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Title: Tree Species-Soils Relationships in Old-Growth Forests of the Oregon Coast Range.

Abstract approved:

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Steven S. Perakis

Tree species directly and indirectly affect soil nutrient cycles. I sought to characterize soils and foliage associated with four common canopy tree species (Douglas-fir, western hemlock, western redcedar, and bigleaf maple) in mixed-species old-growth forests of the Oregon Coast Range and to determine whether and how soils differ among the tree species. Sampling was replicated at eight forest sites to assess the generality of tree-species soils relationships across this region. Forest floor (Oe+Oa horizon) and mineral soils (0 to 10 cm and 10 to 20 cm depth) were analyzed for pools and concentrations of major elements (C, N, P, Ca, Mg, K, and H). Foliar nutrient concentrations, which reflect active nutrient cycling by the trees, were also

determined for C, N, P, Ca, Mg, and K. Results were analyzed with respect to two complementary conceptual models of tree species-soils relationships. In a depth-based model, trees were inferred to influence soil properties if surface mineral soils (0 to 10 cm) differed beneath the canopies of tree species, but deeper mineral soils (10 to 20 cm) did not. Using a context-dependence model, I assessed whether species-based differences in each soil nutrient diverged, converged, or were constant as nutrient status increased across sites.

Douglas-fir soils were characterized by greater mass of forest floor relative to other species and, at high-C and -N sites, large pools of C and N in mineral soils. Western hemlock soils and foliage were generally poor in bases, particularly Ca. Western redcedar soils and foliage were high in Ca and were low in P, and soil P was especially low at high-P sites. Bigleaf maple soils and foliage were rich in P and base cations, and soils had high available nitrate relative to other species at nitrate-rich sites. Overall, the depth-based model was best supported by data for pools of the weatherable elements P and Ca, while the context-dependence model was best supported by data for the atmospherically derived, biologically fixed elements C and N. This apparent dichotomy in patterns for soil pools of rock-derived vs. atmospherically-derived nutrients merits further investigation. Forest management or natural successional processes that foster stand dominance by a single tree species are likely to reduce soil nutrient heterogeneity relative to that of current old-growth forests, and in some cases, may reduce soil fertility.

Tree Species-Soils Relationships in Old-Growth Forests of the Oregon Coast Range

by

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I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

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Alison Cross, Author

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To my family

Tree Species-Soils Relationships in Old-Growth Forests of the Oregon Coast Range

INTRODUCTION

Plants, generally and as individual species, are an important control on soil properties such as structure, water availability, and biota, as well as nutrient cycling. Plant species may influence soil nutrient cycling directly, via nutrient uptake (Turner et al. 1993), litter inputs (Prescott 2002), and induced leaching losses (Lovett et al. 2002, Compton et al. 2003, Templer et al. 2005), and indirectly, via alteration of microclimate and disturbance regime (Chapin et al. 2002), precipitation chemistry (Edmonds et al. 1991), and floral and faunal activities (e.g., Torgersen et al. 1995, e.g., Smolander and Kitunen 2002). Soil nutrient concentrations and pool sizes provide integrated measures of these influences. Concentrations provide indices of nutrient availability as experienced by plant roots and microbes, while pools reflect nutrient supply for ecosystem productivity. Because they are also linked to hydrologic nutrient loss (Lovett et al. 2002, Compton et al. 2003, Templer et al. 2005), tree species influences on soil nutrient availability have implications for future forest and stream productivity. Species-specific data on soil nutrient pools may also inform ecosystem process models such as STANDCARB (Harmon and Marks 2002, Sierra 2006).

Despite continued research into tree species effects on soil nutrient cycles, the generality of these effects remains unknown (Binkley and Menyailo 2005). Of the generalizations proposed by Binkley and Menyailo, the literature on common garden studies offered the strongest support for N-fixing trees increasing soil C and rates of nutrient cycling. In Pacific Northwest forests, nitrogen fixation by early-successional red alder (*Alnus rubra* Bong.) reduces P availability (Compton et al. 1997) and

accelerates N cycling (Binkley et al. 1992, Binkley et al. 1994), soil acidification (Van Miegroet and Cole 1984, 1985, Bormann et al. 1994), and hydrologic loss of N and base cations (Compton et al. 2003). It is not clear whether late-successional tree species in general, and in the Pacific Northwest in particular, foster soil change to a degree that is comparable to those resulting from early successional N fixers.

In studies of tree species effects on soils, conflicting results may stem in part from underlying differences in field site characteristics or from site-mediated species effects. For studies lacking replication within vegetation types (Tarrant et al. 1951, Reich et al. 1997, Knoepp and Swank 1998), inferred vegetation effects are difficult to separate from site effects due to differences in soils or stand history (c.f., Alban 1969, Lovett et al. 2004, Templer et al. 2005). Plants and soils can have reciprocal impacts on each other, and these effects may be context dependent, whereby species effects on soils may be expressed only under a particular set of site conditions. This context dependence of species effects on soils has the potential to either enhance or reduce species differences in nutrient cycling across gradients from low- to high-nutrient status (Figure 1). Species that (1) influence supply of limiting resources (e.g., N-fixers and deep-rooted species) (Chapin et al. 2002), (2) influence nutrient mineralization by microbes via microclimate, root priming, or investment in mycorrhizae, or (3) differ in nutrient uptake or nutrient use efficiency could enhance species effects on soils at low-nutrient sites. Such a pattern would result in convergence at high-nutrient sites (Figure 1, top). Divergence at high-nutrient sites (Figure 1, center) could result from positive feedback loops, as when species differences in litter quality intensify site differences

in soil fertility (Chapin et al. 2002). Positive feedback between plant and soil nutrient cycling along N-availability gradients has been noted in a number of studies (Pastor et al. 1984, Wedin and Tilman 1990, Lovett and Rueth 1999, Prescott et al. 2000). Alternatively, species effects on soils could be independent of underlying site characteristics. These "general" species effects would generate constant species-soils relationships across sites (Figure 1, bottom).

Studies of trees grown in monocultures effectively isolate species effects on soils, but may not adequately capture species effects in mixed stands (Rothe and Binkley 2001). For example, leaf litter decomposition experiments have shown that mixtures of litter of different species can exhibit additive, neutral, and antagonistic effects on overall decomposition that are not easily predicted from the characteristics of the individual litters alone (Gartner and Cardon 2004). More generally, experimental studies of grasslands have shown that species diversity and functional characteristics can impact a range of ecosystem processes that serve as the context for individual species effects on soils (Tilman et al. 1997, Hooper and Vitousek 1998, Tilman et al. 2001). Thus, plants can shape long-term patterns of soil and ecosystem development (Jenny 1941) in ways that may affect subsequent interspecific interactions and plant-soil relationships.

Old-growth forests of the Pacific Northwest provide a unique opportunity to examine tree species-soils relationships in a wide range of mixed-species ecosystems that developed with minimal anthropogenic disturbance. The western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) vegetation zone of the Pacific Northwest is broadly

distributed throughout middle and upper elevations of the Coast and Cascade Ranges of western Oregon and Washington. Old-growth western hemlock forests of the Coast Range generally still include substantial proportions of Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and often western redcedar (*Thuja plicata* Donn ex D. Don.) as well. Succession in forests of the western hemlock zone is thought to proceed ultimately to the shade-tolerant western hemlock, although Douglas-fir, a fast-growing, long-lived (> 750 yr; (Waring 1979)), shade-intolerant seral species, can persist on the driest sites, and western redcedar remains an important forest component on wetter sites. Tree species such as Pacific madrone (*Arbutus menziesii*), Pacific yew (*Taxus brevifolia)*, grand fir (*Abies grandis*), and incense cedar (*Libocedrus decurrens*) are minor components of the canopy at some sites. Understory vegetation varies within and across western hemlock forests of the Coast Range, and may include Pacific swordfern (*Polystichum munitium*), oregongrape (*Berberis nervosa*), salal (*Gaultheria shallon*), rhododendron (*Rhododenron macrophyllum*), vine maple (*Acer circinatum*), oxalis (*Oxalis oregana*), and *Vaccinium spp.* (Franklin and Dyrness 1988).

Old-growth forests currently dominated by Douglas-fir are characterized by high levels of gross productivity, mortality, nutrient retention, and nitrogen-fixing epiphyte abundance, and by large live trees, snags, and logs (Franklin et al. 1981). Forests of the western hemlock zone typically develop old-growth characteristics by 175 to 250 yr after stand initiation (Franklin et al. 2002). For management purposes, old-growth forests are primarily defined by structural heterogeneity in the form of

decurrent crowns, canopy gaps, dead wood, and patchy understories (Spies 2004). Because this definition concerns forest development rather than succession per se, old-growth includes forests dominated by late-successional species, such as western hemlock, as well as forests dominated by seral Douglas-fir. In western Oregon forests, structural and compositional complexity are known to support biodiversity of epiphytes, arthropods, and birds (Muir et al. 2002). Under the Northwest Forest Plan, approximately 3 million ha of federal forest land in western Oregon and Washington were designated late-successional reserves (LSRs) to provide habitat for species dependent on old-growth forest characteristics (Tuchmann et al. 1996). Management of LSRs under the Northwest Forest Plan includes manipulation of young (< 80 yr) stand forest structure and composition to create wildlife habitat and to foster biodiversity. The functional consequences of differences in overstory tree composition have been evaluated for effects on water use (Bond and Kavanagh 1999) and litter decomposition (Valachovic et al. 2004), and long-term studies of log decomposition are in progress (Harmon 1992), but information describing tree species effects on soil nutrient cycling in this region remains poor. Because LSRs currently include late-successional forests as well as younger stands, information on tree species effects on soils should therefore be useful in managing both LSRs and young forests to achieve a desired range of functional diversity and to improve sustainability.

In forests of the western hemlock zone, compositional shifts through succession toward forests dominated by shade tolerant western hemlock may alter soil nutrient dynamics, with implications for ecosystem management. Additionally, fire

suppression in this region will likely increase western hemlock dominance in LSRs that are managed for old-growth structural characteristics. Such ecosystem simplification is of particular concern where important species differences in nutrient cycling would be eliminated. An understanding of the effects of plant species on nutrient cycling should improve our ability to predict ecosystem response to perturbations such as climate change or invasion by exotic species. Such knowledge may also aid in guiding ecosystem management and restoration of late-successional forest composition and function in addition to structural characteristics.

The objectives of this study were (1) to characterize nutrient concentrations and related properties of foliage, forest floor, and mineral soil associated with each of four commonly occurring tree species in mixed old-growth forests of the southern Coast Range of Oregon, and (2) to determine whether relationships between tree species and their associated soils are context dependent or uniform across field sites. I expected trees to influence forest floors and surface mineral soils more strongly than deeper mineral soils, because overstory effects on microclimate, rooting, nutrient uptake, and litter inputs of moist temperate forests are often concentrated in upper soil horizons. Consequently, a depth-based sampling regime was used to evaluate tree species effects on mineral soils (Table 1). Specifically, I tested the hypotheses that (1) after accounting for field site, forest floor and surface mineral soil properties vary with tree species, while deeper mineral soil properties do not, and (2) species-based differences in soils vary systematically across field sites.

METHODS

Study Sites

This research was conducted in old-growth forests of the western hemlock zone in the southern half of the Coast Range of Oregon, USA (Figure 2). Climate in this region is temperate and maritime, with a mean annual temperature of 10°C and mean annual precipitation of 180 cm, falling mostly as winter rains. The Coast Range province extends from the Coquille River in southwest Oregon to the Willapa Hills in southwest Washington. Geology of the province consists largely of Eocene basalts and marine sediments, with Oligocene basalt flows in the north and igneous intrusions in the south, where sharp ridges characterize the deeply dissected topography. On steep slopes, soils are often thin and poorly developed (Franklin and Dyrness 1988).

The forest sites were originally studied by Spies and Franklin (1991) and are included in a larger, ongoing study of Coast Range old-growth forests. All of these sites are dominated by Douglas-fir and typically have 5 to 6 tree species per site (Spies and Franklin 1991). From among those forests, I chose eight sites with four tree species - Douglas-fir, western hemlock, western redcedar (*Thuja plicata* Donn ex D. Don), and bigleaf maple (*Acer macrophyllum* Pursh.) - well represented in the canopy. These sites showed no evidence of logging or other significant human disturbance, although low-intensity fire or fire exclusion may have occurred at the sites since the current stands originated. Four of the sites have soils derived from sedimentary rocks, primarily sandstone and siltstone, and the remaining four have soils derived from mixed sedimentary and volcanic rocks (Table 2). Soils are primarily Ultisols and

Inceptisols but also include Andisols at two sites in Benton County and Alfisols at one site in Douglas County. Updates to the soil surveys are in progress for Benton County and incomplete for Douglas County, but the Coos County and Lane County soil surveys predate the recognition of the Andisols. The Bureau of Land Management administers all sites except 810, which is managed by the USDA Forest Service and lies within the City of Corvallis watershed.

Sample Collection and Preparation

In June–August 2003, soil samples were collected under six individuals of each of the four tree species at each of the eight sites. The sites were sampled from south to north to correspond with seasonal progression of soil drying across the region. Trees were selected from among the largest canopy trees in upland areas. Larger trees had a greater potential to influence soils (Boettcher and Kalisz 1990), as these trees were likely to have returned more litter to the soil over the course of their lives. Immediate neighbor trees were not sampled, and stand edges, large gaps, and draws were avoided. Aspect was recorded and diameter at breast height (1.4 m) was measured from the upslope side of each tree.

Forest floor and mineral soil samples were collected within 30 cm x 30 cm square sampling frames placed within the projected canopy, ≤ 2m from the base of each tree, sideslope rather than up- or down-slope of the bole. Visible logs, large roots, and rocks were avoided when placing the frames. Within each frame, the recently fallen (Oi) and decomposing (Oe+Oa) forest floor horizons were removed to paper bags. At the lab, forest floor samples were oven-dried for 48 hr at 65 °C, sorted to

remove rocks and soil, and weighed prior to analysis. Depths from the surface to each horizon were measured at five points (four corners plus the center of the frame). The underlying mineral soil was sampled at 0 to10 cm and 10 to 20 cm depths using a 6.8 cm-diameter bulb corer and a 4.8 cm-diameter slide-hammer corer, respectively. Two cores were taken at each depth, composited in a polyethylene bag, and placed on ice in a cooler for transport back to the lab, where they were kept in a dark 4 °C refrigerator until analysis.

In July 2004, foliage was collected from six canopy trees of each species at each site. Trees were chosen according to the selection method used in soil sampling but were not necessarily the same individuals as those sampled in 2003. Sun leaves were retrieved from three sides of each tree using a 12-gauge shotgun loaded with steel turkey shot. Samples were composited by tree, sealed in polyethylene bags, and placed in a cooler for transport back to the lab, where they were kept frozen at 0 °C until processing. At that time leaves were separated by hand from twigs, reproductive structures, and any miscellaneous material. For western redcedar, flexible green sprays were separated from brown twigs that had dropped their scale-like leaves. Foliar samples were then dried for 48 hr in a 65 °C oven and stored at room temperature prior to analysis.

Foliar and Forest Floor Chemistry

Approximately 5 to 10 g of each dried foliage or Oe+Oa horizon sample was snipped with scissors, ground on a roller mill to a powder consistency (~1.5 d), and stored in a dessicator until analysis. Samples of the Oi horizon were not analyzed for

nutrients. Tin capsules were packed with 3.5 mg sample, and total C and N were measured against an atropine standard on a Costech ECS-4010 elemental combustion analyzer (Costech Analytical, Valencia, CA, USA).

To determine phosphorus (P) and the base cations calcium (Ca^{2+}), magnesium (Mg^{2+}), and potassium (K^{+}), 0.5 g of each ground sample was weighed into a crucible and ashed for 12 hr at 475 °C in a muffle furnace. Once the samples cooled, 5 mL of 5 M HCl were added to each and swirled gently to dissolve. Each was then diluted with 5 mL of deionized water and the resulting solution was poured, along with four subsequent crucible rinses with 10 mL deionized water, through pre-rinsed Whatman 42 filter paper in funnels. Filtrates were collected in acid-washed 30 mL polyethylene bottles and refrigerated at 4 °C until analysis. Total P was assayed colorimetrically using the molybdenum blue method (QuikChem Method 10-115-01-1-B, Lachat Instruments, Milwaukee, WI, USA). Ca^{2+}, Mg^{2+}, and K^{+} were assayed by flame atomic absorption on a Perkin-Elmer AAnalyst 200 (PerkinElmer Instruments, Shelton, CT, USA). Recovery of apple leaf and alfalfa standards was > 94% and average CV of replicate samples was < 5%.

Mineral Soil Properties

Field-moist mineral soils were weighed and passed through a 2 mm sieve to remove rocks and roots and to homogenize the soil. The < 2 mm fraction was then reweighed. All subsequent chemical analyses were performed using the < 2 mm fraction. Gravimetric soil moisture content was determined by drying a 10 g subsample of the < 2 mm fraction for 48 hr in a 105 °C oven. Bulk density was

calculated as the dry mass of the < 2 mm fraction divided by the volume of the entire soil core. Soil solution pH (2 water: 1 soil) was determined by stirring 20 mL deionized water and 10 g field-moist soil in a 50 mL cup. The mixture was allowed to equilibrate for 30 min, and pH of the supernatant was measured using an Accumet pH meter with a glass-body liquid-filled combination probe (Fisher Scientific, Hampton, NH, USA).

Total Carbon and Nitrogen

Approximately 20 g of field-moist soil was dried for 48 hr at 65 °C, ground on a roller mill to a powder consistency (~2 hr), and stored in a desiccator. Tin capsules were packed with either 11 mg (0 to 10 cm depth) or 14 mg (10 to 20 cm depth) soil for measurement of total C and N as above. In tests using other samples from the same field sites, soils originally dried at 65° C showed mass loss < 2 % when they were dried for another 48 hr at 105° C. For this reason, no additional conversion factor was applied to soil masses in this assay.

Available Nutrients

To estimate nutrients in available pools, soils were assayed for exchangeable C, N, P, and base cations. Carbon and nitrogen were extracted by adding 35 mL of 0.5 M K_2SO_4 to 7 g field-moist soil in snap-cap vials, shaking for 1 h, allowing samples to settle for 30 min, and pouring them through pre-rinsed Whatman 42 filter paper in funnels. Extracts were collected in 20 mL polyethylene scintillation vials and refrigerated at 4 °C for up to one week or kept frozen until analysis. Nitrate (NO_3^-)-N and ammonium (NH_4^+)–N were analyzed colorimetrically by the cadmium reduction

method and the salicylate method, respectively, using a Lachat QuikChem 8000 flow-injection autoanlyzer (QuikChem Methods 12-107-06-2-E and 12-107-04-1-H, Lachat Instruments, Milwaukee, WI, USA). Dissolved organic carbon (DOC) and total dissolved nitrogen (TDN) in soil extracts were analyzed by catalytic oxidation combustion using a Shimadzu TOC-V CSH total organic carbon analyzer with a TNM-1 total nitrogen measuring unit (Shimadzu Scientific Instruments, Columbia, MD, USA). Dissolved organic nitrogen (DON) in soil extracts was calculated as TDN – (NH_4^+–N + NO_3^--N). DON, a calculated variable, lacked a predetermined detection limit. Detection limits for TDN, NH_4^+–N, and NO_3^--N were each 0.1 mg N/L, or ~ 0.65 mg N/kg dry soil for a sample having average moisture (~ 23 % of field-moist mass). I therefore considered DON values < 1 mg N/kg to be unreliable and omitted them (n = 16, or 4 % of samples). Because remaining small DON values would yield artificially high calculated DOC:DON ratios, I instead calculated DON:DOC, which had a more normal distribution.

