

Tree species effects on coupled cycles of carbon, nitrogen, and acidity in mineral soils at a common garden experiment

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Abstract Forest biogeochemical cycles are shaped by effects of dominant tree species on soils, but the underlying mechanisms are not well understood. We investigated effects of temperate tree species on interactions among carbon (C), nitrogen (N), and acidity in mineral soils from an experiment with replicated monocultures of 14 tree species. To identify how trees affected these soil properties, we evaluated correlations among species-level characteristics (e.g. nutrient concentrations in leaf litter, wood, and roots), stand-level properties (e.g. nutrient fluxes through leaf litterfall, nutrient pools in stemwood), and components

of soil C, N, and cation cycles. Total extractable acidity ($\text{acidity}_{\text{tot}}$) was correlated positively with mineral soil C stocks ($R^2 = 0.72$, $P < 0.001$), such that a nearly two-fold increase in $\text{acidity}_{\text{tot}}$ was associated with a more than two-fold increase of organic C. We attribute this correlation to effects of tree species on soil acidification and subsequent mineral weathering reactions, which make hydrolyzing cations available for stabilization of soil organic matter. The effects of tree species on soil acidity were better understood by measuring multiple components of soil acidity, including pH, the abundance of hydrolyzing cations in soil solutions and on cation exchange sites, and $\text{acidity}_{\text{tot}}$. Soil pH and $\text{acidity}_{\text{tot}}$ were correlated with proton-producing components of the soil N cycle (e.g. nitrification), which were

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positively correlated with species-level variability in fine root N concentrations. Soluble components of soil acidity, such as aluminum in saturated paste extracts, were more strongly related to plant traits associated with calcium cycling, including leaf and root calcium concentrations. Our results suggest conceptual models of plant impacts on soil biogeochemistry should be revised to account for underappreciated plant traits and biogeochemical processes.

Keywords Cations · Plant traits · pH · Soil organic matter · Stoichiometry · Weathering · Wood · Stemwood

Introduction

Many studies have documented effects of tree species on ‘biogenic’ (e.g. carbon and nitrogen containing) and lithogenic (e.g. aluminum and calcium containing) chemical species in soil (Augusto et al. 2002; Binkley 1995; Binkley and Giardina 1998; Finzi et al. 1998a, b; Hagen-Thorn et al. 2004; Menyailo et al. 2002a, b; Priha and Smolander 1999; Vesterdal et al. 2008). Fewer studies have addressed how interactions among organic and lithogenic elements determine the impact of tree species on soil biogeochemistry (Dijkstra and Fitzhugh 2003; Hobbie et al. 2007; Mareschal et al. 2010; Moukoui et al. 2006; Reich et al. 2005), despite evidence that many biogeochemical processes link soil carbon (C) and nitrogen (N) cycles with those of aluminum (Al) and calcium (Ca) (Binkley and Richter 1987; Chadwick and Chorover 2001; Chorover et al. 2007; Ross et al. 2008; van Breemen et al. 1983). The result is an incomplete understanding of how different tree species impact soils. This is problematic because the identity and nature of dominant tree species in many forests are changing, with uncertain consequences for forest biogeochemical cycles (Campbell et al. 2009; Ellison et al. 2005).

Tree species can impact several biogeochemical processes that interact to influence both lithogenic and organic soil constituents. For example, protons and organic acids released by plants, or produced during oxidation of plant litter, can lower soil pH, promote mineral dissolution, and increase the concentration of Al and iron (Fe) in soil solution (Binkley and Richter 1987; van Breemen et al. 1983). Monomeric and colloidal Al

and Fe can then react with biomolecules to form complexes that deter microbial degradation, facilitating retention of soil organic C and N (Hobbie et al. 2007; Mikutta et al. 2011; Scheel et al. 2008). Degradation of soil organic substrates can also be inhibited at low soil pH due to toxicity of Al ions (Scheel et al. 2008), reduced exoenzyme activity (Sinsabaugh et al. 2008), or shifts in microbial community composition (Fierer et al. 2009). When soil microbes and fauna do metabolize organic substrates, nutrients such as N are released or immobilized, depending on the stoichiometry of the substrates and decomposers (Manzoni and Porporato 2009). Nutrients that are mineralized from organic substrates, along with nutrients derived from atmospheric deposition or mineral weathering, are then either taken up by plants, subjected to further biogeochemical reactions (e.g. adsorption, nitrification), or leached from the soil, with each pathway having unique implications for the fate of organic and lithogenic chemical species and for soil acidity (Binkley and Richter 1987; Gundersen and Rasmussen 1990). Due to this diversity of biogeochemical interactions, studies of few chemical elements and reactions are likely to insufficiently reveal how tree species impact soils, even if the goal is relatively narrow (e.g. to understand how tree species influence soil N cycling).

Trees species influence soil biogeochemical processes through differences in “functional” traits, such as tissue nutrient concentrations, and stand properties, including the amount of nutrients stored in wood. Yet, different soil processes can be influenced by different plant traits and stand properties, such that a complete understanding of how tree species influence soils will also require assessment of multiple plant traits and stand properties. For example, plant litter nutrient concentrations and annual nutrient fluxes through plant litter are useful for understanding how tree species influence the nutrients that are released to soil via mineralization (Prescott 2005). In contrast, the impact of trees on the net redistribution of nutrients from soils to plants is perhaps more a function of variation in the concentrations and pools of nutrients in wood. Notably, tree species with high nutrient concentrations in leaf litter do not necessarily have high nutrient concentrations in roots (Hobbie et al. 2010) or wood, so different tissues and organs of the same species can have unique effects on soil nutrient mineralization and redistribution.

Here, we explore how tree species impact a suite of interacting biogeochemical pools and processes in soils at a common garden experiment. Earlier work at this site showed that soil pH, abundance of non-hydrolyzing cations (i.e. “base” cations), and organic horizon C stocks and turnover were strongly correlated with earthworm abundance and leaf litter Ca concentrations, which varied considerably among the 14 tree species on-site (Dauer et al. 2007; Hobbie et al. 2006; Reich et al. 2005). Rates of C and N mineralization in the uppermost mineral soil horizons were best correlated with root traits of the tree species, particularly N concentrations, and also with the abundance of exchangeable Al and Fe in soil (Hobbie et al. 2007). These earlier studies did not address effects of tree species on C or hydrolyzing cations (Al and Fe) in mineral soil horizons. This knowledge gap motivates the current work, which also examined interactions among soil C stocks, N transformations, and cations with greater breadth than before.

