

LETTER

Linking litter calcium, earthworms and soil properties: a common garden test with 14 tree species

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Abstract

Tree species can influence biogeochemistry through variation in the quantity and chemistry of their litter, and associated impacts on the soil heterotrophic community. However, the role that different plant traits play in these processes is not well understood, nor is it clear whether species effects on soils largely reflect a gymnosperm vs. angiosperm contrast. Using a replicated, long-term monoculture plot experiment, we examined variation in soils among 14 gymnosperm and angiosperm tree species 30 years after plot establishment, and assessed the role of litter chemistry *vis-à-vis* such variation. Differences in litter calcium concentrations among tree species resulted in profound changes in soil acidity and fertility that were similar within and among tree groups. Tree species rich in calcium were associated with increased native earthworm abundance and diversity, as well as increased soil pH, exchangeable calcium, per cent base saturation and forest floor turnover rate.

Keywords

Calcium, earthworms, pedogenesis, plant-soil, soil, soil acidification, tree species.

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INTRODUCTION

Ecologists and pedologists have long recognized that vegetation can influence the development of soil properties (Jenny 1941; Zinke 1962) and recent evidence suggests that plants can change soils relatively rapidly (Wedin & Tilman 1990; Muys *et al.* 1992; Pastor *et al.* 1993; Berendse 1998; Binkley & Giardina 1998). However, not all studies involving trees support the same hypothesized mechanisms and effects (e.g. contrast Zinke 1962; Finzi *et al.* 1998 with Alban 1982; Bockheim 1997), and our understanding of the generality of effects of given plant traits remains incomplete (Binkley & Giardina 1998). Moreover, the degree to which

differences in soil effects reflect a gymnosperm vs. angiosperm contrast, rather than a continuous response within and among species in both groups, is still unresolved. Regardless, given that a large fraction of the forested biome, especially in the temperate zone, has experienced shifts in species composition following natural disturbance, logging, agricultural cultivation and abandonment (Vitousek 1994), or tree planting, associated changes in soils could have been widespread, albeit inadequately understood (Van Breemen 1993; Binkley & Giardina 1998; Augusto *et al.* 2002). Given the dynamic and interactive nature of plant–soil interactions, increased understanding of the role of different plant traits and of the generality of species effects are critical to the

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development of a more synthetic understanding of the plant–soil system.

In part, our incomplete knowledge of how tree species affect soils is because of the fact that plant species distribution patterns respond to landscape-scale soil variability arising from other state factors of soil formation (soil age, climate, relief and parent material), which confounds our ability to isolate the effect of plants on soil development (Van Breemen *et al.* 1997; Binkley & Giardina 1998; Finzi *et al.* 1998). Hence, natural associations between ecosystem processes and plant species may arise from species effects on those processes, or from underlying differences in some species-independent characteristic of the site (e.g. parent material and microclimate) that favour different species. There is evidence from observational (e.g. Zinke 1962; Finzi *et al.* 1998; Dijkstra 2003), as well as replicated experiments with a relatively small number of species (Binkley & Giardina 1998), in support of a variety of hypothesized effects of trees on soils, but there is also evidence from the same kinds of studies that does not support these hypotheses (Alban 1982; Bockheim 1997; Binkley & Giardina 1998), and it is unclear how much of the supporting evidence reflects successional sorting of species among microsites varying in soil properties. Given the preponderance of non-experimental data, and the inconsistent results to date, it remains unclear whether the oft-hypothesized effects of trees on soils are a general phenomenon (Binkley & Giardina 1998).

'Common garden' experiments provide an opportunity to minimize these confounding effects. In these experiments, different species are planted in adjacent blocks so that climate, parent material, time, hydrology, topography and previous land use are held relatively constant. This allows direct comparison of the effect of species on soil given similar initial conditions (Binkley & Giardina 1998). Such studies with trees have been rare, and somewhat inconclusive, perhaps because of the small number (≤ 5) of species compared, the short time they have run (often < 10 years) and/or lack of replication (Gower & Son 1992; Muys *et al.* 1992; Binkley & Giardina 1998; Augusto *et al.* 2002). Here, we use a long-term replicated 'common garden' experiment with 14 temperate tree species including both angiosperms and gymnosperms (Table 1) to examine whether and how tree species alter soil properties over a 30-year period.