Exchangeable inorganic soil P, an index of plant-available P, was assayed using acid-fluoride extraction (Bray and Kurtz 1945). Bray-1 (0.03 N NH_4F-0.025 N HCl) extracting solution solubilizes P adsorbed to soil particles, complexed with aluminum, and bound with calcium and iron. Twenty-five mL of extracting solution was added to 5 g field-moist soil in 50 mL centrifuge tubes. The samples were shaken vigorously by hand for 1 min and centrifuged at 3400 rpm for 5 min. The supernatant was then poured through Whatman 42 filter paper in funnels and collected in 20 mL polyethylene scintillation vials. Extracts were refrigerated at 4 °C for up to 48 hr or

kept frozen until colorimetric analysis for P as ortho-phosphate by the molybdenum blue method (QuikChem Method 12-115-01-1-A, Lachat Instruments, Milwaukee, WI, USA). Negative values for exchangeable P were replaced by 0.2 mg P/L, one-half the lower detection limit.

Exchangeable base cations were removed from soils via mechanical vacuum extraction (Sampletek 24VE, Mavco Industries, Lincoln, NE, USA) using 1 M ammonium chloride (NH_4Cl). Filter pulp was prerinsed using successive 60 mL washes with 0.5 N HCl, deionized water, and 1 M NH_4Cl. Samples of 2.5 g air-dried soil were then extracted for 12 hr using 60 mL of 1 M NH_4Cl. Extracts were stored in polyethylene bottles and refrigerated at 4° C up to 2 wk until analysis of Ca^{2+}, Mg^{2+}, K^+, and sodium (Na^+) by flame atomic absorption. While Na^+ contributes to the sum of bases and overall charge balance in the soil solution, it is not an essential nutrient to C_3 plants (Taiz and Zeiger 2002) and will not be reported individually. At the time of extraction, additional air-dried soil samples were dried for 48 hr at 105 °C to determine an air-dry mass to oven-dry mass conversion factor.

Nutrients in Microbial Biomass

Concentrations of microbial biomass C, N, and P were determined by the fumigation-direct extraction method (Davidson et al. 1989). Field-moist soils were fumigated in desiccators lined with wet paper towels. A flask containing ~75 mL chloroform was placed in the center of each desiccator. Desiccators were evacuated 4 times; the chloroform was allowed to boil for 2 min during the 4^{th} evacuation. The desiccators were then sealed and samples were incubated in the dark at room

temperature (~25 °C). After 48 hr the soils were allowed to vent to the atmosphere for 10 min and then extracted and analyzed as above for TOC, TDN, and ortho-P. Microbial biomass C and N were calculated as the differences in concentration between extracts of fumigated and unfumigated soils.

Calculations and Statistics

Foliar nutrients were calculated as concentrations per g dry mass, and nutrients in forest floor and mineral soils were calculated both as concentrations and as pools per m^2. Forest floor nutrient concentrations were scaled per mol C to account for some admixing of mineral soil with forest floor material. Mineral soil nutrient concentrations were expressed per kg dry soil. For all compartments, nutrient ratios (e.g., C:N) were calculated on a mol:mol basis.

Species-based differences in each foliar or soil property were evaluated by analysis of variance. This study's generalized randomized block sampling design – 8 sites × 4 species × 6 replicates × 2 depths or horizons (mineral soil and forest floor only) – was described by a linear mixed-effects model (PROC MIXED in the SAS 9.1 software package, SAS Institute, Cary, NC, USA). Fixed effects were *SPECIES, DEPTH,* and *SPECIES × DEPTH;* random effects were *site, site × SPECIES, REPLICATE (site × SPECIES),* and *site × DEPTH(SPECIES),* where parentheses indicate nested effects, e.g. "*REPLICATE* within *site × SPECIES* combinations". The *DEPTH* effects were replaced by *HORIZON* effects for analyses of forest floor properties and were omitted for analyses of foliar properties. The SLICE option in SAS 9.1 was used to test for differences among species within each depth or horizon.

Null hypotheses were evaluated with Type III sums of squares *F*-tests and $\alpha = 0.05$. When species effects within a given depth or horizon were statistically significant, Tukey-Kramer-adjusted *P*-values were used in pairwise comparisons among species.

To assess the importance of site-level replication for interpretation of species effects, all terms in the mixed-effects model above were treated as fixed effects (PROC GLM in SAS 9.1). For foliar properties, site-dependent species effects were tested with *SITE* × *SPECIES* against the *REPLICATE (SITE* × *SPECIES)* error term. Site-dependent effects of depth and species were tested with *SITE* × *DEPTH (SPECIES)* against the default error term, and site-dependent species effects averaged across depths were tested with *SITE* × *SPECIES* against the *REPLICATE (SITE* × *SPECIES)* error term. The null hypotheses of no site interactions were evaluated with Type III sums of squares *F*-tests and $\alpha = 0.05$.

Context-dependence of foliar properties across sites was assessed by linear regression (PROC MIXED in SAS 9.1). For each species, the site mean for each foliar property was regressed against the site mean for a relevant soil property, e.g., foliar N vs. soil N. Context-dependence of trends in surface soil properties across sites were also assessed by linear regression. Species deviations from the site mean were calculated by subtracting the mean of each species at a site from the mean of all species at that site. These deviations were modeled as a function of the fixed effects *SITE MEAN*, *SPECIES*, and a *SITE MEAN* × *SPECIES* interaction. This procedure is comparable to analysis of covariance after centering the response variable by the mean response at each level of the predictor. Absence of autocorrelation between deviations

and the site means was confirmed by Monte Carlo simulation in S-PLUS 7.0.2 (Insightful Corporation, Seattle, WA http://www.insightful.com) and is documented in Appendix A. Regressions were performed for Oe+Oa horizons and 0 to 10 cm mineral soils only. As in the preceding ANOVAs, null hypotheses were evaluated with Type III sums of squares *F*-tests and $\alpha = 0.05$.

Frequency histograms and residual plots were inspected, and natural logarithm transformations were applied where necessary to meet model assumptions of normality and homoscedasticity. Studentized residuals and DFFITS (difference in fit standardized) statistics were checked to identify observations as potentially influential outliers. Those observations generally had values extreme for their species × site group but within the range for all observations, amounted to less than 5 % of observations, and were included in the analyses.

RESULTS

Foliage

Species-based differences were apparent in all foliar nutrient concentrations determined (Table 4). These differences were primarily driven by maple, the only deciduous broadleaf tree, which had significantly lower foliar C and higher N, P, K, and Mg concentrations than did the conifers in pairwise comparison tests. In contrast, redcedar had the lowest foliar N, P, and K concentrations. Species differed in foliar C:N ratios in the order redcedar (high C, low N) > Doulgas-fir = hemlock > maple (low C, high N) (Figure 3). Low redcedar P concentrations resulted in higher N:P ratios for redcedar than for Douglas-fir (Figure 4). Maple and redcedar both had higher foliar Ca than did Douglas-fir and hemlock. Foliar Mg concentrations did not differ among the conifers. Foliar Ca:Mg ratios were ranked: redcedar (high Ca, low Mg) > Douglas-fir > hemlock (low Ca and Mg) = maple (high Ca and Mg). Foliar K concentrations were ranked in the order: maple > Douglas-fir > hemlock > redcedar (Figure 5).

Forest Floor

Species-based differences were also apparent in the thickness and mass of the Oe+Oa horizon but not of the Oi horizon (Table 5). The Oe+Oa horizon was thinner beneath hemlock than beneath maple and was twice as massive beneath Douglas-fir as beneath maple. Forest floor Oe+Oa horizon C:nutrient ratios were consistent among tree species, with the exception of C:Ca, C:Mg, and Ca:Mg ratios (Table 6, Figures 3 through 5). The high C:Ca (or low Ca per unit C) beneath hemlock, low C:Mg (or high

Mg per unit C) beneath maple, and high Ca:Mg beneath redcedar agree with the concentrations of these nutrients as observed in foliage (see Table 4) and mineral soil (see below, Table 7) associated with these species. Species-based differences were significant in all forest floor nutrient pools (Table 6). Again with the exception of Ca and Mg, differences in pool sizes appear to be driven by differences in Oe+Oa horizon mass, with largest pools beneath Douglas-fir and smallest pools beneath maple. Forest floor Ca pools were larger for Douglas-fir than for hemlock and maple, and Mg pools were smaller for redcedar than for the other tree species.

Mineral Soil

Mineral soil properties were determined for 0 to 10 cm and 10 to 20 cm depths. Soil moisture did not differ significantly among species at either depth (Table 7). Concentrations of total C and total N, as well as C:N molar ratios (Figure 3), were consistent among species. Species-based differences were not apparent in available ammonium and nitrate concentrations at either depth. In surface soils, ratios of NH_4^+-N:NO_3^--N concentrations were approximately twice as high beneath redcedar as beneath the other tree species, although pairwise differences were not statistically significant. Concentrations of DON and DOC, as well as DON:DOC ratios, did not differ statistically across species. Microbial C and N concentrations were consistent across species, while ratios of microbial C:N differed among species in surface soils only, where they were highest beneath Douglas-fir.

Exchangeable P concentrations (Table 8, Figure 4) were highest beneath maple and lowest beneath redcedar at both depths. Surface soils had higher Ca (Figure 5) and

Mg beneath maple than beneath hemlock. At both depths, exchangeable Ca:Mg ratios differed among species and were highest beneath redcedar. Exchangeable K concentrations were higher beneath maple than beneath hemlock and redcedar. The sum of base cations decreased with depth beneath all species. Although the sum of bases differed among species at both depths, pairwise differences were significant in the 0 to 10 cm soil only, where the sum of bases was higher beneath maple than beneath hemlock. Species-based differences in the sum of bases appear to be due largely to the difference in exchangeable Ca beneath maple and hemlock combined with the large contribution of Ca, relative to the other base cations, to the sum. Trends in soil pH followed the sum of base cations across species and was lowest beneath hemlock and highest under maple, although differences were not statistically significant

Mineral soil bulk density did not significantly differ among species at either depth (Table 9). For all forms of C and N determined, pools did not differ significantly across all sites (e.g., total C and N, Figure 6). Pools of exchangeable P (Figure 7) differed among species in surface soils only, where pools were smallest beneath redcedar. Exchangeable pools of Ca (Figure 7), Mg, and K also showed species-based differences in surface soils only, where the pools were largest beneath maple and smallest beneath hemlock.

Context Dependence of Tree Species-Soils Relationships

The importance of site-level replication for interpreting species effects on soils was assessed by testing for significance of site-dependent effects of tree species (*SITE*

× *SPECIES)* and of combinations of tree species and depth or horizon [*(SITE* × *DEPTH(SPECIES)* or, for forest floor thickness and mass, *SITE* × *HORIZON(SPECIES)*] in fixed-effects ANOVA. Because forest floor chemistry was determined for Oe+Oa horizon samples only, *SITE* × *SPECIES* was the most complex interaction evaluated for those properties. Significant interactions would suggest context dependence – that any species effects on soils depend on some underlying characteristic of field sites, e.g., geology, climate, disturbance regime, or soil nutrient availability. If interactions are significant, then replication at the site level may help to understand whether species effects as observed at one or more field sites are applicable to other sites in the population of interest. If interactions are not significant, then the values for soil or foliage properties may change depending on field site, even as the relationships among species stay the same from site to site.

Although the present study was not designed to address the mechanisms by which field site characteristics give rise to context dependence of tree species-soils relationships, it is useful to understand the importance of field sites relative to the other effects on soils. More than half of the foliar properties (6 of 10 properties, Table 10) and nearly three quarters of the soil properties (38 of 52 properties, Tables 11 through 13) investigated here showed significant site interactions. For foliage, observed species differences were independent of field site for Ca and K only. For foliar C:N, the dependence of species differences on field site is less clear ($P = 0.050$, Table 10). Species differences in forest floor thickness did not depend on field site, but those in forest floor mass did (Table 11). All forest floor nutrient pools differed among

species independently of field site (Table 12). Species differences for Ca concentrations in forest floor were significantly site-dependent, but those in mineral soil were not site-dependent (Table 13).

Extensive site interactions are not surprising given the broad geographic area and the diversity of soil types sampled (Table 2). These site interactions suggest a context-dependent response of nutrient concentrations and nutrient pools in soils, and influence our ability to (1) infer species effects across sites and (2) to compare or transfer these ideas across studies. Studies may be designed to replicate or constrain field sites relative to the soil property of interest in order to allow for comparisons and transfers of ideas from one site to another. Because this study aimed to characterize baseline tree species-soils relationships in a number of soil properties, it was not designed with respect to any single nutrient gradient, for example. Therefore, results of the context-dependence analysis presented next (Tables 14 through 16) evaluate whether species differences in soil properties across sites are related to the site average for each forest floor or mineral soil property considered. Restated, the context-dependence analysis asks whether predictable site-specific variations among species effects arise across gradients in the properties evaluated. This provides a basis for considering broad classes of mechanisms that may structure site-to-site differences in species effects on soils (Figure 1).

Foliar chemistry was largely independent of underlying variation in soil nutrients across sites (Table 14). With the exception of foliar P and N:P, species differences in foliar chemistry were constant with respect to gradients in soil nutrients.

In general, species ranks for foliar nutrient concentrations were highly conserved across these sites. As soil exchangeable P concentrations increased across sites, species diverged for both foliar P and N:P. Foliar P remained constant with respect to soil P for Douglas-fir and redcedar but increased with soil P for hemlock and maple (Figure 8). Foliar N:P ratios increased with soil P for redcedar and decreased for maple (Figure 9). Foliar N:P differences were also apparent at sites on both ends of the gradient in soil N, although the relationships among species changed as soil N pools increased (Figure 9). Soil exchangeable P ranged over an order of magnitude across sites, so the ability to detect *SITE* × *SPECIES* interactions in regression may have been better against P than against other soil properties with smaller ranges. Because foliar P and N:P diverged across the wide gradient in soil P, any related species differences in soil P would more likely manifest at high- rather than low-P sites.

A number of forest floor properties showed significant context-dependent species effects (Table 15). As the average Oe+Oa horizon thickness increased across sites, maple forest floors became thicker and redcedar forest floors became thinner relative to the average of all species (Figure 10). Deviations in forest floor C concentrations were greater beneath maple and redcedar at low-C sites. C:N and C:P both had significant site interactions and appeared to diverge at high values, although no species deviated significantly from the site mean (slopes and intercepts of individual species regressions not different from zero, *t*-tests, $P \geq 0.062$). Deviations in N and P pools were greatest at sites with high N or P, where maple forest floors accumulated more N or P than average and redcedar forest floor accumulated less N or

P than average (Figure 11). At higher-Mg sites (larger pools or lower C:Mg ratios), redcedar forest floors had lower-than-average C:Mg ratios and maple forest floors accumulated more Mg (Figure 12).

Mineral soils did not always follow the patterns observed in forest floors (Table 16). As the average total C and N pools of mineral soils for all species increased from site to site, Douglas-fir and maple soils diverged, with Douglas-fir accumulating relatively more C and N and maple accumulating relatively less (Figure 13). Redcedar soils had smaller-than-average N pools at low-N sites, but larger-than-average N pools at high-N sites. Redcedar soils also had smaller-than-average P pools at low-P sites (Figure 14). Exchangeable Ca pools showed no site × species interactions (Table 15), while exchangeable Mg pools had significant site interactions but no significant species deviations from the site mean (*t*-tests, $P \geq 0.172$).

While species trends in mineral soil total C and N concentrations showed significant site interactions, no species deviated significantly from the site mean (*t*-tests, $P \geq 0.083$). For concentrations of mineral soil exchangeable NH_4^+-N and NO_3^--N, maple soil deviations from the site mean became more pronounced as the site mean concentration increased (Figure 14). Concentrations of exchangeable P diverged at high-P sites, where redcedar soils had much less P than average (Figure 15). Exchangeable Ca concentrations showed no site × species interactions (Table 15), while exchangeable Mg concentrations for Douglas-fir soil dropped slightly below average as the site mean increased (Figure 16). Predictable context-dependence, in the

form of significant site × species interactions, was not detected for other mineral soil properties.

DISCUSSION

In old-growth forests of the Pacific Northwest, individual trees can persist for centuries. Tree species are known to influence the forest floor and mineral soils beneath them, creating spatial heterogeneity in soil properties at the scale of individual trees. Results of this study demonstrate spatial heterogeneity in both concentrations and pools of nutrients in soils. Soil nutrient concentrations are relevant to plant roots and microbes in the short term and may be highly variable across space and time, while soil nutrient pools are more integrative indices of nutrients stored in soils for future production. Tree-scale heterogeneity of soil nutrients may in turn foster diversity in plant, animal, or microbial communities among tree species. Whatever the cause, the soil heterogeneity characteristic of old-growth forests in this study likely differs considerably from that of young, single-species stands.

Support for Two Conceptual Models

Results of this study supported two conceptual models of tree species-soils relationships. The depth-based model highlighted species differences in pools of the weatherable elements P, Ca, Mg, K in 0 to 10 cm but not deeper mineral soils. In contrast, the context-dependence model primarily highlighted large-scale patterns of tree-species soils relationships for the atmospherically derived, biologically fixed elements C and N across sites.

In the first model, mineral soil properties were evaluated at two depths to test a set of hypotheses regarding species-based differences (Table 1). Mineral soil properties supporting each hypothesis are shown in Table 17. Although no evidence

was found to support the hypothesis of generic plant effects on mineral soils, the suite of soil properties that differed among species in surface soils but not in deeper soils supports the hypothesis of differential tree species influences on soils. I found evidence of tree species influences on P, Ca, Mg, and K pool sizes and on concentrations of Ca. For example, redcedar foliage was characterized by low P and high Ca concentrations and Ca:Mg ratios, which were reflected in nutrient concentrations found in forest floor and mineral soil below. Species ranks for P (maple > Douglas-fir > hemlock > redcedar) were conserved in foliage, forest floor, and mineral soil. Calcium concentration species ranks (maple > redcedar > Douglas-fir > hemlock) were conserved for foliage, forest floor, and surface mineral soil, but species differences were not significant in deep mineral soil. Pools of exchangeable P, Ca, Mg, and K, as well as Ca concentrations, differed among tree species in surface soils but not in deeper soils, which suggests that these differences are due to tree species cycling of these elements via uptake, litter turnover, or other mechanisms. Species-based differences in concentrations of P and Mg were significant in all compartments except for P in the forest floor, where concentrations were generally low. That these differences occurred in mixed stands across 8 study sites – as opposed to the more limited 1-2 monoculture-dominated sites usually examined – suggests that late-successional species may impact soils more intensively and extensively than previously recognized in forests of the Pacific Northwest.

The tree species-related differences in soil properties that appeared at both mineral soil depths were confined primarily to P, Mg, and K when expressed on a

concentration (not total pool) basis. Where such concentration differences occur at both depths, they may reflect establishment of the tree species on contrasting substrates (Table 17). I consider such a cause unlikely for three reasons. First, while light and moisture (Gray and Spies 1997) and animal damage and competition (Maas-Hebner et al. 2005) influence tree seedling establishment in old-growth forests of this region, to my knowledge such an influence of soil chemistry has not been reported. If tree species establishment were determined by soil nutrient availability, I would expect such an influence to manifest as completely conserved species ranks across all 8 field sites. However, analyses of context dependence suggested that any general patterns across sites (e.g, Ca) also include a substantial amount of variability (i.e., some changes in species ranks from site to site). Second, the large diameters of the sampled trees suggest potentially large influences on soils via root uptake and nutrient cycling in litterfall. Species effects on soil properties often become manifest within the lifetime of a single tree (Fujinuma et al. 2005, Reich et al. 2005). Third, short residence times of nutrients in exchangeable pools relative to annual litterfall would result in a much stronger biological vs. parent material imprint on soils. Using annual nutrient returns in litterfall of an another old-growth forest dominated by Douglas-fir (Abee and Lavender 1972), I estimated residence times of nutrients in soil exchangeable pools to be several years for N and P and less than one year for Ca, Mg, and K.

