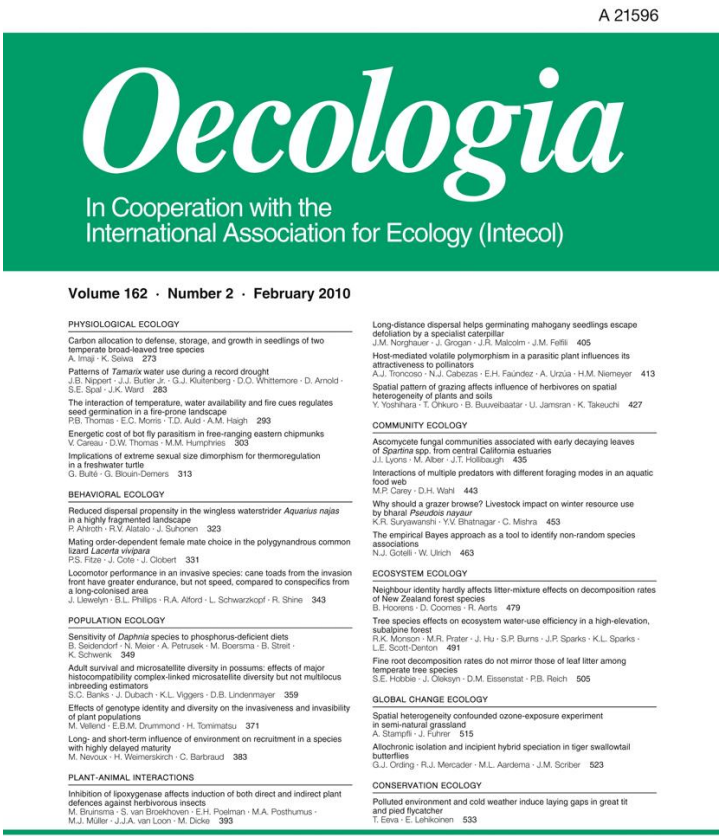
ISSN 0029-8549, Volume 162, Number 2



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Oecologia

In Cooperation with the
International Association for Ecology (Intecol)

Volume 162 · Number 2 · February 2010

Springer

Oecologia (2010) 162:505–513
DOI 10.1007/s00442-009-1479-6

ECOSYSTEM ECOLOGY - ORIGINAL PAPER

Fine root decomposition rates do not mirror those of leaf litter among temperate tree species

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Received: 11 September 2008 / Accepted: 2 October 2009 / Published online: 31 October 2009

Abstract Elucidating the function of and patterns among plant traits above ground has been a major research focus, while the patterns and functioning of belowground traits remain less well understood. Even less well known is whether species differences in leaf traits and their associated biogeochemical effects are mirrored by differences in root traits and their effects. We studied fine root decomposition and N dynamics in a common garden study of 11 temperate European and North American tree species (*Abies alba*, *Acer platanoides*, *Acer pseudoplatanus*, *Carpinus betulus*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*, *Pseudotsuga menziesii*, *Quercus robur*, *Quercus rubra* and *Tilia cordata)* to determine whether leaf litter and fine root decomposition rates are correlated across species as well as which species traits influence microbial decomposition above versus below ground. Decomposition and N immobilization rates of fine roots were unrelated to those of leaf litter across species. The lack of correspondence of above- and belowground processes arose partly because the tissue traits that influenced decomposition and detritus N dynamics different for roots versus leaves, and partly because influential traits were unrelated between roots and leaves across species. For example, while high hemicellulose concentrations and thinner roots were associated with more rapid decomposition below ground, low lignin and high Ca concentrations were associated with rapid aboveground leaf decomposition. Our study suggests that among these temperate trees, species effects on C and N dynamics in decomposing fine roots and leaf litter may not reinforce each other. Thus, species differences in rates of microbially mediated decomposition may not be as large as they would be if above- and belowground processes were working in similar directions (i.e., if faster decomposition above ground corresponded to faster decomposition below ground). Our results imply that studies that focus solely on aboveground traits may obscure some of the important mechanisms by which plant species influence ecosystem processes.

Keywords Ecosystem processes · Nitrogen dynamics · Plant traits · Species effects · Forest

Communicated by Christian Koerner.

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Introduction

While the past decade has seen a flurry of research on patterns and functioning of aboveground plant traits (e.g., Díaz et al. 2004; Güsewell 2004; McGroddy et al. 2004; Reich and Oleksyn 2004; Wright et al. 2004), how the patterns, functioning, and ecosystem consequences of belowground traits relate to those of aboveground traits is unclear. Conceptual frameworks relating plant traits to ecosystem processes and how plant species might differ in their effects on those processes have been based largely on observations of aboveground traits (Aerts and Chapin

2000; Hobbie 1992; Vitousek 1982). Whether belowground traits fit within that framework is less well known.