We expected soil C stocks to vary with tree species traits, biogeochemical processes, and soil properties that influence the primary mechanisms of soil C stabilization, namely organo–mineral and organo–metal interactions (von Lutzow et al. 2006). Specifically, we evaluated the following two hypotheses regarding soil C variability: (1) soil C stocks are positively correlated with estimates of the capacity of soil minerals to bind OM (e.g. the amount of clay-sized particles or of Al and Fe oxides), and (2) soil C stocks are positively correlated with estimates of the capacity of soil cations to bind OM (e.g. the abundance of multivalent cations such as Al, Ca, and Fe). We also expected mineral soil acidity to be correlated not just with leaf and soil Ca concentrations (Reich et al. 2005), but also with aspects of soil C and N cycles, and with variation in other leaf and root traits and stand characteristics. We assessed the following specific hypotheses: (1) soil acidity is positively correlated with estimates of nitrate production (i.e. nitrification) and abundance in soil, (2) soil acidity is positively correlated with the amount of non-hydrolyzing cations stored in tree wood (because accumulation in wood depletes soil buffering capacity), and negatively with the amount of N stored in tree wood (because of depletion of inorganic N pools in soil that can generate acidity via nitrification or nitrate leaching). We evaluated these hypotheses using a variety of measures of soil acidity, each operationally designed to

isolate different components of soil acidity. This is necessary because soil acidity is defined by multiple, interacting chemical species that are differentially associated with organic and mineral soil constituents (Ross et al. 2008).

Methods

Study site

All soil and plant samples were collected from a common garden experiment in central Poland (51°14.87'N, 18°06.35'E, altitude 150 m, mean annual temperature 8.2°C). There, 14 tree species (Table 1) were planted in replicated, monoculture plots (20 × 20 m²) in 1970 and 1971. Eight of the species are angiosperms (all deciduous hardwoods) and six are gymnosperms (five evergreen conifers and one deciduous conifer). Before the experiment was established, the site was occupied by an 80 year old *Pinus sylvestris* plantation. Prior to planting, the pine plantation was clear-cut and soils were plowed. Soils at the site are derived from sandy glacial outwash and are dominated by quartz and feldspar, with smaller mass fractions of mica, layer silicate clay minerals montmorillonite and kaolinite and Fe and Al (oxyhydr)oxides. Each plot was classified by our team as a sandy, mixed, mesic Typic Ustipsamment or a fine-loamy, mixed, mesic Kanhaplic Haplustalf following USDA soil taxonomy. These differences in soil taxonomy are largely a function of variability in percent clay (<10% for the top 20 cm of mineral soil in all plots). The variability in soil texture is an artifact of plowing and the inconsistent depth of the underlying, clay-rich moraine (i.e. in some places the moraine was within plowing depth, in others it was not). Previous studies documented that leaf and fine root chemistry, lifespan, and litter fluxes vary by as much as two-fold or more among the 14 tree species (Hobbie et al. 2010; Reich et al. 2005; Withington et al. 2006).

Soil sampling and focal horizons

One soil pit per plot (53 total) was sampled in August 2002. Each pit was at least 100 cm deep and genetic horizons were described and sampled according to standard procedures. The depth increments of distinct genetic soil horizons varied substantially across plots.

Table 1 Mean values (\pm SD) for soil C and total extractable acidity beneath each species at the common garden experiment

Tree species	n	Total C		Acidity _{tot}	
		Uppermost hor. (g kg ⁻¹)	0–20 cm (kg m ⁻²)	Uppermost hor. (cmol + kg ⁻¹)	0–20 cm (cmol + m ⁻²)
<i>Abies alba</i>	2	8.3 \pm 0.9	1.99 \pm 0.01	6.82 \pm 0.13	1657.2 \pm 48.7
<i>Acer platanoides</i>	3	8.8 \pm 4.4	1.42 \pm 0.26	6.95 \pm 1.79	1342.4 \pm 109.7
<i>Acer pseudoplatanus</i>	3	11.9 \pm 5.9	2.70 \pm 1.04	7.27 \pm 1.26	1870.4 \pm 331.7
<i>Betula pendula</i>	3	10.9 \pm 4.8	2.34 \pm 0.70	7.21 \pm 1.88	1558.8 \pm 386.8
<i>Carpinus betulus</i>	3	12.3 \pm 1.8	2.55 \pm 0.35	7.60 \pm 0.80	1823.7 \pm 47.9
<i>Fagus sylvatica</i>	3	10.9 \pm 4.8	2.51 \pm 1.19	7.31 \pm 2.54	1926.1 \pm 670.1
<i>Larix decidua</i>	6	8.2 \pm 1.7	1.97 \pm 0.37	6.61 \pm 1.07	1715.3 \pm 271.7
<i>Picea abies</i>	6	16.7 \pm 7.4	2.88 \pm 0.88	9.66 \pm 2.68	2097.7 \pm 644.0
<i>Pinus nigra</i>	3	7.7 \pm 3.4	1.85 \pm 0.71	6.46 \pm 2.49	1510.2 \pm 711.6
<i>Pinus sylvestris</i>	3	10.4 \pm 0.8	2.46 \pm 0.80	7.79 \pm 0.18	1890.4 \pm 418.1
<i>Pseudotsuga menziesii</i>	3	13.4 \pm 6.1	2.51 \pm 0.76	9.22 \pm 2.10	2001.9 \pm 385.9
<i>Quercus robur</i>	6	11.0 \pm 2.1	2.48 \pm 0.77	7.39 \pm 0.98	1929.3 \pm 402.9
<i>Quercus rubra</i>	3	8.5 \pm 3.3	2.05 \pm 0.44	5.62 \pm 1.89	1275.7 \pm 494.3
<i>Tilia cordata</i>	3	7.8 \pm 1.4	1.68 \pm 0.40	5.76 \pm 0.47	1344.0 \pm 160.8
Statistics					
Species		$R^2 = 0.38$; $P = 0.07$	ns	$pR^2 = 0.39$; $P < 0.05$	$pR^2 = 0.35$; $P = 0.07$
Soil texture		ns	ns	$R^2 = 0.06$; $P = 0.07$	$R^2 = 0.08$; $P < 0.05$

Statistics for species and soil texture effects are shown at the bottom of the Table. Data shown are for the uppermost mineral soil horizon, typically an A1 horizon, and for the top 20 cm of mineral soil