Tree species, largely through their influences on soil acidity, are among the controls on mineral weathering and therefore on cycling and availability of rock-

derived nutrients in surface soils (Homann et al. 1992, Augusto et al. 2000, Augusto et al. 2002). Although not statistically significant, observed pH differences of ~ 0.4 units in surface mineral soils of maple vs. hemlock are likely important for soil organisms beneath these tree species. The pH values also agree with the pools of weatherable elements observed in surface soils beneath each tree species, with low pH corresponding with small pools of base cations, especially Ca, and high pH corresponding with large pools of base cations. Tree species may also differentially redistribute nutrients throughout the rooting zone and biomass pools (Dijkstra and Smits 2002, Jobbagy and Jackson 2004, Fujinuma et al. 2005). Influences of tree species on deeper soils have been observed in a number of studies. In 30-yr old monocultures of seven tree species replicated at level sites along a nutrient fertility gradient in Denmark, species effects on pH and concentrations of P, Ca, Mg, and K were observed at > 50 cm depth in mineral soils (Vesterdal and Raulund-Rasmussen 1998). Vesterdal and Raulund-Rasmussen also found that concentrations of P, Ca, and K in 0 to 50 cm mineral soil were correlated with the C-weighted concentrations of those nutrients in forest floors. The differences in both surface-soil and deep-soil concentrations of P, Mg, and K observed in this study suggest that tree-species impacts on concentrations of these nutrients may reach deeper than 10 cm in these forests.

I also found limited evidence of species influences on the atmospherically derived, biologically fixed nutrients C and N. For several soil properties – moisture, bulk density, C and N pools, pH, and C and N concentrations – no effect of species on mineral soils was found. Species-based differences in N concentrations, as observed in

foliage, were reduced but detectable in forest floor and undetectable in mineral soil, while differences in C were apparent in foliage only. This suggests that the tree species studied did not strongly influence total pools and concentrations of the biologically fixed elements C and N. Nonetheless, species influences on the relative availability of C and N forms to plants and microbes in surface soil (Wedin and Tilman 1990, Priha et al. 2001, Lovett et al. 2004) were observed for ratios of NH_4^+-N:NO_3^--N and microbial C:N. Exchangeable NH_4^+-N:NO_3^--N ratios reflect relative availability of these N forms for use by plants and microbes, while microbial C:N ratios reflect availability of a nutrient, N, relative to an energy source, C. In field and laboratory studies, redcedar shows no preference for NO_3^--N vs. NH_4^+-N (Turner et al. 1993, Bennett and Prescott 2004), so high NH_4^+-N:NO_3^--N ratios beneath redcedar probably do not result from preferential tree uptake of NO_3^--N vs. NH_4^+-N. Biochemical differences in organic matter quality that influence microbial uptake of different inorganic N forms may give rise to such relative differences, even where overall differences in total C, N, or C:N were not detected.

There was also support for the context dependent model of tree species effects on soils (Fig. 1). Results of the context-dependence analysis suggest that species-based differences in mineral soil C and N pools and inorganic N availability are greater at high-C and high-N sites. At high-C and high-N sites, Douglas-fir stored more total C and N in surface mineral soil than did maple. These results are consistent with the pattern of divergence shown in the conceptual model (Figure 1, center). At low-C sites, maple also appeared to store more C in forest floor than did Douglas-fir,

hemlock, and redcedar, consistent with the pattern of convergence shown in the conceptual model (Figure 1, top). The mechanisms of context dependence in C and N are unclear, as these nutrients showed no clear relationship to the field site characteristics – such as moisture, elevation, annual maximum or minimum temperature, or latitude – expected to influence productivity, decomposition, leaching, or fire regimes and therefore soil C and N.

Context-dependence analysis also lent some support to the generalization that hardwoods promote soil N availability relative to conifers (Binkley and Giardina 1998), although the pattern of divergence among species as a function of increasing N availability suggest the effect may be limited to sites with high N availability. This would be consistent with comparisons of other taxa from forests and grasslands in which species differences in N availability were greatest under high N conditions (Wedin and Tilman 1990, Lovett and Rueth 1999). At N concentrations exceeding those of this study, Templer and others observed higher N retention (i.e., "tighter" or "slower" nutrient cycling resulting in less N loss) in forest floor and mineral soil beneath eastern hemlock vs. sugar maple under both ambient and fertilized conditions (2005). These results are consistent with slow N cycling by eastern hemlock and rapid N cycling by sugar maple reported by Lovett and Mitchell (2004). I speculate that bigleaf maple may play a biogeochemical role in western forests similar to that of sugar maple in eastern forests, despite the fact that underlying variations in N status in these western forests arise primarily from inputs due to biological N fixation and

losses due to fire and other disturbance as opposed to historical land-use and chronic N deposition.

Context dependence with respect to soil P was largely due to the general pattern of low P for redcedar foliage, forest floor, and mineral soil across sites, which appeared strongest at high-P sites and when contrasted with maple. The gradient in mineral soil P, an essential, rock-derived nutrient, did not appear to be related to variation in precipitation, degree of soil development (as judged from soil suborder assignment), or soil parent material across sites. Context-dependence in forest floor and mineral soil Mg, similar to P, was mainly due to a contrast between maple and redcedar. While Douglas-fir soil Mg also diverged from other species as mean Mg concentrations increased across sites, the maximum Douglas-fir deviation amounted to less than 15% of the site mean. The somewhat more constant pattern of species deviations in soil Ca concentrations is shown for comparison with the convergent and divergent patterns (Figure 16, top). Context dependence in remaining soil properties was unpredictable, exhibiting no distinct pattern with respect to underlying variation across sites. Overall, species differences in various mineral soil properties exhibited each of the hypothesized patterns of context dependence: divergent, convergent, constant, and unpredictable or no pattern (Figure 1), suggesting that a broad range of poorly understood mechanisms may be important for structuring plant-soil relationships in old-growth Oregon forests.

Species Profiles

There is great fundamental and practical import for understanding biogeochemical profiles associated with individual tree species. The species is often considered the basic biological unit in nature and provides a useful and long-standing way to organize knowledge of variation in biogeochemical properties characteristic of natural ecological systems. Species-level biogeochemical profiles are also useful for forest management, and management for or against certain species can provide opportunities for controlling soil fertility and long-term productivity. Finally, insight into species influences on soils is important as changes in global climate and disturbance regimes alter species distributions.

Douglas-fir dominates the canopy of most current LSRs and is therefore a major determinant of tree species-mediated nutrient cycling in these forests. For Douglas-fir, foliar nutrient concentrations were similar to those reported for 22 young (≤ 25 yr), unfertilized plantations in the Coast Range (Perakis et al. 2006) and reflected adequate nutrition (Walker and Gessel 1991). Of the four species, Douglas-fir had the lowest foliar N:P. Low N:P ratios are often characteristic of organisms producing P-rich compounds to support rapid growth (Sterner and Elser 2002), and Douglas-fir is known for its rapid growth and can maintain substantial height growth beyond 250 yr (De Mars and Herman 1987). Although Douglas-fir forest floors are reported to have high N concentrations due to high N and low lignin:N ratios in leaf litter (Prescott 2005), no species-based differences in forest floor C:N ratios were apparent in this study. Nonetheless, Douglas-fir forest floors were

most massive and held large pools of C and nutrients. In surface (0 to 10 cm depth) mineral soils, Douglas-fir had lower NH_4^+-N and higher P and Ca concentrations in these mixed-species old-growth forests than in young, managed Douglas-fir stands on comparable parent materials in the Oregon Coast Range (Perakis et al. 2006). As compared to the other tree species, Douglas-fir mineral soils had higher microbial C:N ratios across sites and had large C and N pools at high-C and -N sites. When considered in conjunction with the large nutrient pools stored in massive forest floors beneath Douglas-fir, high microbial C:N and large C and N pools suggest that Douglas-fir slows decomposition, perhaps by producing low-nutrient sloughed bark (Abee and Lavender 1972, Walker and Gessel 1991) and slowly-decomposing litter (Fried et al. 1990) and wood (Harmon and Hua 1991). Douglas-fir's fire resistance, which could allow single individuals to persist longer than other co-occurring species in these forests, may intensify these changes.

Western redcedar represents another important species in the canopies of many old-growth forests of the Pacific Northwest, and its differential cycling of P vs. Ca likely contributes to heterogeneity in nutrient resources. In this study, high Ca, high Ca:Mg ratios, and low P characterized foliage, forest floors, and mineral soils associated with redcedar. Foliar nutrients for redcedar reflected adequate nutrition at these sites (Walker and Gessel 1991). Redcedar foliar Ca concentrations were comparable to those for maple and more than twice as high as for hemlock. This contrast with hemlock was also reported for old-growth conspecifics at three sites in eastern Washington and Idaho (Alban 1969). Redcedar at Coast Range sites in this

study had much (> 2 ×) higher foliar N and K concentrations, but similar Ca and Mg concentrations, as compared with Alban's Washington and Idaho sites. Redcedar forest floors are known to be high in pH and Ca relative to Douglas-fir, western hemlock, and a number of other Pacific Northwest conifers (Prescott 2005). This change primarily in Ca availability, but not in other weatherable elements, raises the possibility that western redcedar preferentially cycles Ca but does not accelerate weathering overall, and may reflect the unique nutritional requirements of Cupressaceae species (Kiilsgaard et al. 1987). The high pH and Ca of cedar forest floors are believed to decrease NH_4^+-N:NO_3^--N ratios and fungi:bacteria ratios and to increase N concentrations and net N mineralization (Prescott 2005). It is not clear why redcedar soils in this study had high NH_4^+-N:NO_3^--N ratios together with high Ca availability. In mineral soils beneath redcedar, N pools were highly variable with respect to site N status, while the low P concentrations and small P pools were especially low at low-P sites.

Results of this study distinguished bigleaf maple, the only angiosperm sampled, from the conifers. Maple foliage had lower C and higher nutrient concentrations than did the conifers, a pattern which has also been observed for bigleaf maple growing on basalt-derived soils at the eastern margin of the Coast Range (Fried et al. 1990), as well as for other *Acer* species (Blinn and Bucker 1989, Fujinuma et al. 2005). The bigleaf maple foliar N concentrations I measured were similar to those reported for sugar maple in a mature northern hardwood forest (Lovett et al. 2004). Mineral soils beneath maple were generally rich in P and base cations,

and could signal an enhanced ability to weather primary minerals in addition to recycling weatherable nutrients through foliage and litterfall. Observed patterns in mineral soil pH, Ca, and Mg – high beneath maple and low beneath hemlock – are consistent with those reported for forest floors (Prescott 2005) and mineral soils (Alban 1969, Finzi et al. 1998). This raises the possibility that maple and hemlock may generally have divergent effects on soil pH and base status where these taxa coexist across different forest types.

Western hemlock is predicted to play an increasingly important role as succession proceeds in these old-growth forests. The western hemlock foliar N concentrations I measured reflected adequate nutrition (Walker and Gessel 1991) and were similar to those reported for eastern hemlock in a mature northern hardwood forest (Lovett et al. 2004). Of the four tree species in this study, hemlock had the lowest Ca and Mg concentrations in foliage and forest floor, as well as the smallest forest floor Ca pools. Forest floors beneath hemlock were generally thinner than beneath other species across all field sites. Like cedar, hemlock at these Coast Range sites displayed similar Ca and Mg concentrations and much (> 2 ×) higher foliar N and K than at three site in Washington and Idaho (Alban 1969). In contrast to redcedar, low pH and Ca of hemlock forest floors are believed to increase NH_4^+-N:NO_3^--N ratios and fungi:bacteria ratios and to decrease N concentrations and net N mineralization (Prescott 2005). In an old-growth forest near the Oregon coast, Turner and others found slightly lower pH beneath hemlock and no differences in Ca concentrations for fallen litter and mineral soil beneath Douglas-fir, cedar, and

hemlock (Turner et al. 1993). However, that site had very high N (> 1 % in litter and mineral soil) and very low Ca (≤ 4 $cmol_c/kg$) – perhaps to due a legacy of N-fixing red alder – compared with the field sites in this study. I observed low concentrations of Ca, Mg, K, and total bases, as wells as small pools of Ca, Mg, and K, in mineral soils beneath hemlock. Overall, the pattern of low Ca was maintained in hemlock foliage, forest floor, and mineral soils and suggests slow cycling of Ca beneath hemlock.

Fire is the primary disturbance agent in many western conifer forests, and patterns of vegetation recovery and tolerance to fires can explain the widespread dominance of Douglas-fir at sites such as those we studied (Spies 1991). Fire suppression has been in place in western Oregon since the early 1900s and most effective since the 1950s (Weisberg and Swanson 2003), and in addition to possible direct effects on forest biogeochemistry (Giesen 2006), such suppression may contribute to changes in species composition that indirectly affect soils and biogeochemical cycling. Continued fire suppression in coastal Oregon forests is likely to shift composition of LSRs to increased dominance by western hemlock, a fire intolerant yet highly shade-tolerant species. These data raise the possibility that increases in western hemlock dominance could foster widespread decreases in the availability of most major plant nutrients in forest floor, mineral soils, or both relative to the Douglas-fir dominated forests they would replace. In particular, results of this study suggest the potential of increased hemlock dominance to slow N cycles and enhance N retention may be greatest at high-N sites. Any potential increase in

hemlock dominance that was also associated with loss of bigleaf maple would further reduce patchiness in N availability. These results also suggest that hemlock has the potential to slow Ca cycling and reduce Ca availability regardless of underlying site conditions. Reductions in N and Ca availability to future forests could limit both productivity and nutrient loss.

Implications for Management

Results of this study suggest that tree species composition, like stand structure, influences ecological function of old-growth forests of the Pacific Northwest. Early-successional species such as red alder are known to dramatically alter forest nutrient cycles, but shifts in species composition of late-successional forests are also likely to affect forest nutrition. Management for old-growth characteristics, combined with continued fire suppression, is expected to increase dominance of shade-tolerant, fire-intolerant western hemlock in LSRs. These future hemlock forests are likely to differ substantially in function from LSRs with canopies currently composed of young Douglas-fir or of old trees of multiple species. Hemlock's increasing dominance, combined with its potential to slow N and Ca cycles and to acidify surface soils, may limit productivity and reduce the small-scale heterogeneity that currently supports diverse communities of plants, animals, and microbes.

Species differences in nutrient cycling mean fostering different species can affect soil heterogeneity, with broader impacts on other organisms and on ecosystem nutrient cycling. In this study, the significance of both general species differences, as described by the depth-based model, and context-dependent species differences

suggest that successful management of these tree species would consider field site characteristics. Moreover, the mechanisms driving tree species effects on particular soil properties have important management implications and therefore deserve further study. For example, trees species that increase nutrient availability may "hoard" nutrients or "provide" them to other organisms. A "hoarding" scheme might emerge if a tree species enhances both weathering and uptake of mineral nutrients, while a "providing" scheme might emerge if a tree species fixes (C, N) or weathers (P, Ca) nutrients but does not match enhanced availability with enhanced uptake by that species. Mechanisms driving context-dependence also warrant exploration, because the de facto gradients in this study were not clearly linked to ecologically relevant site characteristics. The ecological process underpinning these patterns merit further study in either an experimental framework or in an observational study designed with respect to a particular resource gradient. The mechanisms whereby tree species influence soils will determine how species-based management practices affect stand-level nutrition, with important consequences for future nutrient availability and future forest productivity.

CONCLUSION

Results of this study provide insight into current and future functional roles of individual tree species in old growth forests of the Pacific Northwest. Overall, for the tree species I studied, I conclude that species-soils relationships as observed at a single field site are not necessarily indicative of general patterns across sites. Qualitatively significant variations in underlying site characteristics (e.g., soil parent material, fire history) across these study sites may contribute to species-soils relationships across the range of sites. As shown in this study, context-dependence, or site-to-site variation, in species-soils relationships may be general, predictable, or neither general nor predictable, depending on the soil property of interest. I therefore caution against making general inferences about species effects from studies at one or a few field sites. Successful detection and interpretation of species-soils relationships will require consideration of an appropriate scale of inquiry, and vice versa.

Conservation of species ranks in foliar chemistry despite considerable underlying variation in soils across sites suggests strong species differences in nutrient cycling through the active foliar pool. These differences in turn suggest the potential of tree species to control species-based differences in soil properties. Tree species-level variations in soil properties of current late-successional forests in the Oregon Coast Range may contribute to local biodiversity in soil- and litter-dwelling organisms by creating heterogeneous habitats at scales of one to several m^2, the projected zones of influence of individual trees (Zinke 1962, Torgersen et al. 1995, Reich et al. 2005). In young Douglas-fir stands set aside as LSRs, fostering multiple tree species could in

turn enhance habitat diversity. Such variations may, however, decrease in the future as continued fire suppression promotes dominance by shade-tolerant western hemlock in LSRs. Taken together, these results may contribute to the development of species-based approaches to sustainable ecosystem management for long-term production, conservation, and watershed goals.

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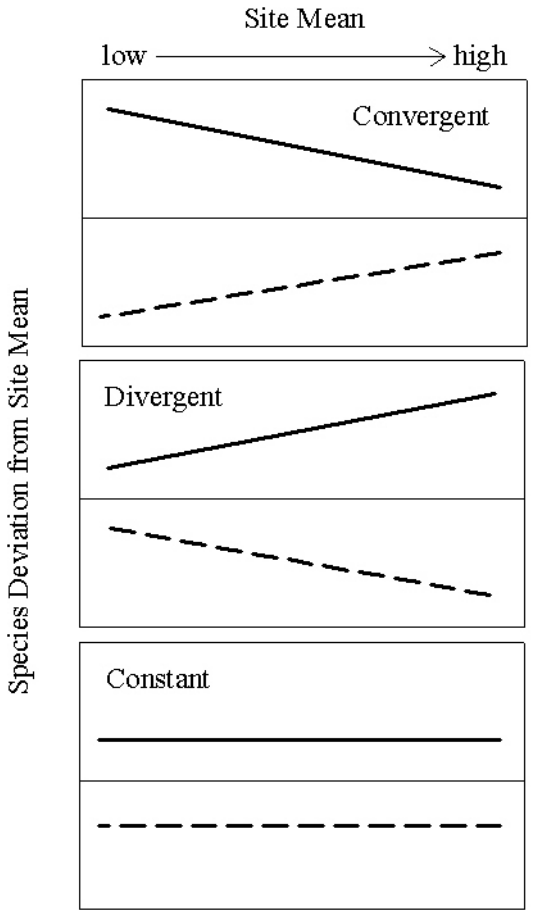

Figure 1. Hypotheses for context dependence analysis. As the mean value for a soil property increases across field sites, the deviations from the mean in soils associated with individual tree species may exhibit convergent (top), divergent (center), or constant (bottom) patterns, or no consistent pattern (not shown).