Plant species can influence ecosystem biogeochemistry through variation in both the quantity and chemistry of litter returned to soil (Pastor *et al.* 1993; Berendse 1998), and the associated impacts on the identity, abundance and activities of diverse soil heterotrophic organisms. Litter-specific decay and nutrient release rates are influenced by C : nutrient ratios and secondary C compounds such as lignin which often reduce decomposition and mineralization rates

(Melillo *et al.* 1982). Because of the importance of N availability as a constraint over plant growth, plant traits that influence the N cycle, such as litter percentage of N and C chemistry are often the focus of studies of species effects on biogeochemical processes (Wedin & Tilman 1990; Pastor *et al.* 1993; Berendse 1998).

However, plant species can also influence cycling of C and nutrients through litter and soils by influencing the distribution and concentrations of Ca, Mg, K and Al, which appear as cations in exchange reactions between soil solids and solution. The concentration of Ca in soil affects soil pH because it is a non-hydrolysing (i.e. 'base') cation that competes with H^+ and Al^{3+} cations for exchange sites on soil particle surfaces, especially 2 : 1 layer-type clays and organic matter. One popular hypothesis holds that gymnosperm tree species create acidic soils because their litter contains lower amounts of exchangeable base cations than that of angiosperm species. Some studies (Zinke 1962; Muys *et al.* 1992; Finzi *et al.* 1998), but not all (Alban 1982; Bockheim 1997) have supported this hypothesis. More generally, there is evidence that plant species can affect mineral weathering of parent materials, and Ca mineralization and recycling (Quideau *et al.* 1996; Dijkstra 2003). Litter and soil Ca content and pH can in turn potentially influence C and N cycling because in forest soils, higher pH is often associated with greater microbial biomass and higher rates of litter decomposition, soil respiration and net N mineralization (Persson *et al.* 1989; Simmons *et al.* 1996; Andersson *et al.* 2000).

To assess the effects of tree species, including both angiosperms and gymnosperms, on soils, we measured plant and soil attributes in a replicated long-term field experiment in which 14 temperate tree species (Table 1) were planted in 1970–1971 in replicated monoculture plots. We hypothesized that angiosperms and gymnosperms would differ in litter traits and associated effects on soils but, more importantly, that species differences in litter N, lignin and Ca would cause divergence in soil properties from initial conditions, and that effects of both angiosperms and gymnosperms on soil would have a common origin as identified by similar relations of plant traits and soil factors. The experiment was located at the Siemianice Experimental Forest, in western Poland.

MATERIALS AND METHODS

The experiment was initiated in 1970 in the Siemianice Experimental Forest (51°14.87' N, 18°06.35' E, elevation 150 m) near the village of Biadaszki, Poland. Climate of the region is transitional between maritime and continental, and the average annual precipitation was 591 mm with about half falling from May to August (weather data recorded 300 m from the field site from 1968–1997). Average

Table 1 Mean stand characteristics, forest floor metrics, selected foliage litter chemistry, earthworm biomass, and soil CO₂ flux data for 14 tree species growing in monoculture plots at Siemianice, Poland

