TREE SPECIES EFFECTS ON DECOMPOSITION AND FOREST FLOOR DYNAMICS IN A COMMON GARDEN

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Abstract. We studied the effects of tree species on leaf litter decomposition and forest floor dynamics in a common garden experiment of 14 tree species (*Abies alba, Acer platanoides, Acer pseudoplatanus, Betula pendula, Carpinus betulus, Fagus sylvatica, Larix decidua, Picea abies, Pinus nigra, Pinus sylvestris, Pseudotsuga menziesii, Quercus robur, Quercus rubra,* and *Tilia cordata*) in southwestern Poland. We used three simultaneous litter bag experiments to tease apart species effects on decomposition via leaf litter chemistry vs. effects on the decomposition environment. Decomposition rates of litter in its plot of origin were negatively correlated with litter lignin and positively correlated with mean annual soil temperature (MAT_{soil}) across species. Likewise, decomposition of a common litter type across all plots was positively associated with MAT_{soil}, and decomposition of litter from all plots in a common plot was negatively related to litter lignin but positively related to litter Ca. Taken together, these results indicate that tree species influenced microbial decomposition primarily via differences in litter lignin (and secondarily, via differences in litter Ca), with high-lignin (and low-Ca) species decomposing most slowly, and by affecting MAT_{soil}, with warmer plots exhibiting more rapid decomposition. In addition to litter bag experiments, we examined forest floor dynamics in each plot by mass balance, since earthworms were a known component of these forest stands and their access to litter in litter bags was limited. Forest floor removal rates estimated from mass balance were positively related to leaf litter Ca (and unrelated to decay rates obtained using litter bags). Litter Ca, in turn, was positively related to the abundance of earthworms, particularly *Lumbricus terrestris*. Thus, while species influence microbially mediated decomposition primarily through differences in litter lignin, differences among species in litter Ca are most important in determining species effects on forest floor leaf litter dynamics among these 14 tree species, apparently because of the influence of litter Ca on earthworm activity. The overall influence of these tree species on leaf litter decomposition via effects on both microbial and faunal processing will only become clear when we can quantify the decay dynamics of litter that is translocated belowground by earthworms.

Key words: calcium; decomposition; earthworms; lignin; litter; N-immobilization; Poland; trees.

INTRODUCTION

Ecosystem ecology has a rich history of studies relating decomposition of leaf litter to its chemistry. For example, variation in decomposition rate among plant species is often positively related to initial nitrogen (N) concentrations and negatively related to initial lignin concentrations (e.g., Meentemeyer 1978, Melillo et al. 1982, Aerts 1997). Although there are exceptions, this general pattern of lignin and/or N control over decomposition rates has been demonstrated in a wide variety of ecosystems (Van Cleve 1974, McClaugherty and Berg 1987, Taylor et al. 1991, Hobbie 1996, Austin and Vitousek 2000), and we refer to it hereafter as the lignin–N paradigm.

Substrate chemistry, along with site factors, also contributes to species differences in N-immobilization into decomposing litter. For example, some studies have shown greater immobilization in litter with low initial N concentrations (Berg and Eckbom 1983, Hobbie and Vitousek 2000, Schwendener et al. 2005; but see Pastor et al. 1987). Other studies suggest that initial lignin concentration determines N-immobilization (Melillo et al. 1982).

Relationships of litter lignin and N to decomposition and litter N dynamics, although not universal, pervade thinking about species effects on biogeochemistry (Vitousek 1982, Hobbie 1992, Scott and Binkley 1997, Berendse 1998) and form a basis for many ecosystem models. For example, the partitioning of litter into different detrital pools and the decay constants assigned to those pools often depends on litter lignin or lignin:N ratios (Moorehead et al. 1996).

Besides substrate chemistry, plant species may alter decomposition rates through their effects on the physical environment or the soil community, particularly if they form monospecific patches (Eviner and Chapin 2003). For example, species effects on microclimate can have significant consequences for biogeochemistry (Mack and D'Antonio 2003). A number of experiments have used reciprocal litter transplants to compare substrate vs. environmental effects on decomposition across environmental gradients (Vitousek et al. 1994, Austin and Vitousek 2000, Hobbie and Vitousek 2000, Pouyat and Carreiro 2003). However, experiments that examine environmental effects on decomposition caused by *species* are more rare.

We used a common garden experiment of 14 tree species in southwestern Poland to explore species effects on leaf litter decomposition and N dynamics. Our specific objectives were to (1) compare species effects on decomposition via litter chemistry vs. the environment and (2) to determine whether the lignin–N paradigm of decomposition control holds true across diverse deciduous and evergreen, angiosperm and gymnosperm trees. Because earthworms are present at this site, we also determined whether the same litter chemistry characteristics explain species differences in leaf litter dynamics when earthworms are excluded from litter vs. when litter is accessible to earthworms.

MATERIALS AND METHODS

Site description

We studied a common garden experiment of 14 European and North American tree species at the Siemianice Experimental Forest near Biadaszki, Poland (51°14.87′ N, 18°06.35′ E, elevation 150 m) (Reich et al. 2005). In 1970–1971, 20×20 m monospecific plots 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 replicates per species) with four species (*Picea*, *Larix*, *Pseudotsuga*, and *Q. robur*) grown in both blocks.