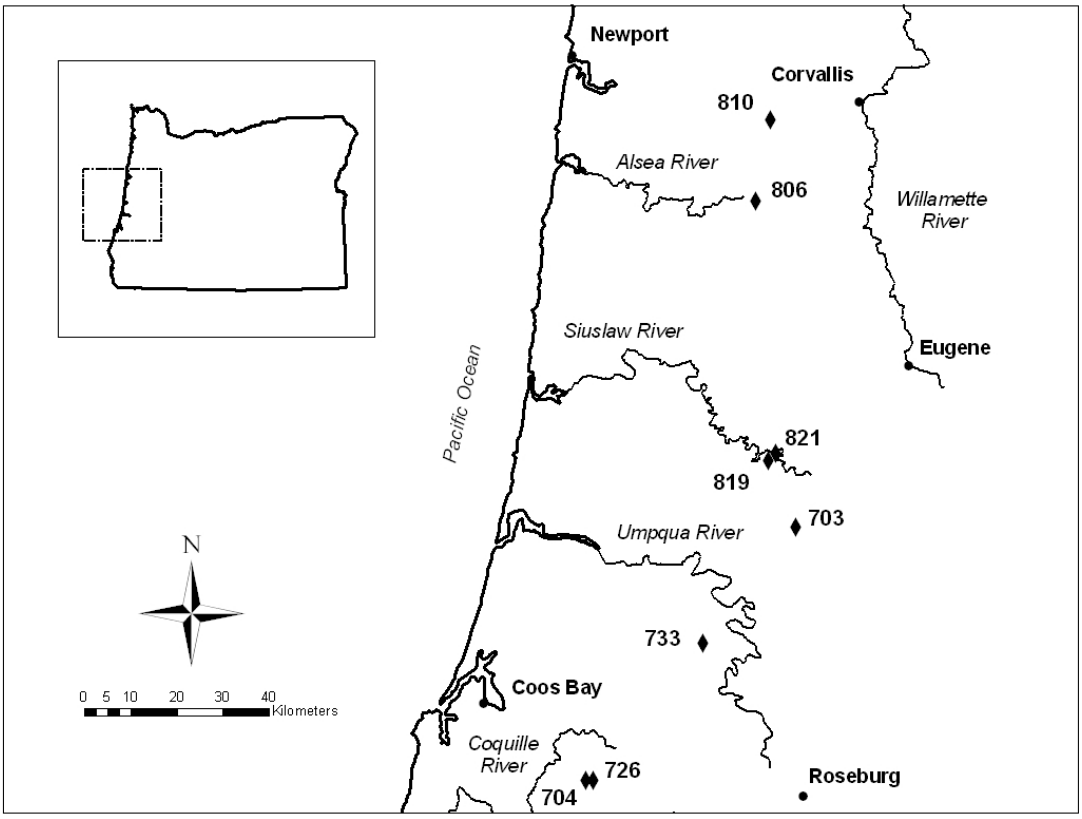

Figure 2. Locations of the eight old-growth forest sites sampled in the field study, southern Coast Range, Oregon, USA.

Figure 3. C:N molar ratios of foliage (top), Oe+Oa horizons (center), and mineral soils (bottom) associated with four tree species at eight field sites. Symbols are Tukey-Kramer adjusted least-squares means with 95% confidence intervals (n = 6 per species). *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. *Filled* symbols indicate significant differences among species (mixed-effects ANOVA, $P < 0.05$).

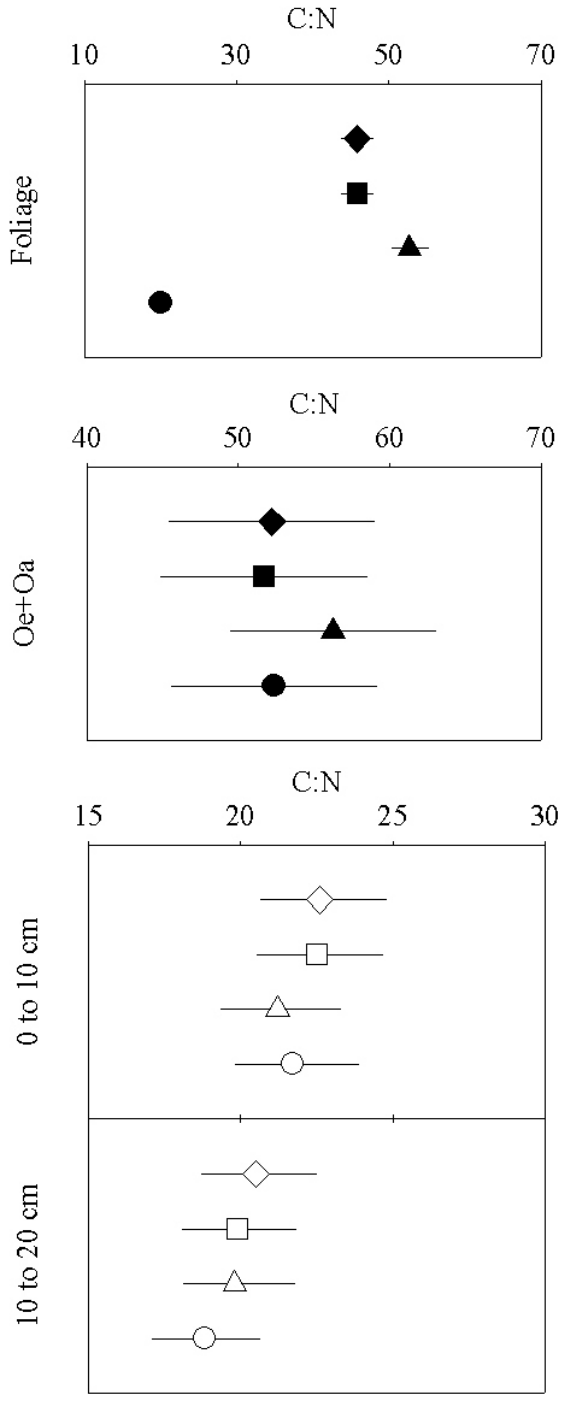
C:N
10
30
50
70
Foliage
C:N
40
50
60
70
Oe+Oa
C:N
15
20
25
30
0 to 10 cm
10 to 20 cm

Figure 3

Figure 4. P concentrations of foliage (top), Oe+Oa horizons (center), and mineral soils (bottom) associated with four tree species at eight field sites. Concentrations for Oe+Oa horizons are expressed per unit C. Symbols are Tukey-Kramer adjusted least-squares means with 95% confidence intervals (n = 6 per species). *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. *Filled* symbols indicate significant differences among species (mixed-effects ANOVA, $P < 0.05$).

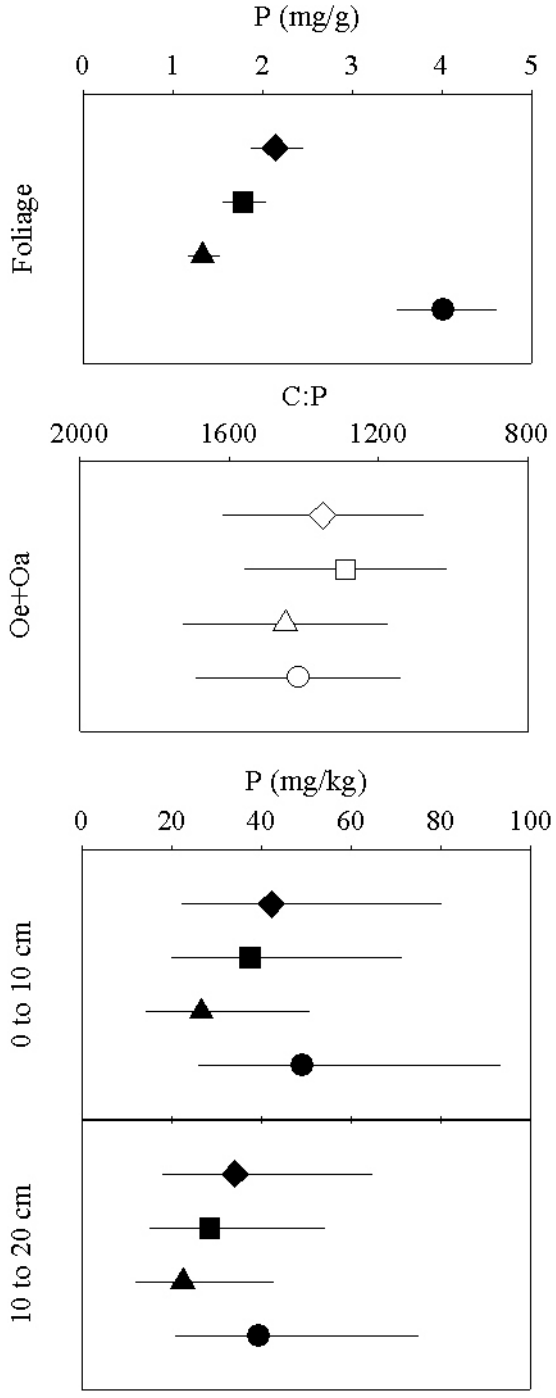
P (mg/g)
0
1
2
3
4
5
Foliage
C:P
2000
1600
1200
800
Oe+Oa
P (mg/kg)
0
20
40
60
80
100
0 to 10 cm
10 to 20 cm

Figure 4

Figure 5. Ca concentrations of foliage (top), Oe+Oa horizons (center), and mineral soils (bottom) associated with four tree species at eight field sites. Concentrations for Oe+Oa horizons are expressed per unit C. Symbols are Tukey-Kramer adjusted least-squares means with 95% confidence intervals (n = 6 per species). *Diamond*s = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. *Filled* symbols indicate significant differences among species (mixed-effects ANOVA, $P < 0.05$).

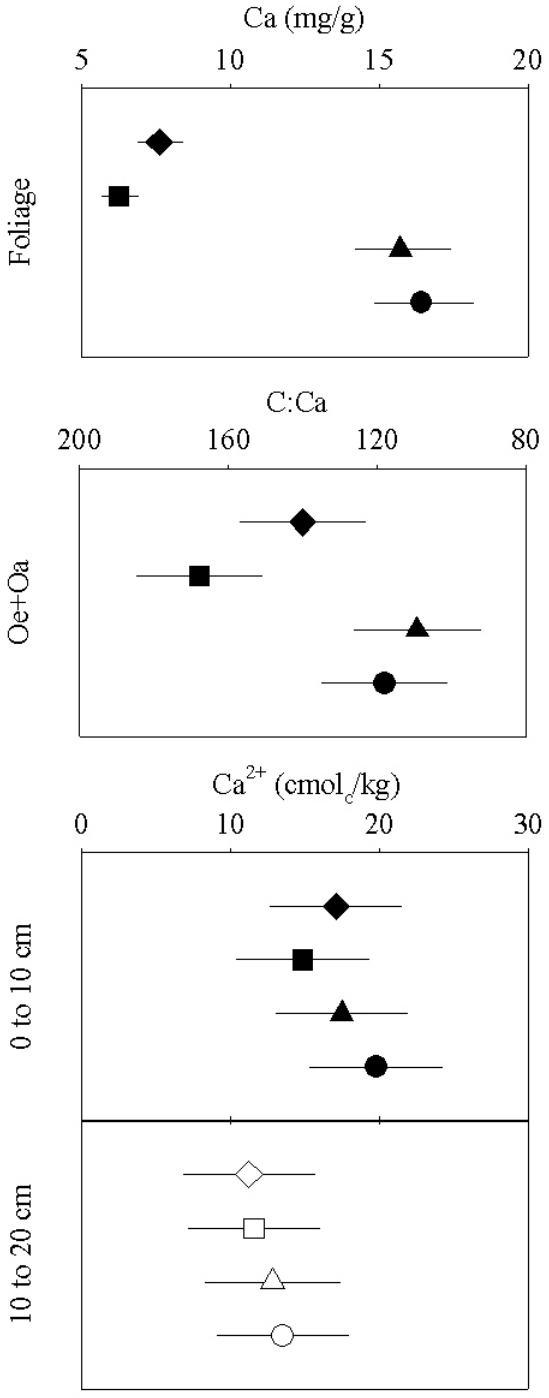
Ca (mg/g)
5
10
15
20
Foliage
C:Ca
200
160
120
80
Oe+Oa
Ca2+ (cmolc/kg)
0
10
20
30
0 to 10 cm
10 to 20 cm

Figure 5

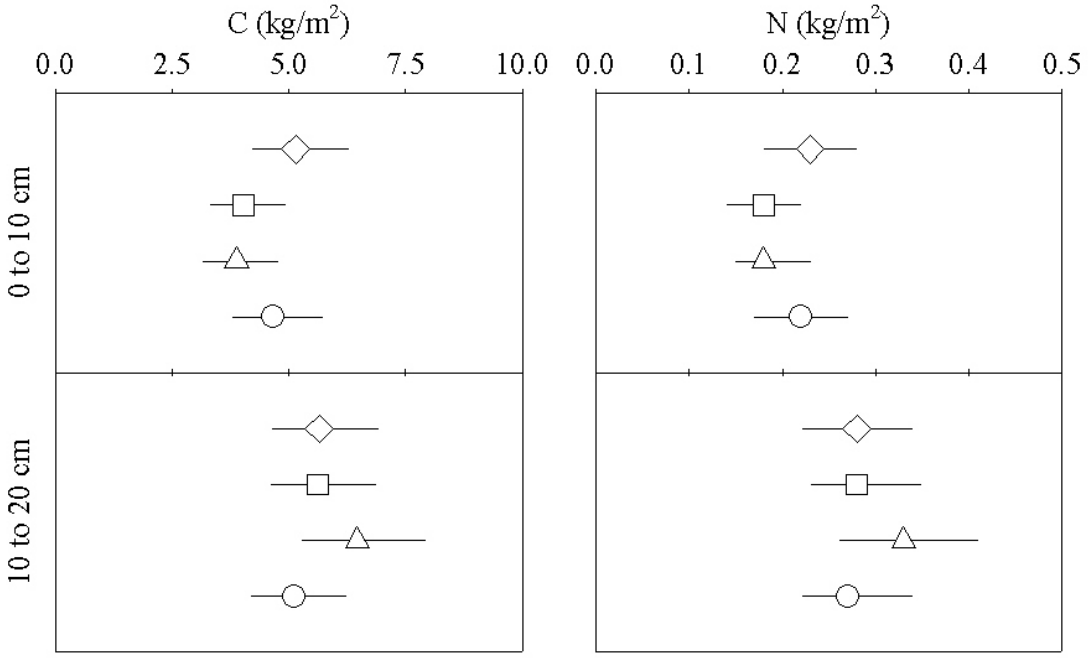

Figure 6. Total C (left) and N (right) pools of mineral soils associated with four tree species at eight field sites. Symbols are Tukey-Kramer adjusted least-squares means with 95% confidence intervals (n = 6 per species). *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. *Filled* symbols indicate significant differences among species (mixed-effects ANOVA, $P < 0.05$).

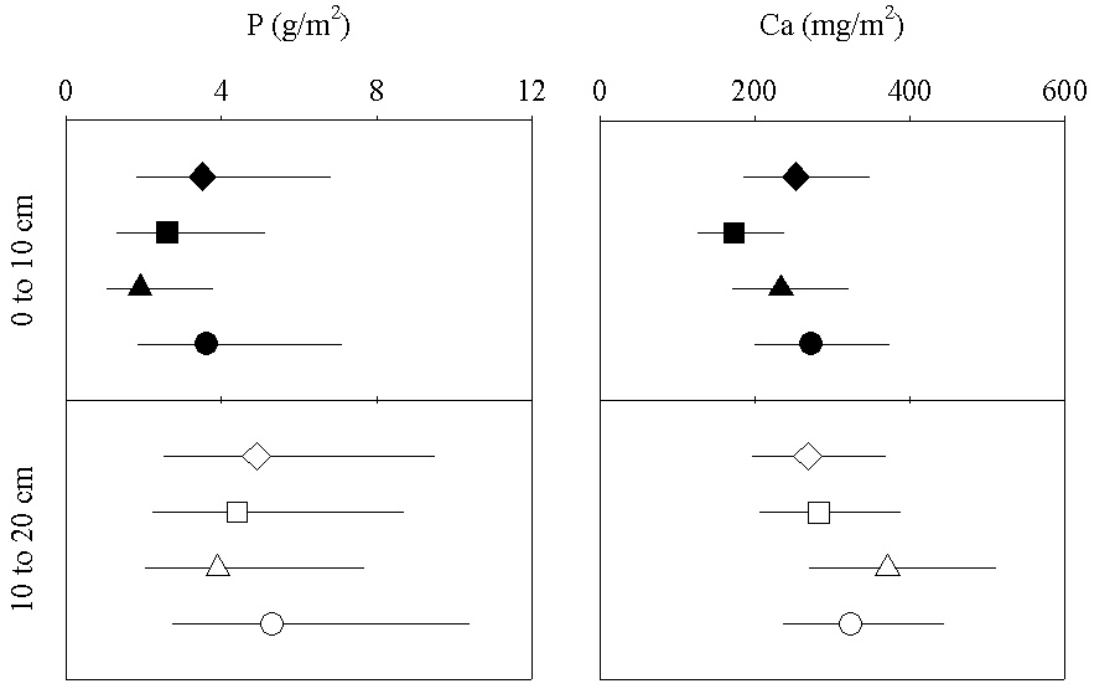

Figure 7. Exchangeable P (left) and Ca (right) pools of mineral soils associated with four tree species at eight field sites. Symbols are Tukey-Kramer adjusted least-squares means with 95% confidence intervals (n = 6 per species). *Diamond*s = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. *Filled* symbols indicate significant differences among species (mixed-effects ANOVA, $P < 0.05$).

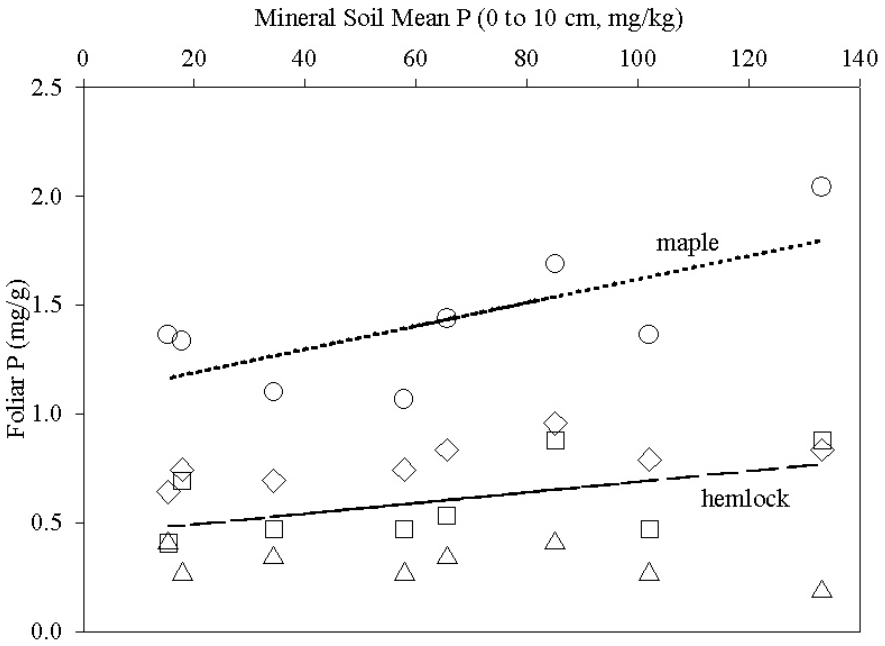

Figure 8. Foliar P for each of four tree species vs. the mean mineral soil (0 to 10 cm) exchangeable P of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t-tests, $P < 0.05$).