Species	Type	Stand characteristics		Forest floor		Foliage litter (mg g ⁻¹)			Earth-worm biomass ash-free dry mass (g m ⁻²)	Soil CO ₂ flux (μmol m ⁻² s ⁻¹)
		Basal area (m ² ha ⁻¹)	Litter production (kg ha ⁻¹ year ⁻¹)	Mass (g m ⁻²)	Turn-over rate constant (k) (1 year ⁻¹)	N	Ca	Lignin		
<i>Tilia cordata</i>	DH	34.0	2901	33.3	0.92	12.2	22.4	375	4.81	4.6
<i>Acer pseudoplatanus</i>	DH	19.6	3715	26.0	0.88	9.4	20.5	164	7.38	6.0
<i>Acer platanoides</i>	DH	19.8	2801	10.9	1.09	6.5	19.0	124	3.41	6.2
<i>Fagus sylvatica</i>	DH	25.6	3091	33.1	0.23	8.4	12.7	242	3.37	5.2
<i>Betula pendula</i>	DH	31.3	2559	35.8	0.35	12.6	12.6	384	0.46	7.1
<i>Abies alba</i>	EC	11.8	802	42.9	0.06	12.5	12.5	304	5.03	4.7
<i>Quercus robur</i>	DH	19.9	2237	35.9	0.36	12.7	11.5	230	2.34	4.7
<i>Picea abies</i>	EC	29.1	1845	58.6	0.10	9.9	11.0	213	0.49	3.9
<i>Quercus rubra</i>	DH	31.0	5595	57.5	0.13	7.1	10.8	196	0.08	5.2
<i>Pseudotsuga menziesii</i>	EC	32.1	1181	54.8	0.07	7.2	9.7	246	1.18	3.6
<i>Carpinus betulus</i>	DH	6.8	1662	80.7	0.05	11.0	9.0	140	0.03	5.9
<i>Larix decidua</i>	DC	42.6	1293	36.3	0.09	8.7	7.0	316	0.06	5.6
<i>Pinus sylvestris</i>	EC	35.8	3293	56.9	0.10	6.8	5.8	176	0.05	4.7
<i>Pinus nigra</i>	EC	31.0	2794	55.8	0.08	5.4	3.7	238	0.12	4.1

DH, deciduous hardwood; DC, deciduous conifer; EC, evergreen conifer.

Species in all tables ordered from highest to lowest based on litter Ca concentration. All attributes were significantly different among species (ANOVA $P < 0.05$) and were not significantly different between gymnosperms (conifers) and angiosperms (hardwoods), except for forest floor turnover rate, litter Ca and soil CO₂ flux. The average standard error for each species was generally between 5 and 15% of the species mean for each variable. Attributes are mean values of three or six plots.

temperature was 8.2 °C with a mean growing season of about 213 days, calculated as the number of days with an average temperature > 5 °C. Ten species were planted in three plots and four species in six plots, for a total of 14 species and 54 plots. The plots were located in two adjacent blocks (nine species per block, three plots per species), each of which contained 27 20 × 20 m plots. Four of the species were planted in both blocks. Prior to the experiment the site was a mature pine-dominated (*Pinus sylvestris* L.) forest with a mean A horizon soil pH of 4.3. Soils formed in sandy glacial outwash overlying finer textured glaciofluvial sediments and were generally loamy sands (83% sand on average, standard deviation of 8%). The species included 12 European and two North American species, comprised of eight angiosperms and six gymnosperms (see Table 1).

Trees were planted with 1 × 1 m spacing and had good survival in all but one of the 54 plots, which we did not measure. The stands grew and self-thinned naturally without fertilizer amendments, weed control, or other silvicultural treatments except for light thinnings in *Larix*, *Betula* and *P. sylvestris* plots. In 1995, plants averaged *c.* 4000 trees ha⁻¹ (*c.* 1.5 m spacing). Between 1995 and 2002 we measured canopy leaf chemistry, litterfall production and chemistry, root chemistry, forest floor dynamics, soil properties and earthworm abundances. Soil properties were

measured in both the underlying mineral soil and in the highly decomposed surface organic horizon (O horizon). Detailed description of litterfall, forest floor and soil sampling and analytical measures are provided in Appendix S1 (see Supplementary Material).

Using analysis of variance to examine the 24 plots of the four species with three replicates in each block, there were no significant ($P < 0.05$) differences among blocks in %C, %N, pH, exchangeable Ca, or any other metric in the O horizon. Given this, we combined data from both blocks to enable comparison of relationships of O horizon soil properties with plant traits for all species. For these same 24 plots, there were significant differences in mineral soil texture (e.g. %clay or %sand) between the two blocks. Regardless, soil %C and %N did not differ among blocks in the mineral soil horizons, nor did soil pH in the 0–20-cm horizon; but blocks did differ ($P < 0.05$) in soil pH at 20–40-cm depth and in soil Ca at both depths in the mineral soil. However, adding %clay as a covariate in the analysis of variance (ANCOVA), removed block as a significant term in these latter analyses.