Evolutionarily, there is reason to believe that selection might cause roots and leaves to be correlated with one another across species in terms of key traits that influence ecosystem processes. For example, low soil fertility might select for efficient use of nutrients in both roots and leaves, leading to leaves and roots with low nutrient concentrations and low turnover (Withington et al. 2006; Reich et al. 2003b; Aerts and Chapin 2000; Chapin 1980; Grime 1977). Because these traits in turn influence ecosystem processes such as decomposition and nutrient cycling (Cornwell et al. 2008), similar traits above and below ground could lead to divergent species effects on these processes.

Evidence for correlated suites of aboveground and belowground traits across plant species is mixed. Plant species that are adapted to infertile soils generally have nutrient-poor, long-lived leaves (Aerts and Chapin 2000; Reich et al. 1992), and slow growth rates (Reich et al. 1992; Chapin 1980). Similarly, such species have low investment in nutrient absorption capacity per unit mass of root, and presumably relatively low root protein content (Chapin 1980), which in turn has been linked to greater root longevity (Eissenstat et al. 2000; Withington et al. 2006). Indeed, among forbs and grasses, leaf and root N are positively related, while other chemical and morphological traits are not (Craine et al. 2005). Yet, in a common garden study of temperate trees, leaf and root lifespan were not related (Withington et al. 2006), indicating that understanding of leaf-root trait relationships is still incomplete.

Because belowground productivity can be of similar magnitude to foliar productivity (e.g., Norby et al. 2004), understanding above- and belowground trait relationships could be important for understanding the strength of species effects on ecosystem processes such as decomposition, that are influenced by these traits. For example, if high detritus lignin or low detritus N concentration is associated with slower decomposition above and below ground, then correlations among these traits between leaf litter and roots should strengthen the differences among species in decomposition.

On the other hand, leaf litter and root decomposition might show little correspondence (among species) for several reasons. First, even if the same traits influence ecosystem processes above and below ground, there might not be a correspondence of values of these traits in leaf litter and fine roots (i.e., a species with high values of a key trait in leaf litter may not have a high value for the same trait in roots). Second, environmental differences above versus below ground could overwhelm tissue chemistry effects on decomposition. Third, if different traits are important for decomposition above versus below ground, species are not likely to differ in parallel for all of these traits (i.e., species with leaf litter traits that lead to fast decomposition will not necessarily have different kinds of traits in their fine roots that also lead to fast decomposition). Such differences in trait importance could arise because of different community composition and therefore different nutritional requirements of decomposers above versus below ground.

We compared fine root (<2 mm diameter) and leaf litter decomposition in a common garden of temperate tree species in southwestern Poland, focusing on 11 gymnosperm and angiosperm taxa. We focused on fine roots because with their more rapid turnover rates (Eissenstat et al. 2000; Gill and Jackson 2000; Guo et al. 2008; Wells and Eissenstat 2001; Anderson et al. 2003) compared to coarse roots, fine roots can dominate total tree root productivity. They also represent a substantial proportion of total net primary productivity. For example, for these tree species, fine root productivity (and presumably detritus inputs) in the top 15 cm of soil averaged 30% of aboveground litterfall (unpublished root ingrowth data), so fine roots should contribute substantially to influencing the strength of tree species effects on decomposition. Our objectives were to determine: (1) whether rates of leaf litter and fine root decomposition are correlated among tree species, and (2) whether such correlations are driven by similarities in traits that influence decomposition rates of leaf litter versus fine roots. Lack of correspondence between leaf litter and root decomposition could arise because either: (1) the same plant traits influence leaf litter and root decomposition, but there is little relationship between above- and belowground traits; or (2) species traits above ground are related to those below ground, but different traits influence above- versus belowground decomposition.