The site was prepared by clear-cutting an 81-year-old *P. sylvestris* stand followed by stump removal and soil plowing (up to a depth of 60 cm). Seedlings for the experiment were obtained from the Pelplin nursery (53°55′ N, 18°41′ E, elevation 55 m) except *P. nigra*, which was obtained from the Kraszkowice nursery (51°12′ N, 18°43′ E, elevation 171 m). (The Pelplin and Kraszkowice nurseries are part of the Polish State Forest system.) In the spring of 1970, one-year-old seedlings of nine species (*Betula*, *P. nigra*, *P. sylvestris*,

Q. rubra, *Carpinus*, *Picea*, *Larix*, *Pseudotsuga*, *Q. robur*) were planted in one of the blocks (399 seedlings per plot). In the following year, two-year-old seedlings of nine species (*A. pseudoplatanus*, *A. platanoides*, *Fagus*, *Tilia*, *Q. robur*, *Pseudotsuga*, *Larix*, *Abies*, *Picea*) originating from the same seed lots were planted in the adjacent block. Therefore, trees at both sites were of the same age. Because of poor survival of *Abies* seedlings, only two replicate plots survived.

The climate of the region is transitional between maritime and continental. Mean annual precipitation is 591 mm, of which half falls from May to August, and mean annual temperature is 8.2°C. Soils at the site formed on sandy outwash overlying finer textured glacial deposits. Before establishment of the common garden, the soil pH of the A horizon averaged 4.3. However, since plot establishment, soil pH, exchangeable base cations, and earthworm abundances have diverged among species, with *A. platanoides*, *A. pseudoplatanus*, and *Tilia* plots having the most basic soils with the highest exchangeable Ca concentrations and earthworm abundances, and *P. sylvestris*, *P. nigra*, and *Larix* plots having the most acidic soils with low exchangeable base cation concentrations and earthworm abundances (Reich et al. 2005).

Litter decomposition experiments

We established three simultaneous leaf-litter decomposition experiments using litter bags. In the first experiment (hereafter, "Home Plot"), we determined the combined effects of different species on decomposition via their influence on the environment for decomposition and on substrate chemistry by decomposing each plot's litter in situ. In the second (hereafter, "Common Plot"), we isolated tree species effects on decomposition via their influence on substrate chemistry by decomposing litter from all plots in a common plot (one *A. pseudoplatanus* plot). In the third (hereafter, "Common Substrate"), we isolated the influence of tree species on the decomposition environment by decomposing a common leaf litter (*A. pseudoplatanus*) in all of the plots.

Litter for litter bags was obtained from collections of total fine litterfall made monthly from 31 May 1996 through 30 November 1998 using litter traps (0.38-m² traps, eight traps per plot). Litter was dried (65°C) and leaf litter of the dominant species in the plot was separated and pooled across collection dates for use in litter bags. For the Common Substrate experiment, litter from all plots of *A. pseudoplatanus* was pooled across collections. Litter bags were constructed from nylon tent netting (0.3-mm mesh) and bags were filled with 5 g (Home and Common Plots) or 2.3 g (Common Substrate) of litter. A small mesh was used because of the large number of needle-leaved species in the experiment. We constructed sufficient bags for two bags per plot and five harvests for the Home Plot and Common

Substrate experiments, and one bag per plot and five harvests for the Common Plot experiment.

Subsamples of initial litter from each plot were ground and analyzed for (1) carbon fractions (Van Soest 1994) on an ANKOM Fiber Analyzer (Ankom Technology, Macedon, NY, USA) (cell solubles, hemicellulose and bound protein, cellulose, and lignin and other recalcitrants, determined on an ash-free dry mass basis); (2) phosphorus, calcium, potassium, and magnesium by ICP (Applied Research Laboratory 3560, ThermoElectron, Waltham, Massachusetts, USA) following digestion in 10% HCl (Munter and Grande 1981) at the University of Minnesota's Research Analytical Laboratory, St. Paul, Minnesota, USA; and (3) carbon and nitrogen on a Costech ECS4010 Element Analyzer (Costech Analytical, Valencia, California, USA) at the University of Nebraska at Lincoln, Nebraska, USA. Initial litter N and C fractions (on a total mass basis) have been previously reported (Reich et al. 2005).

We placed litter bags in the field on 30 November 2002 and harvested subsets on 14 May, 24 July, and 10 October 2003, then on 14 June and 5 October 2004. Upon harvest, litter was removed from bags, separated from roots and the like, dried (65°C), and weighed. The proportion of initial mass was calculated by dividing the mass at any harvest date by the initial mass. In addition, we determined decay constants (k) by fitting the data for each plot with a negative exponential decay model (using linear regressions of ln-transformed proportions of initial mass remaining against time). Harvested litter was ground and analyzed for N. The proportion of initial N at each harvest date was calculated by multiplying percentage of N by litter mass and comparing it to the initial litter N pool.

We compared decomposition rates to environmental parameters measured in this study or reported in Reich et al. (2005). Soil temperatures were measured (at a 10 cm depth) using one datalogger centered in each plot (HOBO 8K, Onset Computer Corporation, Bourne, Massachusetts, USA). Temperatures were recorded each hour between February 1999 and November 2000. We also compared decomposition rates to O horizon soil pH (water) and O horizon mass (Reich et al. 2005), presumably a surrogate for O horizon moisture content.

