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Decomposition and nitrogen dynamics of 15N-labeled leaf, root, and twig litter in temperate coniferous forests

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Decomposition and nitrogen dynamics of ^{15}N-labeled leaf, root, and twig litter in temperate coniferous forests

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Abstract Litter nutrient dynamics contribute significantly to biogeochemical cycling in forest ecosystems. We examined how site environment and initial substrate quality influence decomposition and nitrogen (N) dynamics of multiple litter types. A 2.5-year decomposition study was installed in the Oregon Coast Range and West Cascades using ^{15}N-labeled litter from *Acer macrophyllum*, *Picea sitchensis*, and *Pseudotsuga menziesii*. Mass loss for leaf litter was similar between the two sites, while root and twig litter exhibited greater mass loss in the Coast Range. Mass loss was greatest from leaves and roots, and species differences in mass loss were more prominent in the Coast Range. All litter types and species mineralized N early in the decomposition process; only *A. macrophyllum* leaves exhibited a net N immobilization phase. There were no site differences with respect to litter N dynamics despite differences in site N availability, and litter N mineralization patterns were species-specific. For multiple litter × species combinations, the difference between gross and net N mineralization was significant, and gross mineralization was 7–20 % greater than net mineralization. The mineralization results suggest that initial litter chemistry may be an important driver of litter N dynamics. Our study demonstrates that greater amounts of N are cycling through these systems than may be quantified by only measuring net mineralization and challenges current leaf-based biogeochemical theory regarding patterns of N immobilization and mineralization.

Keywords Integrated decomposition rate · Litter chemistry · Gross mineralization · Immobilization · Soil

Introduction

The decomposition process is a key component of the biogeochemical nitrogen (N) cycle and represents an important feedback process at both the plant and ecosystem levels. Decomposition influences N availability and is regulated by geochemical and biochemical properties and biological activity in the soil. Thus, site characteristics (e.g., temperature, moisture, soil properties), plant species composition (through litter quality), and microbial activity are important factors influencing ecosystem N dynamics through their effects on decomposition (Hobbie et al. 2000; Hobbie and Vitousek 2000; Meentemeyer 1978; Melillo et al. 1982; Taylor et al. 1989).

A large proportion of the work on nutrient dynamics associated with decomposition has examined senesced leaf litter. From this work, a general pattern of decomposition N dynamics has emerged: leaf litter tends to immobilize N early in the decomposition process and tends to mineralize

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N during later phases of decomposition (Gosz et al. 1973; Hobbie and Vitousek 2000; Parton et al. 2007; Staaf and Berg 1982). However, leaf litter with high initial N concentrations may be an exception to this pattern, mineralizing N early in the decomposition process (Parton et al. 2007).

Comparatively, there is less knowledge available on the decomposition and nutrient dynamics of other litter types (e.g., fine roots and twigs) and the feedbacks that may occur as a result of the decomposition of these litter types. However, there is evidence that fine roots may mineralize N even in the earliest phases of decomposition (Chen et al. 2001, 2002; Dornbush et al. 2002; Parton et al. 2007; Silver et al. 2005), exhibiting an exception to the pattern of immobilization followed by mineralization that is commonly reported for leaf litter. The Chen et al. (2001) study, which had study sites in the Pacific Northwest, hypothesized that woody roots would exhibit a pattern of immobilization followed by mineralization. However, roots in the Chen et al. (2001) study mineralized N even in the early phases of decomposition, indicating that the N dynamics of root decomposition warrant further investigation.

When attempting to identify patterns of N mineralization and quantify the amount of N immobilized or mineralized during decomposition, it is important to distinguish between net and gross N transformations. The rates of N mineralization reported from decomposition studies are generally net rates that do not account for the multiple N transformations taking place (Chen et al. 2002; Hart and Myrold 1996; Parton et al. 2007). Consequently, net N cycling rates may underestimate the total amount of N cycling through an ecosystem. The stable isotope ^{15}N can be used to examine these transformations occurring during the decomposition of litter (Hart and Myrold 1996). This approach can be used to discern simultaneous processes of N immobilization and mineralization and to determine the fate of N mineralized from litter (Zeller et al. 2000, 2001). Further, by using ^{15}N it is possible to distinguish between net and gross transformations of N and account for net and gross fluxes of N within a system. Understanding these processes provides insight into the contributions of decomposing litter to ecosystem N dynamics.

In the study reported here, we used ^{15}N-labeled litter in a field time series study in temperate coniferous forests of western Oregon to examine N dynamics during litter decomposition. More specifically, we evaluated: (1) how site environment and initial litter chemistry influenced mass loss and N dynamics of leaf, fine root, and twig litter; (2) whether N is mineralized from litter in the early phases of decomposition; (3) the degree to which N immobilization and mineralization exist simultaneously during the decomposition process. This analysis of litter decomposition allowed us to re-examine the 'leaf-centric' view of decomposition N dynamics and confirm whether fine root litter mineralizes N in the early phase of decomposition. Further, by using ^{15}N, we were able to quantify both net and gross N mineralization associated with decomposing litter and thus provide a more detailed account of N cycling processes in these forest ecosystems.

Methods

Site description

We conducted this research in the Coast Range (Cascade Head Experimental Forest, 45°12′ N, 123°12′ W) and West Cascades (H. J. Andrews Experimental Forest, 44°12′ N, 122°12′ W) in Oregon. The Oregon Coast Range region has a maritime climate, with a mean annual temperature of 10 °C and a mean annual precipitation of 245 cm. The dominant forest type from the coast to 3 km inland is a mixture of *Tsuga heterophylla* (Raf.) Sarg. (western hemlock) and *Picea sitchensis* (Bong.) Carr. (Sitka spruce) and also includes *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir), *Alnus rubra* Bong. (red alder), and *Thuja plicata* Donn ex. D. Don (western redcedar). Soils are Inceptisols with Andic properties; they are moderately well-drained and high in organic matter and N. The West Cascades also have a maritime climate, with a mean annual temperature of 8.5 °C and a mean annual precipitation of 230 cm at lower elevations and 355 cm at higher elevations. At low elevations, the forests are dominated by *P. menziesii* and *T. heterophylla* (Franklin and Dyrness 1988). Soils are deep, well-drained Andisols. At each site, three plots representative of the site's forest composition were established for the litter decomposition experiment. Plots in the Coast Range were located between 250 and 300 m a.s.l.; plots in the West Cascades were located between 560 and 1,000 m a.s.l.

