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Tree Species Effects on Soil Organic Matter Dynamics: The Role of Soil Cation Composition

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Abstract

We studied the influence of tree species on soil carbon and nitrogen (N) dynamics in a common garden of replicated monocultures of fourteen angiosperm and gymnosperm, broadleaf and needleleaf species in southwestern Poland. We hypothesized that species would influence soil organic matter (SOM) decomposition primarily via effects on biogeochemical recalcitrance, with species having tissues with high lignin concentrations retarding rates of decomposition in the O and A horizons. Additionally, because prior work demonstrated substantial divergence in foliar and soil base cation concentrations and soil pH among species, we hypothesized that species would influence chemical stabilization of SOM via cation bridging to mineral surfaces in the A-horizon. Our hypotheses were only partially supported: SOM decomposition and microbial biomass were unrelated to plant tissue lignin concentrations, but in the mineral horizon, were significantly negatively related to the percentage of the cation exchange complex (CEC) occupied by polyvalent acidic (hydrolyzing) cations (Al and Fe), likely because these cations stabilize SOM via cation bridging and flocculation and/or because of inhibitory effects of Al or low pH on decomposers. Percent CEC occupied by exchangeable Al and Fe was in turn related to both soil clay content (a parent material characteristic) and root Ca concentrations (a species characteristic). In contrast, species influenced soil N dynamics largely via variation in tissue N concentration. In both laboratory and in situ assays, species having high-N roots exhibited faster rates of net N mineralization and nitrification. Nitrification:mineralization ratios were greater, though, under species with high exchangeable soil Ca^{2+}. Our results indicate that tree species contribute to variation in SOM dynamics, even in the mineral soil horizons. To our knowledge the influence of tree species on SOM decomposition via cation biogeochemistry has not been demonstrated previously, but could be important in other poorly buffered systems dominated by tree species that differ in cation nutrition or that are influenced by acidic deposition.

Key words: aluminum; carbon; decomposition; microbial biomass; nitrogen; Poland; respiration; soil organic matter; trees.

Introduction

Although it is well-established that plant species can have differing effects on carbon (C) and nitrogen (N) cycling through litter because of

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interspecific variation in litter chemistry (for example, Hobbie 1992), the influence of plant species on soil C and N pools and their dynamics is less clear for at least two reasons. First, although litter decomposition processes can be studied relatively easily over short time scales using litter isolated from plants, studying plant species influences on soil processes requires research on monospecific stands on the timescales of soil organic matter (SOM) turnover, decades to millennia (Parton and others 1988; Hsieh 1992; Trumbore 2000). Second, SOM is mostly derived from plant inputs that have undergone processing by microorganisms in the presence of potential reactions with soil minerals (Stevenson 1994); thus, whether plant species should have a discernable signature on SOM is unclear. Nevertheless, understanding how species influence soil organic matter dynamics is important to predicting how soil C sequestration and fertility will respond to management decisions and as well as global environmental changes that alter plant species composition across the landscape (Eviner and Chapin 2003).

Research to date suggests that different plant species can clearly influence soil nutrient cycling. For example soil base cation status and pH may diverge under different plant species (Lelong and others 1990; Finzi and others 1998a; Augusto and others 2002; Dijkstra and Smits 2002; Dijkstra and others 2002; Reich and others 2005; Oostra and others 2006). Numerous studies have demonstrated divergence in soil N cycling under different species of both herbaceous and woody plants (for example, Wedin and Tilman 1990; Gower and Son 1992; van Vuuren and others 1992; Scott and Binkley 1997; Finzi and others 1998b; Hooper and Vitousek 1998; Mack and others 2001; Mack and D'Antonio 2003; Lovett and others 2004).

Compared to nutrient cycling studies, studies of plant species effects on SOM pools and their dynamics are less common. O-horizon mass can vary substantially among tree species (Augusto and others 2002; Binkley and Giardina 1998; Finzi and others 1998b; Gärdenäs 1998; Raulund-Rasmussen and Viejre 1995). However, Finzi and others (1998b) found no variation among tree species in mineral soil C pools in the northeastern USA. Similarly, Chen and Stark (2000) found no differences in C mineralization rates between soils under crested wheatgrass and sagebrush. In contrast, a study in grasslands demonstrated significant variation in mineral soil C pools, C mineralization rates, and C:N ratios associated with different plant species (Vinton and Burke 1997). Woody encroachment into grasslands sometimes alters soil C pools (Jackson and others 2002) but at other times does not (Briggs and others 2005). Oostra and others (2006) demonstrated variation among European tree species in mineral soil C content in unreplicated plots.

Plant species have the potential to influence soil C pools and their dynamics through variation in C inputs (that is, net primary production) and by influencing C losses, including SOM decomposition. Among tree species, O-horizon pool sizes are largely controlled by the difference between inputs via litterfall and outputs via litter decomposition (Olson 1963) and thus should exhibit marked differences among species that vary in those attributes (Binkley and Giardina 1998). The influence of species on mineral horizon SOM dynamics is likely more complex. Plant species could potentially influence three general mechanisms of SOM stabilization (that is, decomposition): biochemical recalcitrance, chemical stabilization, and physical protection (Sollins and others 1996; Six and others 2002). Species may influence biochemical recalcitrance via the chemistry of organic matter inputs. For example, organic inputs via root turnover and exudation influence labile soil C pool sizes (Neff and Asner 2001; Eviner and Chapin 2003, Dijkstra and others 2006) and current theories of SOM formation suggest the potential for plant species effects on stabilization of soil C into more recalcitrant pools (that is, humus), as well. It has long been thought that plant lignin is an important source of polyphenols that ultimately form quinones that in turn react with amino-compounds to form humus (Stevenson 1994). Therefore, variation among plant species in both detritus lignin concentrations and plant influence over the availability of N-compounds could influence the formation of more stable humus (Eviner and Chapin 2003), with species having higher lignin concentrations or those species that stimulate N mineralization promoting the formation of more stable SOM. However, soil microbes also produce polyphenols (Kögel-Knabner 2002), and the importance of plant- versus microbe-derived polyphenols in forming reactive quinones is unknown. In addition, plant species could indirectly influence humus formation through their influence on the composition of the microbial community, even if plants themselves are not an important source of polyphenols.

Plants species could also influence the chemical stabilization of organic matter at mineral surfaces. Because SOM constituents differ in their affinity for mineral surfaces, species-induced variation in the contribution of organic acids, proteins and poly-

saccharides to the SOM pool is expected to influence sorptive interactions at mineral surfaces (Chorover and Amistadi 2001). Further, because plant species cause divergence in the concentrations of cations in soils (Alban 1982; Lelong and others 1990; Finzi and others 1998b; Dijkstra and Smits 2002; Dijkstra and others 2002; Reich and others 2005), they could influence polyvalent cation ''bridging'' of negatively charged SOM to negatively charged clay particles, thereby reducing its accessibility to decomposers (Oades 1988; Muneer and Oades 1989; Stevenson 1994; Clough and Skjemstad 2000; Mulder and others 2001). Polyvalent cations can also complex directly with SOM molecules, inducing their coagulation and reducing their solubility (Oste and others 2002). Thus, plant species could potentially cause differences in the degree to which SOM is chemically stabilized via their influence on cation chemistry.

Finally, plant species could differ in their influence over the physical protection of SOM into aggregates. For example, Jastrow and others (1998) demonstrated that fine root and mycorrhizal hyphal length (characteristics that vary among plant species) are important in promoting aggregate formation. Earthworms have also been shown to influence soil aggregate formation (Bossuyt and others 2005) and their abundance and composition can also be influenced by plant species composition (Reich and others 2005), indicating a potential indirect route for such effects.

We used a common garden of replicated plots of fourteen European and North American tree species in southwestern Poland to study the influence of tree species on soil element cycling. The garden was established over 30 years before the present study, sufficiently long ago that we expected some signature of plant species on SOM dynamics. Species in the common garden have caused marked divergence in soil pH and exchangeable base cation status: species with Ca-rich tissues have raised soil pH and enriched surface horizons in Ca^{2+}, promoting greater abundance of earthworms and faster forest floor turnover (Reich and others 2005; Hobbie and others 2006). Here, we focus on tree species effects on soil C and N cycling including both organic and near-surface mineral horizons. We hypothesized that species having litter with high concentrations of lignin- and/or N or species that increased the concentrations of polyvalent soil cations would slow rates of SOM decomposition. Specifically, we hypothesized that species would influence O-horizon SOM dynamics through variation in litter chemistry, with lignin-rich species causing slower O-horizon decomposition. Species would influence A-horizon SOM dynamics through both biochemical and chemical stabilization, with lignin- or polyvalent cation-rich species having slower SOM decomposition. Exploring species effects on physical protection of SOM was beyond the scope of the present study; however, we explore whether organic matter dynamics were related to fine root or earthworm biomass, two factors that have been shown to promote physical stabilization of SOM. Because there is some variation across our study site in soil texture and mineralogy (J.C. Chorover and O.A. Chadwick, unpublished data), we compare potential effects of plant species with those of soil physical factors on soil C and N dynamics.