For instance, exchangeable Ca in the 0–20 and 20–40-cm depths and soil pH at 20–40-cm depth did not differ among blocks but did differ with %clay, when both block and %clay were included in the ANCOVA. Given that the blocks differed to our knowledge only in soil texture and that for

the four species common to both blocks mineral soil horizon measures did not differ among blocks when soil texture was accounted for, we combined data from both blocks to enable comparison of relationships of soil properties with plant traits for all species, and used soil texture of each plot as a covariate to check whether each trait in question remained significant once texture was accounted for. This was performed using simple regressions of each soil metric vs. each plant trait both alone and with %clay as a covariate. We also used %clay as a covariate in multiple regression analyses described below. All analyses were made using data at the plot level, but for simplicity results are shown for species mean values in the figures.

RESULTS

The Ca concentration of leaf litter varied sixfold among the species (Table 1), and was correlated with green leaf Ca concentrations ($r = 0.90$) and fine root Ca concentrations ($r = 0.60$) (data not shown). Angiosperm litter N, cell solubles, cellulose or lignin did not differ from those of gymnosperm litter ($P > 0.10$), but angiosperms did have greater litter Ca concentrations than gymnosperms ($P = 0.02$), although approximately half of the species in each group had overlapping values with members of the other group.

After 30 years, the soils beneath different species varied greatly in O horizon acidity, with pH ranging from 3.9 beneath *Larix* to 6.1 beneath *Tilia*, and in mineral soil acidity, from *c.* pH 4.0 in *Picea* and *P. sylvestris* to *c.* pH 5.0 beneath *Acer platanoides* (Table 2). Exchangeable Ca, total cation exchange capacity and per cent base saturation (exchangeable base cations normalized to cation exchange capacity) also varied markedly in the soils beneath the different species (Table 2). Soils beneath gymnosperms differed significantly from those beneath angiosperms in pH ($P < 0.05$ all horizons) and in exchangeable Ca in the O horizon, but not in soil Ca in mineral soil horizons or in cation exchange capacity (analyses not shown).

Soil pH, exchangeable Ca and per cent base saturation in both the O and both mineral soil horizons increased with the Ca concentration of foliage litter ($P < 0.05$) (Table 3, Fig. 1a–d). For all nine of these relationships, litter Ca remained a significant ($P < 0.05$, usually much less) term even once the %clay content of the soil was also included as a covariate in a simple model. Moreover, litter Ca and clay content were only modestly correlated ($r = 0.51$, $P < 0.05$). In a mixed model, tree species ($P < 0.0001$) explained 92% of plot-to-plot variation in litter Ca whereas clay content explained 1% ($P = 0.05$), suggesting that parent material effects were small compared with species effects on litter Ca. Soil %C in the O horizon and cation exchange capacity

Table 2 Mean soil pH, cation exchange capacity, and per cent base saturation in organic horizon (O horizon) and in two mineral soil horizons for 14 tree species growing in monoculture plots at Siemianice, Poland

Species	Type	Soil pH			Cation exchange capacity (meq kg ⁻¹)			Base saturation (%)		
		O horizon	0–20 cm	20–40 cm	O horizon	0–20 cm	20–40 cm	O horizon	0–20 cm	20–40 cm
<i>Tilia cordata</i>	DH	6.13	4.64	4.53	783	102	70	81.0	53.2	60.8
<i>Acer pseudoplatanus</i>	DH	5.65	4.36	4.50	807	87	74	78.8	51.0	58.3
<i>Acer platanoides</i>	DH	5.54	4.99	4.89	747	91	69	75.3	47.9	54.0
<i>Fagus sylvatica</i>	DH	5.40	4.14	4.23	719	93	68	74.6	40.1	47.5
<i>Betula pendula</i>	DH	5.05	4.55	4.35	893	58	43	83.3	35.5	42.4
<i>Abies alba</i>	EC	4.72	4.12	4.13	704	106	66	68.8	46.8	55.0
<i>Quercus robur</i>	DH	4.84	4.22	4.24	822	77	53	67.4	40.0	47.9
<i>Picea abies</i>	EC	4.32	3.85	3.92	875	84	53	54.6	28.1	34.6
<i>Quercus rubra</i>	DH	4.86	4.18	4.10	885	48	33	65.6	33.4	40.5
<i>Pseudotsuga menziesii</i>	EC	4.01	3.96	4.02	807	78	56	47.3	34.0	39.4
<i>Carpinus betulus</i>	DH	4.67	4.15	4.16	837	62	47	69.9	41.5	45.3
<i>Larix decidua</i>	DC	3.94	4.03	4.19	827	91	68	59.8	41.5	51.1
<i>Pinus sylvestris</i>	EC	3.95	4.01	3.97	853	56	41	48.2	28.9	37.4
<i>Pinus nigra</i>	EC	4.08	4.11	4.08	755	56	38	53.3	27.9	39.2

