study, we may need to change the way we view N cycling in the leaf litter layer; N mineralized from foliar litter may not be immediately plant-available as we now assume.

INTRODUCTION

Decomposition of foliar litter is a microbial process in which microbes use litter carbon (C) as a source of energy (Gallardo and Schlesinger 1994). While feeding on litter C, soil microbes sequester nitrogen (N) from the environment for the formation of new cells, resulting in a net increase in litter N (Berg and Staff, 1981). As decomposition progresses and labile C in litter is used up, N in the litter-microbe complex starts to decline in the process of N mineralization (Gosz and others 1973, Edmonds 1980, Berg and Staff 1981, Moore and others 2006, Piatek and others 2009).

The fate of the N that becomes mineralized from fresh foliar litter is unknown. It is typically said that leaf litter plays an important role in forest nutrition and productivity, the assumption being that mineralization of leaf litter yields plant-available forms of N. If litter N is not taken up by plants, as the case may be after forest harvest, mineralized N is nitrified and leached, potentially impacting surface water quality. However, decomposition of leaf litter proceeds within a matrix of other C pools, which constitute sources of energy for microbial growth and opportunities for further N immobilization. Therefore, partially decomposed old leaf litter layers, downed wood, roots, root exudates, and annual litter fall are possible alternative transfer pathways for leaf-mineralized N. Since forests are N-limited (Vitousek and others 1997, Oren and others 2001), and the presence of labile C is expected to result in immobilization by microbial biomass of any available N in

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N-limited systems, it seems unlikely that N mineralized from foliar litter becomes plant-available. Rather, N released from decomposing foliar litter may be rapidly re-immobilized into microbial biomass, which utilizes the next most labile source of C.

Theoretically, this re-immobilization process could continue until all labile C is exhausted. Since a new leaf litter layer is formed each fall in standing deciduous forests, in theory this closed N cycling can continue in perpetuity, or until the forest is cut and C in annual litterfall is no longer available. Downed wood may also be attractive for microbes because woody biomass contains up to 50 percent C. However, N dynamics in wood remains poorly understood due to lack of methods for accounting for loss of wood volume during decomposition (Krankina and others 1999, Creed and others 2004). Addition of N tracers showed negligible immobilization of N into fine woody debris several years later (Currie and others 2002). However, increases in wood N of up to 180 percent of initial N mass were observed in Douglas-fir early in decomposition (Edmonds and Eglitis 1989). Wood chips are apparently also capable of immobilizing N (Homyak and others 2008). A greater understanding of the role of wood in N retention is of considerable interest in intensively managed forests where sites are cleared of woody residues in preparation for tree planting. Furthermore, with a growing interest in using woody biomass for the production of biofuels, extraction of woody residues is likely to increase with as yet unknown consequences for N retention and nitrate exports.

Decomposition studies of foliar litter, however, rarely trace the fate of *released* N, making the term *N-release from litter* potentially misleading. Possible fates of litter N include mineralization to ammonium, re-immobilization, nitrification to nitrate, leaching of dissolved organic N (DON), and a migration of N bound within fungal filaments (Hart and Firestone 1991). A few studies also suggest that foliar litter does not interact with other soil or forest floor N processes (Currie and Nadelhoffer 1999, Fisk and Fahey 2001), increasing the uncertainty of the fate of litter-released N. Fates of litter-released N may determine such ecological conundrums as controls on short- and long-term N availability in N-limiting systems, and nitrate production and export after disturbance or in N-saturated systems.

Nitrogen transfers and cycling in ecosystems can be elucidated using a ^{15}N-labeling technique. Nitrogen-15 is a naturally occurring stable isotope of N which has been used to trace the fate of atmospherically deposited inorganic N (Currie and Nadelhoffer 1999, Piatek and others 2005). It has not been widely used to produce leaf-organic N compounds. To produce labeled organic N, an individual tree is injected with a ^{15}N-enriched solution early in the growing season to allow for the formation of organic N compounds in leaves. Subsequently, leaves can be collected after natural abscission and leaf fall (Christenson and others 2002). Sufficient amounts of the enriched material need to be produced to conduct a decomposition experiment, which typically lasts 1 to 2 years with several collections. Moreover, initial material must contain sufficient levels of label for label recovery among several possible pools in the forest floor. Enriched materials are analyzed by mass spectrometry at select laboratories across the country. Given these challenges, considerable amount of time and costs of isotopic analyses render the labeling technique difficult and expensive to employ and therefore still not widely used. Initial evidence, however, can provide an important justification for a further study.

To provide initial evidence for the fate of N mineralized from leaf litter and the role of downed wood in N retention, I conducted an exploratory experiment using ^{15}N-enriched oak leaf litter to trace N movement from decomposing leaf litter to downed wood, old forest floor layers, freshly deposited leaf litter, and soil. The central hypothesis tested was that N mineralized from leaf litter is re-immobilized into other available C pools, including downed wood.