The effects of soil texture were evaluated in least squares linear regression analyses. When soil texture effects were non-significant (ns, $P > 0.1$), species effects were evaluated using ANOVA. When soil texture effects were significant ($P < 0.1$), species effects were evaluated using ANCOVA with percent clay as a covariate and partial R^2 (pR^2) and P values for the species effect reported in the Table are derived from these ANCOVA results. R^2 values were calculated by dividing the sum of squares attributable to species (when %clay is already in the model), by the total sum of squares of the ANCOVA

For example, A horizon depth ranged from 3 to 42 cm (mean = 17.3 cm, SD = 8.5). The depth of the uppermost mineral soil horizon, typically an A1 horizon, ranged from 3 to 14 cm (mean = 7.6 cm, SD = 2.3). Some of the variability in A and A1 horizon depth was related to soil texture ($R^2 = 0.26$, $P < 0.001$ and $R^2 = 0.07$, $P = 0.05$, respectively; based on linear regression with percent clay), but tree species did not have a significant effect on the depth of these horizons when percent clay was used as a covariate (ANCOVA $P > 0.1$). Thus stocks (mass per unit ground area) of C, N, and hydrolyzing cations in these horizons were strongly influenced by horizon depth, which was unaffected by tree species. To account for this potentially confounding variation in horizon depth, we analyzed the data in the following two forms: (1) as concentrations (i.e. mg C per g soil) for the uppermost mineral soil horizon only (usually

an A1 horizon) and (2) as stocks normalized to a common depth (i.e. mg C per m² from 0 to 20 cm). Both of these soil zones fall within the plowing depth of all plots (typically 30–40 cm). The stocks for the 0–20 cm depth increment were estimated by calculating a depth-weighted average of the data from each soil horizon in that depth increment. Hobbie et al. (2007) previously reported some aspects of the data from the uppermost mineral horizons (but not, for example, acidity_{tot}). None of the data for the 0–20 cm depth increment have been discussed elsewhere.

Soil analyses

For each horizon within a plot, one sample was analyzed for soil chemical parameters (see Hobbie et al. 2007). Briefly, water-soluble ions were measured on the aqueous phase of a saturated soil paste (method

4C1a1a2; Soil Survey Staff 2004). Exchangeable cations were extracted with 0.1 M BaCl₂ (1:10 soil to BaCl₂ solution; (Amacher et al. 1990). BaCl₂ extracts contain a larger fraction of soil cations compared to saturated paste extracts because Ba²⁺ ions displace soil cations from cation exchange sites. We also measured the abundance of Al and Fe in three other extracts (sodium pyrophosphate, ammonium oxalate, citrate–dithionate) according to Soil Survey Staff (2004) methods 4G1a1-3, 4G2a1a1-5, and 4G3a1-3. These extractions target Al and Fe in organic complexes, poorly crystalline solids, and reducible ‘free’ Fe(III) (oxyhydr)oxides, respectively. Soil pH was measured in the saturated soil pastes (pH_{SP}) and a 1:1 mixture of soil to water (mass to volume; pH_{water}). While soil pH measures the intensity of soil acidity, this component does not reflect the capacity of a soil to buffer against changes in pH, i.e. the quantity of reactive soil constituents that contribute to the resistance of soils to a change in the intensity factor (pH). To measure the capacity factor of soil acidity, which derives dominantly from the proton production of hydrolyzing Al and Fe ions, the acidity_{tot} was also measured. This parameter was estimated by reacting soil samples with a buffered (pH 8.2) BaCl₂–triethanolamine solution and back-titrating the solution with HCl (method 4B2b1a1; Soil Survey Staff 2004). This method quantifies the protons as well as Al and Fe ions released from permanent and pH-dependent exchange sites.

Inorganic N availability was assessed using ion-exchange resin bags during the growing season in 2003. The resins (14.8 mg, Dowex Marathon MR-3) were placed in nylon bags, washed in 10% HCl and rinsed with deionized water. At three locations within each plot, one resin bag was buried at 10 cm depth in the mineral soil and another was placed in the litter layer. Resin bags were first deployed in mid-May, collected and replaced with fresh bags in early July and again in late August, with final collection in mid-October. Resin bags were stored in a freezer after collection. For extraction, resins were removed from bags, rinsed with deionized water, air-dried, weighed and extracted with acidic 1.0 M NaCl. Extracts were analyzed for dissolved inorganic nitrogen (DIN) on an Alpkem FS3000 autoanalyzer (Alpkem, College Station, Texas, USA). DIN accumulation in resin bags was averaged within plots for each collection date and then summed to determine total growing season DIN accumulation in

the litter layer and mineral soil. To complement this ion-exchange resin data, we also utilized previously published data for net N mineralization and nitrification (Hobbie et al. 2007) in our analyses.

Plant sampling and analyses

Leaf litter and fine roots (<2 mm) were collected from each plot in 2002 and analyzed for the concentrations of C, N, Ca, and other plant nutrients. We supplemented these previously reported data (Hobbie et al. 2006; 2007) with new data on nutrient concentrations in stemwood. Stemwood was collected from six trees per plot in March 2009 by coring with 40 cm Pressler borers (5 mm diameter). The cores were taken from one side of the trunk to the center of the bole at a height of 130 cm. The cores were divided into two composite samples per plot (stem cores of three trees combined) and oven dried (65°C) to a constant mass prior to being homogenized in a mill. Each composite sample ($n = 106$) was analyzed for elemental concentrations by the Penn State Agricultural Analytical facility. Carbon and N concentrations in wood were measured with a thermal conductivity detector following sample combustion and reduction of oxidized N forms to N₂. Other elements, including Na, K, Ca, Mg, Al, and Fe were measured by inductively coupled plasma mass spectrometry after dry ashing. The duplicate samples per plot were averaged to produce one value for each plot ($n = 53$).

The mass of nutrients stored in wood was estimated by multiplying nutrient concentrations of stemwood by aboveground wood biomass estimates for each plot. Wood biomass was calculated using biometric measurements of individual trees (DBH and height) and allometric biomass equations (Muukkonen 2007; Ter-Mikaelian and Korzukhin 1997; Zianis et al. 2005).

Statistical methods

All statistics were estimated using JMP (version 7.0.2, ©SAS). First, variables with non-normal distributions were transformed using the natural log, log₁₀ or square-root. Correlations among variables were evaluated at the plot level ($n = 53$) using least squares regression and, for variables with significant tree species effects in ANOVA models, at the species level ($n = 14$). Effects of soil texture on dependent variables were evaluated using regression and ANCOVA models (using %clay

as a proxy for soil texture). Effects were deemed ‘significant’ when P values were <0.05 and ‘marginally significant’ when $0.05 < P < 0.1$.