DH, deciduous hardwood; DC, deciduous conifer; EC, evergreen conifer.

As in Table 1, species ordered from highest to lowest based on litter Ca concentration. All attributes were significantly different among species (ANOVA $P < 0.05$) and were not significantly different between gymnosperms (conifers) and angiosperms (hardwoods), except for soil pH (all horizons) and % base saturation (O horizon). The average standard error for each species was generally <0.05 pH units for all depths and between 5 and 10% of the species mean for cation exchange capacity and % base saturation at all depths. Values are mean values of three or six plots.

Table 3 Correlations of selected soil parameters in three horizons with leaf litter chemistry, soil texture (per cent clay in upper mineral soil horizon), and earthworm biomass for 14 tree species growing in monoculture plots at Siemianice, Poland

Traits	Cation exchange capacity (meq kg ⁻¹)	Base saturation (%)	pH _{H₂O}	Soil C (%)	C : N	Exchangeable Ca (cmol kg ⁻¹)
Organic horizon						
Earthworm biomass (g m ⁻²)	-0.57*	0.58*	0.73*	-0.84*	-0.45	0.86*
Litter Ca (%)	-0.22	0.76*	0.92*	-0.79*	-0.53*	0.96*
Litter N (%)	0.09	0.55*	0.37	-0.13	-0.30	0.32
Litter cellulose (%)	0.03	-0.60*	-0.54*	0.62*	0.64*	-0.54*
Clay (%)	-0.40	0.31	0.46	-0.79*	-0.56*	0.55*
Mineral soil, 0–20 cm						
Earthworm biomass (g m ⁻²)	0.70*	0.81*	0.43	0.04	-0.48	0.56*
Litter Ca (%)	0.58*	0.81*	0.71*	-0.10	-0.64*	0.75*
Litter N (%)	0.35	0.46	0.13	0.41	-0.16	-0.05
Litter cellulose (%)	-0.50	-0.68*	-0.46	-0.09	0.67*	-0.49
Clay (%)	0.45	0.49	0.58*	-0.36	-0.63*	0.83*
Mineral soil, 20–40 cm						
Earthworm biomass (g m ⁻²)	0.77*	0.82*	0.57*	-0.14	-0.53*	0.77*
Litter Ca (%)	0.67*	0.76*	0.78*	-0.15	-0.58*	0.75*
Litter N (%)	0.24	0.39	0.10	0.32	-0.18	-0.03
Litter cellulose (%)	-0.57*	-0.55*	-0.54*	-0.04	0.58*	-0.54*
Clay (%)	0.61*	0.45	0.74*	-0.40	-0.51	0.91*

*Pearson correlation coefficients with $P \leq 0.05$. Lignin was not significantly correlated with any soil property; hence it is not shown in the table. Correlations for three soil horizons for 14 tree species growing in monoculture plots at Siemianice, Poland, using species mean values ($n = 3\text{--}6$ per species). Earthworm biomass as ash-free dry mass.

in the mineral soil were also significantly correlated with litter Ca (Fig. 1e, Table 3).

Soil properties were correlated with litter Ca for both angiosperms and gymnosperms as well as across all species. There were no significant differences in the slopes of these relations for the angiosperm and gymnosperm groups, and the effects of litter Ca remained statistically significant and dominant in the models that included group as a factor (Fig. 1). Hence, variation in litter Ca explained most of the variation in the above soil properties, regardless of tree type.

Variation in litter Ca among the different tree species also was significantly correlated with soil C : N ratio, forest floor turnover rate and soil CO₂ flux (Tables 1 and 3). Soils beneath species with Ca-rich litter and high per cent base saturation had faster forest floor turnover rates, low C : N ratios in all soil depths, and high CO₂ flux, indicating rapid movement and cycling of carbon (Tables 1–3, see Appendix S2).