Methods

Site Description

Field measurements and soil collections for laboratory studies were conducted at the Siemianice Experimental Forest near Biadaszki, Poland (51°14.87′N, 18°06.35′E, elevation 150 m) (Reich and others 2005) in a common garden experiment of fourteen European and North American tree species. In 1970 and 1971, the site was prepared by clear-cutting an 81-year-old *Pinus sylvestris* stand followed by stump removal and soil plowing. Soil plowing was intended to reach 60 cm, but visual examination of soils pits indicate that the plow layer typically reached between 30 and 60 cm, likely due to variation in soil mineralogy. Monospecific 400-m^2 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.). The plots were set up in two adjacent blocks (nine species/block, three replicates/species) with four species (*Picea*, *Larix*, *Pseudotsuga* and *Q. robur*) grown in both blocks. Further details regarding site preparation, seed source, and stand management can be found in Reich and others (2005).

The region has a climate transitional between maritime and continental with mean annual precipitation of 591 mm and mean annual temperature of 8.2°C. Soils at the research site are formed in sandy glacial outwash that overlies loam to clay

loam textured ground moraine. The outwash filled in some of the rough topography left by the glacier creating a gently undulating terrain with differing thickness of outwash over moraine. In some places the top meter of soil formed entirely within the outwash whereas in some plots the outwash was confined to the top 30 or 40 cm. In the latter case, plowing upon site establishment mixed the sandy outwash with the underlying loam or clayey material, creating heterogeneity in surface horizon clay content. Thus, soils in the A-horizon ranged in field texture from loamy sand to loam and one block (containing *Abies*, *Acer* spp., *Fagus*, *Picea*, *Pseudotsuga*, *Quercus robur*, *Tilia*, and *Larix*) had higher and more variable (among plots) clay content (4.80% clay, CV = 60.40) than the other block (1.91% clay, CV = 27.97). In late August 2002, we excavated one pit per plot to a depth of at least 100 cm. Each pit was described and sampled by horizon following standard procedures (Schoneeberger and others 1998). The soils classified as sandy, mixed, mesic Typic Ustipsamments for the deep outwash plots and fine-loamy, mixed, mesic Kanhaplic Haplustalfs for the shallow outwash plots (Soil Survey Staff 1999).

Before establishment of the common garden, soil pH of the A-horizon averaged 4.3. However, since the plots were established, 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, cation exchange capacity (CEC) and earthworm abundances, and *P. sylvestris*, *P. nigra*, and *Larix* plots having the most acidic soils with the lowest exchangeable base cation concentrations, CEC and earthworm abundances (Reich and others 2005). More abundant earthworms in plots dominated by Ca-rich species appear to cause more rapid forest floor turnover than in more acidic Ca-depleted plots (Hobbie and others 2006).

Soil C and N Dynamics: Laboratory Assays

We collected soil from the O- and uppermost A-horizons for laboratory measurements of C and N pools and dynamics, exchangeable cations, pH, water-soluble ions extracted from a saturated soil paste, particle size, and concentrations of poorly crystalline minerals as interpreted from measures of Fe and Al in ammonium oxalate extracts, metal-organic complexes as interpreted from Fe and Al in pyrophosphate extracts, and iron oxides as interpreted from Fe extracted by dithionite citrate (see Soil Survey Laboratory Staff 1992 for specific methods). The O_i, O_e and O_a subhorizons were combined to form a single composite organic horizon sample that was readily separated from the top of the mineral soil (A-horizon) because of a sharp bulk density boundary. The lower boundary of the uppermost A-horizon was distinguished on the basis of transition in soil morphological characteristics such as color, structure, texture, and consistency. A-horizon soils were sieved (2 mm) in the field and all soils were kept at 4°C or on ice in coolers during transport back to the University of Minnesota, St Paul, MN, USA. Within five days of collection, we began processing soils, subsampling for microbial biomass determination, 30-day net N mineralization and nitrification potential assays, and long-term incubations for determining respiration, dissolved organic C (DOC) production, dissolved inorganic N (DIN) production, and total C and N. Microbial biomass was determined using chloroform-fumigation, direct extraction in 0.5 M K_2SO_4 (Brookes and others 1985) following a four-day fumigation. Extracts were analyzed for DOC on a Shimadzu TOC/TN analyzer (Shimadzu TOC-V_{CPN}, Shimadzu Scientific Instruments, Columbia, MD). Microbial biomass C was determined by subtracting the total dissolved C in fumigated from non-fumigated samples (we present chloroform-labile C uncorrected for extraction efficiency, but refer to it as microbial biomass). Total C and N in the O-horizon were determined by combustion on a Costech ECS4010 element analyzer (Costech Analytical, Valencia, California) at the University of Nebraska, Lincoln. Total C and N in the A-horizon were determined using a Shimadzu TOC/TN analyzer equipped with a solid sample module (Shimadzu TOC-V_{CPN}, Shimadzu Scientific Instruments, Columbia, MD).

We determined short-term (30-day) net N mineralization and nitrification rates using aerobic incubations of soil at field capacity (−30 kPa) in the dark at room temperature (22°C). One soil subsample was extracted with 2 M KCl and a second was incubated for 30 days prior to extraction with 2 M KCl. The concentrations of (NH_4^+ + NO_3^-)-N in the extracts were determined colorimetrically on an Alpkem FS3000 autoanalyzer (Alpkem, College Station, TX, USA). Final concentrations were subtracted from initials to calculate net N mineralization and nitrification rates.

Subsamples for long-term incubations were placed over glass wool in Pall microfunnel™ filter funnels (100 ml) fitted with ashed GF/F filters. Soils were immediately leached with 75 ml deionized water for 1 h, extracted to −30 kPa, and stored

in the dark at 22°C. After 1, 3, 7, 14, 28, 42, 57, 77, 105, 147, 175, 210, 238, 279, 307, 335, and 387 days, respiration rates were measured by placing filter funnels into 1-l mason jars, and temporarily capping with lids fit with silicone septa. Initial and final (24 h) samples of the headspace were withdrawn using a syringe, and were immediately analyzed for CO_2 concentrations on a gas chromatograph (Shimadzu GC14A, Shimadzu Scientific Instruments, Columbia, MD) using a thermal conductivity detector and a Poropak N column. We calculated respiration rate from the change in headspace CO_2 concentration over time. Cumulative respiration was calculated by determining the average respiration rate for each interval between sampling, multiplying this rate by the duration of the sampling interval, and summing all intervals. Between measurement dates, filter funnels were removed from mason jars, covered with polyethylene film, and stored in the dark. In the O-horizon, cumulative respiration, microbial biomass and DOC production expressed per unit mass of soil and per unit mass of C were highly correlated ($r = 0.85$, 0.90, 0.91, respectively, $P < 0.0001$ in all cases), indicating little variation in C content of the O-horizon. In the A-horizon, cumulative respiration, microbial biomass, and DOC production expressed per unit soil mass and per unit soil C also were correlated, although less tightly ($r = 0.58$, 0.75, 0.78, respectively, $P < 0.0001$) presumably because of greater variation in soil C content in the A-horizon. We present analyses for variables expressed per unit mass of C only.

After days 2, 8, 16, 30, 44, 62, 79, 107, 149, 177, 212, 240, 281, 309, 344, and 392, we leached samples with 75 ml deionized water. Samples were equilibrated with water for 1 hour before extraction at −30 kPa. Leachates were analyzed for dissolved inorganic N (DIN, $NH_4^+ + NO_3^-$) on an Alpkem FS3000 autoanalyzer (Alpkem, College Station, Texas, USA) and for DOC on a Shimadzu TOC/TN analyzer (Shimadzu TOC-V_{CPN}, Shimadzu Scientific Instruments, Columbia, MD). Cumulative DIN was calculated by summing DIN leached at each date.