METHODS

EXPERIMENTAL MATERIAL

Enrichment methods are treated in detail in Christenson and others (2002). Briefly, the bole of a northern red oak tree (*Quercus rubra*), 10 cm in diameter, was injected with a ^{15}N-enriched $(^{15}NH_4)_2SO_4$ solution in spring and summer 2004, and leaf litter was collected in fall. Fallen litter was air-dried for several months prior to use.

Availability of air-dried branch wood at the time when labeled leaf litter was available reduced the choice to a wild-grown *Malus* species. While not widely present in the central hardwood forest, it is found in now-forested old homestead sites across the northeastern United States. *Malus* then satisfied the need for a source of wood-derived C for potential microbial use.

About 6 grams of ^{15}N enriched litter, weighed to the nearest 100th of a gram, were placed in 1-mm mesh bags made of nylon window screening into 20-cm x 20-cm pockets. Twenty-two litter bags contained ^{15}N-enriched litter alone; the contents of these bags became litter type "leaves (-)," or without wood. Twenty-two other litter bags received three air-dried woody pieces 10 cm long, one in each diameter class – small (up to 2 cm in diameter), medium (2 - 4 cm), and large (4 - 6 cm) with intact bark; the contents of these bags became litter type "leaves (+)," or with wood. Each woody piece was individually weighed. Two samples of each litter type were then oven-dried at 65-70 ^{o}C until constant weight to determine the air-to-oven-dry weight adjustment for all other samples.

The remaining 20 litter bags of each litter type were placed on the forest floor at the West Virginia University Research Forest outside of Morgantown, WV (39°41'N, 79°45'W) in early November 2004, and secured with landscape pins. Placement was not random; rather, each type of litter was placed in a 40-m-long row, with each bag 2 m away from another bag in that row, and rows at least 5 m apart, for final plot size of about 60 m x 20 m, without replication. The objective behind this placement was to prevent ^{15}N from transfer between mesh bags. Bags within rows were randomized according to their number (from 1 to 20).

The forest type where the study took place is a mature central hardwood forest, with a high red oak component, and little understory. Average tree diameter at breast height is estimated at 36 cm. The forest floor depth is less than 2 cm. Dead downed wood is amply represented, though the amounts were not quantified.

SAMPLE COLLECTION AND PROCESSING

Two bags of each type [leaves(+) and leaves (-)] were collected every 3 to 4 months, with the first collection in December 2004, and the last in June 2007, for a total of 10 collections. New litter fallen on top of the mesh bags, foliage under the mesh bags (old forest floor or Oe + Oa horizons), and soil beneath bags to 20 cm depth were also collected for analysis of ^{15}N. Additionally, new litter, old forest floor, and soil were collected in six places away from any litter bags for analysis of background ^{15}N levels. Fresh unconfined litter did not contain any fine roots. Partly decomposed "old" forest floor layers, however, are made of materials tightly pressed together, and any separation becomes impossible. Soils were sieved prior to further analysis.

Materials from mesh bags were separated into leaf and wood components. Any fine roots growing into the bags were taken out, although with increasing litter decomposition that process becomes less complete. Samples from mesh bags and nonconfined background materials were oven-dried at 65-70 ^{o}C until constant

weight. All materials were subsequently weighed and ground. Due to substantial hygroscopicity, mass in dried wood fluctuated over time; to account for this fluctuation, a mass loss function was derived with an r^2 of 0.7.

Nitrogen content in decomposed materials was calculated as N mass at collection time over N mass at the start of decomposition, in percent. Net immobilization is reflected in increasing mass of litter N as decomposition progresses, while net mineralization is reflected in decreasing N mass.

^{15}N ANALYSES

Subsamples of the ground samples were analytically weighed into 5-mm x 9-mm tin capsules (Costech Analytical International) and analyzed by mass spectrometry at the University of California–Davis stable isotope facility. Results are obtained as the ratio of ^{15}N to ^{14}N in sample versus that of an international standard (Air; http://stableisotopefacility.ucdavis.edu, accessed Dec. 1, 2009):

$$\delta^{15}N\ [‰] = (^{15}N/^{14}N_{\ sample}) / (^{15}N/^{14}N_{\ standard} - 1) * 1000$$

The magnitude and timing of the decrease in ^{15}N in enriched litter indicates ^{15}N dilution during N immobilization (microbial input of litter-external N). An increase in ^{15}N in wood, freshly fallen litter, old forest floor, or soil indicates a transfer by microbes of ^{15}N from litter. Such transfer serves as initial evidence of the potential role of wood in N retention in hardwood forests.