We sampled the mineral soil at each site in August 2008 to obtain general soil data. After removal of surface litter, four soil cores were collected randomly to a depth of 10 cm from each plot at each site using a 6.7-cm-diameter bulb corer. Two cores from each plot were composited in a polyethylene bag (for a total of six samples for each site) and kept on ice for transport bag to the lab. Prior to analysis, composited samples were sieved (pore diameter 2 mm). The fraction that passed through the sieve (<2 mm) was used for all subsequent soil analyses. Gravimetric soil moisture content was determined by drying a 10-g subsample of soil for 48 h at 105 °C. Bulk density was determined using the excavation method (Elliott et al. 1999).

Extractable NH_4^+–N, NO_3^-–N, total nitrogen (TN) and total carbon (TC) were determined in a 7-g subsample of field-moist soil extracted with 35 mL of 0.5 M K_2SO_4. Samples were shaken for 1 h, allowed to settle

Table 1 Mineral soil properties (depth 0–10 cm) for the Coast Range (Cascade Head Experimental Forest) and the West Cascades (H.J. Andrews Experimental Forest)

Site	Bulk density (g cm^{-3})	DOC (kg ha^{-1})	Extractable NH_4^+-N (kg ha^{-1})	Extractable NO_3-N (kg ha^{-1})	DIN (kg ha^{-1})	DON (kg ha^{-1})	Total C (kg ha^{-1})	Total N (kg ha^{-1})	C:N (mass:mass)
Coast Range	0.32 (0.06)	502 (125)	5.1 (1.8)	0.2 (0.08)	5.4 (1.9)	31.5 (10)	105,128 (18,889)	3,824 (485)	26.7 (1.6)
West Cascades	0.68 (0.05)	426 (135)	0.4 (0.08)	0.03 (0.0001)	0.5 (0.08)	10.7 (1.0)	57,241 (5,460)	1,865 (142)	30.6 (1.4)

DOC dissolved organic carbon, *DIN* dissolved inorganic nitrogen, *DON* dissolved organic nitrogen

Values are presented as the mean with the standard error (SE) in parenthesis ($n = 6$)

for 30 min, and then filtered through pre-rinsed Whatman 42 filter paper (Whatman, New York, NY) in funnels into 20-mL polyethylene scintillation vials. Extracts were analyzed immediately or frozen until analysis. Extracts were analyzed colorimetrically for NH_4^+-N using the salicylate method (QuikChem Method 12-107-06-2-E; Lachat Instruments, Milwaukee, WI) and for NO_3^-–N using the cadmium reduction method (QuikChem Method 12-107-04-1-H; Lachat Instruments). Extracts were analyzed for dissolved organic carbon (DOC) and total dissolved N (TDN) by catalytic oxidation combustion using a Shimadzu TOC-V CSH total organic carbon analyzer with a TNM-1 total N measuring unit (Shimadzu Scientific Instruments, Columbia, MD). Values for dissolved inorganic N (DIN) and dissolved organic N (DON) were obtained by calculation, where DIN is equivalent to the sum of extractable NH_4^+–N and NO_3^-–N, and DON is the difference between TDN and DIN. To analyze soils for TC and TN, subsamples of field-moist soil were dried at 65 °C for 72 h and ground to a powder on a roller mill. Tin capsules were filled with 4 g (Coast Range) or 11 g (West Cascades) of the ground soil and analyzed for TC and TN against an Atropine standard on a Costech ECS-4010 elemental combustion analyzer (Costech Analytical, Valencia, CA). See Table 1 for site mineral soil properties.

Litter decomposition

Two-year-old seedlings of *Acer macrophyllum* Pursh. (bigleaf maple), *P. sitchensis*, and *P. menziesii* were obtained from a local nursery planted in pots of peat. The seedlings were maintained in an open-air greenhouse and fertilized with 6.25 g N m^{-2} using a ^{15}N-labeled NH_4NO_3 (99 atom %) solution, applied four times from May to September 2003. Seedlings and this labeling technique were used to facilitate uniform labeling of plant material, with the aim of obtaining labeled material within a reasonable time frame and because this approach was cost-effective. In addition, this technique could be used by collaborators for a companion study, facilitating comparison of results. Seedlings were harvested, separated into litter types [leaves, fine roots (<2 mm diameter), and twigs (<5 mm diameter)] by species, and the ^{15}N-labeled litter was air-dried. Dried litter was composited for each litter type × species, and 5-g subsamples of a single litter type × species combination were placed in mesh litterbags. Leaf litter subsamples from each species were put in litterbags with 1-mm nylon mesh tops and 55-μm Dacron mesh bottoms. Root and twig litter subsamples were placed in 1-mm nylon mesh litterbags. Subsamples of litter from the seedlings were retained to analyze for moisture content, lignin, total C and N, and ^{15}N.

Litterbags to be collected at a particular date were strung together using a nylon string. Each string held nine (3 litter types × 3 species) litterbags. Two strings for each collection were placed in each plot at each site in May 2004. Litterbags were strung 1 m apart, with the order of the bags on the strings randomized. Those litterbags containing roots were buried at a depth of 10 cm. Litterbags were collected at 0.25, 0.5, 0.75, 1, 1.5, 2, and 2.5 years after initial placement. At each collection, litterbags were carefully cleaned of moss, ingrowing roots, and soil, placed in polyethylene bags, and kept on ice for transport to the laboratory. Litter was then removed from the litterbags, gently brushed free of soil, oven-dried at 65 °C to a constant mass, and weighed. After drying and weighing, replicate litter samples from each plot were composited ($n = 3$) for subsequent analyses.