Results

Effects of tree species and soil texture on mineral soil C

Mean values of soil C for the 14 tree species at the common garden varied approximately two-fold, whether expressed as mass concentrations in the uppermost horizon or as stocks in the 0–20 cm depth increment (Table 1). However, the variability of soil C among plots of the same species was relatively high, so the differences of soil C among species approached statistical significance only for the uppermost mineral soil horizon ($0.05 < P < 0.1$). Soil texture was not correlated with mineral soil C (expressed as depth-normalized stocks or concentrations; Table 1).

Effects of species and soil texture on soil acidity

As shown in previous studies at the common garden (Reich et al. 2005), the pH of mineral soils differed significantly among species ranging from 3.8 to 5.4 (pH_{SP}) and 4.2 to 4.9 (pH_{water}). Significant differences among tree species were also apparent for acidity_{tot}, which varied nearly two-fold among species (Table 1), and for saturated paste Al, which varied 20-fold among species (Table S1 in Online Resource 1), but not for Al or Fe abundance in other extracts. Percent clay was positively correlated with Al in BaCl_2 extracts ($r = 0.56$) and more moderately correlated with acidity_{tot}, Al in saturated pastes, and Fe in BaCl_2 extracts ($r < 0.4$, Table 1, Table S1 in Online Resource 1).

Correlations among soil biogeochemical parameters

Total extractable acidity was tightly positively correlated with soil C concentrations in the uppermost mineral horizons and with C stocks in the upper 20 cm of mineral soil ($r = 0.85$, $P < 0.001$), such that a two-fold increase in acidity_{tot} was associated with a more than two-fold increase in organic C (Fig. 1; Table 2). Other measures of soil acidity were more modestly correlated with soil C ($|r| < 0.65$), but

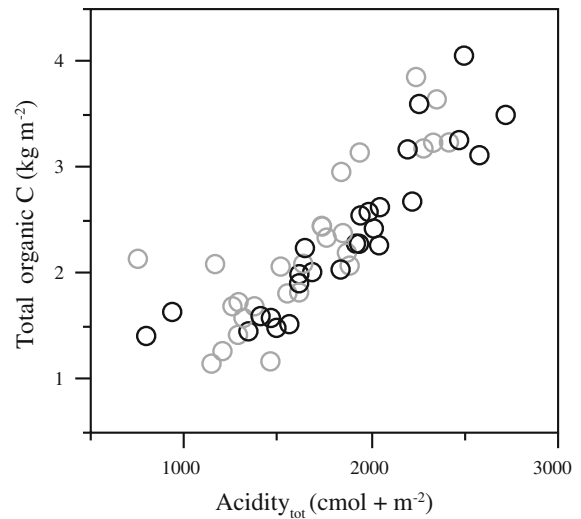


Fig. 1 Relationship between stocks of total extractable acidity (acidity_{tot}) and total organic carbon in the 0–20 cm mineral soil depth increment ($R^2 = 0.72$, $P < 0.001$ from linear regression using \log_{10} -transformed soil C values, $n = 53$). Plots planted with angiosperm species are shown in gray and those planted with gymnosperm species are shown in black. Similar results were observed for data reported as concentrations for the uppermost mineral soil horizon (Table 2)

in a manner consistent with the relationship between acidity_{tot} and soil C (Table 2, including pH_{water} and the abundance of hydrolyzing ions in saturated paste, BaCl_2 , and sodium pyrophosphate extracts). The abundance of Al and Fe in citrate–dithionate extracts was not significantly correlated with soil C concentrations or stocks ($P > 0.1$). Fe abundance in ammonium oxalate extracts was positively correlated with soil C concentrations in the uppermost mineral horizon ($r = 0.34$, $P < 0.05$) and with soil C stocks in the upper 20 cm of mineral soil ($r = 0.53$, $P < 0.01$), but Al abundance in these extracts was not correlated with soil C (Table 2).

Relationships between soil acidity and soil N cycling were also apparent. Total extractable acidity was positively correlated with potential net N mineralization, potential nitrification and accumulation of NO_3^- on ion-exchange resins (Fig. 2, Table S2 in Online Resource 1). Consistent with these relationships between acidity_{tot} and soil inorganic N cycling, soil pH was negatively correlated with soil N transformations and resin NO_3^- (especially pH_{water} ; Table S2 in Online Resource 1).

The strength of correlations between different measures of soil acidity was variable. Only one

Table 2 Correlations between soil C and other soil properties

	pH _{SP}	pH _{water}	Acidity _{tot}	SP Fe	BaCl Fe	Na _{pyro} Fe	Am-Ox Fe	SP Al	BaCl Al	Na _{pyro} Al	Am-Ox Al	%Clay
%C uppermost horizon	ns	-0.36	0.85	0.34	ns	0.36	0.34	ns	ms	-0.29	ns	ns
kg C m ⁻² 0–20 cm	ns	-0.39	0.85	0.64	0.57	0.51	0.53	0.40	0.52	ns	ns	ns

Pearson correlation coefficients are reported at the plot-level ($n = 53$) due to a lack of significant species effects in ANOVA for several variables reported herein. Coefficients are shown only for correlations with $P < 0.05$, otherwise relationships are considered marginally significant (ms, $0.1 > P > 0.05$) or not significant ($P > 0.1$, ns). Data shown are for the uppermost mineral soil horizon, typically an A1 horizon, and for the top 20 cm of mineral soil

SP Saturated paste extracts, BaCl barium chloride extracts, Na_{pyro} sodium pyrophosphate extracts, Am-Ox ammonium-oxalate extracts