MICROBIAL BIOMASS DYNAMICS

To evaluate microbial biomass dynamics in the experimental tissues, the method of Aber and Melillo (1982) was used. In this method, tissue initial N concentration is assumed constant, so that the increase in total substrate N over time is due to microbial biomass growth and N. N concentration in decomposing tissue is plotted against the remaining weight, and the equation parameters with N concentrations over time divided by original litter concentration are used to generate polynomial regression plots for microbial biomass (Aber and Melillo 1982). Obtained in this matter, microbial biomass dynamics helps in interpreting the observed ^{15}N data. Namely, when 15N increases in a new (previously unlabeled) tissue, and is accompanied by microbial biomass growth in that tissue, it serves as an indication that the microbial transfer of label has occurred.

TREATMENT OF DATA

The study's objective was to provide initial evidence for a larger inquiry into N transfer pathways in the forest floor. The limited amount of enriched materials made replication impossible. Therefore, statistical evaluation of main effects of 'row' and 'tissue type' could not be conducted, as replication was only within the time of collection. The combined use of labeling and microbial biomass dynamics techniques provides synergistic evidence, but results were interpreted with due caution.

RESULTS

MASS LOSS

Twenty-four months after start of decomposition, 60 percent of leaf litter mass was lost in litter decomposing with (+) and without wood (-) (Fig. 1). The small starting sample size and relatively long decomposition period resulted in highly fragmented tissue, which did not allow some of the analyses to go beyond 24

months. Approximately 40 percent of wood mass was lost after 24 months, increasing to 50 percent by the end of the study, at 32 months of decomposition.

NITROGEN DYNAMICS IN DECOMPOSING LEAVES AND WOOD

Nitrogen concentrations in oak leaf litter increased from the initial 0.58 percent to the highest level of 2.32 percent for leaves (+) and 2.41 percent for leaves (-) in the 24th month of decomposition. Subsequently, N concentrations in leaf litter started to decline slowly (Fig. 2). Nitrogen concentrations in wood ranged from the initial 0.19 percent to an average for all diameter classes of 1.2 percent (Fig. 2).

Leaf litter immobilized N for 24 months of decomposition, observed as an increase in litter N mass (litter mass x N concentration). Leaf litter with (+) and without (-) wood had similar net N immobilization rates over the study period, except at 11 months, when leaves decomposing without wood immobilized 36 percent more N than leaves decomposing with wood (Fig. 3). After 24 months, an average of 163 percent of original N mass was present in leaf litter. Wood N contents in the large- and medium-diameter classes were similar, but the small-diameter wood exhibited large N increases and decreases. After 24 months of decomposition, an average of 125 percent of initial N mass was present in large- and medium-diameter wood. The highest net N immobilization in the small-diameter wood was 274 percent of original N mass at 11 months. Net mineralization over the next 9 months resulted in a decrease in total N content in small-diameter wood (Fig. 3).