Earthworms (whose biomass is dominated by *Lumbricus terrestris*) are present in the Siemianice site (Reich et al. 2005; C. M. Hale, *unpublished data*), but were excluded from our litter bags (i.e., we never observed earthworms in the bags upon harvest). Therefore, our experiments measured decomposition resulting exclusively from microbial and microfaunal activity. To determine whether the same litter chemistry characteristics that explain species differences in leaf litter decomposition when litter is contained in litter bags (i.e., earthworms excluded) also explain differences in forest floor dynamics when litter is accessible to earthworms, we compared the results from the Home Plot experiment with estimates of forest floor dynamics

obtained under steady state assumptions (i.e., that litterfall inputs to the forest floor equal litterfall outputs via decomposition/removal) using measurements of annual litterfall and forest floor mass data presented in Reich et al. (2005). Litterfall inputs to the forest floor have likely been relatively constant for over two decades, since the dense planting in these stands resulted in canopy closure after 10 years (Szymanski 1982) and six years of litterfall data collected between 1996 and 2004 show no significant temporal trend (J. Oleksyn, *unpublished data*); thus, the litterfall data used in our calculations (collected in 1996–1997, Reich et al. 2005) should be representative of steady state litterfall. Sensu Olson (1963), we calculated forest floor decay rates (k_1) assuming continuous litterfall mass (L) where F is forest floor mass (i.e., $O_e + O_i + O_a$ horizon mass; Reich et al. [2005]):

$$k_1 = L/F. \qquad (1)$$

Since litterfall is relatively discrete in this temperate system, particularly for the deciduous taxa, we also calculated decay rates (k_2) using Olson's equation for discrete autumn litterfall, where T is the maximum forest floor mass, approximated as late-summer (August; Reich et al. 2005) forest floor mass plus litterfall mass ($T = F + L$):

$$k_2 = -ln(1 - L/T). \qquad (2)$$

We recognize that these decay rates might more accurately be termed forest floor "removal rates," since the fate of lost litter could be its translocation to deeper soil horizons by soil organisms and hereafter we refer to these removal rates as such. We further recognize that actual forest floor removal rates are likely an intermediate between k_1 and k_2 for the evergreen taxa, and closer to k_2 for the deciduous taxa. Therefore, we present both.

Plowing prior to planting likely eliminated the preexisting *Pinus sylvestris* forest floor. Thus, the forest floor dynamics estimated here should reflect those of the current canopy species. Our steady state assumption is reasonable for the more rapidly decomposing species, but may have caused us to overestimate removal rates of more slowly decomposing species: after 31 years (the stand age at which forest floor mass was sampled; Reich et al. 2005), forest floor mass should have reached steady state for species with $k_1 > 0.17$ (given that $F/F_{ss} = 1 - e^{-kt}$, where F_{ss} is steady state forest floor mass and t is stand age; Olson 1963). However, even for a species with k_1 as slow as 0.05, forest floor mass would have been at 79% of its steady state value in a 31 yr-old stand.

Analyses

Initial t test comparisons between the two blocks for mass remaining at the final harvest and decay rates for those species present in both blocks indicated no statistically significant differences between blocks ($P > 0.05$). Therefore, in all subsequent analyses, we ignored

blocking. Because we were primarily interested in species-level effects on decomposition (rather than within-species variation), we analyzed the data using species means.

We used stepwise multiple regression with backwards elimination to determine which factors explained significant variation among species in decomposition, after screening potential independent variables for significant autocorrelation ($r > 0.80$). For the Home Plot experiment, we considered all initial litter chemistry variables, mean annual soil temperature (MAT_{soil}), O horizon pH, and O horizon mass for the initial model. For the Common Plot experiment, we considered only initial litter chemistry variables, and for the Common Substrate experiment, we considered only MAT_{soil}, O horizon pH, and O horizon mass in the initial model. We conducted analyses using decay constants determined by assuming negative exponential decay as the independent variable. Because the error associated with fitting the regression models used to obtain decay constants is not accounted for when using decay constants as independent variables in subsequent analyses, we confirmed the results of these analyses using the proportion of initial mass remaining after the final harvest (averaging the two litter bags per plot per harvest).

We calculated the maximum amount of N immobilized into decomposing litter (milligrams of N per gram of initial litter mass) by identifying the harvest date at which the proportion of initial N was at its maximum. We then multiplied the maximum proportion of initial N during the experiment by the initial litter N content, subtracted the initial N content, and normalized by initial litter mass. If litter N declined from the initial content during the experiment, we scored immobilization for that plot as zero. We compared the maximum N-immobilization among plots and species in the Home and Common Plot experiments to litter chemistry using backwards stepwise regression.

RESULTS

Litter bag experiments

Negative exponential decay models generally described the litter bag data well. For the Home Plot experiment, all regressions were significant ($P < 0.03$) and the fits were generally good (R^2 mean = 0.83, median = 0.86, range 0.49–0.97). For the Common Substrate experiment, all regressions were also significant ($P \leq 0.05$) and the fits were also good (R^2 mean = 0.84, median = 0.85, range 0.55–0.98). For the Common Plot experiment, the significance of the regressions was lower, since there was only one (as opposed to two) litter bag per plot per harvest to use in developing regressions (mean $P = 0.02$, median $P = 0.01$, maximum $P = 0.14$) and the fits were good (R^2 mean = 0.90, median = 0.92, range 0.57–1.00).