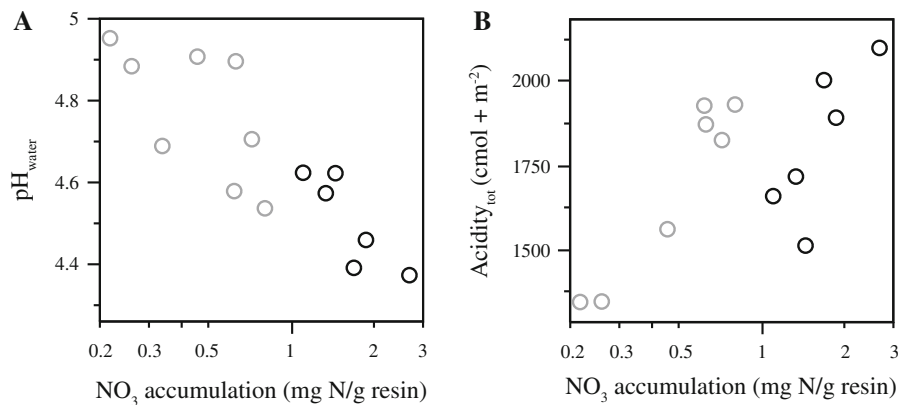


Fig. 2 Relationship between NO₃⁻ accumulation on ion-exchange resins (buried at 10 cm in the mineral soil) and soil pH (a) and total extractable acidity (b) for the top 20 cm of mineral soil. Note log₁₀ scale on the X-axis. Since species means differed significantly for NO₃ accumulation on ion-exchange

resins, total extractable acidity, and soil pH (Table 1 and not shown), here *each circle* mean value for each species (angiosperms shown in gray and gymnosperms shown in black). For plot-level correlations ($n = 53$), see Online Resource 1

correlation coefficient (r) was greater than 0.7, many relationships had r values less than 0.5, and several were not significant (Table 3). Soil pH was negatively correlated with acidity_{tot} and Al and Fe in saturated paste and BaCl₂ extracts (Table 3). The amount of Fe in ammonium oxalate extracts was positively correlated with acidity_{tot} (Table 3). None of the measures of soil acidity were correlated with Al in ammonium oxalate extracts (Table 3) or with Al or Fe in Al in citrate–dithionate extracts (not shown).

Correlations between plant traits and soil biogeochemical parameters

Fine root N concentrations, expressed alone or relative to C or lignin concentrations, were strongly correlated with acidity_{tot} (Table 4). Specifically, a two-fold

increase of root N concentration was associated with an increase in acidity_{tot} of nearly the same magnitude (Fig. 3). Soil pH was also significantly correlated with fine root N concentrations (negatively, Table 4). Nutrient concentrations of leaf litter and stem wood were not well correlated with acidity_{tot}, although Ca concentrations in leaf litter, fine roots, and wood were positively correlated with soil pH and negatively correlated with saturated paste Al (Table 4; not shown).

Discussion

Species effects on mineral soil C

The limited effects of tree species on mineral soil C stand in contrast with the large effects of species on

Table 3 Correlations among different measures of soil acidity

	Acidity _{tot}	SP Fe	BaCl Fe	SP Al	BaCl Al	Na _{pyro} Fe	Am-Ox Fe	Na _{pyro} Al	Am-Ox Al	%Clay
pH _{SP} uppermost horizon	ns	ns	-0.37	-0.63	-0.3	ns	ns	ns	ns	0.32
pH _{SP} 0–20 cm	ns	ns	-0.35	-0.59	ns	ns	ns	ms	ns	0.4
pH _{water} uppermost horizon	-0.5	0.33	ns	-0.64	-0.32	ns	ns	ms	ms	ns
pH _{water} 0–20 cm	-0.51	0.37	-0.28	-0.77	-0.36	ns	ns	ns	ns	ns
Acidity _{tot} uppermost horizon	-	0.55	0.36	0.28	0.51	0.56	0.45	ms	ns	ms
Acidity _{tot} 0–20 cm	-	0.49	0.35	0.36	0.69	0.56	0.70	ns	ms	0.28

Pearson correlation coefficients are reported at the plot-level ($n = 53$) due to a lack of significant species effects in ANOVA for several variables reported herein. Coefficients are shown for correlations with $P < 0.05$, otherwise relationships are considered marginally significant (ms, $0.1 > P > 0.05$) or not significant ($P > 0.1$, ns). Data shown are for the uppermost mineral soil horizon, typically an A1 horizon, and for the top 20 cm of mineral soil

SP Saturated paste extracts, BaCl barium chloride extracts, Na_{pyro} sodium pyrophosphate extracts

Table 4 Correlations between plant stoichiometry and soil properties

Soil properties	Root N	Root C:N	Root lignin:N	Root Ca	Leaf litter N	Leaf litter C:N	Leaf litter lignin:N	Leaf litter Ca
Acidity _{tot} uppermost horizon	0.33/0.64	-0.39/-0.68	-0.48/-0.69	ns/ns	ns/ns	ns/ns	ns/ns	ns/ns
Acidity _{tot} 0–20 cm	0.50/0.83	-0.5/-0.83	-0.55/-0.79	ns/ns	ns/ns	ns/ns	ns/ns	ns/ns
pH _{SP} uppermost horizon	ns/ns	ns/ns	0.28/ns	0.54/0.84	ns/ns	0.30/ns	ns/ns	0.48/0.87
pH _{SP} 0–20 cm	ns/ns	ns/ns	ns/ns	0.54/0.85	ns/ns	0.30/ns	ns/ns	0.55/0.90
pH _{water} uppermost horizon	-0.49/-0.62	0.52/0.64	0.57/0.64	0.35/ns	ns/ns	ns/ns	ns/ns	0.32/0.54
pH _{water} 0–20 cm	-0.50/-0.60	0.51/0.57	0.57/0.67	0.33/0.60	ns/ns	ns/ns	ns/ns	0.39/0.66
Al _{SP} uppermost horizon	0.39/ns	-0.41/ns	-0.45/ns	-0.41/-0.71	ns/ns	ns/ns	ns/ns	-0.45/-0.71
Al _{SP} 0–20 cm	0.47/0.53	-0.47/-0.53	-0.52/-0.60	-0.39/ns	ns/ns	ns/ns	ns/ns	-0.45/ns

Pearson correlation coefficients are given for analyses performed at the plot and species levels (plot/species). $n = 53$ and for plot-level correlations and $n = 14$ for species-level correlations. Coefficients are shown only for correlations with $P < 0.05$, otherwise relationships are considered marginally significant (ms, $0.1 > P > 0.05$) or not significant ($P > 0.1$, ns). Data shown are for the uppermost mineral soil horizon, typically an A1 horizon, and for the top 20 cm of mineral soil

organic horizon C stocks observed by Reich et al. (2005) at the same site. Species effects on mineral soil C stocks are likely smaller and operate more slowly because the mechanisms of organic matter stabilization in mineral soils, primarily organo–mineral and organo–cation interactions, are determined by pedogenic processes (e.g. mineral weathering, aggregate formation, acidification) that operate on longer time-scales than processes responsible for organic matter preservation in organic horizons (e.g. biochemical

constraints on microbial decomposition and faunal activity). Within mineral soils, effects of tree species on soil C were more apparent for the uppermost genetic horizon (usually an A1 horizon) than for the top 20 cm of mineral soil (Table 1), likely because living and senescent plant organs are concentrated in upper soil horizons. Similar studies also observed the greatest species effects on soil biogeochemistry in shallow soil horizons (Alriksson and Eriksson 1998; Finzi et al. 1998a, b; Hagen-Thorn et al. 2004;