Materials and methods

Experimental setup

We compared decomposition rates of fine roots decomposing in a common site among species and to previously published leaf litter decomposition rates (Hobbie et al. 2006) for tree species in southwestern Poland. Briefly, the source of fine roots and leaf litter used in the study was a common garden of 14 European and North American tree species established in 1970–1971 at the Siemianice Experimental Forest near Biadaszki, Poland (51°14.87′N, 18°06.35′E, elevation 150 m, mean annual temperature 8.2°C, mean annual precipitation 591 mm). Monospecific plots (20 × 20 m) were established of Scots pine (*Pinus sylvestris* L.), silver birch (*Betula pendula* Roth.), European hornbeam (*Carpinus betulus* L.), Austrian black pine

(*Pinus nigra* Arn.), red oak (*Quercus rubra* L.), silver fir (*Abies alba* Mill.), European beech (*Fagus sylvatica* L.), sycamore (*Acer pseudoplatanus* L.), Norway maple (*Acer platanoides* L.), small-leafed lime (*Tilia cordata* Mill.), Norway spruce [*Picea abies* (L.) Karst.], European larch (*Larix decidua* Mill.), Douglas fir (*Pseudotsuga menziesii* Franco), and English oak (*Quercus robur* L.). Plots were set up in two blocks (nine species per block, three replicate plots per species) with four species (*Picea*, *Larix*, *Pseudotsuga* and *Q. robur*) grown in both blocks (six replicates per species). Further details regarding plot establishment and soil structure and chemistry are given in Reich et al. (2005) and Hobbie et al. (2006, 2007).

We established a root decomposition study using fine roots collected in 2002 in eight cores per plot (4.7 cm diameter, 15 cm depth). We used fresh roots to compare with leaf litter in our decomposition analysis because there is no evidence that roots senesce, abscise, and are shed discretely the way that leaves do and are. Rather, roots gradually lose function as they age (Eissenstat and Volder 2004) and are colonized by saprotrophic fungi while still living (Resendes et al. 2008). Therefore, the difference between a live root and a decomposing root represents a continuum, making it impossible to collect dead roots that have not already begun to decompose or for which the stage of decomposition can be controlled. We recognize that there is no perfect solution for comparisons of root and leaf litter decomposition, and opted to use fresh roots because they best represent roots that have not yet begun to decompose. Roots were sieved, dried (65°C), and sorted into the <2-mm fraction. We constructed root decomposition bags using 10 × 5-cm polyester mesh bags (50-μm mesh; Ankom Technology, Macedon, N.Y.). Approximately 0.5 g of root material was placed into the bag, which was heat-sealed 5 cm from one end of the bag, creating a 5 × 5-cm enclosure.

Bags were deployed on 14 May 2003, into an arbitrarily chosen common site, one of the plots dominated by *A. pseudoplatanus*, by inserting them vertically into a 10-cm-deep slit in the mineral soil. Three bags containing root material from a given source plot (three to five replicate source plots per species, see below) were deployed in the common site to allow three harvests, in July and October 2003 and in October 2004 (total experiment duration = 510 days). Upon harvest, roots were removed from bags, dried (65°C), weighed, ground and milled, and analyzed for N as above. The proportion of initial N at each harvest date was calculated by multiplying root N concentration by root mass and comparing it to the initial root N pool.

We could not collect sufficient root biomass from some plots to prepare root decomposition bags from all plots. Therefore, the realized replication was $n = 3$ source plots, except for *Picea abies*, *Q. robur*, and *Pseudotsuga menziesii* ($n = 5$) and *L. decidua* ($n = 4$). We excluded three species altogether (*B. pendula, Pinus sylvestris and Pinus nigra*) from the experiment because of insufficient root mass from any of those source plots.

A subsample of fine roots used from each source plot for the decomposition study was ground and analyzed for: (1) C fractions (Van Soest 1994) on an ANKOM fiber analyzer (Ankom Technology; cell solubles, hemicellulose plus bound protein, cellulose, and lignin plus other recalcitrants, determined on an ash-free dry mass basis); (2) P, Ca, K, Mg, and Mn by ICP (Applied Research Laboratory 3560) following digestion in 10% HCl (Munter and Grande 1981) at the University of Minnesota's Research Analytical Laboratory; and (3) C and N on a Costech ECS4010 element analyzer (Costech Analytical, Valencia, Calif.) at the University of Nebraska, Lincoln. Means and coefficients of variation for chemical parameters across all plots in the common garden were reported previously in Hobbie et al. (2007); however, the species-level data presented here have not been previously published.

Statistical analyses

We fit the proportion of initial mass remaining over time to single exponential, double exponential, and asymptotic decomposition models (Wieder and Lang 1982) using nonlinear modeling in JMP 7.0 (SAS Institute) and combining all replicates of a species. Double exponential models were unable to describe the root decomposition results without having biologically unrealistic parameters (and even in those instances, the models were poor fits to the data), whereas both single exponential and asymptotic models fit the results. As our temporal resolution (four time points) was too low to distinguish between these models, we present parameters from both. For the single exponential model, $X = e^{-k_s t}$, X is the proportion initial mass remaining at time t and k_s is the exponential decomposition rate. For the asymptotic model, $X = A + (1 - A)e^{-k_a t}$, A is the fraction of the initial mass whose decomposition rate is zero (the asymptote) while the remaining fraction $(1 - A)$ decomposes at rate k_a. Note that these models constrain the proportion of initial mass remaining at time zero to be 1.