After two years, there were significant differences among species in decomposition in the Home Plot experiment (one-way ANOVA, $P = 0.01$), with P.

sylvestris, Quercus rubra, Carpinus, Acer spp., and *Betula* having the most rapid decay rates, and *Larix, Abies,* and *Fagus* having the slowest decay rates (Fig. 1, Table 1). In stepwise regression analysis, litter lignin (Table 2) was significantly negatively related ($P = 0.03$, Table 3), while MAT_{soil} was positively, albeit weakly, related to litter decay rates ($P = 0.06$, Table 3). Leaf litter K, O horizon pH, and forest floor mass were excluded from the analysis because of tight correlations with litter Ca ($r = 0.82$, 0.89, and -0.80, respectively; $P < 0.001$); litter cell-soluble content was excluded because of tight correlation with litter lignin ($r = -0.83$, $P < 0.001$); and litter Mg was excluded because of tight correlation with litter P ($r = 0.79$, $P < 0.001$). We obtained similar results analyzing mass remaining at the final harvest: lignin was negatively and MAT_{soil} was positively related to mass loss ($P = 0.02$ and $P = 0.03$, respectively; $R^2 = 0.49$).

Decay rates in the Common and Home Plot experiments were significantly correlated (Fig. 1; $r = 0.61$, $P = 0.02$), suggesting that much of the variation among species in decomposition of litter in situ arose from variation in substrate chemistry. In the Common Plot experiment, decay rates were negatively related to litter lignin and positively related to litter Ca ($P = 0.01$ and $P = 0.04$, respectively; Table 3). Similarly, mass loss at the final harvest was negatively related to litter lignin and positively related to litter Ca ($P = 0.006$ and $P = 0.03$, respectively; $R^2 = 0.63$).

By contrast, decay rates in the Common Substrate and Home Plot experiments were unrelated ($r = -0.15$, $P = 0.62$). In stepwise regression analysis, only MAT_{soil} was significantly (positively) related to decay rates of a common substrate across different species plots ($P = 0.02$, Table 3). Similarly, only MAT_{soil} was significantly (positively) related to mass loss at the final harvest in the Common Substrate experiment ($P = 0.008$, $R^2 = 0.46$).

Mass balance estimates

In addition to measuring litter decomposition using litter bags, we estimated forest floor removal rates by mass balance. Values of k_1 (assuming continuous litterfall) and k_2 (assuming discrete autumn litterfall) were similar at the lower range, but k_1 exceeded k_2 at higher values (Table 1). Decay constants determined using litter bags (in the Home Plot experiment) were unrelated to k_1 or k_2 ($P = 0.22$ and 0.24, Table 1). Using the same statistical model used to analyze the Home Plot experiment (excluding forest floor mass, which was used to calculate removal rates), litter Ca alone was significant in explaining variation in k_1 among species, being positively related to removal rate ($P < 0.0001$, $R^2 = 0.73$). The difference between decay rates estimated using litter bags and k_1 was also significantly positively related to leaf litter Ca, because at high litter Ca, k_1 greatly exceeded litter bag decay rates, but at low litter Ca, k_1 was less than litter bag decay rates (Fig. 2; $P < 0.0001$, $R^2 = 0.72$). Litter Ca was highly significantly (positively) related to k_2 ($P < 0.0001$); MAT_{soil} was weakly (positively) related
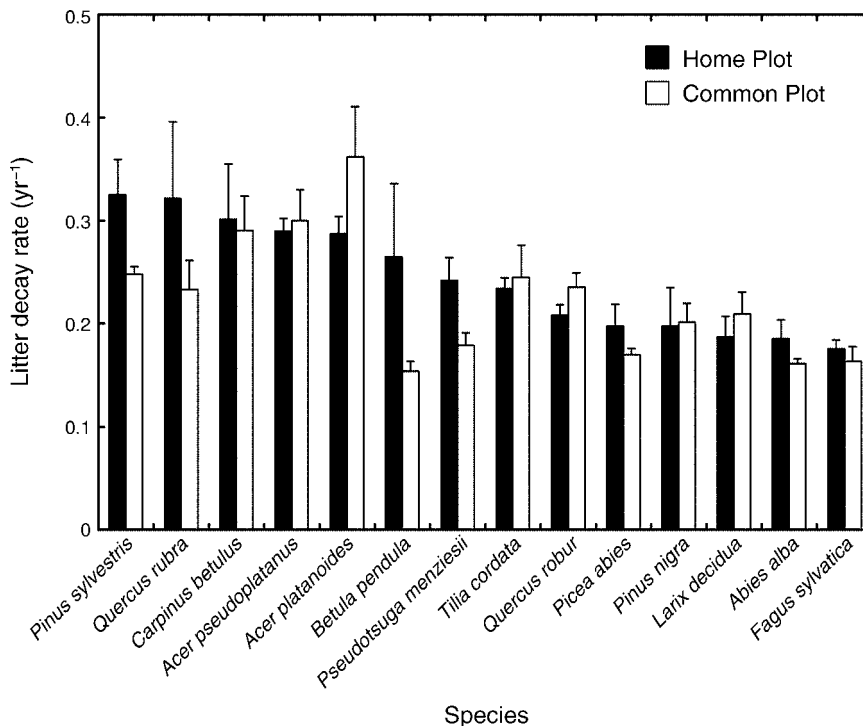
FIG. 1. Decay rate (mean + SE) of litter of 14 species decomposed in its plot of origin (Home Plot experiment) or in a common site (Common Plot experiment). Species are ranked from the most rapidly to the most slowly decomposing in the Home Plot experiment.

($P = 0.05$) while litter N was significantly negatively related to k_2 ($P = 0.01$, $R^2 = 0.88$).