Field Measurements of N Dynamics

In Situ Net N Mineralization. In situ net N mineralization was measured using capped PVC cores for one year beginning in mid-May, 2003. In each plot, 4.5-cm diameter cores were driven into the soil to a depth of 20 cm at three random locations (after removal of the O_i-horizon) and capped. Simultaneously, three 2.22-cm diameter cores were collected to 20 cm depth around each of the PVC cores. These three cores were composited among cores and across all horizons (O_a, O_e, and A), sieved (2 mm) and subsampled for immediate extraction with 2 M KCl and determination of DIN. After the incubation interval, PVC cores were collected and soils were sieved and subsamples extracted with 2 M KCl. This process (of deploying and incubating cores with initial and final extractions) was repeated for 4, 5-week intervals between mid-May and mid-October, 2003, and for one longer over-winter interval from October 2003 to May 2004 (cores obtained at later dates were placed near each of the three original locations). Extracts were frozen, shipped to Minnesota and analyzed for DIN on an Alpkem FS3000 autoanalyzer (Alpkem, College Station, Texas, USA). We determined net N mineralization and nitrification rates by subtracting final from initial DIN concentrations for each interval, averaging among locations within plots, and summing over all intervals to determine annual rates of N cycling. Rates expressed per g soil were converted to area-based rates using bulk density and depth measurements (see below) and compared to depth-weighted total C and N.

Ancillary Data. We measured a number of litter and soil parameters to use as predictor variables in analyses of soil C and N dynamics (Table 1). Some have been previously published, including leaf litter chemistry (C fractions and nutrient concentrations) (Hobbie and others 2006) and earthworm biomass (Reich and others 2005). Other data included in our analyses, below, were fine root biomass and chemistry, soil exchangeable cation composition and pH, aspects of soil texture and mineralogy, soil temperature and soil moisture.

Fine roots were collected in 2002 in eight cores/plot (4.7 cm diameter, 15 cm depth). Roots were sieved and sorted into the smaller than 2 mm diameter fraction. Roots of canopy trees were isolated based on macroscopic morphology, dried, weighed, ground, and analyzed for (1) C fractions (Van Soest 1994) (ANKOM Fiber Analyzer, Ankom Technology, Macedon, NY) (cell solubles, hemicellulose + bound protein, cellulose, and lignin+other recalcitrants, presented on an ash-free dry mass basis); (2) phosphorus (P), calcium (Ca), potassium (K), and magnesium (Mg) by inductively coupled plasma-atomic emission spectrometry (ICP-AES, Applied Research Laboratory 3560, Fisons, Sunland, CA) following digestion in 10% HCl (Munter and Grande 1981) at the University of Minnesota's Research Analytical Laboratory; and (3) C and N (Costech ECS4010, Costech Analytical, Valencia, CA) at the University of Nebraska,

Table 1. Mean, Coefficient of Variation [CV], and Range across all Plots of Predictor Variables used in Analyses of Organic Matter and N Dynamics grouped by Subsets used for Initial Stepwise Regressions

Predictor subset	Predictor variable	Mean (CV, range) for all plots
Leaf litter chemistry	Cell solubles (%)	40.0 (20.5, 21.4–57.8)
	Cellulose (%)	21.9 (18.5, 16.1–32.3)
	Hemicellulose (%)	13.2 (17.3, 8.0–17.9)
	Lignin (%)	24.6 (34.4, 11.5–48.8)
	N (%)	0.93 (29.80, 0.43–1.45)
	Ca (%)	1.13 (43.60, 0.26–2.49)
	K (%)	0.36 (50.81, 0.07–0.84)
	Mg (%)	0.13 (41.42, 0.04–0.27)
	P (%)	0.13 (30.84, 0.04–0.20)
Root chemistry	Cell solubles (%)	32.9 (19.3, 19.6–44.8)
	Cellulose (%)	21.8 (19.3, 12.7–30.7)
	Hemicellulose (%)	9.4 (22.8, 4.9–13.1)
	Lignin (%)	36.0 (13.9, 24.4–48.1)
	N (%)	0.79 (23.08, 0.46–1.19)
	Ca (%)	0.49 (33.60, 0.20–0.93)
	K (%)	0.16 (43.50, 0.03–0.38)
	Mg (%)	0.12 (28.52, 0.06–0.21)
	P (%)	0.12 (21.80, 0.07–0.18)
Soil cations (A-horizon)	Ca (mmol c/kg)	2.29 (169.51, 0.04–22.57)
	Mg (mmol c/kg)	0.82 (167.49, 0.10–8.90)
	Al (mmol c/kg)	10.95 (35.55, 2.51–21.93)
	Fe (mmol c/kg)	0.29 (78.11, 0.01–0.89)
	% Exchangeable Fe + Al	78.9 (20.7, 27.2–95.9)
	$pH_{saturated\ paste}$	4.35 (12.78, 3.63–6.44)
Soil mineralogy (A-horizon)	% Clay	3.3 (75.7, 1.1–13.6)
	Σ Oxalate extractable Fe, Al, Mn (g kg^{-1})	1.7 (26.2, 0.8–2.8)
	CDB extractable Fe (g kg^{-1})	1.5 (83.6, 0.0–6.4)
	CDB extractable Al (g kg^{-1})	0.8 (33.7, 0.4–1.3)
	Σ Na pyrophosphate extractable Fe, Al, Mn (g kg^{-1})	1.3 (25.5, 0.6–1.9)
Other	Earthworm biomass (g/m^2)	1.5 (151.5, 0.0–10.5)
	Fine Root Biomass (g/m^2 to 15 cm)	312 (60, 94–995)
	Soil %N (depth-weighted to 20 cm)	0.08 (27.90, 0.04–0.14)
	Soil C:N (depth-weighted to 20 cm)	15.02 (29.61, 6.39–26.96)
	O-horizon soil %N	1.32 (18.62, 0.57–1.90)
	O-horizon soil C:N	29.47 (17.31, 22.25–52.83)
	A-horizon soil %N	0.03 (46.35, 0.02–0.10)
	A-horizon soil C:N	33.92 (25.54, 15.28–55.90)
	Mean annual soil temperature (°C, 10 cm)	10.1 (3.4, 9.51–11.34)
	Mean annual soil gravimetric moisture (%, to 20 cm)	6.4 (21.6, 4.08–9.62)

See text for further explanation of predictor variables

Lincoln. Note that because of the low cover of understory vegetation in these plots, identifying tree roots was relatively straightforward.

Soil physical and chemical parameters were determined on samples collected by genetic horizon from pits excavated in each plot (data for the uppermost mineral horizon are presented here). Soil exchangeable cations were analyzed on sieved, air-dried soils subjected to $BaCl_2$ extraction (Amacher and others 1990) followed by inductively coupled plasma mass spectrometry (ICP-MS, Perkin Elmer DRC II, Wellesley, MA) analysis. Percent exchangeable Fe + Al was calculated as the charge fraction of the cation exchange complex occupied by Fe and Al, multiplied by 100. Soil pH was measured using the saturated paste method (Rhoades 1996). Selected soil physical and mineralogical characteristics were measured on sieved, air-dried soils, including soil texture by the pipette method (Gee and Or 2002), mass fraction of poorly crystalline minerals by oxalate extraction, mass fraction of metal-organic complexes by Na-pyrophosphate

extraction, and mass fraction of Fe oxides by citrate dithionite bicarbonate (CDB) extraction (Loeppert and Inskeep 1996).

We recorded soil temperatures (10 cm depth) using one datalogger centered in each plot (HOBO 8K, Onset Computer Corporation, Bourne, MA, USA) hourly from February 1999 to November 2000. We measured soil moisture gravimetrically in the 9 cores/plot used for initial KCl extractions at each net N mineralization measurement interval. Moisture was averaged by plot and then averaged over the five measurement dates during the growing season, 2003.

Statistical Analyses

Our general approach was to examine relationships between important aspects of C and N dynamics and various potential predictors (Table 1) first at the species (mean) level ($n = 14$) and second across all plots ($n = 53$). The large number of highly correlated potential predictor variables relative to the small number of species made use of multivariate techniques to tease apart the relative importance of potential predictors infeasible at the species level. Thus, we used simple bivariate regression to provide an overview of patterns among species. We followed these simple regressions with analyses of interplot ($n = 53$) variation in soil C and N dynamics using backwards stepwise regression to simultaneously assess species and parent material effects with a greater overall sample size than was possible at the species mean level. Our hypotheses focused on how species influence soil C and N dynamics, and indeed, some of our predictors were clearly plant species traits (for example, tissue nutrient concentrations). However, because there was heterogeneity across plots in parent material (and thus in clay content), we also included as predictors in our analyses soil factors that are largely independent of species (for example, % clay) or are influenced by both parent material and plant species (for example, soil pH).