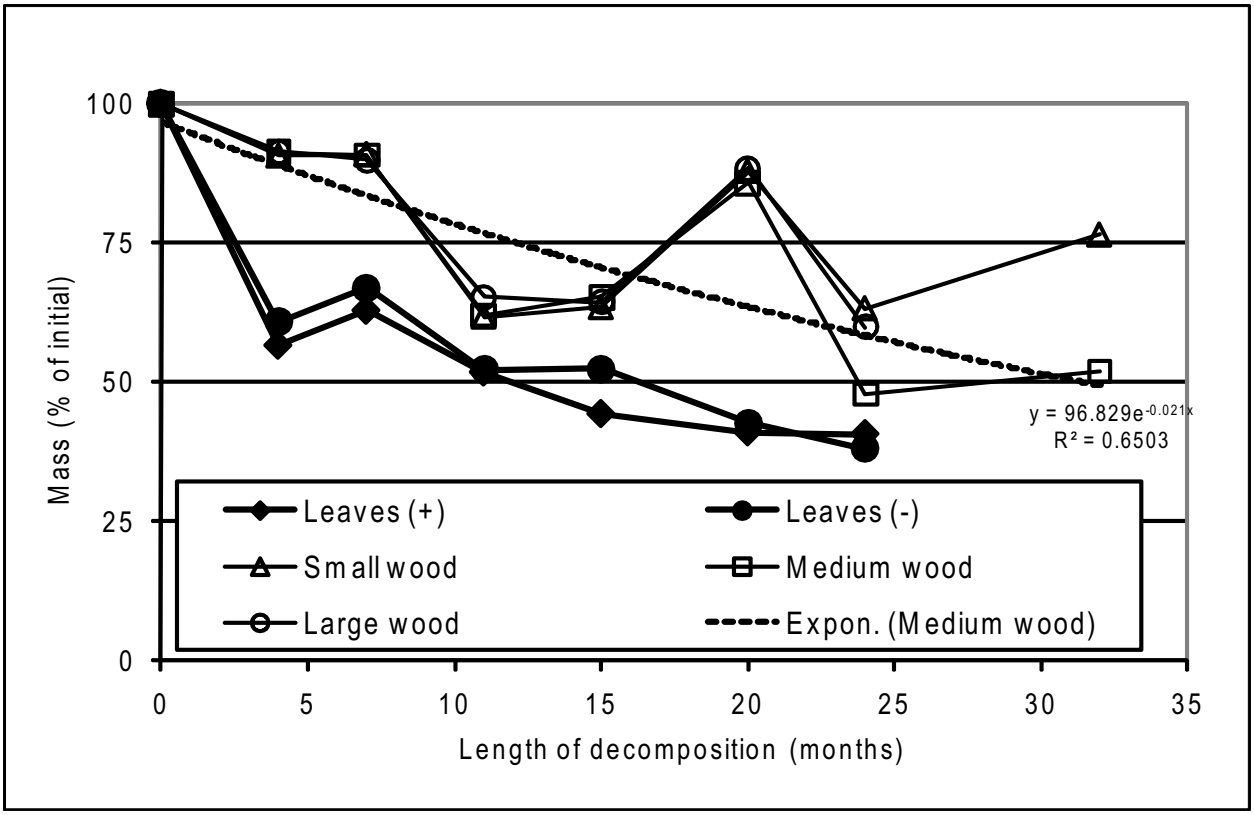

Figure 1.—Mass loss dynamics of leaves decomposing with wood (+) – dark solid diamonds, and without wood (-) – dark solid circles, and wood in three size classes (small – triangles, medium – squares, and large – circles) over time. Regression line denotes average wood decomposition.

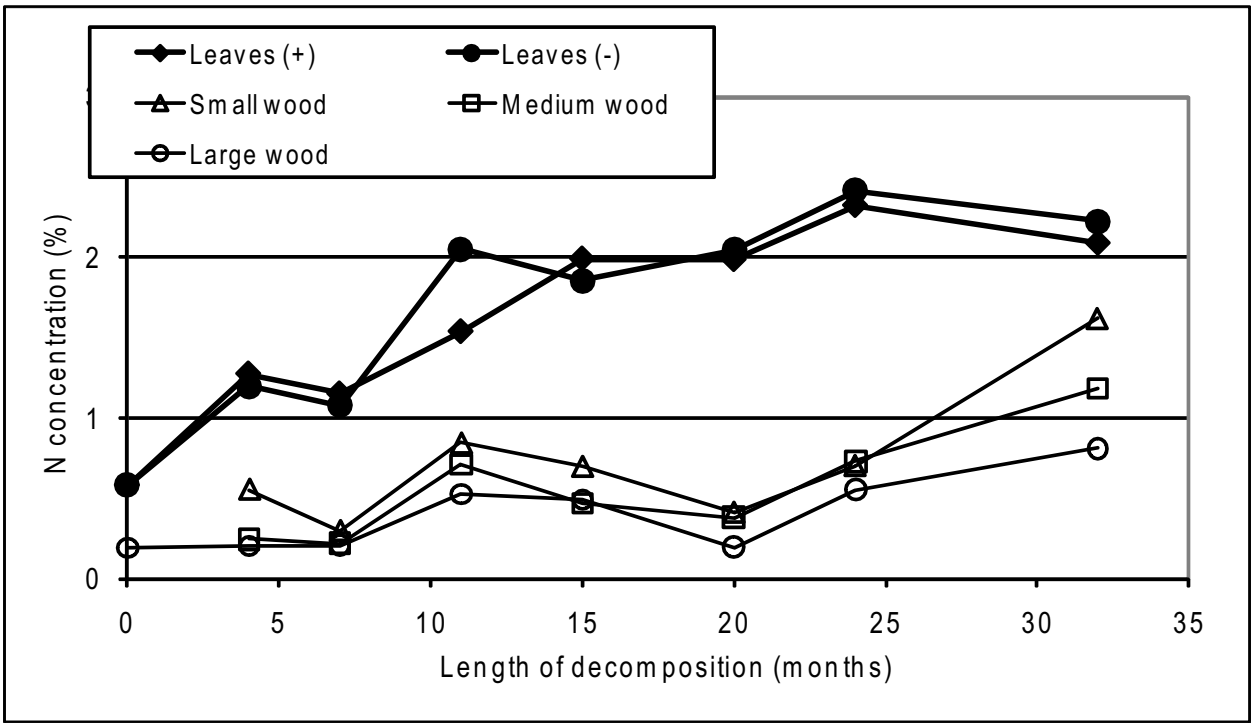

Figure 2.—Nitrogen concentration in leaves and wood during decomposition.