We compared k_s, k_a, A, and the maximum N immobilized by decomposing roots to initial root chemical characteristics and to morphological characteristics reported in Withington et al. (2006; specific root length, root diameter, and root tissue density) using bivariate linear regressions. Additionally, we compared rates of belowground fine root decomposition in this study with rates of aboveground leaf litter decomposition measured for the same species in the same common site (one of the

plots dominated by *A. pseudoplatanus*) during an overlapping time period (Hobbie et al. 2006). Leaf litter and fine roots used in decomposition studies were collected from the same source plots. Although they were collected in different years (1998–1999 versus 2002, respectively), relative differences among species should not have changed significantly. Hobbie et al. (2006) measured leaf litter decomposition rates in litter bags on the soil surface with five harvests over a 675-day period beginning in November 2002. Their first, second, third, and fifth (last) harvest dates correspond to the deployment, and first, second, and third (last) harvest dates, respectively, of this study. Because Hobbie et al. (2006) used linear models with ln-transformed data to obtain exponential decomposition rate constants, we reanalyzed those data to obtain decomposition rates using nonlinear modeling to compare directly with fine root decomposition rates obtained in this study. Decomposition rates obtained using nonlinear and linear models were highly correlated with one another ($r = 0.91$, $P < 0.0001$) and use of linear data did not substantively influence the results of our comparison. Both the leaf litter bags and root decomposition bags excluded earthworms, an important processor of detritus in this system (Hobbie et al. 2006), so our above- versus belowground decomposition comparison applies only to microbially mediated decomposition. Furthermore, because this study focused on fine root and leaf litter decomposition measured in a common site, we restrict our comparison of species effects on decomposition to those caused by interspecific variation in substrate quality, rather than those caused by species effects on the decomposition environment. Understanding the latter would require decomposing the suite of substrates under the canopies of each of the tree species studied, which was beyond the scope of the present study.

Results

Asymptotic models of fine root decomposition provided a better fit (R^2, actual vs. modeled: mean = 0.64, median = 0.65, range = 0.39–0.76) than single exponential decomposition models (R^2, actual vs. modeled: mean = 0.54, median = 0.52, range = 0.26–0.74). This occurred because most species exhibited initially rapid rates of fine root mass loss (k_a between 1.56–3.32 year^{-1}) followed by rates of decomposition that approached zero with 0.58–0.80 of the initial mass remaining (Table 1). Moreover, decomposition constants (k_s) obtained by fitting a single exponential decomposition model were tightly negatively correlated with the asymptotes (A) determined by fitting the asymptotic model ($r = -0.94$, $P < 0.0001$), i.e., a faster exponential decomposition rate corresponded to a lower fraction of initial mass remaining whose decomposition rate was effectively zero.

Q. rubra, *L. decidua*, and *P. menziesii* exhibited the slowest and *C. betulus*, *F. sylvatica*, and *T. cordata* the fastest rates of fine root decomposition according to both models (Table 1). Angiosperms and gymnosperms did not differ significantly from one another in k_s ($t_{1,9} = 1.33$, $P = 0.22$). However gymnosperms tended towards higher A (0.68 vs. 0.78, $t_{1,9} = -2.13$, $P = 0.06$) and had significantly greater k_a (2.98 vs. 1.91, $t_{1,9} = -4.91$, $P = 0.003$) than angiosperms.

Few initial chemical (Table 2) and morphological fine root characteristics (Withington et al. 2006) were related to decomposition dynamics. Initial hemicellulose concentrations were positively related to k_s ($r = 0.61$, $P = 0.05$) and negatively related to A ($r = -0.63$, $P = 0.04$), i.e., higher hemicellulose concentrations were associated with more rapid rates of fine root decomposition. Initial fine root concentrations of soluble cell contents were positively related to k_a ($r = 0.65$,

Table 1 Parameters obtained from fitting fine root decomposition data over 2 years to single exponential and asymptotic decomposition models and maximum rates of N immobilization by decomposing fine roots for each tree species (means with SE)