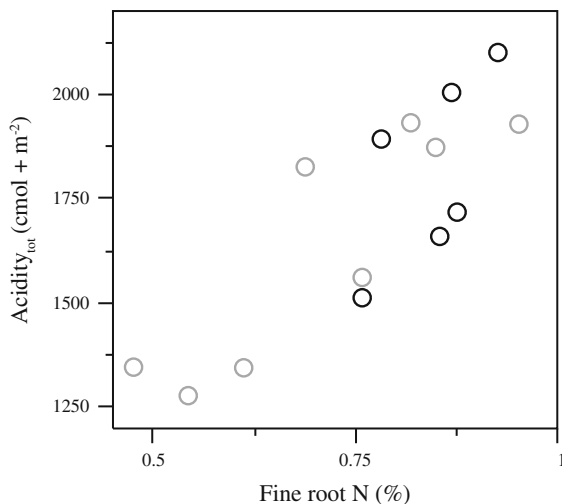


Fig. 3 Relationship between fine root nitrogen concentration and total extractable acidity ($\text{acidity}_{\text{tot}}$) in the 0–20 cm mineral soil depth increment ($R^2 = 0.69$, $P < 0.001$ from linear regression, $n = 14$). Since both root N and $\text{acidity}_{\text{tot}}$ differ significantly among the 14 tree species planted at the common garden (not shown and Table 1), here *each circle* mean value for each species (angiosperms shown in *gray* and gymnosperms shown in *black*). For plot-level analyses ($n = 53$) and correlations with other plant traits, see Table 4

Vesterdal et al. 2008) and in older stands (Priha and Smolander 1999), although there are exceptions (Menyailo et al. 2002b).

Soil acidity as a predictor for SOM stabilization

The strong correlation between $\text{acidity}_{\text{tot}}$ and mineral soil C stocks and concentrations (Fig. 1) indicates that increasing extractable acidity is coupled to soil organic matter (SOM) accumulation at the common garden. Soil organic C and $\text{acidity}_{\text{tot}}$ are likely coupled through polyvalent cation-bridging between negatively-charged organic matter moieties (e.g. carboxyl, phenolic hydroxyl) and Al and Fe ions, an interaction that stabilizes SOM against decomposition (Scheel et al. 2008; von Lutzow et al. 2006). This interpretation is consistent with the positive correlations of both soil C and $\text{acidity}_{\text{tot}}$ with the amount of Fe in sodium-pyrophosphate extracts (Tables 2, 3). Al in sodium-pyrophosphate extracts was not strongly correlated with soil C or $\text{acidity}_{\text{tot}}$, perhaps because sodium-pyrophosphate also extracts inorganic, colloidal Al from forest soils (Ross et al. 2008).

Mineral soil C concentrations and stocks were also correlated with soil pH (negatively), which can affect

SOM preservation through its negative effect on exoenzyme activity (Sinsabaugh et al. 2008) or its influence on microbial community composition (Fierer et al. 2009). Other research at the Polish common garden shows that soil pH was positively correlated with microbial biomass C and C mineralization rates in the uppermost soil horizons (Hobbie et al. 2007), lending additional support for a pH-mediated effect of microbial activity on soil C preservation. However, soil C stocks and concentrations were much more strongly correlated with $\text{acidity}_{\text{tot}}$ ($r > 0.8$) than with soil pH ($r < 0.4$). Likewise, microbial biomass C and C mineralization rates were more tightly correlated with the fraction of cation exchange capacity occupied by Al and Fe than with pH (Hobbie et al. 2007). Thus, it seems pH effects on microbial decomposition of SOM may be less important as a mechanism of soil C preservation than interactions of organic matter with hydrolyzing cations.

The absence of strong correlations of percent clay with soil C or soil acidity (Table 1; Table S1 in Online Resource 1) suggests that variation in soil texture across the study site had at most a minor role in controlling soil chemistry and soil C pools. The sandy soils at this site (clay mass fraction < 0.1) and resulting low levels of aggregation (“personal observation”) probably minimize the role of organo-mineral interactions in SOM preservation. Alternatively, there is some evidence that poorly crystalline minerals could contribute to soil C stabilization at this site: Fe abundance in ammonium oxalate extracts was positively correlated with soil C concentrations and stocks (Table 2). However, two lines of evidence suggest that the effect of soil acidity on soil C is at least partially independent of variation in amorphous iron oxides. First, the correlation between soil C and $\text{acidity}_{\text{tot}}$ was stronger ($r = 0.85$) than that between soil C and ammonium oxalate extractable Fe ($r \leq 0.53$). Second, tree species differed significantly with respect to $\text{acidity}_{\text{tot}}$ (Table 1) but not ammonium oxalate extractable Fe ($P > 0.2$).

Others have hypothesized that plant litter traits and their influence on microbial and faunal decomposition of organic matter should have consequences for soil C stocks (Wardle et al. 2004). However, we observed no correlations between litter traits and soil C that were consistent with this hypothesis. Other studies at the common garden experiment showed that earthworm abundance, as mediated by tree species-variation in