Dried litter samples were ground to fine powder, following which 6-mg subsamples were weighed into tin capsules and analyzed for total C, N, and ^{15}N using a Thermo Electron gas isotope–ratio mass spectrometer (Thermo Fisher Scientific, Waltham, MA) at the Colorado Plateau Stable Isotope Laboratory. Due to the cost of isotope analysis, only litter subsamples from litterbags collected at 0.25, 1, and 2.5 years were analyzed for total C and N, and ^{15}N. To correct for ash content and determine ash-free litter dry mass (AFDM), 1-g subsamples of dried litter were ashed in a muffle furnace for 4 h at 500 °C. Initial litter samples were dried, ground, and analyzed for total C and N, and ^{15}N as described above. Lignin content of initial samples was assayed using the acid detergent method (Goering and Van Soest 1970) at the University of Nebraska–Lincoln

Table 2 Initial litter chemistry

Litter type	Species	Lignin (%)	C (mg g^{-1} litter)	N (mg g^{-1} litter)	^{15}N (mg g^{-1} litter)	Atom $\%^{15}N$	C:N (mass:mass)	Lignin:N
Leaves	*Acer macrophyllum*	21.3 (0.6)	435 (0.5)	10.0 (0.47)	0.05 (0.0009)	0.53 (0.03)	43.6 (2.1)	21.4 (1.6)
	Pseudotsuga menziesii	20.3 (1.3)	492 (0.9)	13.6 (0.35)	0.07 (0.003)	0.53 (0.01)	36.2 (1.0)	15.0 (1.3)
	Picea sitchensis	17.3 (0.4)	483 (0.7)	13.7 (0.58)	0.08 (0.02)	0.56 (0.08)	35.4 (1.6)	12.7 (0.8)
Roots	*A. macrophyllum*	26.1 (0.8)	469 (3.5)	11.7 (0.70)	0.35 (0.02)	2.90 (0.33)	40.3 (2.7)	22.5 (2.0)
	P. menziesii	35.2 (1.2)	456 (14.5)	10.5 (0.24)	0.19 (0.02)	1.81 (0.18)	43.7 (2.4)	33.7 (1.9)
	P. sitchensis	29.2 (0.5)	465 (0.2)	10.4 (0.95)	0.15 (0.02)	1.49 (0.31)	45.1 (4.1)	28.4 (3.1)
Twigs	*A. macrophyllum*	11.0 (0.9)	461 (0.5)	8.1 (0.38)	0.10 (0.01)	1.25 (0.23)	57.4 (2.8)	13.7 (1.8)
	P. menziesii	23.2 (0.6)	485 (0.4)	8.2 (0.81)	0.08 (0.01)	0.97 (0.08)	59.5 (5.8)	28.4 (2.0)
	P. sitchensis	25.8 (0.1)	492 (2.5)	6.2 (0.001)	0.04 (0.003)	0.58 (0.05)	79.1 (0.4)	41.5 (0.1)

Values are presented as the mean with the SE in parenthesis ($n = 2$)

Soil and Plant Analytical Laboratory. We recognize that the recalcitrant residue classified as lignin by this method may include a variety of polymers; thus, we use 'lignin' as an operational term for litter material that resisted degradation by a strong acid. Initial litter chemistry values are presented in Table 2.

Calculations and statistical analyses

Mass loss is expressed as the proportion of initial litter mass remaining and was calculated using ash-corrected litter mass values. To calculate decomposition rates, the proportion of mass remaining data was transformed to the natural logarithmic scale, resulting in a value of zero for initial mass on the log scale. This value of zero represented the *y*-intercept. Linear regression was used to test whether the intercepts for regression lines fitted to the log-transformed proportion data were significantly different from zero. This intercept test was used to determine whether linear or non-linear regression was appropriate for analyzing the mass loss data and calculating decomposition rate constants. If the intercept of the regression line was significantly different from zero ($P < 0.05$), non-linear regression was used to describe mass loss dynamics. Except for *P. menziesii* root litter, all litter types and species had intercepts significantly different from zero. However, data on *P. menziesii* root litter mass remaining were analyzed using non-liner regression to allow for comparisons across all species and litter types.

Based on the results of the intercept test described above, non-linear regression in the form of a two-pool, double-exponential decomposition model (Wieder and Lang 1982) was used to describe the mass loss dynamics of the decomposing litter. Although the single exponential model (Olson 1963) is widely use to describe decomposition dynamics, a two-pool double-exponential model often better describes decomposition dynamics over a wide range of litter types (Harmon et al. 2009). The regression model used was:

$$\text{percent mass remaining} = F_{slow}e^{-k_{slow}t} + (100 - F_{slow})e^{-k_{fast}t} \quad (1)$$

where F_{slow} is the slowly decomposing litter fraction, k_{slow} ($year^{-1}$) is the decomposition rate of the slow fraction, k_{fast} ($year^{-1}$) is the decomposition rate of the fast fraction, and t is time (years). The fast fraction is equivalent to the model term $100 - F_{slow}$. Mass loss data and the estimates obtained from the double-exponential regression were used to predict integrated k (k_I) values (Harmon et al. 2009). The k_I value represents the k value, or decomposition rate constant, when the litter pool reaches steady-state. This rate thus provides a single value to compare complex decomposition dynamics.