Figure 9. Foliar N:P for each of four tree species vs. the mean mineral soil (0 to 10 cm) total N (top) and exchangeable P (bottom) of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t-tests, $P < 0.05$).

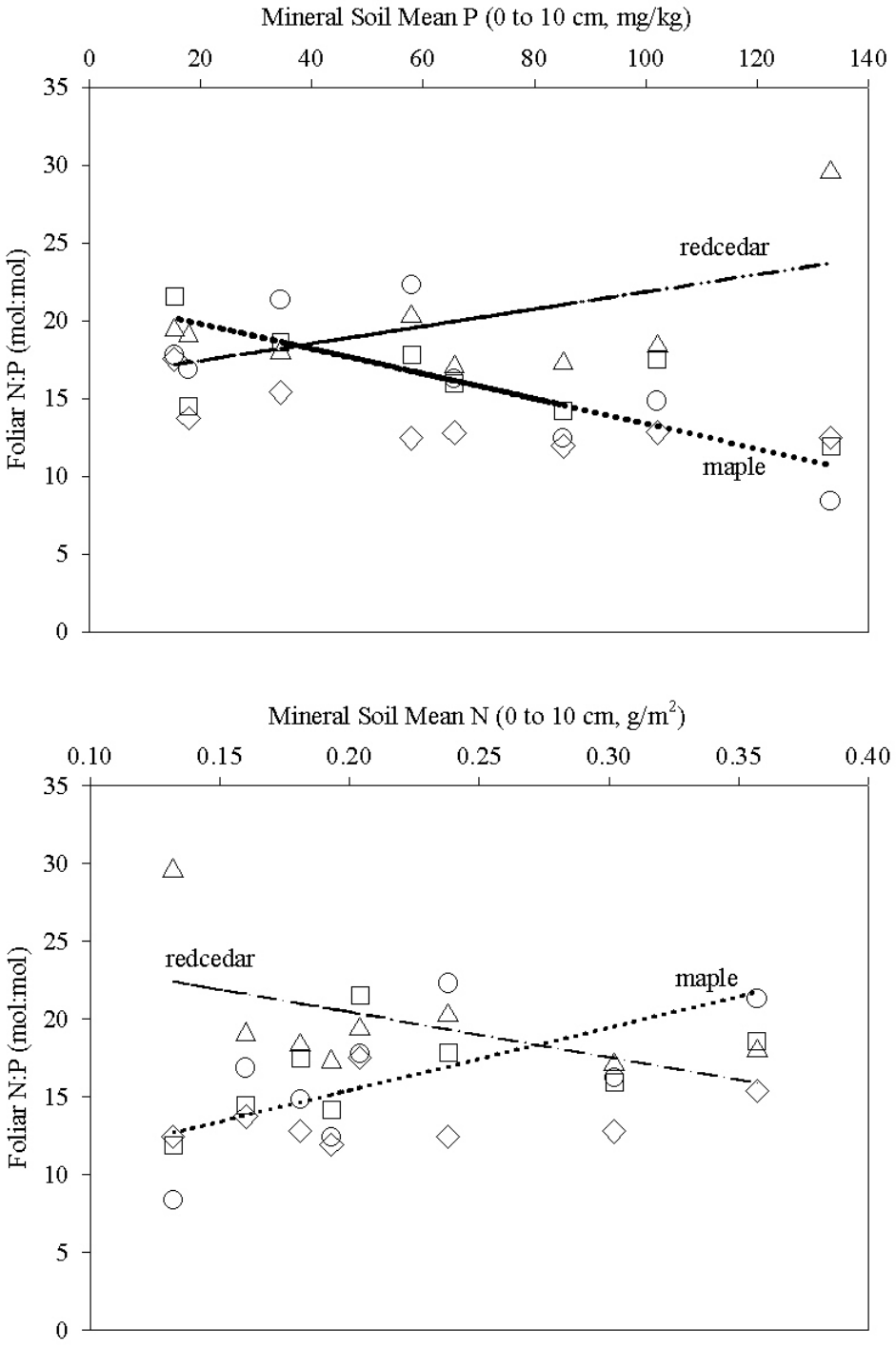
Mineral Soil Mean P (0 to 10 cm, mg/kg)
0
20
40
60
80
100
120
140
35
30
25
20
15
10
5
0
Foliar N:P (mol:mol)
redcedar
maple
Mineral Soil Mean N (0 to 10 cm, g/m2)
0.10
0.15
0.20
0.25
0.30
0.35
0.40
35
30
25
20
15
10
5
0
Foliar N:P (mol:mol)
redcedar
maple

Figure 9

Figure 10. Deviations in thickness (top) and C % (bottom) for forest floor Oe+Oa horizons beneath each of four tree species vs. the mean of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t-tests, $P < 0.05$).

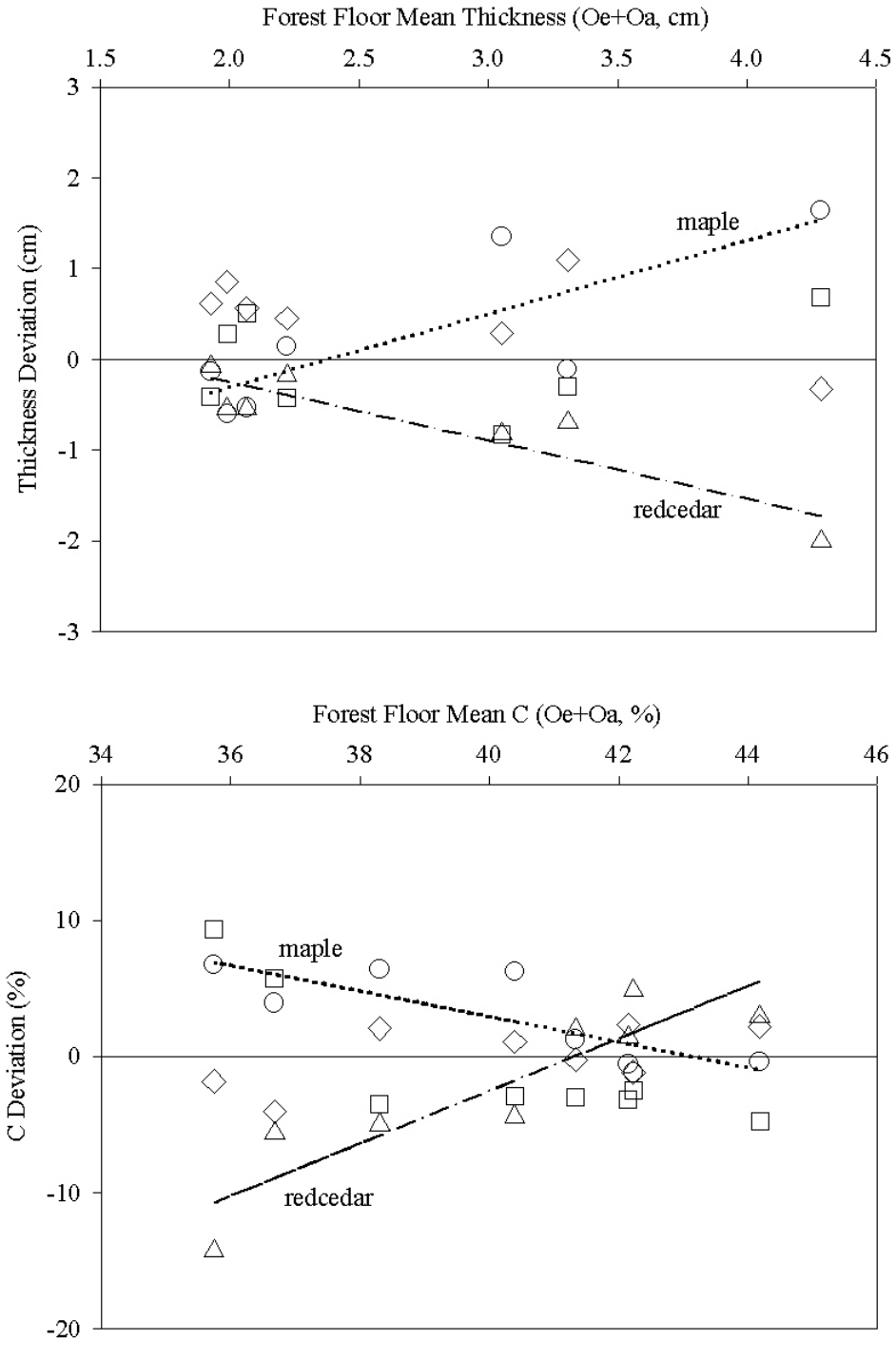
Forest Floor Mean Thickness (Oe+Oa, cm)
1.5
2.0
2.5
3.0
3.5
4.0
4.5
3
2
1
0
-1
-2
-3
Thickness Deviation (cm)
maple
redcedar
Forest Floor Mean C (Oe+Oa, %)
34
36
38
40
42
44
46
20
10
0
-10
-20
C Deviation (%)
maple
redcedar

Figure 10

Figure 11. Deviations in N (top) and P pools (bottom) for forest floor Oe+Oa horizons beneath each of four tree species vs. the mean of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t-tests, $P < 0.05$).

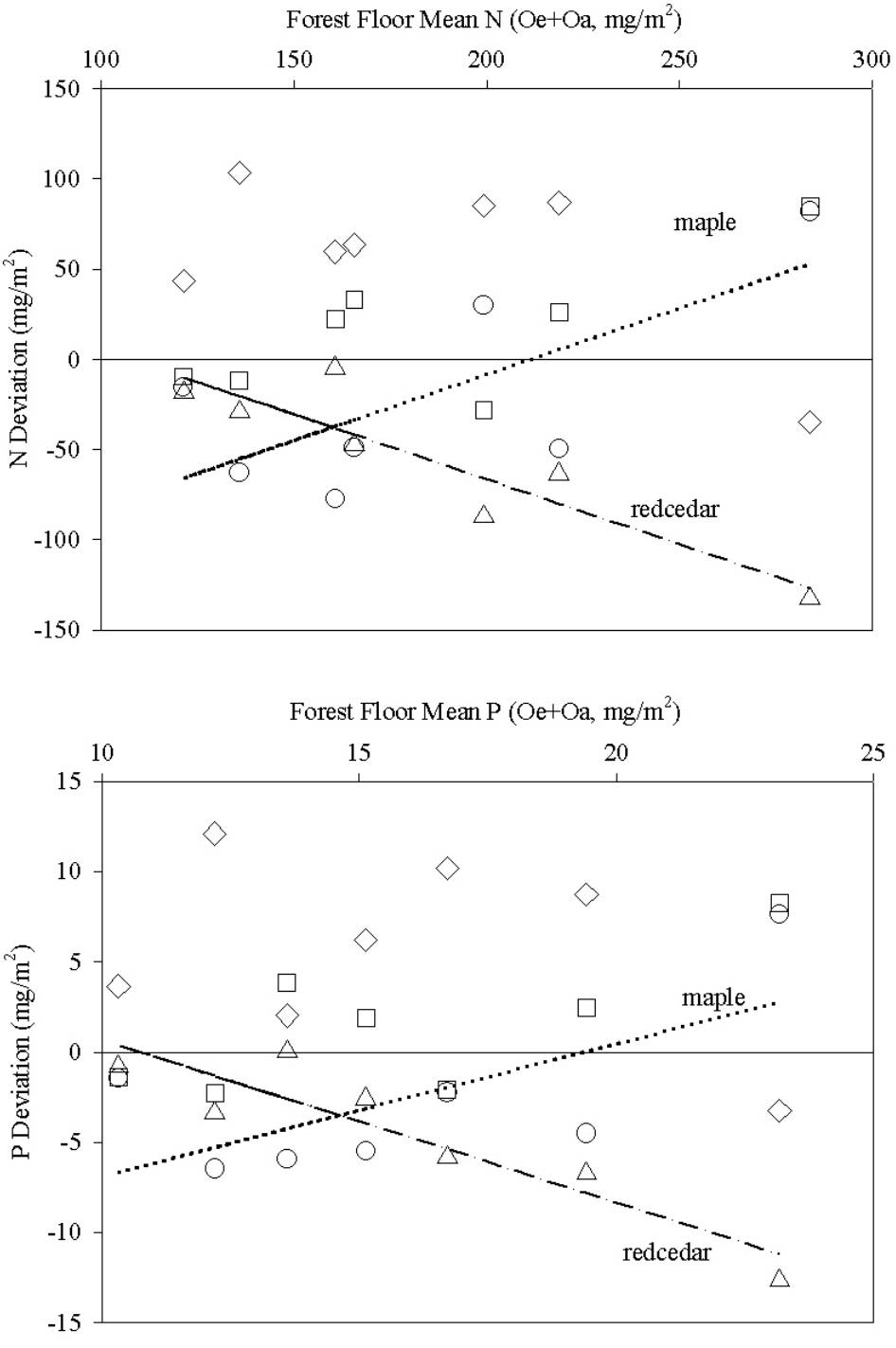
Forest Floor Mean N (Oe+Oa, mg/m2)
100
150
200
250
300
150
100
50
0
-50
-100
-150
N Deviation (mg/m2)
maple
redcedar
Forest Floor Mean P (Oe+Oa, mg/m2)
10
15
20
25
15
10
5
0
-5
-10
-15
P Deviation (mg/m2)
maple
redcedar

Figure 11

Figure 12. Deviations in C:Mg ratios (top) and Mg pools (bottom) for forest floor Oe+Oa horizons beneath each of four tree species vs. the mean of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t-tests, $P < 0.05$).

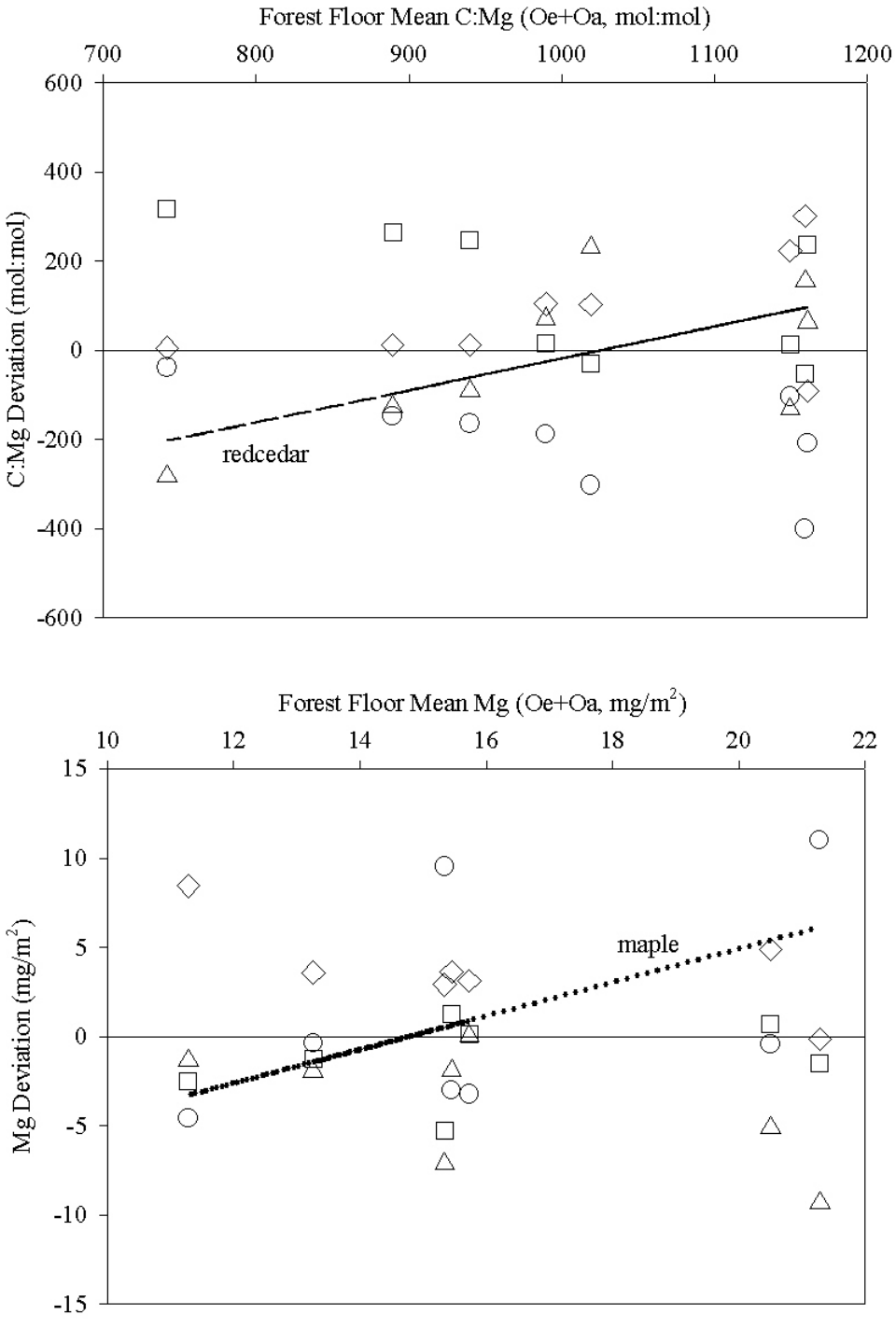
Forest Floor Mean C:Mg (Oe+Oa, mol:mol)
700
800
900
1000
1100
1200
600
400
200
0
-200
-400
-600
C:Mg Deviation (mol:mol)
redcedar
Forest Floor Mean Mg (Oe+Oa, mg/m2)
10
12
14
16
18
20
22
15
10
5
0
-5
-10
-15
Mg Deviation (mg/m2)
maple

Figure 12

Figure 13. Deviations in total C (top) and N (bottom) pools for 0 to 10 cm mineral soils beneath each of four tree species vs. the mean of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t tests, $P < 0.05$).