Species	Single exponential model k_s (year^{-1})	Asymptotic model		Maximum N immobilization (mg N g^{-1} initial litter)
		A (proportion initial mass remaining)	k_a (year^{-1})	
Abies alba	0.24	0.75	3.32	1.60 (0.00)
Acer platanoides	0.23	0.75	2.57	4.22 (0.59)
Acer pseudoplatanus	0.23	0.72	1.74	1.71 (0.83)
Carpinus betulus	0.30	0.67	1.99	2.28 (0.57)
Fagus sylvatica	0.30	0.63	1.35	−1.01 (1.19)
Larix decidua	0.20	0.78	2.58	2.46 (0.84)
Picea abies	0.29	0.72	3.31	2.17 (0.58)
Pseudotsuga menziesii	0.18	0.80	2.69	2.23 (0.91)
Quercus robur	0.29	0.66	1.56	1.84 (0.32)
Quercus rubra	0.20	0.77	2.31	2.37 (0.57)
Tilia cordata	0.40	0.58	1.85	3.03 (0.49)

Table 2 Initial fine root chemistry (means with SE) for 11 species grown in a common garden experiment

Species	C:N	Initial root nutrients (mg element g^{-1} root)						Initial root C fractions (mg compound g^{-1} ash-free dry mass)				Ash (mg g^{-1} root)
		N	Ca	K	Mg	Mn	P	Cell solubles	Cellulose	Hemicellulose	Lignin	
Abies alba	56.3 (9.0)	8.6 (1.3)	5.9 (0.9)	1.8 (0.8)	1.3 (0.3)	0.4 (0.0)	1.4 (0.3)	406.2 (29.1)	174.3 (10.6)	78.3 (3.7)	341.2 (14.8)	27.5 (4.5)
Acer platanoides	76.2 (1.5)	6.1 (0.2)	7.6 (0.9)	3.0 (0.2)	1.6 (0.2)	0.7 (0.0)	1.1 (0.2)	273.6 (5.7)	262.2 (8.7)	106.4 (3.6)	357.8 (1.3)	36.2 (9.6)
Acer pseudoplatanus	56.6 (6.9)	8.5 (1.2)	7.4 (0.8)	1.6 (0.3)	1.5 (0.1)	0.5 (0.03)	1.1 (0.1)	268.2 (0.4)	228.5 (5.3)	77.0 (1.1)	426.3 (4.5)	32.1 (1.7)
C. betulus	68.6 (3.8)	6.9 (0.4)	3.5 (0.6)	1.5 (0.1)	1.2 (0.1)	0.5 (0.1)	1.1 (0.1)	349.4 (12.2)	217.9 (10.7)	84.9 (1.9)	349.5 (0.4)	13.4 (3.3)
F. sylvatica	51.5 (6.4)	9.5 (1.2)	5.6 (0.2)	1.7 (0.2)	1.2 (0.1)	0.5 (0.0)	1.3 (0.1)	274.0 (11.9)	222.6 (24.0)	92.9 (9.0)	410.6 (39.1)	39.9 (13.8)
L. decidua	54.7 (2.8)	8.5 (0.4)	4.9 (0.5)	1.0 (0.2)	1.2 (0.1)	0.4 (0.0)	1.2 (0.1)	344.1 (13.6)	235.0 (4.6)	90.6 (0.6)	331.2 (9.3)	20.2 (4.7)
Picea abies	53.3 (6.2)	9.0 (1.0)	4.6 (0.5)	1.4 (0.2)	1.0 (0.1)	0.7 (0.1)	1.4 (0.1)	364.2 (37.7)	205.4 (8.8)	87.8 (1.9)	343.7 (44.1)	59.4 (28.6)
Pseudotsuga menziesii	54.8 (5.2)	8.7 (0.8)	5.0 (0.5)	1.0 (0.1)	1.1 (0.1)	0.3 (0.1)	1.2 (0.1)	346.5 (8.1)	200.0 (8.8)	65.3 (6.3)	389.3 (7.0)	39.4 (12.6)
Quercus robur	63.1 (4.6)	8.1 (0.7)	4.4 (0.4)	2.0 (0.1)	1.3 (0.0)	0.3 (0.1)	1.3 (0.0)	345.6 (12.1)	171.7 (11.8)	114.7 (3.4)	369.1 (8.3)	28.1 (12.6)
Quercus rubra	91.9 (6.1)	5.4 (0.4)	4.3 (0.5)	1.8 (0.2)	1.7 (0.1)	0.4 (0.1)	1.6 (0.1)	296.5 (7.0)	160.9 (9.6)	66.0 (2.7)	478.5 (7.2)	14.2 (3.6)
T. cordata	99.7 (1.4)	4.8 (0.1)	6.7 (0.4)	2.3 (0.2)	1.2 (0.0)	0.3 (0.0)	1.1 (0.0)	269.7 (12.0)	255.7 (8.9)	105.3 (7.7)	369.8 (4.4)	27.3 (9.0)