We began with general hypotheses about the relationships of soil C and N cycling, plant traits, and soil characteristics. However, we had many potential predictor variables but lacked explicit hypotheses to help us eliminate predictors, and were concerned about possible collinearity because many of these predictor variables were closely related. Because of both of these issues, our general approach was to (1) log-transform variables with relatively large ranges (Weisberg 2005), (2) divide the entire set of potential predictor variables into smaller subsets of related predictors for preliminary stepwise multiple regressions (Table 1), and (3) combine those predictors retained during preliminary stepwise regressions into a final stepwise multiple regression model. We used Akaike's Information Criterion (AIC), which rewards good model fit while penalizing for more model terms, to select predictors to retain in preliminary multiple regressions and to include in the final multiple regression model in a stepwise manner. Specifically, we started with a multiple regression model that included all potential predictors within a given subset (Table 1) and eliminated predictors one at a time in the order of which one produced the greatest reduction in AIC (Weisberg 2005). We proceeded until predictor elimination resulted in no further reduction in AIC. Then we combined the predictors retained in each of the models created using the predictor subsets into a single new multiple regression model and again used AIC to eliminate predictors in a stepwise manner to generate a final model. We used variance inflation factors (for example, Weisberg 2005) as well as pairwise correlations of predictors retained in the model as a final check against the inclusion of highly correlated (for example, collinear) predictors in the same model.

For O-horizon cumulative respiration, cumulative DOC production, and microbial biomass, predictor subsets included leaf litter chemistry, root chemistry, and earthworm biomass from the ''other'' subset (see Table 1). For A-horizon cumulative respiration, cumulative DOC production, and microbial biomass, predictor subsets included those used for the O-horizon along with soil cations, soil mineralogy, and (from the ''other'' subset) root biomass.

For in situ net N mineralization and nitrification (and their ratio), we included all predictor subsets and (from the ''other'' subset) earthworm biomass, fine root biomass, soil %N and C:N (depth-weighted to 20 cm), mean annual soil temperature, and mean annual soil moisture. For O-horizon short-term (30-day) laboratory net N mineralization and nitrification and long-term (1-year) cumulative DIN production, we included leaf litter chemistry and root chemistry subsets and (from the ''other'' subset) earthworm biomass and O-horizon %N and C:N. For A-horizon short-term (30-day) net N mineralization and nitrification and long-term (1-year) cumulative DIN production, we included all subsets and (from the ''other'' subset) earthworm biomass, fine root biomass, and A-horizon %N and C:N.

Results

Tree species influenced SOM C and N dynamics, but via markedly different mechanisms, with C dynamics influenced largely via species influence on chemical stability and N dynamics determined largely via effects on substrate chemistry. These patterns, and their relations to our original hypotheses, are discussed separately in the following sections.

Carbon Dynamics

O-Horizon. In contrast to our hypothesis, neither leaf litter lignin nor root lignin concentration was an important predictor of O-horizon organic matter decomposition in analyses of species means or of all plots. In bivariate regressions of species means, leaf litter K, root Mg and earthworm biomass were significantly ($P < 0.05$) positively related to O-horizon cumulative respiration; leaf litter Ca, leaf litter K and root K were positively related to microbial biomass; and no potential predictor was significantly related to cumulative DOC production. In multivariate analyses (Table 2), our predictors explained one-third of the variation in cumulative respiration in the O-horizon and only two predictors were significant: root N was negatively and earthworm biomass was positively related to O-horizon respiration, perhaps because in plots with greater earthworm biomass, the O-horizon is dominated by fresh, relatively undecomposed litter (Hobbie and others 2006). Microbial biomass was significantly (positively) related to leaf litter K only. Cumulative DOC leached from O-horizon soils was negatively related to leaf litter Ca and positively related to leaf litter P and root lignin concentrations. Although different predictors ended up explaining significant variation in respiration, microbial biomass and DOC production, cumulative respiration in the O-horizon was significantly correlated with both microbial biomass ($r = 0.72$, $P < 0.0001$) and cumulative DOC production ($r = 0.40$, $P < 0.003$).

A-Horizon. Tree species ranged two-fold in cumulative respiration rates and nearly four-fold in microbial biomass in the A-horizon (Table 3). In bivariate regressions of species means, A-horizon cumulative respiration and microbial biomass were significantly ($P < 0.05$) positively related to % clay, saturated pasted pH, root and leaf litter Ca and K, exchangeable Ca and Mg, CDB Fe, and fine root biomass and negatively correlated with exchangeable Fe and % exchangeable Fe + Al. Microbial biomass was additionally positively related to earthworm biomass. Of these significant predictors, % exchangeable Fe + Al was the best single predictor of cumulative respiration (Figure 1, $P = 0.002$, $R^2 = 0.58$) and microbial biomass ($P < 0.0001$, $R^2 = 0.77$). However, it was impossible to use multiple regression to tease apart the relative importance of various predictors at the species level, because many potential predictors were highly correlated with one another (for example, soil texture, exchangeable cations, pH, litter and root cation concentrations; analyses not shown). Hence, we use the following multiple regression analyses, at the plot level.

The multiple regression analyses indicate that in the A-horizon, our hypothesis was partially supported in that respiration and microbial biomass were both strongly inhibited by high concentrations of trivalent Al and Fe on the CEC (that is, high % exchangeable Fe + Al). In contrast, respiration and microbial biomass were unrelated to aspects of leaf litter or root chemistry, indicating little role of plants in influencing biochemical recalcitrance of SOM. Specifically, cumulative respiration and microbial biomass C were strongly negatively related to % exchangeable Fe + Al and positively related to fine root biomass (Table 2), and unrelated to aspects of leaf litter or root chemistry. These relationships are illustrated by the bivariate scatterplots of the dependent variables in relation to the significant predictors from the full model (Figure 2A–D).

Cumulative DOC production was significantly correlated with cumulative respiration ($r = 0.44$, $P = 0.001$), but not with microbial biomass ($r = -0.0007$, $P = 1.00$) and was negatively related to leaf litter cell soluble, cellulose, and Mg concentrations and earthworm biomass, although only one-fourth of its total variation could be explained by these variables (Table 2).

As noted above, A-horizon percent exchangeable Fe + Al was strongly associated with both cumulative respiration and microbial biomass at species and plot levels (Figures 1, 2; Table 2) and thus appears to play an important role in governing A-horizon C dynamics. Given our interest in characterizing species effects, it is important to ask whether variation in exchangeable Fe + Al was a function of innate microsite properties or of species. Based on several analyses, exchangeable Fe + Al appears to be a function of plant species characteristics as well as of soil mineralogy and texture. When we used exchangeable Fe + Al as the dependent variable in a stepwise multiple regression that included leaf litter and root base cation concentrations and % clay as predictors (overall $R^2 = 0.64$), % exchangeable Fe + Al was significantly negatively related to root

Table 2. Results of Stepwise Regressions using Plots as Observations (n = 53)

Study component	Dependent variable	Units	Significant predictors in final model	R^2
O-horizon laboratory C pools/dynamics (1-year incubation)	Cumulative respiration	g C kg soil C^{-1}	Root N* (−), earthworm biomass*	0.34
	Microbial biomass C	g C kg soil C^{-1}	Litter K***	0.23
	Cumulative DOC production	g C kg soil C^{-1}	Litter Ca** (−), litter P**, root lignin*	0.32
A-horizon laboratory C pools/dynamics (1-year incubation)	Cumulative respiration	g C kg soil C^{-1}	% Exchangeable Fe + Al*** (−), fine root biomass**	0.46
	Microbial biomass C	g C kg soil C^{-1}	% Exchangeable Fe + Al*** (−), fine root biomass***	0.66
	Cumulative DOC production	g C kg soil C^{-1}	Litter cell solubles** (−), litter cellulose* (−), litter Mg** (−), earthworm biomass * (−)	0.24
In situ N dynamics	Net N mineralization	g N m^{-2} y^{-1}	Litter cellulose* (−), litter P* (−), root N***, root K***, root P* (−), CDB Fe* (−)	0.52
	Net nitrification	g N m^{-2} y^{-1}	Litter P** (−), root N***, root Ca*, root K***, root P** (−), CDB Fe** (−)	0.75
	Net nitrification/net N mineralization	None	Litter P* (−), root hemicellulose** (−), root cellulose*, root N***, root Ca*, root K***, exchangeable Fe* (−), fine root biomass* (−)	0.66
O-horizon laboratory N dynamics (long-term incubation)	Cumulative DIN production	mg N g $soil^{-1}$	Root Mg**, soil %N*	0.22
O-horizon laboratory N dynamics (30-day incubation)	Net N mineralization	μg N g $soil^{-1}$ d^{-1}	Litter P*, root N***	0.37
	Net N mineralization	μg N g soil N^{-1} d^{-1}	Litter P**, root N***	0.34
	Nitrification	μg N g $soil^{-1}$ d^{-1}	Root N***, root K**	0.24
	Nitrification	μg N g soil N^{-1} d^{-1}	Root N**	0.15
A-horizon laboratory N dynamics (long-term incubation)	Cumulative DIN production	mg N g $soil^{-1}$	% Exchangeable Fe + Al*** (−), soil %N***	0.82
A-horizon laboratory N dynamics (30-day incubation)	Net N mineralization	μg N g $soil^{-1}$ d^{-1}	Root N*, root K**, fine root mass* (−), soil %N***	0.60
	Net N mineralization	μg N g soil N^{-1} d^{-1}	Exchangeable Mg***, fine root mass (−)***	0.54
	Nitrification	μg N g $soil^{-1}$ d^{-1}	Fine root mass* (−), soil %N***	0.61
	Nitrification	μg N g soil N^{-1} d^{-1}	Exchangeable Ca***, $\sum$ Na pyr.* (−)	0.42
	%N	g N 100 g $soil^{-1}$	Root cell solubles**, root Mg** (−), exchangeable Fe*, %exchangeable Fe + Al*** (−), fine root mass**	0.68