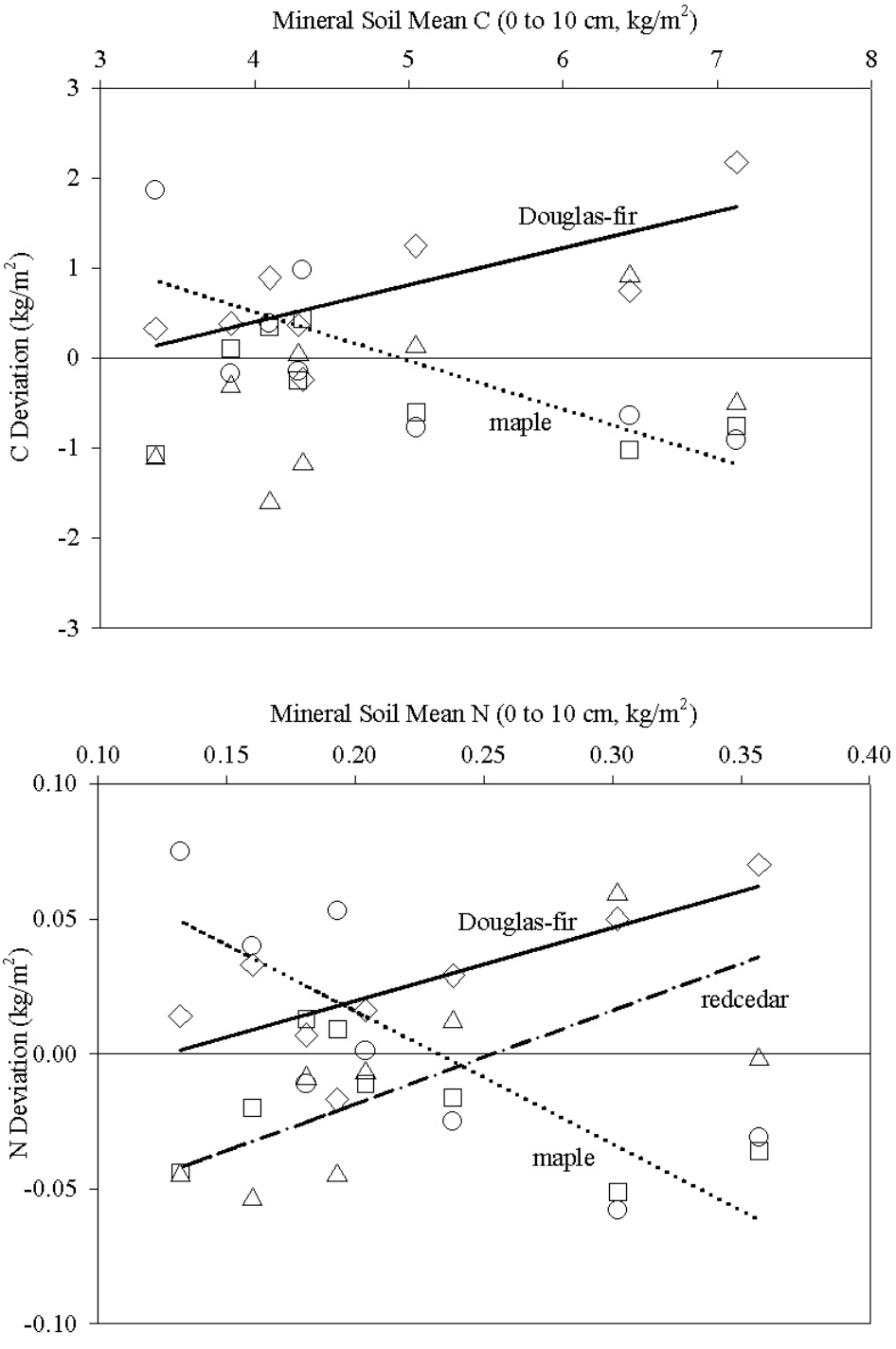
Mineral Soil Mean C (0 to 10 cm, kg/m2)
3
4
5
6
7
8
3
2
1
0
-1
-2
-3
C Deviation (kg/m2)
Douglas-fir
maple
Mineral Soil Mean N (0 to 10 cm, kg/m2)
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.10
0.05
0.00
-0.05
-0.10
N Deviation (kg/m2)
Douglas-fir
redcedar
maple

Figure 13

Figure 14. Deviations in exchangeable NH4+-N (top) and NO3--N (bottom) concentrations for 0 to 10 cm mineral soils beneath each of four tree species vs. the mean of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t tests, $P < 0.05$).

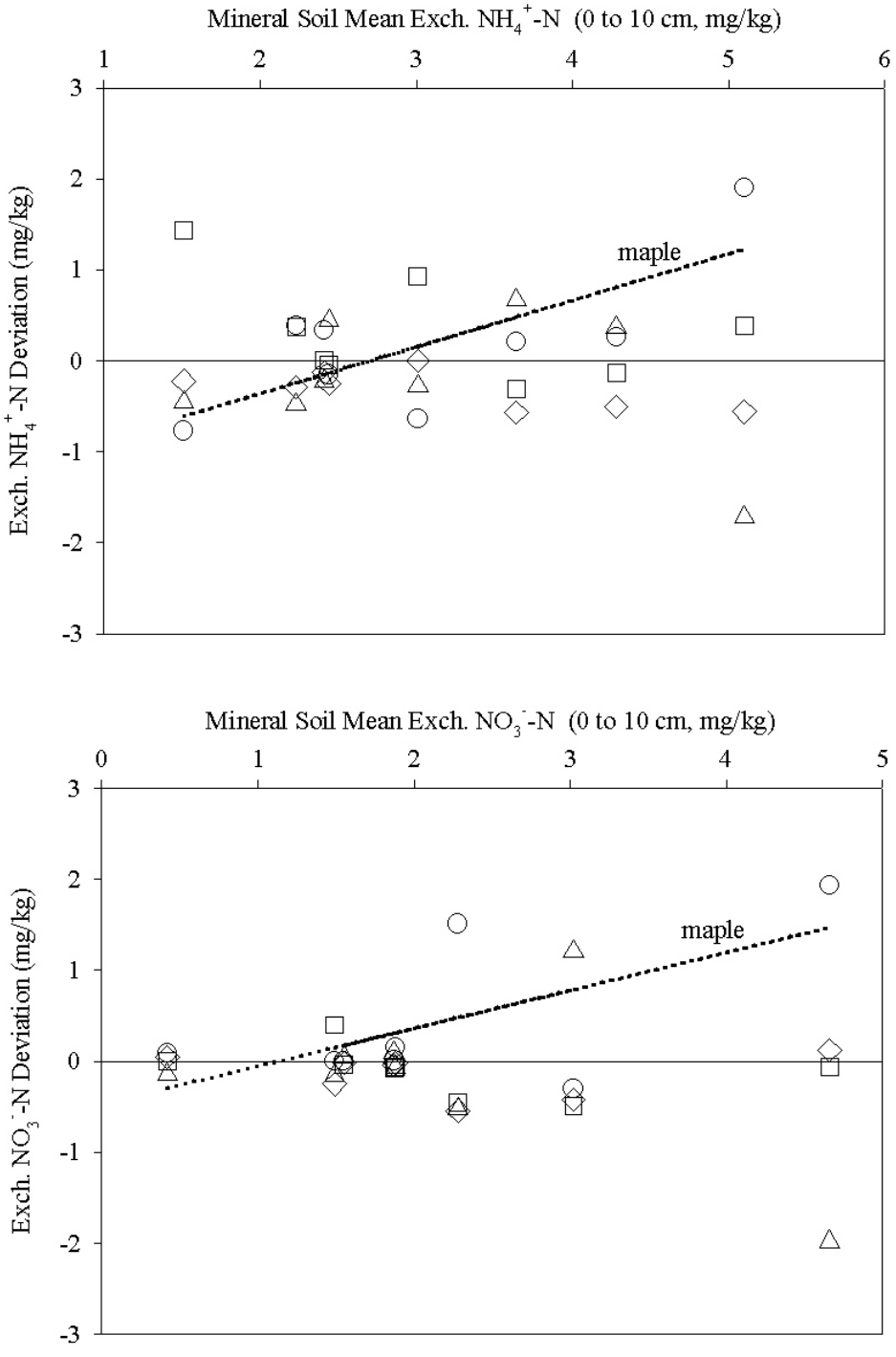
Mineral Soil Mean Exch. NH4+-N (0 to 10 cm, mg/kg)
Exch. NH4+-N Deviation (mg/kg)
maple
Mineral Soil Mean Exch. NO3--N (0 to 10 cm, mg/kg)
Exch. NO3--N Deviation (mg/kg)
maple

Figure 14

Figure 15. Deviations in exchangeable P pools (top) and concentrations (bottom) for 0 to 10 cm mineral soils beneath each of four tree species vs. the mean of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t tests, $P < 0.05$).

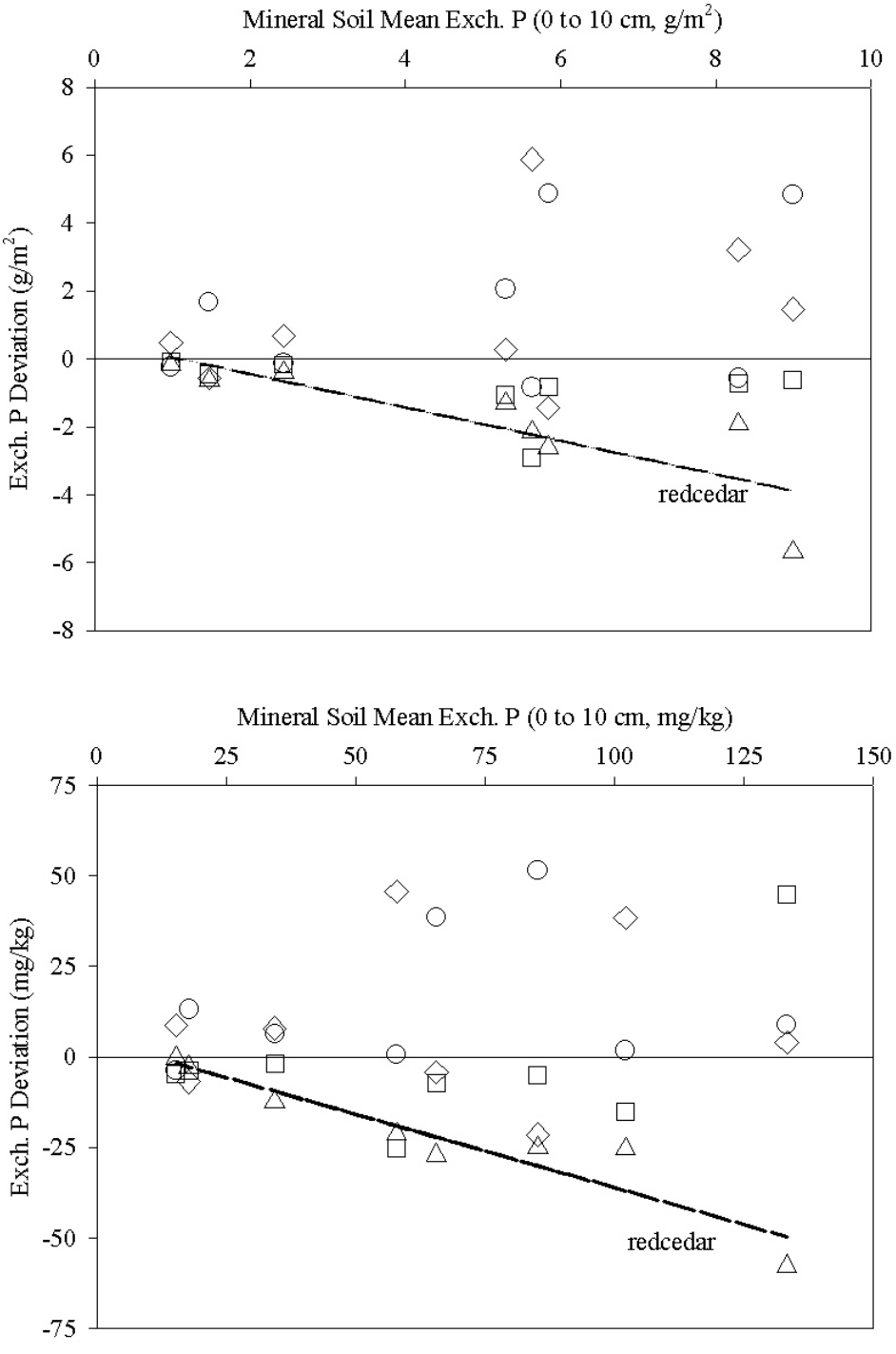
Mineral Soil Mean Exch. P (0 to 10 cm, g/m2)
0
2
4
6
8
10
8
6
4
2
0
-2
-4
-6
-8
Exch. P Deviation (g/m2)
redcedar
Mineral Soil Mean Exch. P (0 to 10 cm, mg/kg)
0
25
50
75
100
125
150
75
50
25
0
-25
-50
-75
Exch. P Deviation (mg/kg)
redcedar

Figure 15

Figure 16. Deviations in exchangeable Ca (top) and Mg (bottom) concentrations for 0 to 10 cm mineral soils beneath each of four tree species vs. the mean of all species. Symbols are means of six trees per species at each site. *Diamonds* = Douglas-fir; *squares* = western hemlock; *triangles* = western redcedar; *circles* = bigleaf maple. A linear regression of the form *DEVIATION* = *SITE* + *SPECIES* + *SITE MEAN* × *SPECIES* was fit to the data. *Regression lines* are shown where slopes differ significantly from zero (t tests, $P < 0.05$).

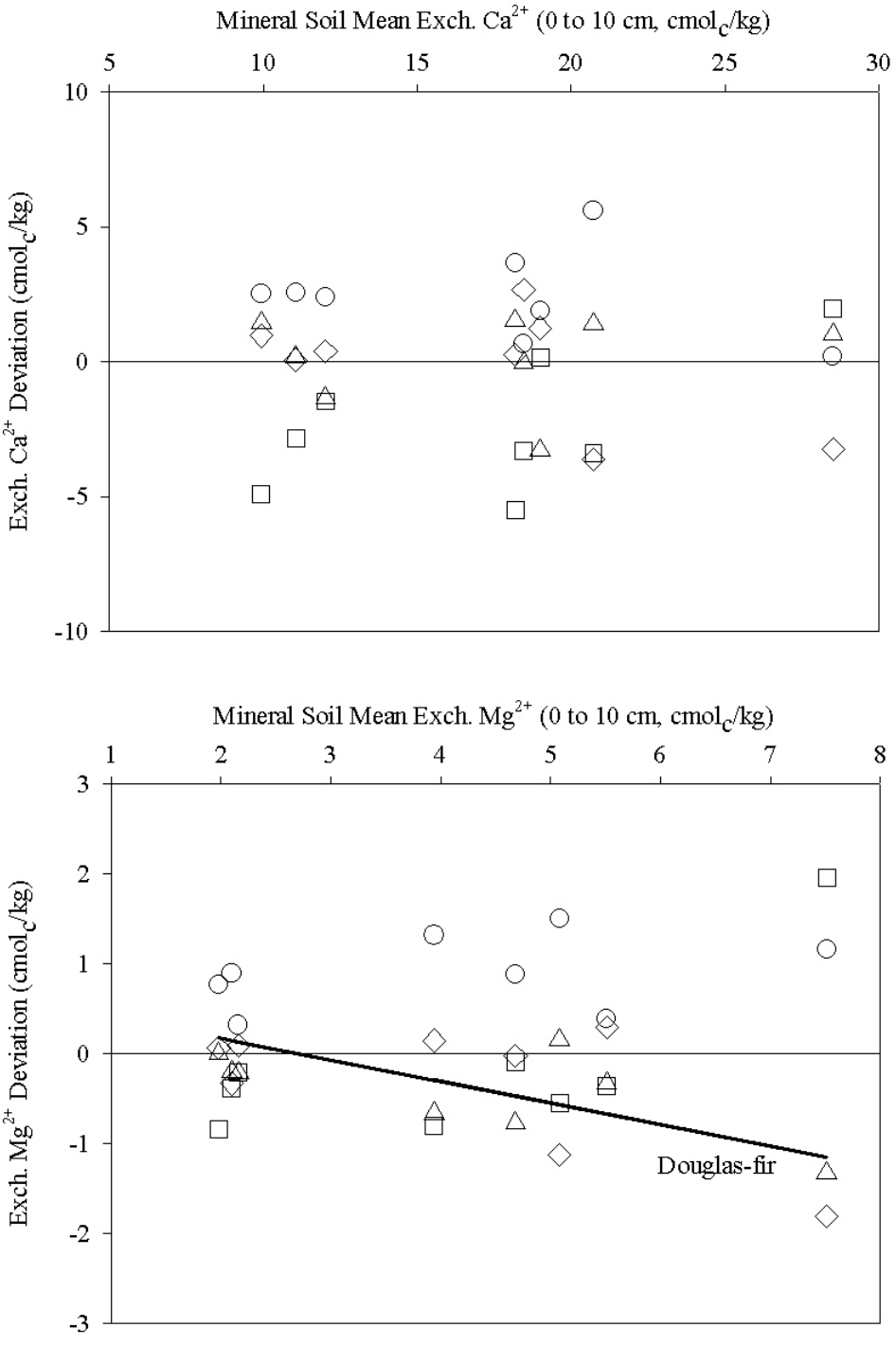
Mineral Soil Mean Exch. Ca^{2+} (0 to 10 cm, $cmol_c/kg$)
5
10
15
20
25
30
10
5
0
-5
-10
Exch. Ca^{2+} Deviation ($cmol_c/kg$)
Mineral Soil Mean Exch. Mg^{2+} (0 to 10 cm, $cmol_c/kg$)
1
2
3
4
5
6
7
8
3
2
1
0
-1
-2
-3
Exch. Mg^{2+} Deviation ($cmol_c/kg$)
Douglas-fir

Figure 16

Table 1. Depth-Based Soil Sampling Rationale.

Species differences in deeper mineral soils?	Species differences in surface mineral soils?	
	Yes	No
No	Differential species effects	No pattern OR Low power
Yes	Differential species establishment OR Species effects reach deep soils	Generic plant effects

Table 2. Characteristics of the Eight Field Sites.

Site	Latitude (N)	Longitude (W)	Parent Material †	Soil Subgroups (USDA) †	Aspect	Elevation * (m)	Max. Temp.§ (C)	Min. Temp.§ (C)	Precip.§ (mm)
703	43°43’54”	123°23’42”	Sedimentary	Typic Paleudult Dystric Eutrudept Andic Dystrudept	N	400	17	4	1400
704	43°13’18”	123°55’49”	Sedimentary	Andic Dystrudept	N	300	17	5	1900
726	43°13’18”	123°54’38”	Sedimentary	Andic Dystrudept	E	500	17	5	1900
733	43°29’56”	123°38’00”	Sedimentary	Ultic Palexeralf Ultic Haploxeralf Xeric Haplohumult Typic Dystroxerept	W	300	17	4	1300
806	44°21’57”	123°32’07”	Mixed sedimentary & volcanic	Typic Palehumult Xeric Palehumult Alic Hapludand	N	400	17	6	1800
810	44°31’33”	123°30’09”	Mixed sedimentary & volcanic	Typic Palehumult Xeric Palehumult Alic Hapludand	N	300	16	5	1900
819	43°51’35”	123°28’29”	Mixed sedimentary & volcanic	Dystric Eutrudept Typic Halplohumult	W	300	17	5	1400
821	43°52’26”	123°27’18”	Mixed sedimentary & volcanic	Typic Halplohumult Dystric Eutrudept	N	200	17	5	1400

† NRCS Soil Surveys (Soil Survey Staff 1975, 1987, 1989, 2004). * Elevation at nearest township-range-section center (Gustafson 1995), rounded to the nearest 100 m to account for deeply dissected terrain. § Annual average for years 1895 to 2005 (Spatial Climate Analysis Service 2006).

Table 3. Diameter at Breast Height for Trees Sampled in 2003.

	Species			
Site	Douglas-fir	Western hemlock	Western redcedar	Bigleaf maple
703	107.8 (70.4, 153.5)	84.6 (63.0, 104.8)	84.1 (41.0, 120.5)	41.9 (29.8, 56.3)
704	ND	ND	87.3 (54.6, 117.7)	65.2 (47.1, 81.9)
726	149.2 (104.9, 183.0)	86.6 (48.3, 120.5)	139.7 (84.4, 208.3)	61.2 (45.2, 82.6)
733	152.4 (98.3, 219.5)	59.1 (47.5, 86.1)	105.9 (73.8, 168.0)	40.8 (27.9, 61.9)
806	75.8 (54.5, 107.3)	73.2 (56.7, 91.4)	175.7 (97.0, 232.0)	56.9 (38.1, 66.4)
810	148.1 (85.4, 191.4)	60.9 (28.9, 77.3)	88.7 (43.0, 164.0)	50.7 (40.4, 63.2)
819	121.3 (100.6, 161.6)	80.0 (59.0, 97.0)	96.6 (74.5, 109.9)	38.3 (25.5, 48.4)
821	100.8 (63.2, 117.3)	98.6 (62.3, 125.4)	89.0 (36.1, 128.3)	49.0 (29.5, 59.9)

Note*:* Values are means in cm with ranges in parentheses. ND = no data.