The following equation was used to calculate the ^{15}N isotope ratio of the initial litter:

$$R_{initial} = R_{standard} * \left(\left(\delta^{15}N_{initial} + 1000\right)/1000\right) \quad (2)$$

where $R_{initial}$ is the $^{15}N/^{14}N$ isotope ratio of the initial litter for a given species and litter type, $R_{standard}$ is the isotope ratio of the standard (air, 0.0036765), and $\delta^{15}N_{initial}$ is the measured ^{15}N content of the initial litter for a given species and litter type. The $\delta^{15}N_{initial}$ and calculated $R_{initial}$ values from Eq. 2 were then used to calculate gross N mineralization as follows:

$$\text{Gross N mineralization} = \left(\delta^{15}N_{initial} - {}^{15}N_t\right)/R_{initial} \quad (3)$$

where $^{15}N_t$ is the measured content of a litter sample for a given collection time (0.25, 1, or 2.5 years). Net mineralization was calculated as the difference between initial N content ($N_{initial}$) and N content for a given collection time (N_t):

$$\text{Net N mineralization} = N_{initial} - N_t \quad (4)$$

N immobilization was then calculated as the difference between gross and net mineralization:

$$\text{N immobilization} = \text{Gross N mineralization} - \text{Net N mineralization} \quad (5)$$

Mass loss data, double-exponential parameter estimates, k_1 values, gross N mineralization, net N mineralization, and gross N immobilization were each compared with analysis of variance (ANOVA) to determine the effects of site, litter type, and species on the variables of interest. Results from comparisons of N dynamics indicated no site differences; thus, differences between gross and net N mineralization were tested for significance using a single-sample t test ($\alpha = 0.05$). Initial litter C, N, and lignin content were analyzed using two-way ANOVA with a Tukey adjustment was used for multiple comparisons.

The statistical software package SAS ver. 9.1 (SAS Institute, Cary, NC) was used for all analyses. Prior to analysis, normal probability plots were used to check data distributions for normality and residual plots were used to check for homogeneity of variances. Log transformations were applied when necessary. Results were considered significant at $P < 0.05$.

Results

Initial litter chemistry

Initial chemistry varied among litter types and species (Table 2). All initial chemistry variables except atom % differed significantly with respect to the interaction of litter × species (lignin $F_{4,9} = 42.96$, $P < 0.0001$; N concentration $F_{4,9} = 8.51$, $P = 0.0040$; ^{15}N concentration $F_{4,9} = 18.82$, $P = 0.0002$, C:N $F_{4,9} = 7.23$, $P = 0.0069$; lignin:N $F_{4,9} = 29.12$, $P \leq 0.0001$). Atom %^{15}N differed significantly with respect to litter ($F_{2,9} = 79.05$, $P \leq 0.0001$) and species ($F_{2,9} = 10.28$, $P = 0.0047$).

Mass loss dynamics and decomposition rates

After 2.5 years of decomposition, mass loss ranged from 42 to 69 % for leaves, from 47 to 59 % for roots, and from 33 to 53 % for twigs) (Fig. 1). Due to the significance of multiple interactive effects (site × litter $F_{2,24} = 9.80$, $P < 0.0001$; species × litter $F_{4,24} = 59.58$, $P < 0.0001$; species × litter × time $F_{24,241} = 2.00$, $P = 0.0047$), there were few patterns with respect to the amount or rate of mass loss for litter types or species. For both sites, leaves lost the most mass and twigs lost the least mass. With respect to species, *A. macrophyllum* roots lost the most mass, whereas both *P. menziesii* and *P. sitchensis* leaves exhibited the greatest mass loss after 2.5 years. Differences in mass loss between species were more prominent for leaves than they were for roots or twigs (Fig. 1).

When decomposition rates were fitted with the two-pool model, the two sites did not differ in the proportion of litter mass decomposing in the fast and slow pools or in the decomposition constants associated with these pools (Table 3). However, the proportion of mass in the fast and slow pools differed significantly with respect to litter type ($F_{2,32} = 5.23$, $P = 0.011$), and k_{slow} differed significantly

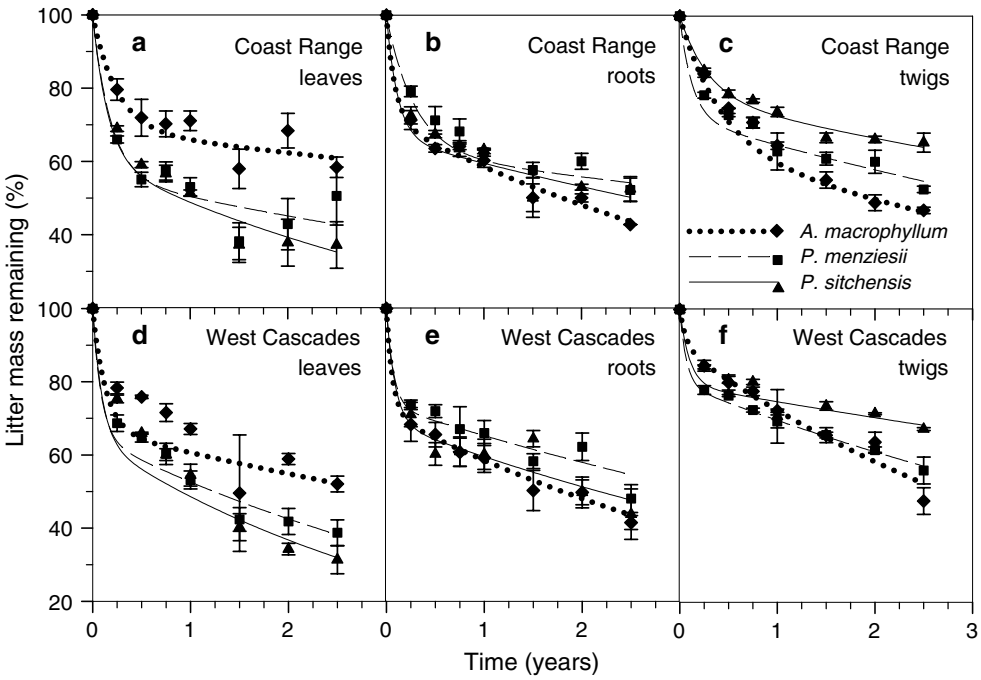

Fig. 1 Mass loss over time and corresponding regression lines of foliage (**a**, **d**), root (**b**, **e**), and twig litter (**c**, **f**) from *Acer macrophyllum* (*filled diamonds*, *dotted line*), *Pseudotsuga menziesii* (*filled squares*, *dashed line*), and *Picea sitchensis* (*filled triangles*, *solid line*) decomposed in temperate coniferous forests in the Coast Range (*top row*, **a–c**) and West Cascades (*bottom row*, **d–f**) of Oregon. *Regression lines* Estimated decomposition (as percentage initial mass remaining over time); these were modeled using the double-exponential regression coefficients in Table 3. *Symbols* means ($n = 3$), *error bars* ±1 standard error (SE)