*Predictor variables that were retained in the final model and that were significant ($P \leq 0.05$) are indicated for each dependent variable analyzed, along with the final model R^2. Negative predictor coefficients are indicated. ***$P \leq 0.001$, **$P \leq 0.01$, *$P \leq 0.05$.*

Table 3. Species Means (SE) for Select Processes and Attributes

Species	A-horizon cumulative respiration (g C kg soil C^{-1})	A-horizon microbial biomass C (g C kg soil C^{-1})	Net N mineralization (g N m^{-2} y^{-1})	Net nitrification (g N m^{-2} y^{-1})	Nitrification: mineralization
Abies alba	144.5 (5.9)	5.2 (2.2)	6.4 (2.5)	1.8 (1.1)	0.23 (0.07)
Acer platanoides	196.8 (52.9)	11.7 (5.3)	11.2 (4.5)	1.5 (0.8)	0.13 (0.04)
Acer pseudoplatanus	179.3 (47.8)	12.2 (2.4)	11.3 (0.8)	3.1 (0.6)	0.25 (0.04)
Betula pendula	140.2 (4.5)	5.0 (0.6)	10.2 (1.8)	1.2 (1.0)	0.09 (0.07)
Carpinus betulus	121.4 (12.6)	5.5 (0.6)	5.9 (1.5)	0.1 (0.1)	0.02 (0.01)
Fagus sylvatica	97.5 (10.8)	5.2 (1.6)	8.3 (0.9)	1.9 (1.2)	0.22 (0.12)
Larix decidua	129.8 (20.1)	5.6 (0.7)	6.7 (2.2)	1.1 (0.5)	0.14 (0.04)
Picea abies	159.2 (16.6)	5.0 (0.7)	10.1 (3.1)	2.1 (1.1)	0.15 (0.05)
Pinus nigra	140.5 (9.9)	4.9 (0.8)	6.2 (0.9)	1.4 (1.0)	0.19 (0.13)
Pinus sylvestris	114.8 (9.0)	3.9 (0.2)	6.3 (1.0)	1.2 (0.6)	0.14 (0.07)
Pseudotsuga menziesii	116.7 (7.0)	4.4 (0.6)	6.5 (1.3)	1.4 (0.4)	0.17 (0.04)
Quercus robur	146.8 (16.0)	8.2 (1.3)	7.7 (1.4)	1.5 (0.7)	0.15 (0.06)
Quercus rubra	135.8 (13.5)	3.2 (0.8)	3.3 (0.6)	0.1 (0.0)	0.02 (0.01)
Tilia cordata	166.4 (34.0)	8.0 (1.9)	5.6 (1.0)	0.9 (0.2)	0.15 (0.02)
Mean of all species (SE)	140.3 (7.5)	6.1 (0.7)	7.7 (0.6)	1.4 (0.2)	0.15 (0.02)

Mineralization and nitrification are in situ rates.

Ca concentration ($P < 0.0001$), % clay ($P < 0.0001$), and root K ($P = 0.02$) concentrations; and positively related to root Mg ($P = 0.01$). When we conducted this same analysis using species (rather than plots) as observations (overall $R^2 = 0.96$), the results were similar: exchangeable Fe + Al was negatively related to root Ca ($P < 0.001$), % clay ($P = 0.02$), and leaf litter K ($P = 0.02$) and positively related to root Mg ($P = 0.01$). Given that exchangeable Al + Fe is a strong driver of A-horizon C dynamics (Figure 2; Table 2), we conclude that species traits (via their influence on exchangeable Al + Fe) play an important role along, with soil mineralogy, in influencing A-horizon SOM C dynamics.

Nitrogen Dynamics. In situ net N mineralization and nitrification rates were significantly correlated with laboratory measures of A-horizon N dynamics (in which the environment was held constant) (Table 4), indicating that variation in substrate quality or other soil chemical properties are important factors contributing to plot-to-plot variation in in situ N dynamics. In situ net nitrification rates were further strongly positively correlated with in situ net N mineralization rates (Table 4), suggesting that NH_4^+ production is a strong constraint over net nitrification among plots. Correlations between O- and A-horizon rates of nitrification indicate that some plots are more favorable for nitrification throughout the surface horizons than others.

Tree species differed three-fold in rates of in situ net N mineralization and 30-fold in rates of net nitrification, with *Acer pseudoplatanus* having the highest and *Quercus rubra* having the lowest rates (Table 3). As with SOM decomposition, at the species level, many potential predictor variables were highly correlated, impeding statistical approaches to discerning their relative importance in explaining species variation in N dynamics. In bivariate regressions, in situ net N mineralization and nitrification rates and cumulative DIN production from incubated A-horizon soils were significantly ($P < 0.05$) positively related to exchangeable Ca, K, and Mg concentrations, earthworm biomass, and % clay and negatively related to % exchangeable Fe + Al. In addition, net N mineralization and DIN production were related positively to soil %N and negatively to soil C:N. Net nitrification and the ratio of nitrification:mineralization were related positively to root N concentration. In short-term laboratory incubations, O- and A-horizon net N mineralization and nitrification were positively related to root N concentration and A-horizon rates additionally were related positively to total A-horizon soil N concentration.

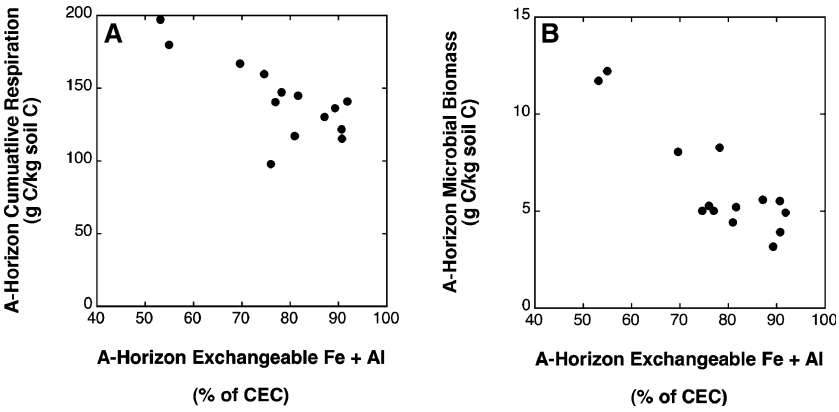

Figure 1. Scatterplots of cumulative respiration and microbial biomass in the A-horizon versus % exchangeable Fe + Al. Each point represents the mean of replicate plots of a species. See text for statistical analyses.