Litter nitrogen dynamics

Nearly all litter types in all experiments were still immobilizing N after two years (Appendix). Some species had approximately their original litter N content after two years (e.g., *Betula*, *Carpinus*, *Q. robur*, *Tilia*), while others were still exhibiting substantial immobilization (e.g., *A. platanoides*, *Larix*, *Pinus* spp., *Pseudotsuga*). The proportion of initial N (across all harvest dates and plots) was correlated between the Home and

TABLE 1. Litter bag decay constants (k) in the three experiments, mass balance decay constants (k_1 and k_2), and annual soil temperature (all values are mean $\pm$ SE).

	k from litter bag experiments (yr^{-1})					
Species	Home Plot	Common Plot	Common Substrate	k_1† (yr^{-1})	k_2 (yr^{-1})	Annual soil temperature (°C)
Abies alba	0.19 ± 0.02	0.16 ± 0.00	0.30 ± 0.02	0.06 ± 0.00	0.06 ± 0.00	9.89 ± 0.14
Acer platanoides	0.29 ± 0.02	0.36 ± 0.05	0.27 ± 0.01	1.09 ± 0.29	0.72 ± 0.14	10.17 ± 0.26
Acer pseudoplatanus	0.29 ± 0.01	0.30 ± 0.03	0.31 ± 0.04	0.88 ± 0.38	0.59 ± 0.20	10.42 ± 0.12
Betula pendula	0.26 ± 0.07	0.15 ± 0.01	0.35 ± 0.03	0.35 ± 0.15	0.28 ± 0.11	10.92 ± 0.27
Carpinus betulus	0.30 ± 0.05	0.29 ± 0.03	0.26 ± 0.03	0.05 ± 0.00	0.05 ± 0.00	10.08 ± 0.11
Fagus sylvatica	0.18 ± 0.01	0.16 ± 0.01	0.33 ± 0.02	0.23 ± 0.10	0.20 ± 0.08	10.13 ± 0.11
Larix decidua	0.19 ± 0.02	0.21 ± 0.02	0.34 ± 0.03	0.09 ± 0.02	0.08 ± 0.01	10.41 ± 0.09
Picea abies	0.20 ± 0.02	0.17 ± 0.01	0.27 ± 0.02	0.10 ± 0.05	0.09 ± 0.04	9.69 ± 0.07
Pinus nigra	0.20 ± 0.04	0.20 ± 0.02	0.28 ± 0.03	0.08 ± 0.01	0.08 ± 0.01	10.00 ± 0.08
Pinus sylvestris	0.33 ± 0.03	0.25 ± 0.01	0.31 ± 0.01	0.10 ± 0.02	0.09 ± 0.02	10.27 ± 0.06
Pseudotsuga menziesii	0.24 ± 0.02	0.18 ± 0.01	0.23 ± 0.03	0.07 ± 0.01	0.07 ± 0.01	9.86 ± 0.05
Quercus robur	0.21 ± 0.01	0.24 ± 0.01	0.34 ± 0.04	0.36 ± 0.14	0.29 ± 0.10	10.19 ± 0.07
Quercus rubra	0.32 ± 0.07	0.23 ± 0.03	0.31 ± 0.02	0.13 ± 0.03	0.12 ± 0.03	10.12 ± 0.09
Tilia cordata	0.23 ± 0.01	0.24 ± 0.03	0.34 ± 0.06	0.92 ± 0.32	0.62 ± 0.17	10.14 ± 0.08

Notes: For mass balance estimates and mean annual soil temperature, "species" refers to the identity of the dominant species in the plot where measurements were made. For litter bag decay rates, "species" refers to the identity of the dominant species in the plot where litter was decomposed (Common Substrate), the identity of the species whose litter was decomposed (Common Plot), or both (Home Plot).

† From Reich et al. (2005).

TABLE 2. Initial litter chemistry parameters (means with SE in parentheses) for 14 species grown in a common garden experiment.