Table 3 Parameter estimates from the double-exponential regression model used to estimate litter decomposition in temperate coniferous forests in the Coast Range and West Cascades of Oregon and associated integrated k (k_I) values

Site	Litter type	Species	F_{fast} (%)	F_{slow} (%)	k_{fast} (year^{-1})	k_{slow} (year^{-1})	Integrated k_I (year^{-1})
Coast Range	Leaves	*A. macrophyllum*	31 (10.7)	69 (10.7)	4.05 (3.9)	0.05(0.1)	0.07 (0.1)
		P. menziesii	44 (10.7)	56 (10.7)	5.36 (3.9)	0.11 (0.1)	0.18 (0.1)
		P. sitchensis	39 (10.7)	61 (10.7)	6.39 (3.9)	0.22 (0.1)	0.30 (0.1)
	Roots	*A. macrophyllum*	29 (4.6)	71 (4.6)	11.06 (3.6)	0.20 (0.03)	0.27 (0.04)
		P. menziesii	37 (4.6)	63 (4.6)	3.43 (3.6)	0.06 (0.03)	0.08 (0.04)
		P. sitchensis	33 (4.6)	67 (4.6)	8.70 (3.86	0.11 (0.03)	0.16 (0.04)
	Twigs	*A. macrophyllum*	35 (5.8)	65 (5.8)	2.43 (3.1)	0.14 (0.03)	0.17 (0.04)
		P. menziesii	28 (5.8)	72 (5.8)	7.83 (3.1)	0.11 (0.03)	0.14 (0.04)
		P. sitchensis	22 (5.8)	78 (5.8)	3.44 (3.1)	0.078 (0.03)	0.10 (0.04)
West Cascades	Leaves	*A. macrophyllum*	33 (10.7)	67 (10.7)	7.61 (3.9)	0.10 (0.1)	0.13 (0.1)
		P. menziesii	35 (10.7)	65(10.7)	11.36 (3.9)	0.21 (0.1)	0.28 (0.1)
		P. sitchensis	36 (10.7)	64 (10.7)	10.18 (3.9)	0.28 (0.1)	0.34 (0.1)
	Roots	*A. macrophyllum*	29 (4.6)	71 (4.6)	15.40 (3.6)	0.20 (0.03)	0.28 (0.04)
		P. menziesii	27 (4.6)	73 (4.6)	13.67 (3.6)	0.12 (0.03)	0.15 (0.04)
		P. sitchensis	31 (4.6)	69 (4.6)	11.29 (3.6)	0.15 (0.03)	0.21 (0.04)
	Twigs	*A. macrophyllum*	10 (5.8)	90 (5.8)	14.90 (3.1)	0.22 (0.03)	0.24 (0.04)
		P. menziesii	20 (5.8)	80 (5.8)	14.50 (3.1)	0.13 (0.03)	0.16 (0.04)
		P. sitchensis	21 (5.8)	79 (5.8)	10.10 (3.1)	0.06 (0.03)	0.07 (0.04)

The regression model used was percent mass remaining $= F_{slow}e^{-k_{slow}t} + (100 - F_{slow})e^{-k_{fast}t}$, where F_{slow} is the slowly decomposing litter fraction, k_{slow} (year^{-1}) is the decomposition rate of the slow fraction, k_{fast} (year^{-1}) is the decomposition rate of the fast fraction, and t is time (years). The fast fraction is equivalent to the model term $100 - F_{slow}$. The k_I values represent the decomposition rates of steady-state litter pools and were predicted using the double-exponential parameter estimates

Values are presented as the mean with the SE in parenthesis ($n = 3$)

with respect to the litter × species interaction ($F_{4,32} = 2.88$, $P = 0.039$). Integrated k values varied with respect to litter type and species (litter × species: $F_{4,32} = 3.25$, $P = 0.024$), with a distinct difference between the deciduous and coniferous species. For *A. macrophyllum* (deciduous), roots exhibited the largest k_I values, followed by twigs and then leaves. For the two coniferous species, leaves had larger k_I values than roots or twigs. Overall, *P. sitchensis* leaves exhibited the fastest decomposition with respect to k_I.

N dynamics

All litter types and species mineralized N in the early phases of decomposition (Fig. 2). With respect to gross N mineralization (litter × species $F_{4,31} = 27.43$, $P < 0.0001$), *A. macrophyllum* root litter mineralized the most N and leaf litter mineralized the least amount of N; roots mineralized 29 % more N than leaves and 16 % more N than twigs. *P. sitchensis* leaf litter mineralized 37 % more N than root litter and 64 % more N than twig litter. Twig litter from *P. menziesii* mineralized 10 % more N than leaf litter and 24 % more N than root litter (Fig. 2).

Net N mineralization (litter × species $F_{4,31} = 39.51$, $P < 0.0001$) patterns are similar to the gross mineralization patterns. Roots from *A. macrophyllum* mineralized 36 % more N than leaves and 3 % more than twigs. *P. sitchensis* leaves mineralized 18 and 32 % more N than roots and twigs, respectively. Twig litter from *P. menziesii* mineralized the most N, mineralizing16 % more N than leaf litter and 18 % more N than root litter (Fig. 2).