All C and nutrient fractions were analyzed as concentrations in dry tissue by mass

$P = 0.03$), likely because soluble compounds are both readily leached and represent a labile energy source to decomposers. Of the morphological characteristics that we considered, specific root length (SRL; length per unit mass, cm g^{-1}) of first- and second-order roots was weakly negatively related to A ($r = -0.63$, $P = 0.07$) and strongly negatively related to k_a ($r = -0.83$, $P = 0.006$). Among the species studied, those with higher SRL had slower initial rates of decomposition rate, but their roots decomposed more quickly in the long term, as their decomposition rate approached zero at a lower proportion mass remaining. This relationship between decomposition and SRL (which can be expressed as the inverse of root tissue density multiplied by π and the square of root radius) arose because of effects of root diameter, rather than root density, on decomposition. Thinner roots decomposed more slowly than thicker ones initially, but more quickly than thicker ones in the long run: diameter of first- and second-order roots was positively related to both A ($r = 0.67$, $P = 0.05$) and k_a ($r = 0.80$, $P = 0.009$), while decomposition was unrelated to tissue density of first- and second-order roots.

k_s of leaf litter (Hobbie et al. 2006) was unrelated to fine root k_s ($r = -0.07$, $P = 0.84$), A ($r = 0.07$, $P = 0.83$), and k_a ($r = -0.13$, $P = 0.70$) among species (Fig. 1). Also, k_s was not consistently larger or smaller for roots compared to leaf litter (paired t-test, $P = 0.72$). Similarly, initial leaf litter and fine root chemical and morphological characteristics mostly were unrelated to one another (among species) with two exceptions: (1) K and Ca concentrations were positively correlated between leaf litter and fine roots, and (2) SRL of first- and second-order roots was positively related to specific leaf area (area per unit mass, cm^2 g^{-1}; data from Withington et al. 2006; Table 3). Although mean decomposition rates across all species did not differ between leaf litter and roots, root decomposition was more variable. The SDs among replicate source plots for fine root mass remaining at the final harvest were greater than for leaf litter mass remaining at the comparable time point (paired t test, $P = 0.0021$).

The maximum amount of N immobilized into decomposing fine roots differed significantly among species (Table 1; one-way ANOVA, $P = 0.03$) with roots of all species exhibiting immobilization except for those of *F. sylvatica*. The maximum amount of N immobilized was negatively correlated with the initial N concentration of roots ($r = -0.65$, $P = 0.03$), with N-rich roots exhibiting less immobilization than roots with low initial N concentrations. The maximum amount of N immobilized by decomposing fine roots was unrelated to that immobilized by decomposing leaf litter (Hobbie et al. 2006) across species ($r = -0.06$, $P = 0.87$).

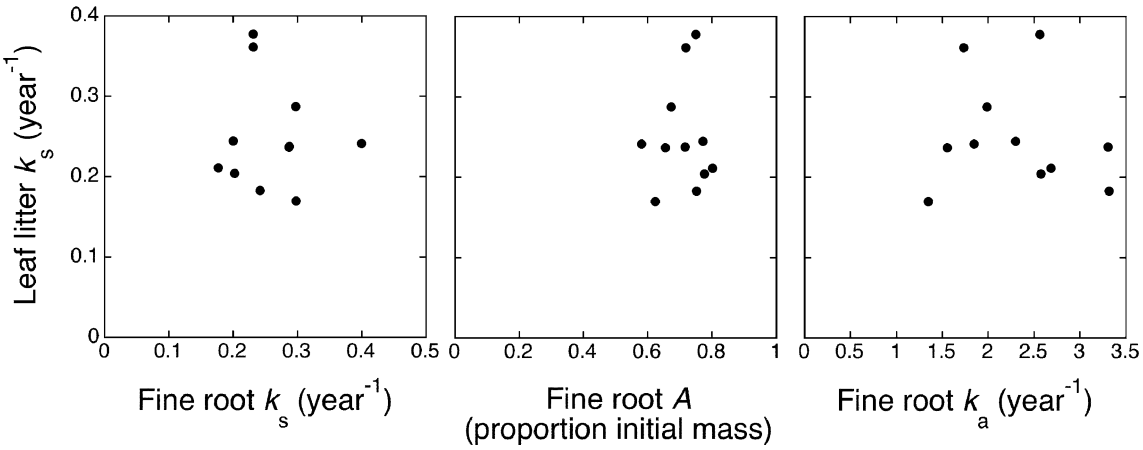

Fig. 1 The relationships between decomposition rates of leaf litter versus fine roots. Exponential decomposition rates of leaf litter were calculated using data from Hobbie et al. (2006). Fine root decomposition data from between three and five plots per species were combined by species and fit to either a single exponential decomposition or to an asymptotic model, where k_s is the exponential decomposition rate, A is the fraction of the initial mass whose decomposition rate is zero (the asymptote), while the remaining fraction of the initial mass ($1 - A$) decomposes at rate k_a. Each point represents one of 11 temperate tree species