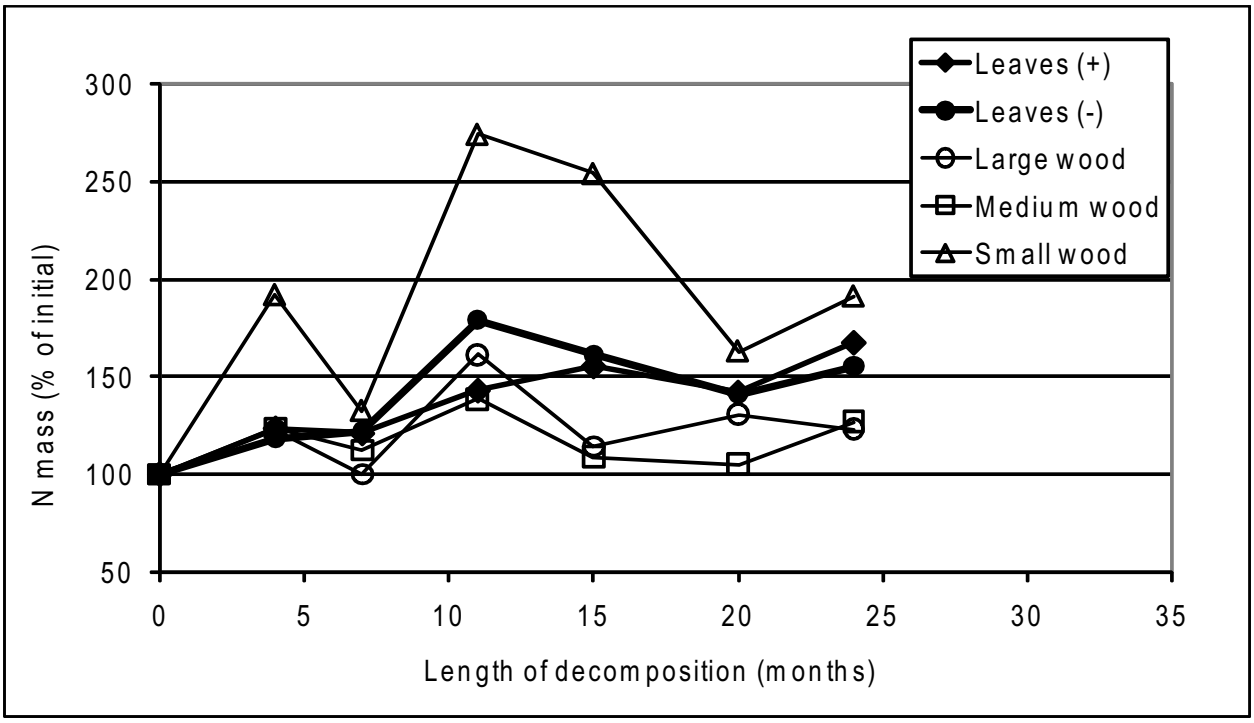

Figure 3.—Nitrogen dynamics during decomposition of leaves decomposing with wood (+) – dark solid diamonds, and without wood (-) – dark solid circles, and wood in three size classes (small – triangles, medium – squares, large – circles) over time.

CHANGES IN $\delta^{15}N$

The average starting level of ^{15}N label in experimentally enriched leaf litter was +162‰, compared to the background levels with the range of -1.4 ‰ in small diameter wood to +8.9 ‰ in the soil at the site (Fig. 4). Early $\delta^{15}N$ dynamics in leaf litter included a dilution of the label by N immobilized by leaf-colonizing microbes. Between 11 and 20 months, ^{15}N levels appeared to stabilize around 82‰ for both leaf litters (decomposing with and without wood), and then decreased to 57‰ after 24 months, and to 48‰ after 32 months of decomposition. During 0-20 months of decomposition, label was not detected in any of the other types of organic matter tested (Fig. 4). After 20 months, a slight increase was noted in wood in all size classes. This increase continued. Label was recovered in wood in all diameter classes after 24 months of decomposition, indicating a transfer of label between leaf litter and wood. After 24 months, $\delta^{15}N$ in wood ranged from 113‰ in the medium wood to 148‰ in small wood. Over the next 8 months, enrichment in wood declined to background levels in all wood sizes.

MICROBIAL BIOMASS DYNAMICS

Leaf litter with and without wood had similar microbial biomass dynamics until N concentrations reached about 1.5 percent in month 9 and 11 for leaves with and without wood, respectively (Fig. 2 and 5). Beyond tissue N concentration of 1.5 percent, microbial dynamics diverged. Leaves decomposing with wood supported less biomass per unit increase in N concentration than did leaves without wood. Wood supported much greater levels of microbial biomass at much lower N concentrations than did the leaves (Fig. 5), with small-diameter wood supporting more than large-diameter wood (Fig. 5). The trajectory for wood-supporting microbial biomass was still increasing, especially for the small-diameter wood, when the experiment ended after 32 months.