No other litter trait (such as lignin or N) nor ecosystem variable (such as total litterfall or basal area, Table 1) was as consistently or as well correlated with soil variables as was litter Ca. Moreover, in multiple regression analyses that included Ca plus four measures of litter C and N chemistry, as well as soil clay content, Ca remained the trait best related to the suite of measured soil properties (Appendix S2). In essence, even after removing effects of these other variables, litter Ca was significantly and positively associated with soil

pH and per cent base saturation and negatively related to soil %C and soil C : N.

Plots containing tree species with Ca-rich detritus had greater density, diversity and biomass of native earthworms than plots containing trees with Ca-poor litter (Fig. 1f and data not shown). Moreover, there were strong correlations between earthworm biomass and their species or functional group richness ($r > 0.9$). Hence, Ca-rich plots had greater numbers of earthworm individuals and species, including representatives of more of the major earthworm functional groups: epigeic species (e.g. *Dendrobaena octaedra*) that live and feed exclusively in the litter layer, endogeic species (e.g. *Aporrectodea* spp.) that live and feed in the mineral soil horizon and anecic species (e.g. *Lumbricus terrestris*) that burrow deeply but feed primarily on fresh surface litter. Plots with high earthworm biomass had lower forest floor mass and O horizon %C, and higher forest floor turnover and exchangeable soil Ca in all horizons (Fig. 2, Tables 1–3).

Differences in soils apparently result from variation among tree species in litter chemistry, and in turn, such differences appear to be influencing tree chemistry in a dynamic and ongoing fashion. Species with higher soil exchangeable Ca and soil pH tended to have increases in green leaf Ca concentrations over the period from 1995 to 2001 (Fig. 3). Thus, the influence of trees on soil processes has apparently led to a positive feedback by which intrinsic