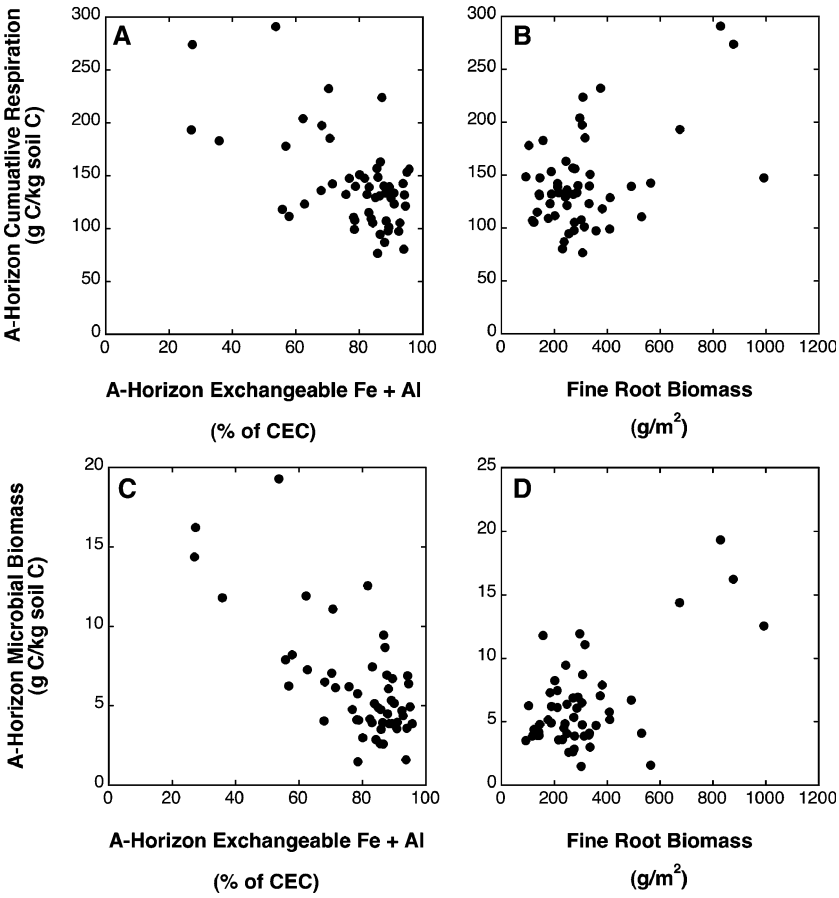

Figure 2. Scatterplots of cumulative respiration and microbial biomass in the A-horizon versus the predictors % exchangeable Fe + Al and fine root biomass. Each point represents a single plot. See Table 2 for statistical analyses.

In stepwise multiple regressions including all plots, in situ net N mineralization and nitrification were related to a similar set of predictor variables, consistent with their tight correlation (Tables 2, 4). Root N and root K were strongly positively related to both aspects of N cycling as well as to the ratio of net nitrification: net N mineralization (Table 2). Other variables (for example, leaf litter P, root P and CDB Fe) were more weakly and negatively correlated with both net N mineralization and nitrification.

In laboratory incubations of O-horizon soils, cumulative DIN production from long-term incubations was related positively to root Mg and soil N (%), whereas in short-term (30-day) laboratory incubations, O-Horizon net N mineralization was related positively to both leaf litter P and root N concentrations (Table 2). Net nitrification was also positively related to root N concentration. In incubations of A-horizon soils, cumulative DIN production from long-term incubations was related negatively to % exchangeable Fe + Al and

Table 4. Correlation Coefficients for Pairwise Correlations between various Field and Laboratory Measures of Soil N Cycling

	NetNMin (gN m^{-2} y^{-1})	NetNit (gN m^{-2} y^{-1})	O DIN production (mgN/g soil)	O potential N Min (μgN g $soil^{-1}$ d^{-1})	O potential Nit (μgN g $soil^{-1}$ d^{-1})	A DIN production (mgN/g soil)	A potential N Min (μgN g $soil^{-1}$ d^{-1})	A potential Nit (μgN g $soil^{-1}$ d^{-1})
NetNMin (gN m^{-2} y^{-1})	1.00							
NetNit (gN m^{-2} y^{-1})	**0.81*****	1.00						
O DIN production (mgN/g soil)	−0.14	−0.11	1.00					
O potential N Min (μgN g $soil^{-1}$ d^{-1})	−0.02	0.05	**0.37****	1.00				
O potential Nit (μgN g $soil^{-1}$ d^{-1})	0.18	**0.38****	0.10	**0.67*****	1.00			
A DIN production (mgN/g soil)	**0.31***	**0.33***	0.03	0.01	0.12	1.00		
A potential N Min (μgN g $soil^{-1}$ d^{-1})	**0.50*****	**0.64*****	−0.09	0.04	**0.29***	**0.69*****	1.00	
A potential Nit (μgN g $soil^{-1}$ d^{-1})	**0.50*****	**0.65*****	−0.17	0.11	**0.35***	**0.65*****	**0.91*****	1.00

NetNMin: in situ net N mineralization rate; NetNit: in situ net nitrification rate; DIN Production: cumulative DIN production in long-term laboratory incubations; Potential N Min: net N mineralization in short-term 30-day incubations; Potential Nit: net nitrification in short-term 30-day incubations; O: O-horizon soils; A: A-horizon soils.
Bold type indicates significance at $P \leq 0.05$.
$^{***}P \leq 0.001$, $^{**}P \leq 0.01$, $^{*}P \leq 0.05$.

positively to soil N (%), whereas in short-term incubations, net N mineralization and nitrification were related positively to soil N (%) and negatively to fine root mass. Net N mineralization was also related positively to root N and root K concentrations.

Discussion

Our overall hypotheses were only partially supported, in that trees species apparently influenced SOM C dynamics primarily through their influence on chemical stabilization rather than on biochemical recalcitrance, but affected N dynamics via tissue N concentrations. For example, plant foliar and root lignin concentrations did not explain variation in SOM dynamics in either the organic or mineral soil horizons. Rather, effects of soils and plants on exchangeable cation chemistry were important in influencing rates of organic matter decomposition and microbial biomass, particularly in the mineral horizons. In contrast, across plots, soil net N mineralization and nitrification rates were consistently influenced by root chemistry and biomass, suggesting an overriding importance of tree effects on substrate chemistry and quantity in driving tree effects on N dynamics.

Carbon Dynamics

In contrast to our hypothesis, tree species did not appear to influence SOM dynamics through variation in the lignin concentration of organic inputs (litter, roots) to soils. Rather, trees influenced SOM dynamics primarily through their influence on soil cation chemistry, but via different mechanisms and to differing degrees in the organic and mineral horizons.

In the O-horizon, organic matter decomposition (as measured by cumulative respiration from long-term laboratory incubations) was positively related to earthworm biomass, likely because greater earthworm biomass, particularly of *Lumbricus terrestris*, is associated with lower forest floor mass (Reich and others 2005), more rapid forest floor disappearance (Hobbie and others 2006), and very little accumulation of an O_e or O_a horizon (personal observation). Thus, in plots with high earthworm abundance, the O-horizon consists mostly of relatively undecomposed leaf litter (O_i) that is likely of higher substrate quality for microbial decomposition than more humified O_e- and especially O_a-horizon material in plots with lower earthworm abundance. Disappearance of the O_e and O_a horizons also has been shown in

studies of invading *Lumbricus rubellus* in North America (Alban and Berry 1994; Gundale 2002; Hale and others 2005).

The relationship of microbial biomass to leaf litter K in the O-horizon may reflect specific nutritional requirements of the microbial community in these sites, although K limitation of the microbial community is unlikely (Harder and Dijkhuisen 1983). The mechanisms responsible for variation in O-horizon DOC production among species and across plots are also unclear. The negative correlation between leaf litter Ca and DOC production may have arisen because plots dominated by Ca-rich species have little O_a horizon. Another study found that the more humified O_a horizon contributes proportionally more to DOC production than the less humified O_i horizon (Park and others 2002).

In the A-horizon, SOM decomposition and microbial biomass were both negatively related to % exchangeable Fe + Al (the % of the CEC occupied by exchangeable acidic hydrolyzing cations, Fe^{3+} + Al^{3+}) and positively related to fine root biomass. Other studies also have shown that Al correlates negatively with microbial respiration and biomass, either across sites that vary naturally in exchangeable Al (Illmer and others 2003) or with experimental Al addition (Boudot and others 1989; Brynhildsen and Rosswall 1997; Mulder and others 2001). The negative relationship between SOM decomposition and % exchangeable Fe + Al could arise for several reasons (Mulder and others 2001), although it is difficult to distinguish among them using correlation analysis alone, and indeed, % exchangeable Fe + Al was negatively correlated with soil pH, % clay and exchangeable Ca and Mg concentrations ($r = -0.66$, -0.67, -0.82, -0.84, $P < 0.001$ in all cases). First, the cations Fe^{3+} and Al^{3+} should be effective at flocculating organic matter and serving as cation bridges between humus and clay minerals, chemically stabilizing organic matter and decreasing its accessibility to decomposers (Boudot and others 1989; Brynhildsen and Rosswall 1997; Mulder and others 2001; Oades 1988; Oades and Waters 1991; Skjemstad 1992). Much of the work done on chemical stabilization via cation bridging has focused on Ca^{2+} (Clough and Skjemstad 2000; Paul and others 2003), perhaps because of the importance of Ca^{2+} in agricultural soils that are subject to liming as well as the importance of calcareous soils in agricultural regions. Indeed, Groffman and others (2006) found that Ca addition to a watershed led to a reduction in microbial biomass. However, it is well known that trivalent Al and Fe can be more effective than bivalent Ca for cation bridging to layer silicate clays such as montmorillonite (Varadachari and others 1991; Stevenson 1994). Second, as the relative proportion of these acidic cations on the cation exchange complex trends inversely with forest soil pH, slower decomposition of SOM in soils with higher % exchangeable Fe + Al could have resulted from direct inhibitory effects of acidic pH on microbial activity or from pH-induced changes in the microbial community (Fierer and Jackson 2006) that slowed rates of decomposition. Third, complexation of organic matter with Al^{3+} may render that organic matter more toxic to decomposers (Illmer and Schinner 1997, but see Brynhildsen and Rosswall 1997), leading to slower decomposition in the presence of greater exchangeable Al^{3+}. It is unlikely that the negative correlation between % exchangeable Fe + Al and SOM decomposition was actually caused by a relationship between % clay and SOM decomposition. Even though % clay and exchangeable Fe + Al were correlated, this relationship was negative. Thus, SOM decomposition was actually positively related to % clay, opposite of the expected relationship, because clay is thought to stabilize organic matter and protect it from decomposition (for example, Burke and others 1989; but see Percival and others 2000). More likely, the positive relationship between % clay and SOM decomposition arose because greater % clay was associated with higher concentrations of base cations and more neutral pH, leading to displacement of Fe and Al on the cation exchange complex and reduced Fe and Al solubility (Dijkstra and Fitzhugh 2003).