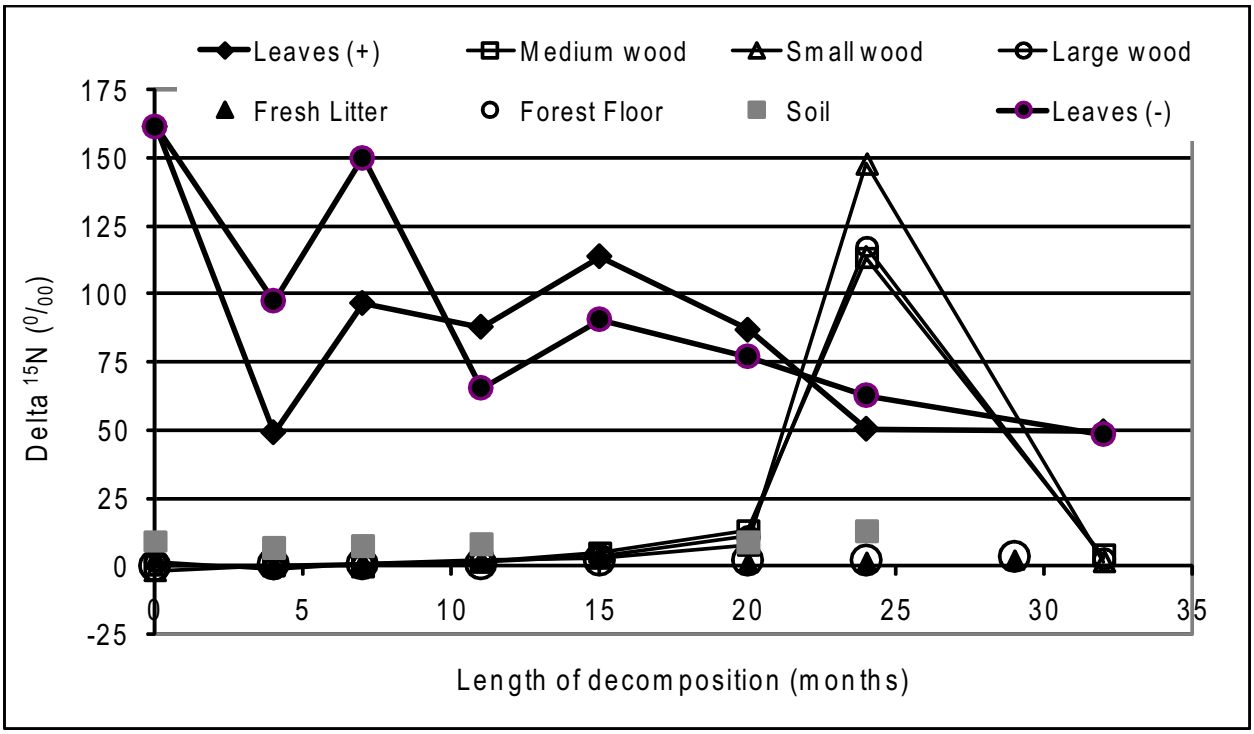

Figure 4.—Delta ^{15}N dynamics during decomposition of leaves decomposing with wood (+) – dark solid diamonds, and without wood (-) – dark empty diamonds, and wood in three size classes (small – triangles, medium – squares, and large – circles) over time, and fresh forest floor (soil – light solid squares, old forest floor – dark solid diamonds, no line, and fresh litter – triangles).