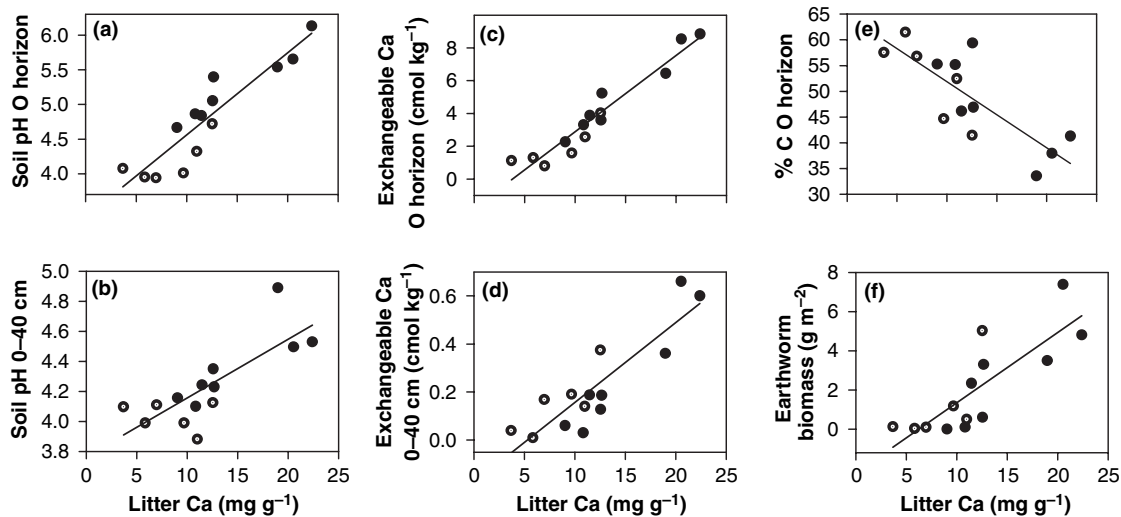


Figure 1 Relationships of soil properties to litter calcium (Ca) concentration. In all panels (a–f), each data point is the average of between three and six plots per species, and angiosperm (hardwood) species are shown in closed symbols, gymnosperms (conifers) in open symbols. For figures, mineral soils data were averaged for the 0–20 and 20–40 cm mineral horizons (data shown separately by horizon in Tables and Supplementary Appendix). Analyses of covariance revealed no significant ($P > 0.10$) difference in slope of the relationships for angiosperm and gymnosperm groups for any of the relationships shown here or in Figs 2 and 3. (a and b) Soil pH (water) in relation to litter Ca (mg g^{-1}) for organic horizon (O horizon) ($r = 0.92$, $P < 0.0001$ for all species combined) and 0–40 cm mineral soil horizon ($r = 0.75$, $P < 0.0001$). (c and d) Soil exchangeable Ca (cmol kg^{-1}) in relation to litter Ca for O horizon ($r = 0.96$, $P < 0.0001$) and 0–40 cm horizon ($r = 0.88$, $P < 0.0001$). (e) O horizon %C in relation to litter Ca (mg g^{-1}) ($r = -0.79$, $P < 0.0001$). (f) Earthworm biomass in relation to litter Ca (mg g^{-1}) ($r = 0.81$, $P < 0.0001$).

differences in tissue chemistry influence soil properties and processes, leading to yet greater divergence in biochemistry among the species.

DISCUSSION

Among 14 temperate tree species, variation in green foliage Ca concentration, and hence in litter Ca concentration, appears to be a key driver of decadal-scale change in soil properties, especially those related to acidity and cation biogeochemistry, but also those related to C and N contents and ratios in forest floor, humic and mineral soil horizons. The differences among species in foliage and litter chemistry to a large part represent intrinsic, species-specific traits because they are present even when species are grown under comparable nutrient supply and identical climate (e.g. Höhne 1962; Reich *et al.* 1998). Moreover, variation in litter Ca serves as a unifying driver of soil processes regardless of whether trees are gymnosperms or angiosperms, or evergreen or deciduous. Variation in litter %Ca likely influences the distribution and concentration of Ca as a cation in exchange reactions between soil solids and solution, thereby affecting cation exchange processes and soil pH.

Although litter Ca was strongly correlated with many soil chemical properties in our study, other litter properties, such

as lignin and N concentrations, have frequently been correlated with litter and soil C and N dynamics (Melillo *et al.* 1982; Pastor *et al.* 1993; Scott & Binkley 1997; Van Breemen *et al.* 1997). However, in our study, neither lignin nor N concentrations in litter were consistently or as well correlated to soil properties as was litter Ca.

The high abundance and biomass of earthworms on plots containing tree species with Ca-rich detritus is consistent with the known influence of litter chemistry on the composition, abundance and activity of earthworm communities (Pearce 1972; Hendriksen 1990; Edwards 1998; Hendrix *et al.* 1999). Differential species effects on soils associated with the Ca concentrations of their litter are likely enhanced by the activities of earthworms (Pearce 1972; Lavelle 1997; Edwards 1998; Ponge *et al.* 1999). High earthworm biomass was associated with lower forest floor mass and O horizon %C, and higher forest floor turnover and exchangeable soil Ca. Earthworms, when present, typically play a major role in the translocation and/or decomposition of fresh detritus (Lavelle 1997; Edwards 1998), and differ strongly in their feeding and habitat preferences (Pearce 1972; Lavelle 1997; Edwards 1998), with high diversity and abundance of earthworms leading to increased organic matter turnover rates (Ponge *et al.* 1999). They also affect organic matter dynamics by incorporating organic material from the forest floor into deeper soil