Differences between gross and net mineralization after 2.5 years were significant for *A. macrophyllum* leaf litter ($t_4 = 4.48$, $P = 0.011$) and root litter ($t_5 = 7.47$, $P = 0.001$), *P. sitchensis* leaf litter ($t_5 = 8.24$, $P < 0.0001$), and *P. menziesii* leaf litter ($t_5 = 6.049$, $P = 0.002$) and twig litter ($t_5 = 3.63$, $P = 0.015$). For these litter × species combinations, gross mineralization ranged from 7 to 20 % more than net mineralization. Overall, net mineralization ranged from 30 to 87 % of gross mineralization in our study.

With respect to N immobilization (litter × species: $F_{4,31} = 3.23$, $P = 0.025$), *A. macrophyllum* and *P. sitchensis* demonstrated similar patterns. Leaves of these two species immobilized the most N and twigs immobilized the least amount of N (Fig. 2). *A. macrophyllum* leaves immobilized 5 % more N than roots and 18 % more N than twigs, while *P. sitchensis* leaves immobilized 15 % more N than roots and 31 % more N than twigs. Leaf litter from *P. menziesii* also immobilized the most N; however, in contrast to *A. macrophyllum* and *P. sitchensis*, the root litter from this species immobilized the least amount of N and was similar

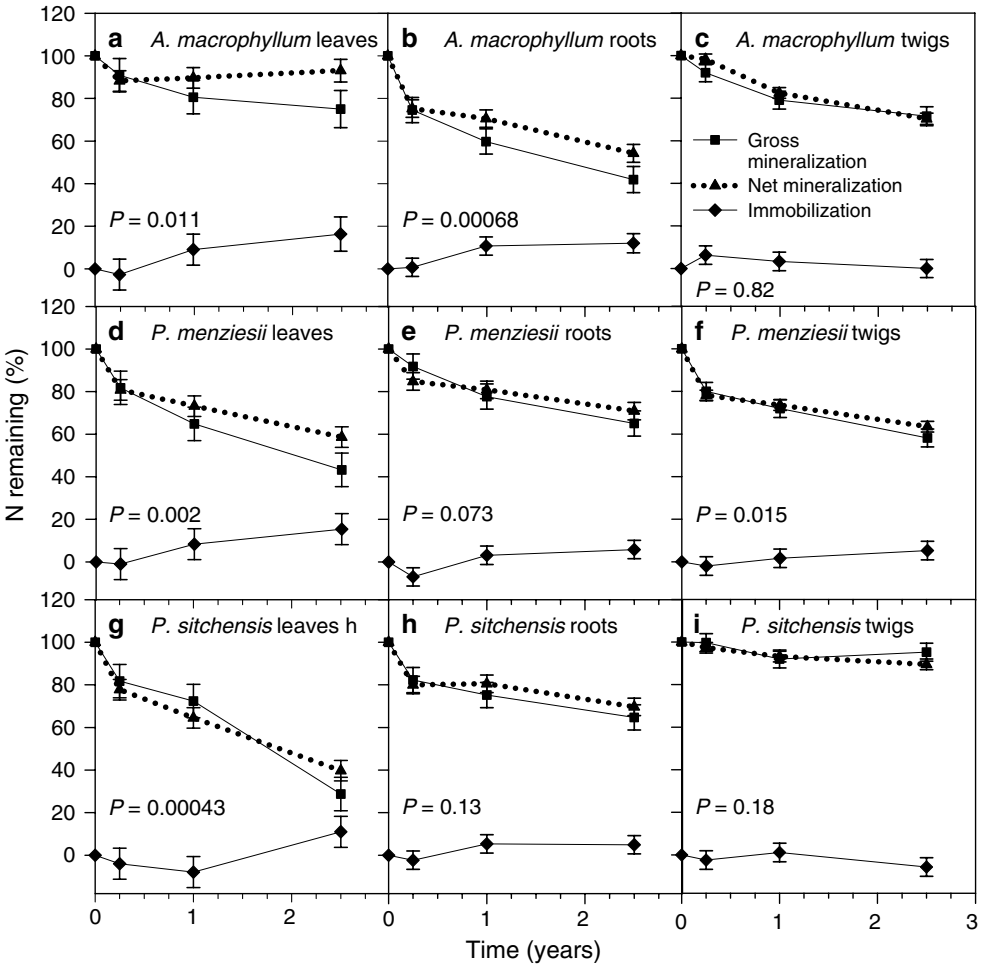

Fig. 2 Gross N mineralization (*filled squares*, *solid line*), net N mineralization (*filled triangles*, *dotted line*), and N immobilization (*filled diamonds*, *solid line*) (as percentage initial N remaining) for foliage (**a**, **d**, **g**), root (**b**, **e**, **h**), and twig litter (**c**, **f**, **i**) from *A. macrophyllum* (*first row*, **a–c**), *P. menziesii* (*second row*, **d–f**), and *P. sitchensis* (*third row*, **g–i**) decomposed in temperate coniferous forests in the Coast Range and West Cascades of Oregon (sites are combined). Statistics are the results from single sample *t* tests on the differences between gross and net N mineralization. *Symbols* means ($n = 6$), *error bars* ± 1 SE

to twig litter. *P. menziesii* leaf litter immobilized 7 and 6 % more N than root and twig litter, respectively. Due to the lack of significant site effects, the data in Fig. 2 are presented for only litter and species.

Discussion

Site versus initial litter chemistry

Our results suggest that site environmental differences were likely not large enough to significantly influence decomposition rates or N mineralization patterns. This confirms results from an earlier fine root decomposition study at these sites (Chen et al. 2002). Climate is often thought of as an important predictor of decomposition rates, particularly for leaf litter (Aerts 1997; Meentemeyer 1978). In contrast, root litter decomposition does not seem to be as affected by climatic differences but more so by initial root chemistry (Chen et al. 2002; Silver and Miya 2001). Thus, it could be that the two sites do not differ enough in climatic attributes to produce measurable differences in decomposition or N mineralization. The West Cascades experience cooler temperatures and more precipitation in the form of snow, but overall the two sites exhibit similar patterns and values for temperature and monthly precipitation. For the duration of this study, mean monthly temperatures differed by <10 °C for the two sites. Additionally, the soil environment could potentially buffer temperature differences. However, this buffering effect would only apply to litter decomposed in buried litterbags. Still, there was little difference between sites for leaves or twigs decomposing aboveground.