Table 3 Correlations between fine root and leaf litter traits

Fine root versus leaf litter trait comparison[a]	Correlation coefficient	*P*
Cell solubles	−0.13	0.71
Hemicellulose	0.27	0.43
Cellulose	−0.46	0.16
Lignin	−0.24	0.48
N	0.01	0.98
P	−0.27	0.42
K	**0.62**	**0.04**
Ca	**0.86**	**0.0006**
Mg	0.40	0.22
Mn	0.09	0.80
SRL versus SLA[b]	**0.69**	**0.04**

$P < 0.05$ indicated in *bold*

SRL Specific root length, *SLA* specific leaf area

[a] Leaf litter chemical traits from Hobbie et al. (2006)

[b] *SRL* and *SLA* from Withington et al. (2006)

Discussion

Leaf litter versus fine root decomposition

Among 11 temperate tree species, we found little correspondence between microbially mediated decomposition rates of leaf litter and fine roots. We know of no other study that has compared above- and belowground decomposition among so many species. Although Vivanco and Austin (2006) measured fine root and leaf litter decomposition on ten grassland species, they did not present correlations between them. An analysis of their ranked data indicates no significant correlation (analysis not shown, although the number of observations is low for a ranked correlation). In contrast to other studies, in our study roots did not decompose consistently faster or slower than leaf litter. Past studies have found that roots decompose more slowly (Vivanco and Austin 2006) and more quickly (Ostertag and Hobbie 1999) than leaf litter in comparisons among species or ecotypes. Our results suggest that these patterns may not be general across a large number of species.

The lack of correspondence between fine root and leaf litter decomposition among species arose partly because different traits influenced decomposition above and below ground and partly because traits important to decomposition showed little similarity among species for leaf litter versus fine roots. Decomposition rates of leaf litter of the same 11 tree species in the same plots over the same time period were negatively correlated with initial lignin and positively correlated with initial cell soluble and Ca concentrations (Hobbie et al. 2006; the independent effects of lignin versus soluble cell contents were not distinguishable because their concentrations were so tightly negatively correlated with each other). Neither lignin nor Ca was a significant predictor of fine root decomposition. Rather, fine root decomposition was influenced by root diameter (but the effects differed between the early and later stages of decomposition) and was faster for roots with high hemicellulose and cell soluble concentrations. Thus, the traits that significantly predicted species variation in decomposition rates differed in part for fine roots and leaf litter: while aspects of initial C chemistry were important for both, morphology was uniquely important for root decomposition and Ca for leaf litter decomposition.

These results contrast with those of other studies showing significant positive relationships between root Ca

and N concentrations and fine root decomposition at a global scale (Silver and Miya 2001). However, among the species studied here, initial root Ca ranged from 3.5 to 7.6 mg g^{-1} (Hobbie et al. 2007), while root Ca in the Silver and Miya (2001) study varied by several orders of magnitude. Similarly, initial root C:N ratios ranged from 52 to 100 among the species in this study, while those reported by Silver and Miya (2001) encompassed a 50-fold greater range (i.e., C:N ratio varied by 2 orders of magnitude). Thus the lack of relationships between root chemical parameters and root decomposition may reflect the relatively limited variation in root chemistry among the tree species studied here. In addition, because Silver and Miya (2001) synthesized data from a number of studies, some of the differences among species in root chemistry and associated differences in decomposition may have arisen from methodological differences or from site effects on both root chemistry and decomposition, rather than solely from inherent differences among species in tissue quality.

The lack of correspondence between some aspects of root chemistry (initial lignin, N, Ca) and root decomposition in this study may also reflect greater variability within a species for root compared to leaf litter decomposition, perhaps because the belowground environment is more variable than the aboveground environment in terms of microclimate or soil biota or because bulk fine roots <2 mm include a heterogeneous mixture of roots that vary in their chemical and morphological characteristics. For example, different root orders vary chemically and morphologically (Withington et al. 2006, Pregitzer et al. 2002), and the relative contribution of different orders to roots <2 mm varies among species. Thus, relationships between root chemistry and root decomposition might become apparent in decomposition studies that resolve roots more finely (e.g., by order or size). Indeed, this was the case for a more detailed analysis of decomposition among first- and second-order roots of four of the tree species studied here (Goebel et al., unpublished data).