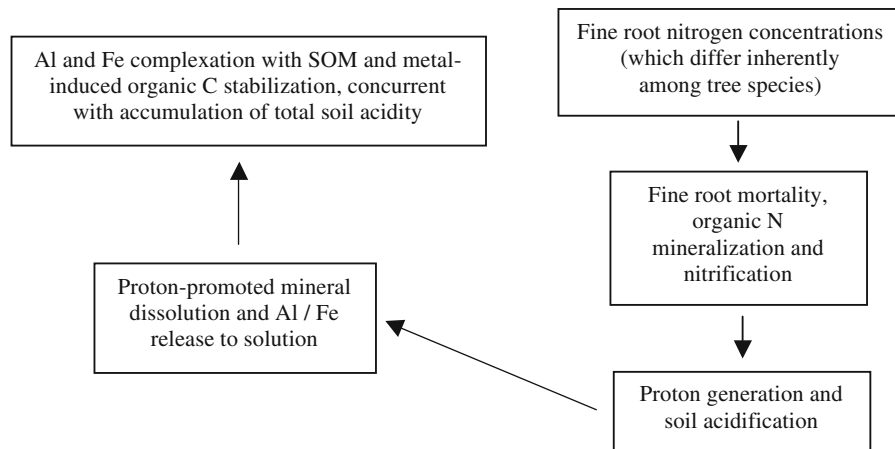


Fig. 4 Proposed conceptual model of the apparent process couplings among nitrogen cycling, soil acidification, mineral weathering, and SOM complexation at the common garden study

leaf litter calcium, determines organic horizon C stocks and turnover (Hobbie et al. 2006; Reich et al. 2005). Yet, earthworm abundance was not strongly correlated with mineral soil C in this study, perhaps because the dominant earthworm on site (*Lumbricus terrestris*) is a surface litter feeder with permanent burrows in the mineral soil (Jegou et al. 2000) and minimal influence on mineral soil mixing.

Mechanisms of species influence on soil acidity

Other studies have documented effects of tree species on soil pH or other components of soil acidity (Binkley and Valentine 1991; Dijkstra and Fitzhugh 2003; Finzi et al. 1998a; Hagen-Thorn et al. 2004), but have generally not addressed the mechanisms by which trees influence soil acidity. Here, we discuss different mechanisms by which tree species could have influenced soil acidity in our study. First we highlight and compare the effects of soil N and Ca cycling on soil pH and the solubility of hydrolyzing cations. Then we briefly discuss whether the effects of tree species on soil acidity could also arise from variability of subsoil properties or cation storage in wood.

Variation in soil acidity at this study site appears to be related to the soil N cycle (Fig. 4). Previously, Hobbie et al. (2007) showed that species with higher N concentrations in fine roots were associated with higher rates of net N mineralization and nitrification, likely because, during decomposition of fine roots, microbial demand for N is exceeded for tree species with high root N concentrations. Species with higher

fine root N also tended to have shorter root lifespans (Withington et al. 2006); thus, increased rates of fine root mortality could also contribute to higher N mineralization and nitrification rates for species with high root N. In this study, we showed that soil N transformations and accumulation of NO_3^- on ion-exchange resins were also correlated with acidity_{tot} and soil pH (Fig. 2; Table S2 in Online Resource 1). Nitrification and nitrate leaching result in proton generation, which can decrease soil pH, promote primary mineral dissolution, and lead to greater aqueous phase and exchangeable concentrations of Al and Fe (Binkley and Richter 1987; Chadwick and Chorover 2001; Gundersen and Rasmussen 1990). Proton production by nitrification and nitrate leaching can represent a substantial portion of the total proton budget for a stand or ecosystem (Gundersen and Rasmussen 1990). Further, the effects of nitrification and nitrate leaching on pH and hydrolyzing cation availability are likely more important in sandy soils with limited buffering capacity. Thus, the effect of root N on proton-generating components of the soil N cycle was likely a major mechanism of species influence on soil acidity (Fig. 3). Soil acidity could also be influenced by effects of tree species on throughfall N (De Schrijver et al. 2011, 2007), but we did not measure throughfall N.

Differences in cycling of non-hydrolyzing cations, also contribute to variation in soil acidity among tree species. Previous work at the common garden experiment showed species-level variation in leaf litter calcium (Ca) was positively correlated with soil Ca

concentrations, while both litter and soil Ca were positively correlated with soil pH (because Ca ions compete with Al ions for exchange sites, limiting the effect of Al on pH) (Reich et al. 2005). Here, we showed that Ca concentrations in plant tissues were strongly correlated with pH_{SP} ($0.5 < r < 0.9$), moderately correlated with pH_{water} ($0.3 < r < 0.7$), and not correlated with $\text{acidity}_{\text{tot}}$ (Table 4). Likewise, plant tissue Ca was more correlated with the abundance of Al in saturated paste extracts (Table 4) than in BaCl_2 extracts (not significant and not shown). Thus, at this site, plant Ca stoichiometry appears to have strong effects on soil solution acidity (e.g. in saturated pastes) but weaker influence on the capacity factor of soil acidity, i.e. the fractions of soil acidity that are more tightly bound and included in $\text{acidity}_{\text{tot}}$.

In contrast to the results for Ca, root N concentrations and soil N transformations were correlated with pH_{water} and $\text{acidity}_{\text{tot}}$, but not with pH_{SP} (Table 4; Table S2 in Online Resource 1). The divergent correlations of different soil acidity metrics with Ca and N parameters suggest the different measures of soil acidity, while clearly linked, represent distinct fractions of acidity with unique biogeochemical interactions. This conclusion is also supported by the correlations among soil acidity, soil C, and percent clay. pH_{water} was correlated with soil C and $\text{acidity}_{\text{tot}}$ while pH_{SP} was not; likewise, pH_{SP} was correlated with %clay but pH_{water} was not (Table 3).

The greater dependence of $\text{acidity}_{\text{tot}}$ on N cycling, as compared to Ca cycling, could be explained if protons derived from soil N transformations are consumed in weathering and buffering reactions that drive lithogenic Al and Fe, but not Ca, into bound fractions associated with organic matter (Ross et al. 2008). Specifically, protons generated from N cycling (e.g. nitrification) could be consumed in weathering reactions that release polyvalent Al and Fe to solution, followed by complexation of those cations with organic matter (thus contributing to the tight correlation between $\text{acidity}_{\text{tot}}$ and soil C at our site; Fig. 1). Regardless of the underlying mechanisms, our results suggest that tree species influence various components of soil acidity through different pathways and that using a variety of methods to measure soil acidity yields a deeper understanding of species effects on soil acidity and related element cycles.

We have emphasized relationships among tree species traits and soil biogeochemical properties in

shallow mineral soil horizons. However, variability in deeper soil horizons, such as B_t horizons rich in clay and non-hydrolyzing cations, could contribute to variability in the biogeochemistry of surface horizons. Yet, we did not observe correlations between characteristics of deeper horizons, such as soil texture or cation exchange capacity, and the parameters of interest in surface soil horizons (e.g. C stocks or soil acidity). In addition, previous studies at this site suggest the species differences in plant and soil Ca were not dependent on differences in subsoil texture or Ca content or on differences in rooting depth or distribution (Dauer et al. 2007; Reich et al. 2005).