Table 4. Foliar Chemistry.

Property	Units	*SPECIES*				$F_{3,21}$	*P*
		Douglas-fir	Western hemlock	Western redcedar	Bigleaf maple		
C †	%	50.08 (49.53, 50.63) [a]	50.85 (50.30, 51.40) [a]	50.29 (49.74, 50.84) [a]	47.25 (46.70, 47.80) [b]	55.63	**<0.001**
N	%	1.27 (1.21, 1.34) [a]	1.29 (1.23, 1.36) [a]	1.12 (1.06, 1.17) [b]	2.75 (2.63, 2.89) [c]	609.23	**<0.001**
P	mg/g	2.14 (1.86, 2.46) [a]	1.78 (1.55, 2.05) [ab]	1.33 (1.16, 1.53) [b]	4.01 (3.49, 4.61) [c]	73.40	**<0.001**
Ca	mg/g	7.61 (6.86, 8.45) [a]	6.26 (5.64, 6.94) [a]	15.71 (14.16, 17.44) [b]	16.42 (14.80, 18.21) [b]	409.60	**<0.001**
Mg	mg/g	1.11 (0.97, 1.26) [a]	1.20 (1.06, 1.67) [a]	1.22 (1.08, 1.39) [a]	3.34 (2.94, 3.79) [b]	160.26	**<0.001**
K	mg/g	8.09 (7.51, 8.70) [a]	6.33 (5.89, 6.81) [b]	5.11 (4.75, 5.50) [c]	16.55 (15.38, 17.80) [d]	116.63	**<0.001**
C:N	mol:mol	45.84 (43.66, 48.12) [a]	45.82 (43.65, 48.10) [a]	52.70 (50.19, 55.33) [b]	20.00 (19.06, 21.00) [c]	733.31	**<0.001**
N:P †	mol:mol	13.62 (11.5, 15.79) [a]	16.50 (14.34, 18.66) [ab]	18.64 (16.47, 20.82) [b]	16.26 (14.10, 18.42) [ab]	6.05	**0.004**
Ca:Mg	mol:mol	4.18 (3.64, 4.79) [a]	3.15 (2.75, 3.61) [b]	7.81 (6.81, 8.95) [c]	2.98 (2.61, 3.42) [b]	57.91	**<0.001**

Note: Model: *Property = site + SPECIES + site × SPECIES* (PROC MIXED in SAS 9.1). Values are back-transformed least squares mean estimates with 95% confidence intervals in parentheses (Type III sums of squares). Boldface type denotes soil properties for which species effects are significant at the $P < 0.05$ level. Different superscript letters within a row denote significant pairwise differences (Tukey-Kramer, $P<0.05$). †Variable was not natural log-transformed for analysis.

Table 5. Forest Floor Thickness and Mass.

Property	Units	***SPECIES***				$F_{3, 18}$	*P*
		Douglas-fir	Western hemlock	Western redcedar	Bigleaf maple		
Oi							
Thickness	cm	2.7 (2.0, 3.6)	2.0 (1.5, 2.7)	1.8 (1.4, 2.4)	2.3 (1.7, 3.0)	2.20	0.115
Mass	g/m^2	7.6 (5.7, 10.1)	5.8 (4.4, 7.7)	5.5 (4.1, 7.3)	5.1 (3.8, 6.8)	2.03	0.136
Oe+Oa							
Thickness	cm	1.5 (1.2, 2.1) [ab]	0.9 (0.7, 1.2) [a]	1.5 (1.1, 2.0) [ab]	1.9 (1.4, 2.5) [b]	6.91	**0.002**
Mass	g/m^2	22.7 (17.1, 30.1) [a]	15.7 (11.8, 20.9) [ab]	13.0 (9.8, 17.3) [ab]	11.1 (8.4, 14.7) [b]	6.32	**0.003**

Note: Model: *Property= site + SPECIES + site × SPECIES + REPLICATE (site × SPECIES) + HORIZON + SPECIES × HORIZON + site × HORIZON (SPECIES), Slice = HORIZON* (PROC MIXED in SAS 9.1). Values are back-transformed least squares mean estimates with 95% confidence intervals in parentheses (Type III sums of squares). Boldface type denotes soil properties for which species effects are significant at the $P < 0.05$ level. Different superscript letters within a row denote significant pairwise differences (Tukey-Kramer, $P < 0.05$).

Table 6. Forest Floor Oe+Oa Horizon Nutrient Concentrations and Pools.

Property	Units	***SPECIES***				$F_{3, 18}$*	*P*
		Douglas-fir	Western hemlock	Western redcedar	Bigleaf maple		
Nutrient concentrations							
C	%	40.18 (36.18, 44.18)	39.55 (35.53, 43.56)	37.85 (33.84, 41.87)	42.93 (38.93, 46.93)	1.28	0.308
C:N	mol:mol	52.23 (45.40, 59.05)	51.69 (44.85, 58.53)	56.24 (49.40, 63.08)	52.34 (45.52, 59.17)	0.74	0.540
C:P	mol:mol	1348 (1076, 1621)	1289 (1015, 1563)	1449 (1176, 1722)	1414 (1143, 1687)	0.37	0.774
N:P	mol:mol	25.12 (22.58, 27.65)	24.30 (21.75, 26.85)	24.85 (22.30, 27.40)	26.48 (23.94, 29.02)	0.59	0.626
C:Ca	mol:mol	140.1 (123.0, 157.2) [a]	167.9 (150.7, 185.1) [b]	109.3 (92.1, 126.5) [a]	118.1 (101.0, 135.3) [a]	9.98	**<0.001**
C:Mg	mol:mol	1089 (937, 1242) [a]	1134 (981, 1287) [a]	993 (840, 1146) [ab]	812 (659, 964) [b]	5.99	**0.004**
Ca:Mg	mol:mol	7.97 (6.93, 9.01) [ab]	7.04 (6.00, 8.08) [a]	9.07 (8.02, 10.11) [b]	7.06 (6.02, 8.09) [a]	8.45	**<0.001**
C:K	mol:mol	2305 (1857, 2752)	2352 (1903, 2801)	2375 (1927, 2824)	2203 (1755, 2650)	0.20	0.896
Nutrient pools							
C	g/m^2	9.13 (6.32, 13.19) [a]	6.01 (4.15, 8.71) [ab]	5.03 (3.48, 7.27) [b]	4.74 (3.29, 6.83) [b]	5.07	**0.010**
N	mg/m^2	203 (143, 288) [a]	139 (98, 198) [ab]	103 (72, 146) [b]	108 (76, 153) [b]	6.35	**0.004**
P	mg/m^2	17.98 (12.94, 24.98) [a]	12.51 (8.96, 17.46) [ab]	8.97 (6.45, 12.46) [b]	9.22 (6.65, 12.79) [b]	6.45	**0.004**
Ca	mg/m^2	230.48 (157.93, 336.35) [a]	127.43 (87.13, 186.39) [b]	152.18 (104.28, 222.08) [ab]	140.77 (96.69, 204.99) [b]	4.40	**0.017**
Mg	mg/m^2	17.11 (12.63, 23.17) [a]	11.25 (8.28, 15.27) [a]	10.05 (7.42, 13.61) [b]	12.04 (8.91, 16.27) [a]	3.90	**0.026**
K	mg/m^2	12.97 (9.81, 17.17) [a]	8.84 (6.67, 11.73) [ab]	6.99 (5.28, 9.24) [b]	7.23 (5.53, 9.64) [b]	5.08	**0.010**

Note: Model: *Property* = ***site*** + ***SPECIES*** + ***site*** × ***SPECIES*** (PROC MIXED in SAS 9.1). Values are back-transformed least squares mean estimates with 95% confidence intervals in parentheses (Type III sums of squares). Boldface type denotes soil properties for which species effects are significant at the $P < 0.05$ level. Different superscript letters within a row denote significant pairwise differences (Tukey-Kramer, $P < 0.05$). * C % and nutrient ratios have df = 3, 21 and were not transformed for analysis.

Table 7. Mineral Soil Moisture and C and N Concentrations.

Property	Units	***SPECIES***				$F_{3, 28}$	***P***
		Douglas-fir	Western hemlock	Western redcedar	Bigleaf maple		
0 to 10 cm							
Moisture	%	19.5 (16.1, 23.0)	20.6 (17.1, 24.1)	20.6 (17.2, 24.1)	20.6 (17.1, 24.0)	2.65	0.078
Total C	%	6.22 (5.10, 7.60)	5.78 (4.73, 7.06)	5.30 (4.33, 6.47)	6.30 (5.16, 7.70)	1.29	0.299
Total N	%	0.28 (0.22, 0.34)	0.26 (0.21, 0.32)	0.25 (0.20, 0.31)	0.29 (0.23, 0.36)	1.46	0.247
C:N	mol:mol	22.6 (20.6, 24.8)	22.5 (20.5, 24.7)	21.2 (19.3, 23.3)	21.7 (19.8, 23.9)	1.05	0.384
NH_4^+-N	mg/kg	2.2 (1.5, 3.2)	2.9 (2.0, 4.4)	2.3 (1.5, 3.5)	2.5 (1.7, 3.8)	2.04	0.131
NO_3^--N	mg/kg	1.6 (0.9, 2.6)	1.6 (1.0, 2.7)	1.6 (1.0, 2.6)	1.9 (1.2, 3.1)	0.93	0.442
NH_4^+-N:NO_3^--N	mol:mol	1.1 (0.7, 1.7)	1.2 (0.8, 1.9)	2.4 (1.5, 3.7)	1.5 (1.0, 2.4)	3.27	**0.036**
Exch. DOC	mg/kg	104.0 (69.3, 156.0)	93.7 (62.4, 140.6)	80.0 (53.3, 120.0)	82.0 (54.7, 123.0)	2.33	0.096
Exch. DON	mg/kg	5.9 (4.0, 8.9)	4.8 (3.2, 7.2)	4.5 (3.0, 6.7)	4.9 (3.3, 7.3)	1.49	0.239
DON:DOC	mol:mol	0.057 (0.051, 0.064)	0.050 (0.044, 0.056)	0.054 (0.048, 0.061)	0.060 (0.053, 0.067)	2.11	0.123
Microbial C	mg/kg	373.1 (303.4, 458.9)	345.5 (280.9, 425.1)	296.3 (240.8, 364.4)	316.5 (257.4, 389.2)	2.20	0.111
Microbial N	mg/kg	50.9 (40.7, 63.6)	50.5 (40.4, 63.1)	46.5 (37.2, 58.2)	49.5 (39.6, 61.9)	0.32	0.813
Microbial C:N	mol:mol	7.3 (6.6, 8.0)	6.9 (6.2, 7.5)	6.4 (5.8, 7.0)	6.4 (5.8, 7.0)	4.39	**0.012**
10 to 20 cm							
Moisture	%	19.7 (16.3, 23.2)	20.2 (16.8, 23.7)	20.8 (17.3, 24.2)	20.7 (17.3, 24.2)	2.44	0.097
Total C	%	3.96 (3.24, 4.84)	3.60 (2.95, 4.40)	3.95 (3.23, 4.83)	3.80 (3.11, 4.64)	0.38	0.766
Total N	%	0.19 (0.15, 0.24)	0.18 (0.14, 0.23)	0.20 (0.16, 0.25)	0.20 (0.16, 0.25)	0.73	0.544
C:N	mol:mol	20.5 (18.7 , 22.5)	19.9 (18.1, 21.8)	19.8 (18.1, 21.8)	18.8 (17.1, 20.6)	1.69	0.191
NH_4^+-N	mg/kg	1.9 (1.3, 2.9)	2.0 (1.4, 3.0)	2.1 (1.4, 3.2)	2.0 (1.3, 2.9)	0.23	0.873
NO_3^--N	mg/kg	1.6 (1.0, 2.6)	1.9 (1.2, 3.1)	1.5 (0.9, 2.5)	1.6 (1.0, 2.7)	1.00	0.406
NH_4^+-N:NO_3^--N	mol:mol	1.3 (0.8, 2.0)	0.9 (0.6, 1.5)	1.6 (1.0, 2.4)	1.2 (0.8, 1.8)	1.32	0.288
Exch. DOC	mg/kg	102.6 (68.4, 153.9)	92.7 (61.7, 139.2)	90.6 (60.4, 136.0)	76.4 (50.9, 114.6)	2.35	0.094
Exch. DON	mg/kg	4.9 (3.3, 7.3)	3.9 (2.6, 5.9)	4.1 (2.7, 6.1)	4.0 (2.7, 6.1)	1.06	0.383
DON:DOC	mol:mol	0.048 (0.042, 0.053)	0.042 (0.038, 0.048)	0.045 (0.040, 0.051)	0.051 (0.046, 0.058)	2.43	0.087
Microbial C	mg/kg	239.9 (195.0, 295.0)	208.5 (169.4, 256.8)	207.8 (168.9, 255.7)	200.6 (163.1, 246.6)	1.35	0.279
Microbial N	mg/kg	34.7 (27.7, 43.3)	32.3 (25.8, 40.4)	33.1 (26.4, 41.4)	32.2 (25.7, 40.2)	0.23	0.875
Microbial C:N	mol:mol	6.9 (6.3, 7.6)	6.5 (5.9, 7.1)	6.3 (5.7, 6.9)	6.2 (5.7, 6.8)	2.56	0.075

Note: Model: *Property= site + SPECIES + site × SPECIES + REPLICATE (site × SPECIES) + DEPTH + SPECIES × DEPTH + site × DEPTH (SPECIES), Slice = DEPTH* (PROC MIXED in SAS 9.1). Values are back-transformed least squares mean estimates with 95% confidence intervals in parentheses (Type III sums of squares). Boldface type denotes soil properties for which species effects at that depth are significant ($P < 0.05$).

Table 8. Mineral Soil pH (H_2O), P, and Base Cation Concentrations.

Property	Units	***SPECIES***				$F_{3, 28}$	***P***
		Douglas-fir	Western hemlock	Western redcedar	Bigleaf maple		
0 to 10 cm							
pH (H_2O)		5.83 (5.65, 6.01)	5.58 (5.40, 5.76)	5.91 (5.73, 6.09)	6.00 (5.82, 6.18)	2.29	0.113
Exch. P	mg/kg	42.1 (22.1, 80.2)	37.4 (19.6, 71.3)	26.6 (13.9, 50.8)	49.0 (25.7, 93.3)	3.41	**0.031**
Exch. Ca^{2+} †	$cmol_c/kg$	17.08 (12.60, 21.57)^{ab}	14.86 (10.36, 19.35)^{a}	17.48 (12.98, 21.98)^{ab}	19.77 (15.28, 24.26)^{b}	5.15	**0.006**
Exch. Mg^{2+}	$cmol_c/kg$	3.36 (2.22, 5.10)^{ab}	3.12 (2.06, 4.73)^{a}	3.27 (2.16, 4.97)^{ab}	4.45 (2.93, 6.75)^{b}	4.78	**0.008**
Exch. K^{+}	$cmol_c/kg$	1.23 (0.98, 1.56)^{ab}	1.03 (0.81, 1.30)^{a}	1.04 (0.82, 1.32)^{a}	1.49 (1.18, 1.89)^{b}	7.36	**<0.001**
∑Base Cations	$cmol_c/kg$	20.23 (14.52, 28.17)^{ab}	16.81 (12.07, 23.42)^{a}	20.59 (14.77, 28.70)^{ab}	24.58 (17.65, 34.25)^{b}	4.42	**0.012**
Ca^{2+}: Mg^{2+}	mol:mol	4.54 (3.90, 5.29)	3.97 (3.41, 4.62)	4.88 (4.18, 5.68)	4.13 (3.54, 4.81)	3.95	**0.018**
10 to 20 cm							
pH (H_2O)		5.87 (5.69, 6.05)	5.69 (5.51, 5.89)	5.89 (5.71, 6.07)	5.98 (5.80, 6.16)	1.85	0.174
Exch. P	mg/kg	34.0 (17.8, 64.8)	28.4 (14.9, 54.2)	22.4 (11.8, 42.8)	39.4 (20.7, 75.1)	2.98	**0.048**
Exch. Ca^{2+} †	$cmol_c/kg$	11.25 (6.76, 15.74)	11.59 (7.10, 16.08)	12.82 (8.32, 17.32)	13.48 (9.00, 17.99)	1.39	0.265
Exch. Mg^{2+}	$cmol_c/kg$	2.52 (1.66, 3.83)^{a}	2.65 (1.75, 4.02)^{ab}	2.68 (1.77, 4.07)^{ab}	3.57 (2.36, 5.42)^{b}	4.71	**0.009**
Exch. K^{+}	$cmol_c/kg$	0.97 (0.78, 1.23)^{ab}	0.80 (0.63, 1.01)^{a}	0.88 (0.69, 1.11)^{a}	1.19 (0.94, 1.50)^{b}	7.04	**0.001**
∑Base Cations	$cmol_c/kg$	13.33 (9.57, 18.57)	12.87 (9.24, 17.93)	15.09 (10.82, 21.03)	17.07 (12.26, 23.78)	3.04	**0.045**
Ca^{2+}: Mg^{2+}	mol:mol	3.76 (3.23, 4.37)	3.43 (2.94, 3.99)	4.17 (3.58, 4.86)	3.37 (2.89, 3.92)	4.38	**0.012**

Note: Model: *Property= site + SPECIES + site × SPECIES + REPLICATE (site × SPECIES) + DEPTH + SPECIES × DEPTH + site × DEPTH (SPECIES), Slice = DEPTH* (PROC MIXED in SAS 9.1). Values are back-transformed least squares mean estimates with 95% confidence intervals in parentheses (Type III sums of squares). Boldface type denotes soil properties for which species effects at that depth are significant ($P < 0.05$). †Variable was not natural log-transformed for analysis.

Table 9. Mineral Soil Bulk Density and Nutrient Pools.