The positive relationship between fine root biomass and SOM decomposition likely arose because, through exudation, sloughing, and turnover, roots were a source of relatively labile C for decomposers. Indeed, microbial biomass and activity often are related to plant detritus production (Johnson and others 2003; Zak and others 2003; Bond-Lamberty and others 2004; Dijkstra and others 2005), and in this system, roots are likely an important C source for decomposers. In addition, labile C produced by roots may be important in priming the decomposition of more recalcitrant SOM (Kuzyakov 2002) such that greater SOM decomposition occurs where there is more root biomass to induce a priming effect. This positive correlation also suggests that any positive effects of fine roots on decomposition via provision of substrate were greater than negative effects that might occur via promotion of aggregate formation and physical stabilization of organic matter (for example, Jastrow and others 1998).

The similar responses of organic matter respiration and microbial biomass are not surprising and suggest that they are closely linked. As in many systems (Zak and others 1994), microbial biomass is likely C-limited in this system. Thus, chemical stabilization of organic matter by polyvalent cations should by definition reduce its availability to microorganisms, inducing C limitation and limiting microbial biomass. Low microbial biomass in turn should lead to slower decomposition of organic matter and lower respiration rates. Increased inputs of labile C associated with greater fine root biomass should stimulate C-limited microbial biomass.

The lack of the hypothesized relationship between plant foliar and root lignin concentrations and SOM decomposition (and microbial biomass) could have resulted from several factors. First, plant lignin may not be the dominant source of polyphenols contributing to humus formation if microbial production of polyphenols (Stevenson 1994; Kögel-Knabner 2002) is of overriding importance in this system. Second, the lack of a significant correlation between leaf litter lignin and root lignin concentrations among plots (data not shown) may have led to relatively small overall differences among plots in total plant lignin concentrations, effects of which we were unable to detect. In addition, as found in other systems, biochemical recalcitrance arising from selective preservation of lignin may be relatively unimportant here (Kiem and Kögel-Knabner 2003; Kramer and others 2003). Third, differences in biochemical recalcitrance caused by species variation in lignin concentrations may simply have been small relative to differences in biochemical recalcitrance and chemical stabilization caused by differences in root biomass and cation-stabilization effects, respectively. Finally, the proximate method used to analyze lignin concentrations presented here (acid hydrolysis) likely leads to an overestimate of actual lignin concentrations, as ''lignin'' measured this way may include cutin and tannin along with lignin (Preston and others 1997, 2000). Other methods of characterizing lignin more reliably such as ^{13}C NMR spectroscopy (Preston and others 1997) and oxidation with cupric oxide (Hedges and Ertel 1982; Johansson and others 1986) could hypothetically have revealed relationships between soil C dynamics and lignin, but were beyond the scope of the current study.

Nitrogen Dynamics

Correlations among the various measurements of N dynamics (Table 4) suggest that interplot differences in in situ net N mineralization rates were related in part to interplot differences in A-horizon substrate chemistry and availability rather than being solely explained by interplot variation in environmental factors (for example, temperature and moisture). Consistent with that interpretation, environmental variables did not explain significant variation in in situ net N mineralization rates across plots.

Rather, our results suggest that trees exerted influence over net N mineralization rates, primarily via interspecific variation in root chemistry and biomass. Across plots, root N was strongly and significantly (positively) related to both in situ and O- and A-horizon laboratory measures of net N mineralization, consistent with a number of other studies showing positive relationships between net N mineralization and soil N:C or detritus N:C or N:lignin (Wedin and Tilman 1990; Reich and others 1997, 2001; Scott and Binkley 1997; Finzi and others 1998b; Lovett and others 2004; Dijkstra and others 2006). These relationships arise because gross N mineralization rates increase whereas immobilization rates decrease with increasing detritus N:C ratios (Booth and others 2005). That net N mineralization rates were unrelated to % exchangeable Fe + Al and were unrelated or negatively related to fine root biomass, the two factors most related to SOM decomposition, suggests an overriding influence of trees on immobilization rather than mineralization (that is, decomposition) processes. Interestingly, in long-term incubations, cumulative DIN production was significantly negatively related to % exchangeable Fe + Al. This could reflect an increasing ratio of net to gross N mineralization (which should in turn be related to SOM decomposition) during the incubation, if declining C availability reduces microbial demand for N (Hart and others 1994). Although plots with greater fine root biomass likely had faster rates of SOM decomposition and thus gross N mineralization rates, these plots had slower net N mineralization, likely because greater root-derived organic matter inputs stimulated N immobilization.

The negative relationship between net N mineralization and fine root biomass may also be reinforced by the significant (albeit loose) negative relationship between root N and fine root biomass across plots (data not shown) and, in turn, the positive relationship between root N and net N mineralization rate. The negative relationship between root N and fine root biomass has been observed in other systems (Reich and others 2001; Craine and others 2002) and likely arises because of the association between high root N and high root

turnover (and thus low fine root biomass) (Reich and others 2001; Withington and others 2006). Indeed, across the fourteen species studied here, high root N is associated with short root lifespan (Withington and others 2006). Thus, the combination of high root biomass and low root N likely operate together to reduce rates of net N mineralization through their stimulation of immobilization rates.

Relationships between net N mineralization and other aspects of root chemistry are less easy to interpret. Root K was consistently positively related to net N mineralization, whereas leaf litter P was significantly positively related to net mineralization in the O-horizon. We have no good suggestions for the mechanisms underlying these relationships.

In short-term laboratory incubations, A-horizon net N mineralization and nitrification rates were positively related to soil N concentrations and negatively related to root biomass. Other studies have shown that gross N mineralization rates are positively related to soil N (Wang and others 2001; Booth and others 2005), likely reflecting a straightforward relationship between gross N mineralization rates and the size of the total and, thus, mineralizable N pool. As discussed above, the negative relationship between net N mineralization and root biomass may reflect greater N immobilization with greater root-derived C inputs.

Patterns of net nitrification largely followed those of net N mineralization as seen in other studies (Walters and Reich 1997; Finzi and others 1998b; Lovett and others 2004; Booth and others 2005), suggesting that nitrification rates are limited by the rate of ammonification across plots. The ratio of in situ nitrification to mineralization was positively related to root N, suggesting that plots with high root N had NH_4^+ in excess of N demand by heterotrophic microbes that was available for nitrification. Both net nitrification and the ratio of net nitrification:mineralization were strongly positively related to both root K and root Ca, which in turn were positively related to soil pH (data not shown). Thus, these relationships could have arisen because nitrification was inhibited at more acidic pH (Robertson 1982), although root K was also strongly related to net N mineralization, so they could also partly reflect the influence of mineralization on nitrification rates.

Are Tree Species Influencing Soil Carbon and Nitrogen Dynamics?