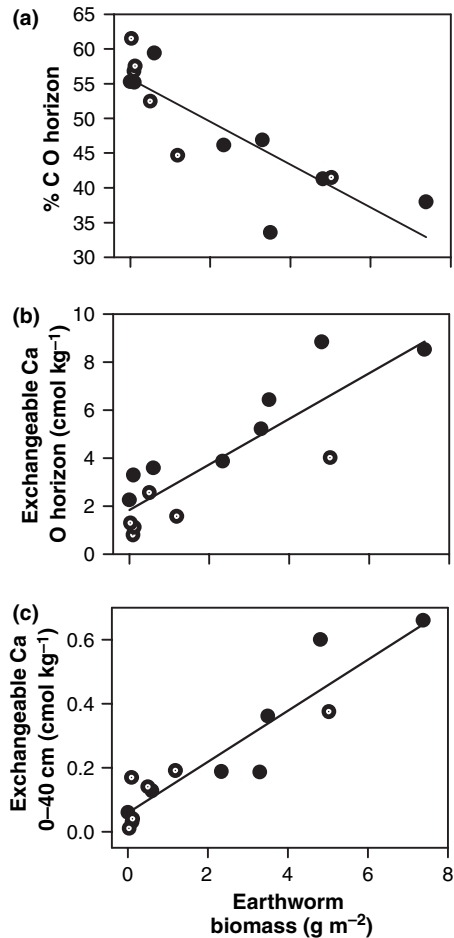


Figure 2 (a) Organic horizon (O horizon) %C in relation to earthworm ash-free biomass ($r = -0.87$, $P < 0.0001$). (b and c) Exchangeable soil Ca in the O horizon ($r = 0.87$, $P < 0.0001$) and in the 0–40 cm horizon ($r = 0.92$, $P < 0.0001$) in relation to earthworm biomass.

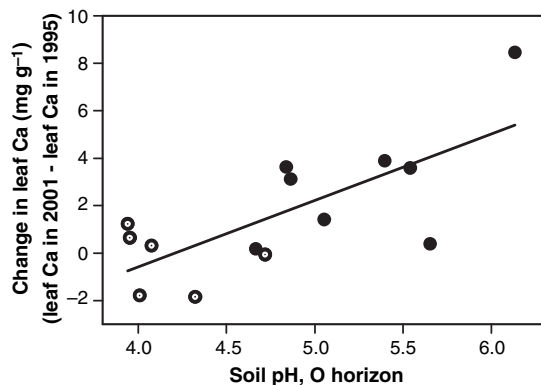


Figure 3 Change in canopy leaf Ca (mg g^{-1}) from 1995 to 2001 (leaf Ca in 2001–leaf Ca in 1995) in relation to the organic horizon pH ($r = 0.73$, $P < 0.0001$).

horizons and by processing litter during passage through the earthworm gut (Devliegher & Verstraete 1997). The net effect in a given ecosystem may depend on the species composition and biomass of earthworms and associated shifts in the composition, biomass and activity levels of the microbial community (Lavelle 1997; Edwards 1998).

From these data, there is evidence that species effects on soils occur in 30 years, largely mediated by litter Ca. Moreover, this influence of trees has apparently led to a positive feedback by which intrinsic differences in tissue chemistry influence soil properties and processes, leading to yet greater divergence in biochemistry (as shown by changes in green leaf Ca) among the species. Whether individual species modifications of soils have positive, neutral or negative impacts on the performance of either conspecific regenerating seedlings or on mature trees are unknown in this instance, and in general will depend on a variety of biotic and abiotic factors.

In summary, we observed rapid (within three decades) and widespread changes in soils beneath different tree species. Species affected soils both directly through the chemistry of their litter and indirectly through the effect of their litter on detritivores, including earthworms. Litter Ca appears to be a critical and general agent in these processes, as its variation led to similar divergence in soils among species within gymnosperm and angiosperm groups, as well as across them. If the fertility and biogeochemistry of soils, particularly those derived from relatively base-rich parent materials, are as generally malleable and influenced by vegetation and associated soil organisms as observed in this study, it supports the idea (Van Breemen 1993; Berendse 1998; Binkley & Giardina 1998; Ponge *et al.* 1999) that vegetation, soil organisms and soil chemistry should be viewed as co-developing components of terrestrial ecosystems even on decadal scales, and highlights the need to consider the role of vegetation change as a driver of regional biogeochemistry (Lovett *et al.* 2002) in broad analyses of global environmental change.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online from <http://www.Blackwell-Synergy.com>:

Appendix S1 Online materials and methods.

Appendix S2a Summaries of multiple regressions of dependent variables (forest floor turnover rate, earthworm biomass, soil pH, and cation exchange capacity) with five leaf litter attributes and soil clay content.

Appendix S2b Summaries of multiple regressions of dependent variables (percentage base saturation, soil C, and soil C/N ratio) with five leaf litter attributes and soil clay content.

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