In contrast to site environmental differences, initial litter chemistry emerged as a strong driver of both decomposition rates and N mineralization. Initial lignin content is a key predictor of decomposition rates (Aber et al. 1990; Melillo et al. 1982; Staaf and Berg 1982; Taylor et al. 1989). In our study, twigs had the highest lignin content and the lowest decomposition rate (smallest values for k_I), while leaves generally were lowest in lignin and decomposed the fastest (Tables 2, 3). Both of these results were expected given the relationship between lignin content and decomposition rates. Initial lignin content was similarly related to N mineralization patterns, with litter higher in

lignin generally exhibiting less N mineralization. In contrast, litter high in initial N content exhibited greater N mineralization. This finding is consistent with findings from the LIDET study, which determined that global-scale patterns in N immobilization and mineralization for leaf litter were primarily driven by initial N concentrations (Parton et al. 2007). In root litter, initial N concentration also correlates with N mineralization (Chen et al. 2002). In contrast to this study and the LIDET results, data from the Canadian Intersite Decomposition Experiment (CIDET) did not indicate a relationship between initial N concentration and N mineralization for multiple species of leaf litter (Moore et al. 2006). Moore et al. (2006) suggested that the narrow range of initial N concentrations used in CIDET may have constrained the ability to distinguish a relationship between initial N content and N mineralization. However, for a given litter type, the ranges of initial N concentrations for our study were also comparatively narrow, yet a relationship was still found between initial N concentration and N mineralization. The CIDET N mineralization results were presented with respect to initial C:N and acid unhydrolyzable residue:N. However, when presented with respect to litter mass remaining, the CIDET results are similar to both our results and the LIDET results (Parton et al. 2007). Given the range of litter types and species used in LIDET, CIDET, and our study, it seems probable that initial N concentration exerts strong control over decomposition N dynamics during decomposition across multiple ecosystems, litter types, and species.

Litter N mineralization

With the exception of *A. macrophyllum* leaves, all litter types and species mineralized N for the duration of our study and did not exhibit a net N immobilization phase (Fig. 2). For leaf litter, these results contrast with the pattern of a net N immobilization phase preceding N mineralization (Gosz et al. 1973; Hobbie and Vitousek 2000; Parton et al. 2007; Staaf and Berg 1982). In the global analysis of N mineralization based on the LIDET data, N dynamics for leaf litter were modeled as a function of initial N concentration and litter mass remaining, with N concentrations ranging from <0.39 to 1.98 % (Parton et al. 2007). Leaf litter at the higher range of N concentration (1.02 and 1.98 %) exhibited very little—if any—immobilization, but litter at the lower range (<0.395 and 0.58–0.80 %) did exhibit a phase of N immobilization prior to mineralization. Similarly, Prescott et al. (1993) found that multiple litter types high in N exhibited an initial N mineralization phase during decomposition in forests of the Canadian Rocky Mountains. Hobbie et al. (2010) found that decomposing roots with higher initial N concentrations immobilized less N than roots with lower initial N concentrations. We used fresh litter from seedlings, and the initial N concentrations for our leaf litter were intermediate between the upper range values for the LIDET study, indicating that little or no immobilization of N should occur; our immobilization results demonstrated such.

In contrast, results from Perakis et al. (2012) showed that lignin-rich *P. menziesii* leaves covering a narrow range of lignin content and a wide range of N content decomposing in the Oregon Coast Range exhibited a net immobilization phase. However, leaves with a higher initial N content did exhibit less immobilization and more rapid mineralization than leaves with a lower N content. What is interesting is that the initial N concentrations for *P. menziesii* leaves in both our study and that of Perakis et al. (2012) were similar, yet different patterns of N mineralization emerged from the two studies. The lignin content of the *P. menziesii* leaves in our study was lower than that reported by Perakis et al. (2012), suggesting that both higher initial N contents and lower lignin contents (i.e., lower lignin:N ratios) facilitated the rapid mineralization of N we observed. Scott and Binkley (1997) demonstrated that N mineralization is strongly related to the leaf litter lignin:N ratio across multiple forest ecosystems, with mineralization decreasing non-linearly as the lignin:N ratio increases. In the same analysis, higher lignin content also resulted in decreased N mineralization (Scott and Binkley 1997). Our lignin:N ratios (Table 2) fall within the range of the values that facilitate the highest annual net N mineralization, as demonstrated by Scott and Binkley (1997). In addition, higher litter lignin:N ratios generally resulted in less mineralization in our study.

The decomposition of fresh, young leaf litter may result in N dynamics that differ from those observed during the decomposition of litter that has undergone senescence and abscission. During senescence, approximately one-half of the N in leaves is resorbed (Aerts 1996; Killingbeck 1996). In our study we used leaf litter that had double the N concentrations than the senesced litter used in other decomposition studies (e.g., Prescott et al. 2004). Thus, it is not entirely unexpected that the leaf litter in our study would exhibit different patterns of N dynamics (e.g., little to no immobilization) than senesced litter relative to initial litter N concentrations. Further, a study by Prescott (1995) provides evidence that green leaf litter decomposes more rapidly than senesced leaf litter, even if the senesced leaf litter has similar or higher N contents that green litter. Prescott (1995) attributed this to a rapid loss of labile materials. While the litter used in our study may not be representative of litterfall that would occur in a mature temperate conifer forest, we can imagine scenarios (e.g., a disturbance in a young stand) where fresher, younger leaf litter may find its way to the forest floor. Our results demonstrate the potential for litter to decompose without exhibiting a net immobilization phase. The next logical, though more

challenging, step would be to examine decomposition N dynamics using ^{15}N-labeled senesced litter and determine whether this potential is realized.