Our analyses indicate that species likely contribute to variation in soil C and N dynamics. Tree species likely influenced SOM decomposition by influencing the concentrations of trivalent acidic cations and thus the chemical stabilization of organic matter: when species rather than plots were analyzed, percent exchangeable Fe + Al was the most significant single predictor of both cumulative respiration and microbial biomass in the A-horizon, being negatively correlated with both. Furthermore, across plots and species, % exchangeable Fe + Al was negatively related to both root Ca (a trait that differed significantly among species, one-way ANOVA, $P < 0.001$) and clay content (a parent material characteristic), which likely contributes to high base cation concentrations, and thus low % exchangeable Fe + Al. Species with high root Ca, in particular, were associated with low % exchangeable Fe + Al, likely because these species enrich surface soils in base cations. This results not only in an increase in soil pH, but also reduced solubility of Fe^{3+} and Al^{3+} bearing mineral phases, leading to replacement of the hydrolyzing trivalent cations on the exchange complex with base cations (Dijkstra and Fitzhugh 2003). However, variation in clay content also contributed to variation in exchangeable Fe + Al, likely because clay minerals are an important source of variation in base cations in these soils (Callesen and Raulund-Rasmussen 2004). Thus, clay-poor soils have higher exchangeable Fe + Al as a fraction of total cation exchange capacity than clay-rich soils.

Given the tight correlation among soil characteristics associated with texture, acidity, and base cation status among species, we cannot rule out that species variation in SOM decomposition may have also arisen from species-induced variation in soil pH, which was highly correlated with both % exchangeable Fe + Al and with A-horizon respiration. Higher pH may have favored microbial activity because of direct physiological tolerance effects, changes in microbial community composition (Fierer and Jackson 2007) or Al toxicity at lower pH (Illmer and Schinner 1997; but see Brynhildsen and Rosswall 1997). At these sites, soil pH is likely influenced by tree species as well as clay content because both leaf litter and root Ca are positively related to soil pH, even when accounting for variation among plots and species in soil clay content (Reich and others 2005, analyses not shown).

Our results contrast those of a study of an overlapping set of tree species showing that SOM mineralization rates were unrelated to soil pH. In that study, soil C:N ratio was negatively correlated with respiration, at least at one site (Ladegaard-Pedersen and others 2005). We found a similar negative relationship in this study (analysis not

shown), although it is unclear whether lower soil C:N ratios contribute to or result from higher SOM decomposition rates. That study did not include the broadleaf deciduous species (*Acer* spp., *Tilia*) that caused the greatest increase in soil pH and exchangeable base cation concentrations in this study. Thus, among species that differ less in cation concentrations than those studied here, effects on other factors besides soil cation status and pH may be more important in explaining species differences in SOM decomposition.

Tree species influenced soil N dynamics through interspecific variation in detritus chemistry. Functional groups, specifically conifers and hardwoods, did not differ on average in net N mineralization rates (one-way ANOVA, $F_{1,12} = 0.40$, $P = 0.54$), although some studies have reported lower rates of net N mineralization under conifers than under hardwoods (for example, Lovett and others 2004). However, our results are consistent with a prior analysis suggesting that these two groups do not differ in this respect when grown on similar substrates (Reich and others 1997). Instead our results suggest that traits that vary within as well as among groups strongly influence soil N dynamics. Net N mineralization rates were positively related to root N concentrations across plots, a result that is consistent with other studies of species effects on N cycling (Wedin and Tilman 1990; Dijkstra and others 2006). However, across species, net N mineralization rates were strongly negatively correlated with soil exchangeable Al + Fe and soil C:N ratio and positively related to base cation status, clay content and soil pH, even though these predictors were not important in explaining plot-to-plot variation in N dynamics. Other studies have also found that gross and net N mineralization and nitrification rates are inversely related to soil C:N ratios among forest stands of different species composition (Finzi and others 1998b; Thomas and Prescott 2000; Lovett and others 2004; Högberg and others 2006) and that soil C:N ratios are lower in sites with higher pH and base cation concentrations (Giesler and others 1998; Högberg and others 2006).

Nitrification rates were strongly correlated with net N mineralization rates across species, as has been seen in previous studies both within (Walters and Reich 1997) and across species (Finzi and others 1998b). Although a previous study reported that North American stands dominated by *Quercus rubra* had lower rates of nitrification than expected from their rates of net N mineralization (Lovett and others 2004), low rates of nitrification in *Q. rubra* plots in the present study could be explained by low rates of net N mineralization (Table 3). However, why *Q. rubra* was associated with such low rates of net N mineralization in this study relative to rates measured in a range of its native sites remains unclear.

Species likely additionally influenced nitrification rates via their influence on base cation status—root Ca was positively related to both nitrification rates and the ratio of nitrification:mineralization. Because root Ca is significantly and strongly correlated with soil pH (data not shown), this could reflect more favorable conditions for nitrification under species that create less acidic soils (Robertson 1982), although some studies have demonstrated significant nitrification in acidic forest soils (De Boer and Kowalchuk 2001) with rates unrelated to pH (Booth and others 2005). Studies in the USA showed that net nitrification rates were positively related to soil pH and the abundance of *Acer* spp. (Venterea and others 2003) and at ten *Acer*-dominated sites in North America with comparably sandy soils, the nitrification:mineralization ratio was even higher than in the current study (Walters and Reich 1997). Here, the congener *Acer pseudoplatanus* was associated with the highest rates of net nitrification and the highest ratio of nitrification:mineralization, and also has the highest soil pH (data not shown). Differences among studies in the strength of pH effects on nitrification likely depend on the community composition of nitrifying microbes (De Boer and Kowalchuk 2001).

The negative relationship between leaf litter P and rates of nitrification and the ratio of nitrification:mineralization is less easily understood. However, higher leaf P could stimulate decomposer demand for N; if decomposers are effective at outcompeting nitrifiers for NH_4^+, that could reduce nitrification. Indeed, in a separate study of leaf litter decomposition in these same plots, N immobilization into decomposing litter was positively related to litter P concentrations (Hobbie and others 2006).

Conclusions

In summary, in a study of replicated monocultures of fourteen tree species, we found that tree species contributed significantly to variation in soil C and N dynamics, but not always via the hypothesized mechanisms. Trees (and tree species) influenced SOM dynamics in the mineral horizons primarily via their influence on soil cation chemistry and chemical stabilization, rather than via variation in detritus chemistry and biochemical recalcitrance.

Among the plots and species studied here, soil pH and exchangeable cation chemistry have diverged considerably, with some plots and species (for example, *Acer* spp.) having high base saturation and low % exchangeable Fe + Al and others (for example, *Pinus* spp.) having high % exchangeable Fe + Al (Reich and others 2005). Plots with high exchangeable Fe + Al were in turn associated with low rates of SOM decomposition and microbial biomass, likely because the hydrolyzing cations, Al^{3+} and Fe^{3+}, were important in stabilizing SOM via cation bridging with clays and flocculation, but also potentially because of the toxic effects of Al^{3+}, direct inhibitory effects of low pH, or pH-induced changes in the soil microbial community. Consistent with our results, total soil C pools in the surface horizons are greater in plots with high extractable Fe + Al (JC Chorover and others unpublished data). In contrast to our hypothesis, tree and species variation in tissue lignin concentrations could not explain variation in SOM decomposition rates.

To our knowledge the influence of tree species on SOM decomposition via changes in cation biogeochemistry has not been considered or demonstrated previously, but is likely important in other ecosystems, particularly those with low soil pH buffering capacity. Tree species are known to differ greatly in their use of cations, such as Ca^{2+} (Broadley and others 2003), and tree species have been shown to differ in soil cation cycling in other systems (Ovington 1958; Nihlgård 1971; Alban 1982; Muys and Lust 1992; Finzi and others 1998a; Dijkstra and Smits 2002; Dijkstra 2003), with potential consequences for SOM dynamics. In addition, acid deposition has greatly altered the cation chemistry of poorly buffered soils in some regions (Likens and others 1996; 1998) with unknown consequences for mineral soil SOM decomposition rates.

In contrast to soil C dynamics, in our study, species influenced N cycling in ways similar to those demonstrated in past studies, primarily via variation in root N concentrations (Wedin and Tilman 1990; Dijkstra and others 2006). That net N mineralization rates were unrelated to the major controls of decomposition (and hence presumably of gross rates of mineralization) suggests an overriding influence of trees and species on N immobilization. Nitrification rates covaried with mineralization rates but were additionally stimulated under tree-induced conditions of high base cation status and pH, likely reflecting more favorable conditions for nitrification in more alkaline soils (Robertson 1982). Nitrification rates were reduced by litter P concentrations, perhaps reflecting competition between litter decomposers and nitrifiers for NH_4^+.

In summary, we found that the fourteen tree species studied here have caused significant divergence in soil organic matter dynamics, influencing soil C dynamics primarily through effects on the chemical stabilization of organic matter and influencing soil N dynamics primarily through variation in detritus chemistry. These results suggest that variation in tree species composition arising from variation in forest management and land use, biological invasion, or global climate or atmospheric change could have substantial consequences for soil C and nutrient cycling.

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