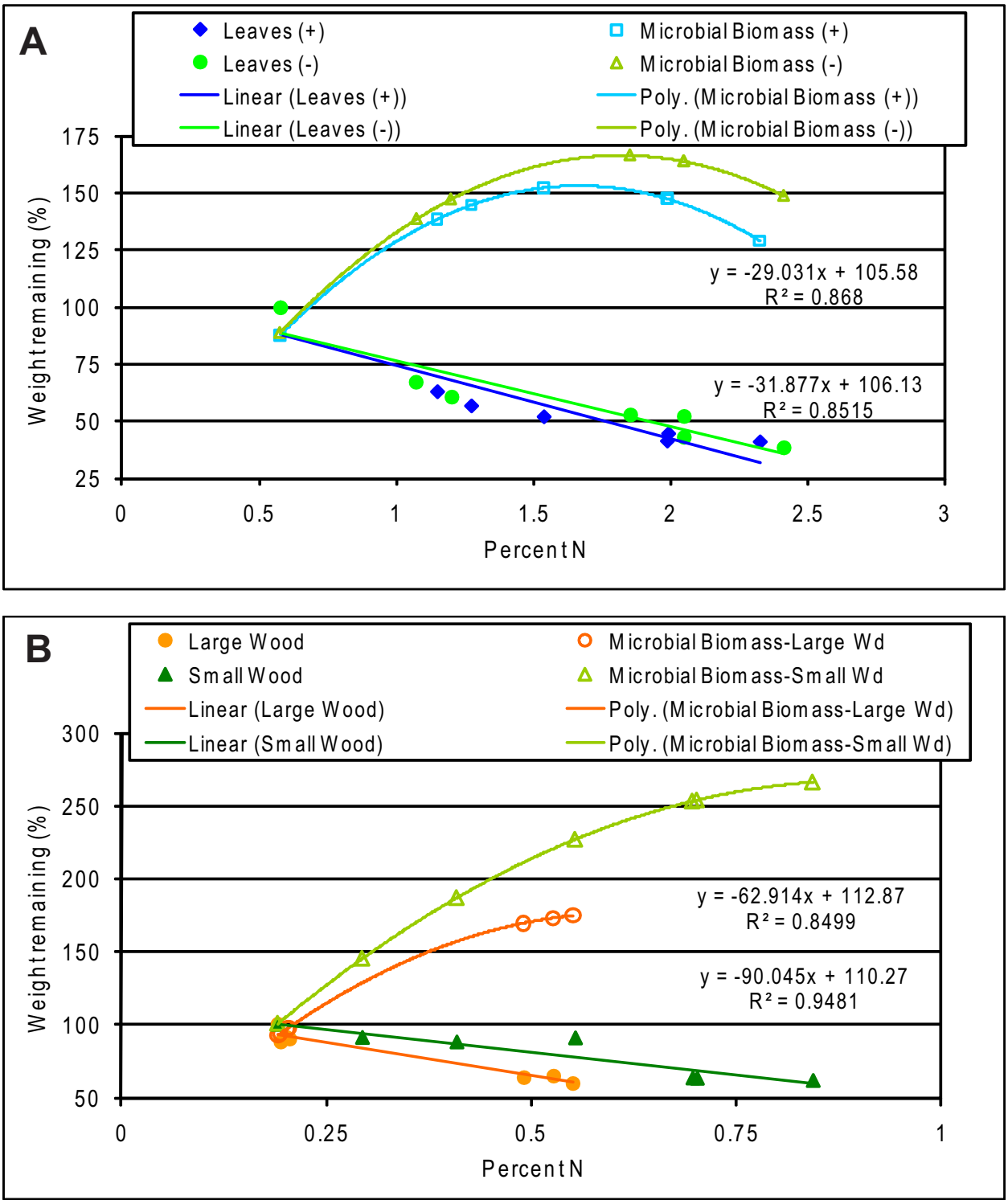

Figure 5.—Estimated microbial biomass N dynamics plotted as N concentration vs. N content (%) (after Aber and Melillo 1982). Top (A): Leaves with wood (+) – dark solid diamonds, leaves without wood (-) – solid circles, leaf microbial biomass with wood (+) – open squares, leaf microbial biomass without wood (-) – open triangles. Bottom (B): Wood pieces: Large wood – solid circles; Small wood – solid triangles. Microbial biomass: Large wood – open circles; Small wood – open triangles.

DISCUSSION

THE FATE OF N MINERALIZED FROM LEAF LITTER

The delayed appearance of N label in wood supports the study hypothesis that N mineralized from leaf litter is re-immobilized into other available C pools, in this case wood. The one-time increase and subsequent decrease in ^{15}N in wood to background levels is difficult to explain given the small overall sample size. However, six pieces of wood per collection responded in the same manner. These observations are consistent with immobilization of N into downed wood observed during decomposition of Douglas-fir and in wood chips of mixed northern hardwoods (Edmonds and Eglitis 1989, Holub and others 2001, Homyak and others 2008). Currie and others (2002) did not observe label transfer to wood, but the observations were made during advanced stages of wood decomposition.

Transfer of N label mineralized from experimental leaf litter to wood was expected to be accompanied by a corresponding decrease in $\delta^{15}N$ in leaf litter. However, the decrease in $\delta^{15}N$ in leaf litter was relatively small compared to the increase in wood. The decrease in early stages of decomposition can be explained by label dilution. Dilution was indicated by a decrease in $\delta^{15}N$ accompanied by an increase in litter total N (i.e., immobilization; Fig. 3), and a lack of label outside of the enriched leaf litter (Fig. 4). The decrease in leaf $\delta^{15}N$ together with the decline in leaf microbial biomass at that stage of decomposition (Fig. 5) suggest that some of the leaf litter-inhabiting microbes either died or migrated to other sources of C. Dead microbial biomass constitutes easily decomposable organic matter that is subject to mineralization, while the released microbial N can be re-immobilized by other microbes. Because the increase in $\delta^{15}N$ occurred in wood alone, the "other" microbes were most likely wood decomposers. The sum of ^{15}N after 24 months indicated that enrichment level in all tissues together reached 425‰, up from the starting 162‰ in leaves. Enrichment can be due to a concentrating effect of decreasing leaf and woody tissue mass on ^{15}N (and ^{14}N), as well as to microbial biomass turnover (Fig. 1 and 5).

Total N dynamics were the same in leaves decomposing in the presence or absence of wood. One exception occurred in the 11th month of decomposition (Fig. 3), when N concentration in leaf litter reached 1.5 percent and microbial biomass started to decline in leaves decomposing with wood (Figs. 2 and 5). This decline is not likely to be due to competition for available N between wood- and leaf-colonizing microbes for at least two reasons. In September, the 11th month of study, ecosystem N-sink activity is probably at its lowest, and N availability at some of the highest during the year due to slowing N uptake by plants and temperatures conducive to soil organic matter mineralization. It is then unlikely that microbial competition for available N operates under these conditions of N supply and demand. At the same time, the content of labile C in leaf litter declined after almost a full year of microbial growth and C utilization. Therefore, the decline in microbial biomass in leaf litter decomposing with wood but not in leaf litter decomposing alone may be associated with a migration of microbes from a low-C substrate to a higher-C substrate in wood.