| Species | C:N | Initial litter nutrients (mg element/g litter) | | | | | Initial litter C fractions (mg/g ash-free dry mass) | | | | Ash (mg/g litter) |
		N	Ca	K	Mg	P	Cell solubles	Cellulose	Hemi-cellulose	Lignin	
Abies alba	41.2	12.5	12.4	2.2	0.8	1.18	370.1	199.9	123.4	304.6	3.4
	(4.1)	(1.3)	(1.1)	(0.4)	(0.1)	(0.07)	(36.5)	(5.9)	(2.9)	(27.6)	(0.7)
Acer platanoides	68.9	6.5	19.0	6.6	1.6	1.29	530.6	180.2	160.8	125.9	16.1
	(4.8)	(0.4)	(1.7)	(0.9)	(0.1)	(0.05)	(30.5)	(14.3)	(9.8)	(6.2)	(4.6)
Acer pseudo-platanus	49.1	9.4	21.8	6.9	1.6	1.16	524.2	184.3	122.7	166.8	16.7
	(6.2)	(1.1)	(2.3)	(0.8)	(0.2)	(0.24)	(5.9)	(9.8)	(2.7)	(7.9)	(1.8)
Betula pendula	38.5	12.6	11.5	3.2	2.4	1.61	278.0	186.8	124.4	408.7	57.1
	(1.1)	(0.2)	(0.4)	(0.6)	(0.1)	(0.02)	(31.9)	(1.9)	(6.2)	(39.7)	(22.0)
Carpinus betulus	42.7	11.0	9.2	3.9	1.5	1.85	496.2	200.8	155.3	143.6	26.8
	(2.0)	(0.5)	(0.5)	(0.8)	(0.1)	(0.05)	(20.1)	(6.8)	(5.1)	(16.0)	(2.9)
Fagus sylvatica	55.9	8.4	12.9	4.2	1.1	1.41	381.5	231.9	138.8	245.7	13.2
	(3.6)	(0.5)	(0.5)	(1.0)	(0.1)	(0.15)	(26.3)	(12.9)	(8.1)	(18.9)	(3.3)
Larix decidua	64.9	8.7	6.9	1.5	1.4	1.39	365.5	222.0	92.6	317.4	3.7
	(10.1)	(1.3)	(0.7)	(0.3)	(0.1)	(0.11)	(21.3)	(9.3)	(5.1)	(18.0)	(0.8)
Picea abies	49.3	9.9	11.1	3.4	0.8	1.10	414.6	231.3	138.1	214.1	4.8
	(2.5)	(0.4)	(0.5)	(0.2)	(0.0)	(0.12)	(15.6)	(12.3)	(2.4)	(6.0)	(1.3)
Pinus nigra	98.7	5.4	3.1	2.3	0.5	0.51	289.7	316.0	153.8	238.7	2.9
	(13.9)	(0.9)	(0.5)	(0.1)	(0.1)	(0.09)	(7.2)	(3.3)	(6.6)	(11.3)	(0.4)
Pinus sylvestris	81.9	6.8	5.4	2.0	0.5	0.62	389.3	298.8	133.2	176.6	2.6
	(15.9)	(1.4)	(0.5)	(0.2)	(0.0)	(0.13)	(7.1)	(7.2)	(5.6)	(7.2)	(0.4)
Pseudotsuga menziesii	72.0	7.2	9.1	2.9	1.1	1.15	455.6	182.2	112.3	247.6	4.7
	(3.0)	(0.3)	(0.7)	(0.2)	(0.0)	(0.11)	(9.0)	(5.3)	(3.3)	(6.6)	(0.7)
Quercus robur	37.7	12.7	12.0	5.0	1.8	1.70	388.5	222.3	153.7	233.5	14.4
	(5.1)	(0.6)	(0.5)	(0.7)	(0.1)	(0.09)	(13.0)	(6.2)	(5.6)	(15.0)	(2.4)
Quercus rubra	68.7	7.1	11.8	3.1	1.4	1.38	417.8	232.2	149.6	198.4	9.5
	(5.5)	(0.5)	(0.6)	(0.6)	(0.1)	(0.05)	(6.4)	(1.6)	(3.2)	(1.0)	(1.2)
Tilia cordata	37.0	12.2	18.8	4.0	1.8	1.47	270.9	193.6	115.5	417.1	94.0
	(1.3)	(0.1)	(0.8)	(1.1)	(0.0)	(0.08)	(46.4)	(11.3)	(4.1)	(41.0)	(31.1)
Mean	57.6	9.3	11.8	3.7	1.3	1.27	398.0	220.2	133.9	245.5	19.3

Common Plot experiments ($r = 0.63$, $P < 0.0001$), but not between the Common Substrate and the other experiments ($P > 0.10$ in both cases). The maximum N-immobilization (milligrams of N per gram of initial litter; data not shown) was significantly positively related to initial litter C:N ($P < 0.0001$) and P ($P =$

TABLE 3. Results of stepwise multiple regressions with backwards elimination ($P > 0.10$) for decay rates after two years in the three litter bag experiments.

| | Experiment | | |
Independent variable	Home Plot	Common Plot	Common Substrate
N (%)			...
Cellulose (%)			...
Hemicellulose (%)			...
Lignin (%)	(−)*	(−)*	...
Ca (%)		(+)*	
P (%)			...
Forest floor mass	X	...	
Mean annual soil temperature	(+)†	...	(+)*
R^2	0.43	0.56	0.39

Notes: Ellipses indicate that a variable was excluded from the original model because of irrelevance. An "X" indicates that a variable was excluded from the original model because of tight correlation with another variable in the model. Blank cells indicate nonsignificance ($P > 0.10$). The sign of the relationship between significant independent variables and decay rate (− or +) is indicated.

* $P < 0.05$; † $P < 0.10$.

0.02) in the Home Plot experiment when all plots were included in the analysis ($R^2 = 0.30$), but when species means were analyzed, N-immobilization was unexplained by any litter chemistry parameters. In the Common Plot experiment, the maximum N-immobilization was positively related to initial litter C:N, Ca, and P, when all plots were included in the analysis ($P < 0.001$, $P < 0.001$, $P = 0.01$, respectively; $R^2 = 0.41$), and to litter C:N and Ca when species means were analyzed ($P = 0.009$, $P = 0.01$, respectively; $R^2 = 0.57$).