Species-level differences in uptake and storage of soil nutrients are another possible mechanism of tree species influence on soil acidity (Fujii et al. 2008). For example, species could reduce nitrate leaching and resulting acidity by maintaining high biomass N stocks that serve as a competing ‘loss’ of DIN from the soil profile over time. Yet, the amount of N in aboveground wood biomass, expressed per kg wood or as the total amount of N in aboveground woody biomass (Tables S3, S4 in Online Resource 1), was not correlated significantly with soil pH, $\text{acidity}_{\text{tot}}$, or other components of soil acidity ($P > 0.1$). Conversely, translocation of non-hydrolyzing cations from soil to wood could increase soil acidity by increasing the relative predominance of Al on cation exchange sites. Pools of Ca and non-hydrolyzing cations in woody biomass were also not correlated with soil pH, $\text{acidity}_{\text{tot}}$ ($P > 0.05$). In contrast, the concentrations of Ca and other non-hydrolyzing cations in wood (Tables S3, S4) were positively correlated with soil pH and negatively correlated with the abundance of Al in saturated soil pastes ($P < 0.05$), but unrelated to $\text{acidity}_{\text{tot}}$ ($P > 0.1$). We suggest these correlations reflect the effects of pH and leaf litter Ca on soil Ca availability (Reich et al. 2005), rather than reflecting a causal relationship between accumulation of non-hydrolyzing cations in wood and soil acidity. As differences in biomass among these monocultures accumulate over time, differences in cumulative nutrient uptake and storage among species could have an influence on soil chemistry. Nonetheless, our estimates of current wood nutrient pools suggest the effect of this pathway has been minimal after nearly four decades of stand development. A series of common garden experiments in Belgium, with a maximum age of 35 years, also showed that soil

acidification was minimally affected by the accumulation of cations in wood (De Schrijver et al. 2011).

Causes of key correlations

Our explanation of how tree species impact soil elements and how soil element cycles interact at this site is based partly on correlation and should be interpreted carefully. For example, the link between soil C and acidity_{tot} could operate in two directions: (1) the amount of soil organic C contributes to variation in acidity_{tot} by providing exchange sites for protons and Al and Fe ions, and/or (2) the amount of soil acidity contributes to variation in soil organic C through cation-bridging or other constraints on microbial decomposition of SOM. There are reasons to speculate that the second direction is dominant, although both could operate simultaneously. First, parameters associated with plant C inputs and other mechanisms of SOM preservation were not associated with variability in soil organic C stocks, including the abundance of clay-sized soil particles, the amount of amorphous Al and Fe, the abundance of lignin in plant litter, and the magnitude of plant litter fluxes (specifically, leaf litterfall and fine root mortality). Thus, it is difficult to explain how the observed variation in soil C could have arisen if not due to effects of soil acidity (although we cannot rule out mechanisms related to unmeasured parameters, such as dissolved organic C fluxes from the organic horizon). Second, the influx of plant litter and organic substrates in all plots is high relative to the stocks of soil organic C. Therefore, it seems more likely that the formation of stable organo-metal complexes is limited by the availability of hydrolyzing cations as opposed to the amount of suitable organic C substrates.

Similarly, it is possible that high root N concentrations are a consequence of high soil N availability that was caused by other factors, such as tree species effects on throughfall N (as opposed to species differences in root N giving rise to differences in soil N availability). However, for root N variation to result from variability in soil N availability, a state of N saturation sufficient to induce nutrient accumulation in roots would be required. This is an unlikely scenario for the sandy, infertile soils at the common garden site and because the relatively young stands (<40 years-old) are still accruing biomass and thus have a high aboveground demand for N. Further, even if root N

concentrations are influenced by differences in soil N availability, this would only serve to reinforce species differences in soil N cycling given the strong evidence for root N as a control of N mineralization rates (Parton et al. 2007).

Our explanation of the links between soil biogeochemical parameters and plant traits is the most parsimonious explanation when evaluated in light of the wealth of data for this site, and is consistent with biogeochemical theory. However, given the complexity of soil acidity, plant–soil interactions, and interactions among element cycles, it is likely that unmeasured plant traits or biogeochemical parameters have an important role at this site. For example, exudation of organic acids by roots or other sources of dissolved organic C could be important. The balance of cation and anion uptake by roots over time could also help determine how trees impact soil acidity.

Conclusions

In our study, stocks of mineral soil C, inorganic N, and hydrolyzing cations beneath different tree species appear to be a function of species effects on soil N transformations and soil pH, which are mediated by species differences in root N concentrations and calcium concentrations of leaves and roots. Mineral soil C, N, and extractable Al stocks were not related to commonly measured leaf litter traits (e.g. N or lignin concentrations), litter fluxes or decomposition rates, or nutrient storage in aboveground woody biomass. Thus, the utility of simple, leaf-centric conceptual models of plant–soil interactions (e.g. Wardle et al. 2004) is eroded by the nature of trait–process relationships and soil element interactions highlighted here. Knowledge of tree impacts on soil elements will be enhanced by consideration of a wider range of plant traits, biogeochemical processes, and element cycles than what is typically measured.

Total extractable acidity in soil (acidity_{tot}) was more closely related to soil C stocks and more influenced by tree species than other hydrolyzing cation fractions (Al and Fe in BaCl₂ or ammonium oxalate extracts, Al in sodium pyrophosphate extracts, and saturated paste Fe), which were more dependent on soil texture. The different measures of soil acidity also diverged in their relationships with plant nutrient concentrations and soil N transformations.

Thus, different measurements of soil acidity offer unique insights into biogeochemical interactions. Measurement of multiple components of soil acidity at other sites should enhance the understanding of tree species effects on soil acidity and interactions among element cycles.

We expect the dominant mechanisms of tree influence on soil biogeochemistry will depend on climate, topography, and parent material type, which serve to determine the dominant pathways of element fluxes into and out of soil. Consequently, the patterns and apparent mechanisms observed in this study are most likely to operate in other coarse-textured soils in the temperate zone. Other plant traits and soil processes could be more important in forests with different soil faunal communities (e.g. in forests without anecic earthworms). Across studies, the diversity of results observed for effects of tree species on soil biogeochemistry likely reflects this dependency of species effects on other state factors of soil formation. Additional studies are needed to more widely assess the impacts of tree species on soil biogeochemistry and synthesize results in a manner that supports predictions of how changes in tree species composition will influence forest biogeochemical cycles and productivity.

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