Although our study compared multiple litter types and species, the results for roots are of particular interest. This is the first study to use ^{15}N to examine N dynamics during fine root decomposition. Up until now, fine root decomposition studies have only examined net N mineralization (Chen et al. 2002; Dornbush et al. 2002; Silver et al. 2005), and the use of ^{15}N has been limited to decomposition studies of leaf litter or lichens (Holub and Lajtha 2003; Zeller et al. 2000, 2001) or to tracer studies to examine N cycling processes and the fate of N cycling through ecosystems (e.g., Holub and Lajtha 2004; Perakis and Hedin 2001; Zeller et al. 2000, 2001). Both the gross and net N mineralization results for roots in our study study (Fig. 2b, e, h) confirm that decomposing fine roots may exhibit rapid mineralization of N in the early phases of decomposition (Chen et al. 2002; Dornbush et al. 2002; Fornara et al. 2009; Silver et al. 2005) and support the notion that patterns of N dynamics during fine root decomposition may differ from patterns commonly observed in leaf litter.

N cycling in forest ecosystems

A large or increasing percentage of net mineralization as a proportion of gross mineralization indicates that microbial N requirements are being met (Hart et al. 1994; Parton et al. 2007). Considering the percentages of net mineralization relative to gross mineralization for litter in the present study, and the relatively rapid onset of net N mineralization overall, it is possible that microbial communities may not be N limited at these two sites and were able to meet their N requirements using only litter-N, rather than immobilizing N from soil N pools. Multiple studies have demonstrated a linear relationship between litter N inputs and net mineralization (Pastor et al. 1984; Perakis and Sinkhorn 2011; Reich et al. 1997; Vitousek 1982). Thus, it seems plausible that net mineralization would be facilitated given our relatively high initial litter N concentrations. With respect to initial N content, net N mineralization from leaf litter in the LIDET study was initiated at C:N values ranging from 31 to 48 (Parton et al. 2007). The leaf and root litter used in our study had C:N values ranging from 35 to 45, and twigs had values ranging from 57 to 79 (Table 2). Thus, the low initial C:N values for leaf and root litter would be expected to facilitate N mineralization, whereas twig litter would be expected to exhibit little if any N mineralization. Our results are consistent with this trend for leaves and roots for all species; however, only *A. macrophyllum* and *P. sitchensis* twigs followed this expected pattern.

Many forests of the Oregon Coast Range do not grow in response to experimental N fertilization and are therefore not considered to be N-limited (Mainwaring et al., in review). Conversely, tight patterns of N cycling in soils in the West Cascades provide indirect evidence that those forests are N-limited (Boyle et al. 2008; Sollins et al. 1980). Estimates of soil N capital for our study (Table 1) indicated twice as much surface soil N in the Coast Range than in the West Cascades, a finding that is consistent with prior reports of differences in the soil C:N ratio and N concentration between the sites (e.g., Hart and Sollins 1998; Sulzman et al. 2005). Soil N capital is linearly related to net N mineralization in western Oregon forests (Perakis and Sinkhorn 2011); however, the lack of site differences with respect to litter N mineralization in our study suggests that N mineralization patterns may be more strongly coupled to initial litter N concentrations than mineral soil N availability, and/or the spatial heterogeneity of soils failed to reflect twofold differences in soil N between the sites with respect to soil N influences on litter N mineralization. Prescott et al. (1993) found that N availability in the forest floor did not affect the rate of N mineralization from a standard litter substrate decomposed at different sites in Rocky Mountain coniferous forests. In Hawaii, litter decomposed at sites where N is either limiting (Thurston site) or non-limiting (Kauai site) to annual net primary productivity immobilized N; increasing soil N by fertilization further stimulated immobilization (Hobbie and Vitousek 2000). In the same study, litter decomposed at the Laupahoehoe site (limited by N and phosphorus together), exhibited net mineralization of N (Hobbie and Vitousek 2000). Perakis et al. (2001) found that *P. menziesii* litter exhibited the strongest N immobilization in N-fertilized plots in the Oregon Coast Range. Thus, while there is evidence that soil N availability may affect litter N mineralization, the direction and magnitude of this effect may be mediated by initial litter N concentration.

Conclusion

Our study confirms that decomposing fine roots mineralize N even in the earliest phases of decomposition and that initial N concentration is an important factor in determining whether N will be mineralized or immobilized during the decomposition process. We have also confirmed that it is possible for leaf litter to decompose without exhibiting a net N immobilization phase. Finally, we have demonstrated that net N mineralization may represent a large percentage of gross N mineralization and that this may be similar to what occurs in some soils.

The true biogeochemical imprint of the patterns of N mineralization observed in our study will largely depend upon the fate of the mineralized N. This will generally be determined by how tightly N is cycled in these systems.

More specifically, N retention mechanisms (e.g., plant uptake or adsorption on to soil particles) and N loss mechanisms (e.g., leaching) will influence the fate of this N. As for decomposition, these mechanisms are regulated by multiple factors that interact at multiple spatial and temporal scales and which contribute to the complexity of the N cycle in forest ecosystems. Additional studies highlighting decomposition using ^{15}N-labeled litter could elucidate the spatial and temporal partitioning of N mineralized from decomposing litter. Finally, this study highlights the importance of both above- and belowground processes and community composition in regulating ecosystem N cycling. While abiotic factors such as temperature and precipitation may be important drivers of N cycling via the process of decomposition, biotic factors are arguably as important and may act as more proximate controls on N cycling by regulating above- and belowground litter chemistry. This interplay between abiotic and biotic factors has implications for how we think about and assess potential effects of global change on N cycling and requires that we consider these effects within an integrated framework that accounts for the multiple factors that regulate the N cycle.

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Conflict of interest None.

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