DISCUSSION

Taken together, the three experiments indicate that the 14 tree species studied here influence microbially-mediated decomposition, primarily through variation in litter lignin (and perhaps litter Ca) and by influencing forest floor temperatures. Species with relatively low litter lignin (*P. sylvestris*, *Acer* spp., *Carpinus*, *Q. rubra*) generally exhibited the most rapid decomposition in both the Home and Common Plot experiments. Since litter lignin and litter cell solubles were so tightly correlated, we cannot rule out the possibility that more rapid decomposition of species with lignin-poor litter was caused by high concentrations of cell solubles. Litter Ca was significant in explaining species differences in litter decomposition in the Common Plot, but not the Home Plot, experiment. Inconsistent results between the two experiments could have arisen for two reasons. First,

there may be litter-type-by-environment interactions that we were unable to assess using our experimental design because we decomposed all litter types in a single common environment (an *A. pseudoplatanus* plot). For example, a high Ca requirement of the microbial community in that plot compared to the average of other plots could have given the results we observed. Alternatively, variation among plots in environmental factors could have masked (statistically) a biologically significant relationship between litter Ca and decomposition across species in the Home Plot experiment. We cannot distinguish between these two alternatives given our experimental design. Species with high light penetration to the forest floor had warmer MAT_{soil} and relatively rapid decomposition in both the Home Plot and Common Substrate experiments (MAT_{soil} was significantly correlated with average growing-season PAR (photosynthetically active radiation) at a height of one meter; $r = 0.78$, $P = 0.001$; J. Modrzynski, *unpublished data*). Species with little light penetration to the forest floor (e.g., *Abies* and *Picea*) had colder soil temperatures and slower decomposition. Although numerous studies have demonstrated relationships between lignin and decomposition (Hobbie 2000) and between temperature and decomposition across sites (Aerts 1997, Gholz et al. 2000), we are unaware of other studies demonstrating that monospecific tree stands significantly affect decomposition via both litter chemistry and effects on soil temperatures.

Plot differences in microbial N-immobilization resulted from differences in litter chemistry, since immobilization patterns were correlated between the Home and Common Plot experiments, but not between the Common Substrate and the other experiments. Specifically, differences within and among species in litter N led to differences in N-immobilization, with high C:N litter increasing N-immobilization over two years, likely because of greater N demand by microbes decomposing litter with relatively lower N content. Additionally, high litter Ca and/or P promoted N-immobilization, perhaps because decomposers had a higher N demand, when they were supplied with adequate amounts of these other nutrients. Thus, while litter lignin was important in explaining variation in microbial decomposition rates among species, litter nutrient concentrations (C:N ratio, Ca, and P) were important in explaining variation in litter N dynamics. Some unknown environmental differences among plots may have also contributed to variation in litter N dynamics, since the common substrate, *A. pseudoplatanus*, showed different patterns of immobilization depending on its plot of decomposition.

The match between decomposition assessed using litter bags and forest floor removal estimated by mass balance was extremely poor. The removal rates calculated by mass balance for many litter types were slower than were decay rates calculated from litter bags. This discrepancy is not surprising given that decomposition
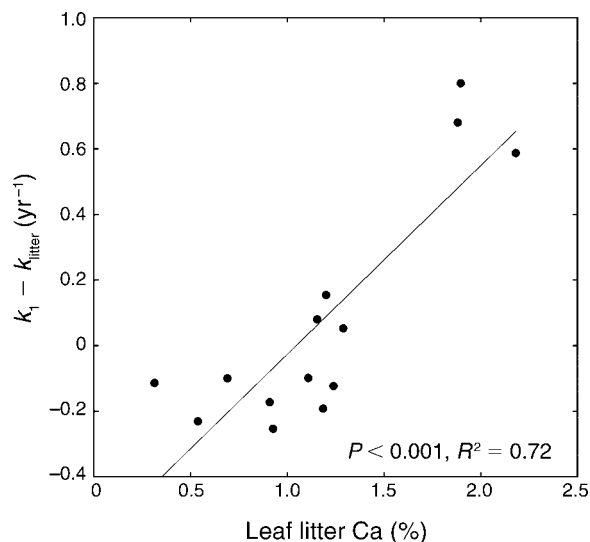

FIG. 2. The difference between decay rates obtained using litter bags in the Home Plot experiment (k_{litter}) and k_1, estimated by mass balance as a function of leaf litter Ca. Each point represents the mean of replicate plots for one of 14 tree species.

in litter bags was measured for only two years, by which point litter had lost only 29–48% of the initial mass. Presumably, if left to decompose longer, decay rates would have slowed as the relative amount of recalcitrant material in the litter increased. Mass balance estimates, by contrast, include the O_a horizon that has begun to humify and is likely decaying at a slower rate than fresh litter.

More surprising were those species that exhibited faster decomposition estimated by mass balance. In particular, mass balance removal rates for *A. plata-noides*, *A. pseudoplatanus*, and *Tilia* were two to three times faster than litter bag estimates of decay constants. What accounts for this large discrepancy? We believe that it is a straightforward consequence of the fact that litter uncontained by litter bags was accessible to earthworms, and that earthworms were responding more to species differences in litter Ca rather than to differences in litter lignin (or any other aspect of litter chemistry). Specifically, high litter Ca concentrations in *Tilia* and *Acer* spp. promoted high earthworm abundances that in turn led to rapid forest floor consumption and thus rapid apparent "decay" rates calculated by mass balance (Reich et al. 2005). However, when earthworms were excluded from litter (i.e., by litter bags), species with Ca-rich litter exhibited decomposition rates more in line with those expected, based on their lignin concentrations.

Numerous studies have demonstrated that earthworms enhance leaf litter or forest floor disappearance (Swift et al. 1979, Staaf 1987, Alban and Berry 1994, Liu and Zou 2002, Bohlen et al. 2004b, Hale et al. 2005). However, to our knowledge, few studies have linked variation in litter Ca concentrations to variation in the

processing of litter by earthworms. Past studies have related earthworm abundance to soil pH and base cations (Piearce 1972a, Muys and Lust 1992, Robinson et al. 1992, Ponge et al. 1999, Curry 2004); however, studies of litter selection by earthworms have largely focused on litter N (Hendriksen 1990, Bohlen et al. 1997, Curry 2004).