The transfer of N label with microbes migrating from leaf litter was expected into the freshly deposited litter layer (on experimental litter bags). Fresh litter is expected to have higher contents of labile C than wood. Lack of transfer to the older forest floor below the mesh bags is consistent with earlier findings suggesting little interaction between N cycling processes in fresh litter with the underlying layers (Currie and Nadelhoffer 1999, Fisk and Fahey 2001, Christenson and others 2002). The lack of interaction may extend in the other direction as well. Lack of N transfer to soil is best confirmed with data allowing calculations of ^{15}N pools

which were not quantified in this study; neverthless, estimates (data not shown) revealed no changes between soils away from enriched litter and soils directly under litter bags. Again, these results are not surprising if N in our initial litter (in litter bags) does not interact with the forest floor or soils below.

Types of decomposers are likely to differ among substrate types, especially when substrate types vary in their chemistry as much as do leaf litter and wood. Therefore, as microbial biomass in leaf litter declines (Fig. 5), probably as a result of a decrease in available C, the products of microbial biomass turnover in leaf litter may be immobilized by and translocated by wood-decomposing fungi, thus appearing in wood (as evidenced by changes in $\delta^{15}N$). Translocation of N within fungal filaments has been observed (Hart and Firestone 1991). Thus, neighboring wood materials may not necessarily be more "attractive" to decomposers because of their accessibility than labile C sources farther away, but wood-inhabiting fungal decomposers may be capable of accessing the products of microbial turnover in leaf litter. The described potential N transfer pathways are supported by patterns of estimated microbial biomass growth in leaves and in wood (Fig. 5); namely, when leaf microbial biomass started to decline, wood-supported biomass was expanding. However, different N transfer pathways may operate depending on the type of physical barriers and on chemical properties of decomposition microsites.

POTENTIAL IMPLICATIONS OF THE FINDINGS

A transfer of leaf-litter-mineralized N to wood and wood immobilization of N were observed in this study. The carrier of N label in this study was foliar litter of northern red oak. Northern red oak is the dominant species in the central hardwood forest type (Hicks 1998), and its relative component may reach up to 93 percent (Kromroy and others 2008). Therefore, it is a good choice for an exploratory study of N transfers in the litter layer. However, decomposition is slower and N dynamics in oak exhibits higher rates of immobilization and slower mineralization than other leaf litter types in the central hardwood forests (Piatek and others 2009, Piatek and others 2010). For example, red maple or yellow-poplar leaf litter, both common in the central hardwoods, could be expected to initially immobilize and mineralize N faster than observed here, and at smaller levels (Piatek and others 2009). As a result of faster dynamics but lesser amounts involved, label dilution in leaf litter would be less in these other species, and mineralization and re-immobilization of N to other C sources may be observed earlier in decomposition than in oak litter. Therefore, some of the results related to the timing of N transfers may be particular to the decomposition dynamics in oak litter. Overall dynamics and N transfers, however, are likely to be preserved.

The observed N immobilization into wood merits a further study into the role of wood as an N retention mechanism in forests. Mechanisms of N retention are of considerable interest on sites that either have high rates of N turnover (such as clearcut forests) or receive high rates of N deposition (Magill and Aber 1998, Piatek and others 2009); both situations may result in potentially hazardous levels of nitrate leaching into drinking water supplies or aquatic habitats. A potential N-immobilization capacity of downed wood, especially at 140-250 percent of initial mass as observed here, would mean that 45-60 kg N ha^{-1} can be retained on a site with a hypothetical 25-kg initial N mass in fresh downed wood. (At average wood concentrations of 0.1 percent N, 2,500 kg downed wood ha^{-1} would be needed). This amount of N retention would account for substantially more than current rates of atmospheric N deposition of about 12 kg N ha^{-1} in the central hardwood forest region (Adams and others 2000). With subsequent mineralization of N (as indicated in this study), these rates would not translate into a long-term N sink.

Large amounts of woody residues are currently left on the ground each time forests are harvested (Grushecky and others 1997, Ares and others 2007). With the increased interests in biofuels, however, harvesting residues may be increasingly sought after for conversion to wood energy. It is therefore important to fully elucidate the role of downed wood in N cycling in our forests. This initial evidence suggests that removal of downed wood and its N immobilization capacity may have important consequences for water quality, among other ecological impacts.

CONCLUSIONS

The results of this study serve as initial evidence of potentially tight N cycling within microbial biomass between C pools in the decomposition matrix of the forest floor. If confirmed, these results may necessitate a change in the way we view N cycling after mineralization from the leaf litter layer. Contrary to current assumptions, N mineralized from foliar litter may not be immediately available to plants.

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