The single trait that explained significant variation in both fine root and leaf litter decomposition rates among species, the initial concentration of cell solubles, was unrelated between fine roots and leaf litter ($r = -0.13$, $P = 0.71$). These results suggest that patterns of detritus processing across these species, at least by soil microbes, may show little correspondence above versus below ground.

The pattern of decomposition differed between fine roots and leaf litter, as an asymptotic model better described fine root decomposition while a single exponential model better described leaf litter decomposition. This difference arose because roots exhibited a period of rapid mass loss between deployment and the first and second harvests (i.e., high k_a), but little mass loss between the second and third harvests. In contrast, leaf litter followed a typical exponential decomposition pattern through time. The period of rapid mass loss in roots could have been caused by chemical characteristics of the roots themselves or by some attribute of the belowground decomposition environment. As concentrations of nutrients and soluble cell contents were generally lower for roots (Table 2) than for leaf litter (Hobbie et al. 2006), chemical differences between roots and leaf litter likely cannot explain the different patterns of mass loss below and above ground. Alternatively, the belowground environment may have been more conducive to rapid mass loss, either because of moister conditions that promoted leaching and/or microbial activity or more rapid colonization of decomposing material by microbes.

Leaf litter versus fine root N dynamics

N immobilization into decomposing roots versus leaf litter was unrelated across species. This lack of correspondence above and below ground occurred because, although similar traits (i.e., tissue N concentrations) influenced immobilization into fine roots and leaf litter, patterns of these traits differed for roots and leaf litter. The concentration of N in roots was negatively related to the maximum amount of N immobilized into decomposing fine roots, presumably because of lower demand for N by microbes breaking down N-rich roots. This pattern is predicted by theory (Manzoni et al. 2008) and is similar to that found for leaf litter in a related study (Hobbie et al. 2006) and in cross-site comparisons of litter N dynamics (Hobbie 2008; Manzoni et al. 2008; Parton et al. 2007). However, there was no correspondence in the N concentrations of leaf litter and fine roots, leading to a lack of consistency between immobilization above and below ground. Thus above- and belowground traits may not reinforce each other to enhance interspecific differences among the 11 tree species in rates of soil N transformations that are influenced by N immobilization into detritus (e.g., net N mineralization rates).

The lack of relationship between leaf litter and fine root N found here is consistent with some studies, but not others. For example in a study of seedlings of 34 savanna species, leaf and root N were unrelated as found in this study (Reich et al. 2003a). By contrast, among both co-occurring tree species grown as seedlings (Reich et al. 1998) and among dozens of herbaceous species at regional and global scales (Craine et al. 2005; Craine et al. 2002), leaf and root N were positively related. The reasons for inconsistencies among studies are unclear. Root N concentrations are influenced not just by protein concentrations within the root, but also by chitin concentrations of root-associated mycorrhizal fungi. Thus, mycorrhizal type

(ectomycorrhiza vs. arbuscular mycorrhiza) and taxon may contribute to variation in root N that is unlinked to plant growth strategies and thus aboveground traits.

Conclusion

Our study suggests that among these 11 temperate tree species, effects on C and N dynamics in decomposing fine roots and leaf litter, as mediated by microbes, may not reinforce each other to cause divergence in species effects on these dynamics. In other words, differences among plant species in effects on microbial belowground litter processing and N immobilization do not necessarily mirror differences among species in their effects on the same microbially mediated processes aboveground. Because root detritus contributes significantly to total detritus inputs, species differences in rates of microbially mediated decomposition may not be as large at they might be if above- and belowground processes were working in similar directions (if faster decomposition above ground corresponded to faster decomposition below ground). The lack of correspondence above and below ground largely arose because there was little correlation above versus below ground for traits that influence decomposition and detritus N dynamics between leaves and fine roots. In addition, different traits were important above versus below ground in influencing decomposition. We do not know whether this lack of correspondence also would occur if detritivore-mediated decomposition were compared above versus below ground. Nevertheless, our results imply that studies linking plant traits to ecosystem processes that focus solely on aboveground traits may obscure some of the important mechanisms by which plant species influence ecosystem processes.

Acknowledgments This material is based upon work supported by the National Science Foundation under DEB 0128958. We thank Andrzej Jagodzinski, Piotr Karolewski, Brian Kloeppel, Megan Ogdahl, Michal Oleksyn, Mark Tjoelker, Ewa Turzanska, and Roma Zytkowiak for assistance. The experiment complies with the current Polish law.

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