Nevertheless, several lines of evidence support our interpretation that litter Ca drove plant species effects on earthworm litter consumption, despite lignin control over microbial decomposition. Litter Ca was the sole significant predictor of k_1 and the most highly significant predictor of k_2. Because earthworm abundance was highly correlated with litter Ca ($r = 0.81$, $P < 0.0001$; Reich et al. 2005), we could not use both litter Ca and earthworm abundance in a stepwise regression. However, when we replaced litter Ca with earthworm abundance in the stepwise regression model, then earthworm abundance became the sole significant predictor of forest floor removal rates ($P = 0.007$, $R^2 = 0.47$ and $P = 0.01$, $R^2 = 0.41$ for k_1 and k_2, respectively). Hendricksen (1990) also found a preference for Tilia litter over other hardwoods, but explained the results based on variation in litter N and phenolics. Litter Ca was not measured in that study, and was likely quite high in Tilia. Similarly, in a North American field study, when earthworm communities that included Lumbricus terrestris were offered litter of Tilia americana, Acer saccharum, and Quercus rubra, litter of Tilia and Acer (the two Ca-rich litter types) disappeared rapidly, with complete disappearance of Tilia after one year, while Quercus showed little mass loss over the same time period (A. R. Holdsworth, P. B. Reich, and L. E. Frelich, unpublished data).

Whether earthworms in this site are responding directly to higher litter Ca or to the concomitant higher concentrations of soil Ca (Reich et al. 2005) is unknown (Ponge et al. 1999). Regardless, the positive relationship between forest floor removal and litter Ca likely arises from the nutritional requirements of the earthworms at the site. Although there are several species of earthworms in the Siemianice Experimental Forest (Reich et al. 2005), earthworm biomass is dominated by Lumbricus terrestris (C. M. Hale, unpublished data). Lumbricus is an anecic species that makes deep burrows, but consumes litter on the soil surface. Lumbricus has well-developed calciferous glands that produce calcium carbonate (Robertson 1936, Canti and Piearce 2003). It has been suggested that Lumbricus and other species with well-developed calciferous glands produce calcium carbonate to reduce their blood CO_2 levels and regulate blood pH when faced with high soil CO_2 levels, and thus they have a high Ca requirement (Crang et al. 1968, Robertson 1936, Piearce 1972b).

The decomposition rate of litter removed from the surface by Lumbricus is unknown. However, litter removed from the soil surface likely decays more rapidly than surface litter because of partial digestion, fragmen-

tation, more favorable moisture conditions, and enhanced microbial activity after passage through the earthworm gut (Bohlen et al. 2004a).

Our results have important implications for the generality and applicability of the lignin–N paradigm of litter decomposition control. First, the paradigm may be most important in predicting species effects on decomposition in those ecosystems lacking abundant Ca-demanding earthworms or where microbial activity dominates litter processing. It is possible that many studies that have been influential in developing the lignin–N paradigm were earthworm-free or inhabited by earthworms without high Ca requirements, either for geographic reasons (McClaugherty and Berg 1987) or because they were conducted in ecosystems dominated by species like Scots pine (Pinus sylvestris), that seem to inhibit Lumbricus terrestris (Meentemeyer and Berg 1986). Second, the lignin–N paradigm may reflect, in part, the prevalent use of litter bags in decomposition studies (including our own). The effects of litter bags on earthworm activity are likely complex, depending on both mesh size and earthworm species identity and its feeding strategy. For example, we never observed earthworms in the litter bags in this study. However, in a Hawaiian study, the same small mesh size used here was ineffective at excluding earthworms (S. E. Hobbie, unpublished data). Some studies report access by earthworms to litter in bags with 1–2 mm mesh (Liu and Zou 2002, Pouyat and Carreiro 2003), while others used 1-mm mesh to exclude earthworms (Staaf 1987). Clearly more research is needed to determine interactions between earthworm species, feeding strategy, litter bag mesh size, and litter chemistry. Finally, our results provide insights into ongoing invasions by European earthworms in parts of North America (Bohlen et al. 2004c), suggesting that preferences for Ca-rich litter by some earthworm species could explain the predominance of non-native earthworms in hardwood-dominated stands in northern forests (Hale et al. 2005).

In conclusion, our comparison of the effects of 14 tree species on leaf litter decomposition suggests that differences among species in litter lignin (and perhaps Ca) and soil temperatures explain much of the variation in species effects on microbial decomposition rates. Differences within and among species in litter nutrients (C:N, Ca, and P) explain much of the variation in microbial immobilization of N into decomposing litter. However, differences among species in forest floor dynamics are overwhelmingly related to differences in leaf-litter Ca that are driven, in turn, by differences in the abundance of Lumbricus terrestris. Ca-rich species like Tilia and Acer spp. exhibited rapid forest floor removal related to high earthworm abundance, while species like Abies, Picea, and Pinus spp. exhibited accumulation of a substantial forest floor mass and are associated with low earthworm abundance. Thus, while litter lignin is important in explaining species effects on microbially mediated decomposition, differences among species in

litter Ca appear most important in determining species effects on forest-floor leaf-litter dynamics among the 14 tree species in this system. The overall influence of these tree species on leaf-litter decomposition via effects on both microbial and faunal processing will only become clear when we can quantify the decay dynamics of litter that is translocated belowground by earthworms.

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APPENDIX

A figure showing litter N dynamics in the three experiments (*Ecological Archives* E087-139-A1).