Property	Units	***SPECIES***				$F_{3, 28}$	P
		Douglas-fir	Western hemlock	Western redcedar	Bigleaf maple		
0-10 cm							
Bulk density	g/cm^3	0.83 (0.71, 0.96)	0.70 (0.60, 0.81)	0.73 (0.60, 0.81)	0.74 (0.63, 0.86)	1.18	0.335
Total C	kg/m^2	5.14 (4.20, 6.30)	4.03 (3.29, 4.95)	3.88 (3.16, 4.76)	4.66 (3.81, 5.72)	1.98	0.141
Total N	kg/m^2	0.23 (0.18, 0.28)	0.18 (0.14, 0.22)	0.18 (0.15, 0.23)	0.22 (0.17, 0.27)	2.00	0.137
NH_4^+-N	g/m^2	0.18 (0.12, 0.26)	0.20 (0.14, 0.30)	0.17 (0.12, 0.24)	0.19 (0.13, 0.27)	0.76	0.525
NO_3^--N	g/m^2	0.13 (0.08, 0.20)	0.11 (0.07, 0.18)	0.11 (0.07, 0.18)	0.14 (0.09, 0.22)	0.79	0.509
Microbial C	g/m^2	30.8 (24.2, 39.3)	24.1 (18.9, 30.8)	21.6 (17.0, 27.6)	23.4 (18.4, 29.9)	2.41	0.088
Microbial N	g/m^2	4.2 (3.3, 5.3)	3.5 (2.8, 4.5)	3.4 (2.7, 4.3)	3.7 (2.9, 4.6)	0.93	0.441
Exch. P	g/m^2	3.5 (1.8, 6.8)	2.6 (1.3, 5.1)	1.9 (1.0, 3.8)	3.6 (1.8, 7.1)	4.60	**0.010**
Exch. Ca^{2+}	mg/m^2	253.1 (184.1, 348.1)	173.0 (125.7, 238.0)	233.3 (169.4, 321.4)	272.3 (197.8, 374.8)	3.21	**0.038**
Exch. Mg^{2+}	mg/m^2	33.8 (22.8, 50.1)	26.5 (17.8, 39.3)	29.0 (19.6, 43.1)	40.0 (26.9, 59.3)	3.00	**0.047**
Exch. K^+	mg/m^2	39.9 (31.2, 50.9)	28.0 (21.9, 35.8)	29.7 (21.2, 38.0)	43.1 (33.7, 55.1)	4.63	**0.010**
10-20 cm							
Bulk density	g/cm^3	1.43 (1.22, 1.67)	1.56 (1.34, 1.82)	1.65 (1.41, 1.93)	1.34 (1.15, 1.57)	1.92	0.149
Total C	kg/m^2	5.65 (4.61, 6.93)	5.62 (4.58, 6.89)	6.46 (5.26, 7.94)	5.10 (4.16, 6.25)	1.08	0.374
Total N	kg/m^2	0.28 (0.22, 0.34)	0.28 (0.23, 0.35)	0.33 (0.26, 0.41)	0.27 (0.22, 0.34)	1.11	0.360
NH_4^+-N	g/m^2	0.27 (0.19, 0.40)	0.33 (0.23, 0.48)	0.35 (0.24, 0.51)	0.26 (0.18, 0.38)	2.18	0.113
NO_3^--N	g/m^2	0.23 (0.14, 0.36)	0.30 (0.19, 0.47)	0.25 (0.16, 0.40)	0.22 (0.14, 0.34)	1.47	0.244
Microbial C	g/m^2	34.4 (27.0, 43.9)	32.8 (25.7, 41.9)	34.4 (26.9, 43.9)	26.9 (21.1, 34.3)	1.42	0.259
Microbial N	g/m^2	5.0 (3.9, 6.3)	5.1 (4.0, 6.4)	5.5 (4.3, 6.9)	4.3 (3.4, 5.5)	1.01	0.402
Exch. P	g/m^2	4.9 (2.5, 9.5)	4.4 (2.2, 8.7)	3.9 (2.0, 7.7)	5.3 (2.7, 10.4)	0.88	0.463
Exch. Ca^{2+}	mg/m^2	268.1 (194.9, 368.9)	282.4 (205.1, 388.8)	371.2 (269.3, 511.7)	323.5 (235.3, 444.9)	1.71	0.188
Exch. Mg^{2+}	mg/m^2	43.3 (29.2, 64.3)	50.1 (33.7, 74.3)	53.6 (36.1, 79.6)	58.3 (39.3, 86.5)	1.45	0.249
Exch. K^+	mg/m^2	54.2 (42.5, 69.2)	48.4 (37.9, 61.9)	56.1 (43.8, 71.9)	62.3 (48.8, 79.5)	1.09	0.369

Note: Model: *Property = site + SPECIES + site × SPECIES + REPLICATE (site × SPECIES) + DEPTH + SPECIES × DEPTH + site × DEPTH (SPECIES), Slice = DEPTH* (PROC MIXED in SAS 9.1). Values are back-transformed least squares mean estimates with 95% confidence intervals in parentheses (Type III sums of squares). Boldface type denotes soil properties for which species effects at that depth are significant ($P < 0.05$).

Table 10. Results of Fixed-Effects ANOVA (Type III sums of squares) for Foliar Chemistry.

		SITE × SPECIES	
Property	Units	$F_{21, 158}$	*P*
C*	%	1.87	**0.017**
N	%	1.67	**0.040**
P	mg/g	3.00	**<0.001**
C	mg/g	1.06	0.398
Mg	mg/g	2.30	**0.002**
K	mg/g	0.78	0.744
C:N	mol:mol	1.62	*0.050*
N:P †	mol:mol	3.16	**<0.001**
Ca:Mg	mol:mol	1.76	**0.027**

Note: Model: *Property* = *SITE* + *SPECIES* + *SITE* × *SPECIES* (PROC GLM in SAS 9.1). Boldface type denotes significance at the $P < 0.05$ level. * Variable was not natural log-transformed for analysis.

Table 11. Results of Fixed-Effects ANOVA (Type III sums of squares) for Forest Floor Thickness and Mass.

		SITE × SPECIES		***SITE × HORIZON (SPECIES)***	
Property	Units	$F_{18, 140}$	*P*	$F_{24, 140}$	*P*
Thickness	cm	1.41	0.138	1.27	0.199
Mass	g/m^2	1.00	0.465	2.08	**0.005**

Note: Model: *Property = SITE + SPECIES + SITE × SPECIES + REPLICATE (SITE × SPECIES) + HORIZON + SPECIES × HORIZON + SITE × HORIZON (SPECIES)* (PROC GLM in SAS 9.1). The *SITE × SPECIES* effect was tested against *REPLICATE (SITE × SPECIES)* as an error term. Analyses include data from 7 of 8 sites. Boldface type denotes significance at the $P < 0.05$ level.

Table 12. Results of Fixed-Effects ANOVA (Type III sums of squares) for Forest Floor Oe+Oa Horizon Nutrient Concentrations and Pools.

		SITE × SPECIES	
Property	Units	$F_{21, 160}$*	*P*
Nutrient Concentrations			
C	%	3.24	**<0.001**
C:N	mol:mol	2.35	**0.002**
C:P	mol:mol	2.89	**<0.001**
N:P	mol:mol	2.58	**<0.001**
C:Ca	mol:mol	2.67	**<0.001**
C:Mg	mol:mol	1.77	**0.026**
Ca:Mg	mol:mol	1.46	0.100
C:K	mol:mol	2.64	**<0.001**
Nutrient Pools			
C	g/m^2	1.04	0.424
N	mg/m^2	0.96	0.508
P	mg/m^2	1.22	0.251
Ca	mg/m^2	0.87	0.621
Mg	mg/m^2	0.98	0.499
K	mg/m^2	1.43	0.129

Note: **Model*: Property* = *SITE* + *SPECIES* + *SITE* × *SPECIES* (PROC GLM in SAS 9.1). * Nutrient pool data include 7 of 8 sites and have df = 18, 140. Boldface type denotes significance at the P < 0.05 level.**

Table 13. Results of Fixed-Effects ANOVA (Type III sums of squares) for Mineral Soil Properties.

		SITE × SPECIES		***SITE × DEPTH (SPECIES)***	
Property	Units	$F_{21, 160}$	*P*	$F_{28, 160}$	*P*
Moisture	%	2.77	**<0.001**	2.18	**0.001**
Bulk density	g/cm^3	1.68	**0.0385**	2.82	**<0.001**
pH (H_2O)		1.40	0.126	1.79	**0.014**
Nutrient Concentrations					
Total C	%	1.65	**0.044**	2.58	**0.001**
Total N	%	2.02	**0.008**	2.45	**0.001**
C:N	mol:mol	1.58	0.060	2.24	**0.001**
NH_4^+-N	mg/kg	1.21	0.252	1.50	0.065
NO_3^--N	mg/kg	2.54	**<0.001**	5.24	**<0.001**
NH_4^+-N:NO_3^--N	mol:mol	5.38	**<0.001**	2.17	**0.002**
Exch. DOC	mg/kg	2.19	**0.003**	2.26	**0.001**
Exch. DON	mg/kg	2.20	**0.003**	2.82	**<0.001**
DON:DOC	mol:mol	1.23	0.235	2.17	**0.002**
Microbial C	mg/kg	2.01	**0.009**	4.13	**<0.001**
Microbial N	mg/kg	2.35	**0.002**	3.46	**<0.001**
Microbial C:N	mol:mol	0.95	0.532	3.72	**<0.001**
Exch. P	mg/kg	1.17	0.288	0.81	0.736
Exch. Ca^{2+}	$cmol_c/kg$	1.45	0.104	1.46	0.079
Exch. Mg^{2+}	$cmol_c/kg$	2.57	**<0.001**	2.06	**0.003**
Ca^{2+}: Mg^{2+}	mol:mol	1.21	0.252	0.86	0.668
Exch. K^+	$cmol_c/kg$	1.22	0.244	2.13	**0.002**
∑Base Cations	$cmol_c/kg$	2.25	**0.003**	2.02	**0.004**
Nutrient Pools					
Total C	kg/m^2	2.42	**0.001**	4.91	**<0.001**
Total N	kg/m^2	2.04	**0.007**	2.16	**0.002**
NH_4^+-N	g/m^2	0.73	0.799	1.80	**0.013**
NO_3^--N	g/m^2	1.55	0.070	4.43	**<0.001**
Exch. DOC	g/m^2	1.52	0.077	2.91	**<0.001**
Exch. DON	g/m^2	1.88	**0.016**	3.09	**<0.001**
Microbial C	g/m^2	2.16	**0.004**	5.30	**<0.001**
Microbial N	g/m^2	2.24	**0.003**	4.69	**<0.001**
Exch. P	g/m^2	1.15	0.306	1.30	0.162
Exch. Ca^{2+}	mg/m^2	2.78	**<0.001**	3.23	**<0.001**
Exch. Mg^{2+}	mg/m^2	2.85	**<0.001**	2.84	**<0.001**
Exch. K^+	mg/m^2	1.67	**0.041**	3.34	**<0.001**

Note: Model: Property = SITE + SPECIES + SITE × SPECIES + REPLICATE (SITE × SPECIES) + DEPTH + SPECIES × DEPTH + SITE × DEPTH (SPECIES) (PROC GLM in SAS 9.1). The SITE × SPECIES effect was tested against REPLICATE (SITE × SPECIES) as an error term. Boldface type denotes significance at the $P < 0.05$ level.

Table 14. Results of Linear Regression of Foliar Chemistry vs. Soil Properties**.**

				SOIL SITE MEAN × SPECIES	
Foliar Property (dependent)	Units	Soil Property* (independent)	Units	$F_{3, 24}$	*P*
C †	%	Total C	%	2.11	0.126
			kg/m^2	1.49	0.243
N	%	Total N	%	1.36	0.278
			kg/m^2	1.72	0.189
P	mg/g	**Exch. P**	**mg/g**	3.28	**0.038**
			g/m^2	1.71	0.192
Ca	mg/g	Exch. Ca^{2+}	$cmol_c/kg$	0.01	0.999
			mg/m^2	0.08	0.971
Mg	mg/g	Exch. Mg^{2+}	$cmol_c/kg$	1.71	0.193
			mg/m^2	2.14	0.121
K	mg/g	Exch. K^+	$cmol_c/kg$	0.60	0.621
			mg/m^2	1.28	0.305
C:N	mol:mol	Total C	%	0.32	0.810
			kg/m^2	0.46	0.714
		Total N	%	0.28	0.840
			kg/m^2	0.37	0.776
		C:N	mol:mol	0.15	0.928
N:P †	mol:mol	**Total N**	%	2.35	0.098
			kg/m^2	3.39	**0.034**
		Exch. P	**mg/g**	4.95	**0.008**
			g/m^2	2.89	0.057
Ca:Mg	mol:mol	Exch. Ca^{2+}	$cmol_c/kg$	1.61	0.213
			mg/m^2	1.80	0.175
		Exch. Mg^{2+}	$cmol_c/kg$	1.30	0.298
			mg/m^2	1.57	0.222
		Ca:Mg	mol:mol	0.27	0.846

Note: Model: *Foliar Property = SOIL SITE MEAN + SPECIES + SOIL SITE MEAN × SPECIES* (PROC MIXED in SAS 9.1).Boldface type denotes significance ($P < 0.05$). * Mineral soil at 0 to 10 cm depth. †Variable was not natural-log transformed for analysis.

Table 15. Results of Linear Regression of Forest Floor Oe+Oa Horizon Property Deviations from the Site Mean.

		SITE MEAN × SPECIES	
Property	Units	$F_{3,24}$*	*P*
Thickness	cm	7.73	**0.001**
Mass	g/m^2	1.82	0.176
Nutrient Concentrations			
C	%	21.89	**<0.001**
C:N	mol:mol	3.21	**0.041**
C:P	mol:mol	4.52	**0.012**
N:P	mol:mol	1.24	0.316
C:Ca	mol:mol	2.52	0.082
C:Mg	mol:mol	4.31	**0.015**
Ca:Mg	mol:mol	2.53	0.081
C:K	mol:mol	1.71	0.191
Nutrient Pools			
C	g/m^2	1.13	0.361
N	mg/m^2	7.99	**0.001**
P	mg/m^2	5.46	**0.007**
Ca	mg/m^2	1.05	0.392
Mg	mg/m^2	3.17	**0.047**
K	mg/m^2	2.49	0.089

Note: Model: *Deviation = SITE MEAN + SPECIES + SITE MEAN × SPECIES* (PROC MIXED in SAS 9.1).Boldface type denotes significance ($P < 0.05$). * Thickness, mass, and nutrient pools include 7 of 8 field sites and have df = 3, 20.

Table 16. Results of Linear Regression of Mineral Soil Property Deviations from the Site Mean.

		SITE MEAN × SPECIES	
Property	Units	$F_{3, 24}$	*P*
Moisture	%	1.90	0.156
Bulk density	g/cm^3	2.32	0.101
pH (H_2O)		2.25	0.108
Nutrient Concentrations			
Total C	%	3.17	**0.043**
Total N	%	3.58	**0.029**
C:N	mol:mol	2.36	0.097
NH_4^+-N	mg/kg	3.52	**0.030**
NO_3^--N	mg/kg	3.28	**0.038**
NH_4^+:NO_3^-	mol:mol	0.93	0.441
Exch. DOC	mg/kg	2.60	0.075
Exch. DON	mg/kg	2.51	0.083
DON:DOC	mol:mol	2.08	0.130
Microbial C	mg/kg	1.24	0.318
Microbial N	mg/kg	0.49	0.693
Microbial C:N	mol:mol	0.63	0.604
Exch. P	mg/kg	2.69	0.069
Exch. Ca^{2+}	$cmol_c/kg$	2.38	0.095
Exch. Mg^{2+}	$cmol_c/kg$	5.78	**0.004**
Exch. K^+	$cmol_c/kg$	0.74	0.540
∑Base Cations	$cmol_c/kg$	3.18	**0.042**
Ca^{2+}: Mg^{2+}	mol:mol	0.43	0.731
Nutrient Pools			
Total C	kg/m^2	5.86	**0.004**
Total N	kg/m^2	9.18	**<0.001**
NH_4^+-N	g/m^2	0.24	0.868
NO_3^--N	g/m^2	0.63	0.604
Microbial C	g/m^2	1.32	0.292
Microbial N	g/m^2	2.94	0.053
Exch. P	g/m^2	2.81	0.061
Exch. Ca^{2+}	mg/m^2	2.48	0.085
Exch. Mg^{2+}	mg/m^2	4.82	**0.009**
Exch. K^+	mg/m^2	0.29	0.829

Note: Model: *Deviation = SITE MEAN + SPECIES + SITE MEAN × SPECIES* (PROC MIXED in SAS 9.1).Boldface type denotes significance ($P < 0.05$).

Table 17. Summary of Results of Depth-Based Soil Sampling.

Species differences in 10 to 20 cm soils?	Species differences in 0 to 10 cm soils?	
	Yes	No
No	**Differential species effects:** • NH_4^+-N:NO_3^--N • Microbial C:N • Ca concentrations • P pools • Ca, Mg, K pools	**No pattern or Low power:** • Moisture • pH • C & N concentrations • Bulk density • C & N pools
Yes	**Differential species establishment or Species effects reach deep soils:** • P concentrations • Mg & K concentrations • Sum of base cations • Ca:Mg	**Generic plant effects:** • No evidence

APPENDICES

Appendix A: Documentation of Monte Carlo Simulation

The following commands in S-PLUS were used to simulate the context dependence analysis using random numbers drawn from normal distributions. "N1" through "N8" are sets of 4 random numbers (means for each species at a field site) drawn from a normal distribution. The vector "N" is composed of these random numbers. Deviations of each species mean from the mean of all species at a site is given by "dif." "Dif" is plotted against "meansN", the means for the 8 distributions (means of all 4 species at a field site) in Figure A1. The plot of "N" vs. "meansN," which shows clear autocorrelation, is given for comparison in Figure A2.

```
> N1<-rnorm(4,mean=1, sd=0.5)
> N2<-rnorm(4,mean=2, sd=0.5)
> N3<-rnorm(4,mean=3, sd=0.5)
> N4<-rnorm(4,mean=4, sd=0.5)
> N5<-rnorm(4,mean=5, sd=0.5)
> N6<-rnorm(4,mean=6, sd=0.5)
> N7<-rnorm(4,mean=7, sd=0.5)
> N8<-rnorm(4,mean=8, sd=0.5)
> meansN<-c(1,1,1,1,2,2,2,2,3,3,3,3,4,4,4,4,5,5,5,5,6,6,6,6,7,7,7,7,8,8,8,8)
> N<-c(N1,N2,N3,N4,N5,N6,N7,N8)
> dif<-(meansN-N)
> plot(meansN,dif)
> plot(meansN,N)
```

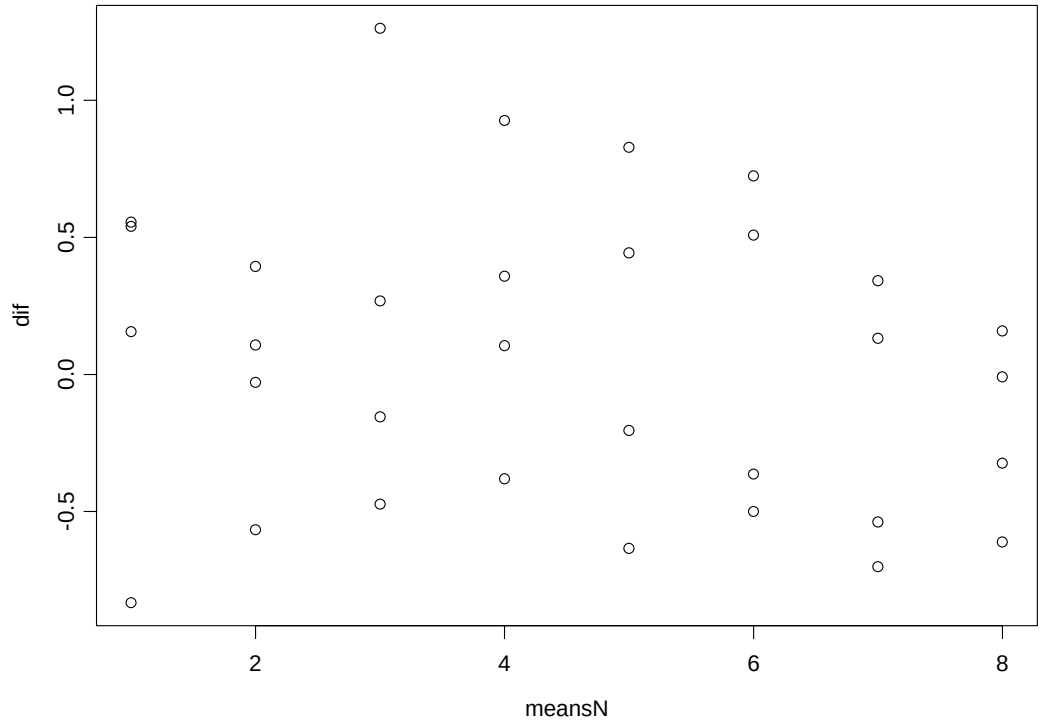

Figure A1. Deviation in mean of each species at a site from the mean of all species at that site (dif) is not correlated with the mean of all species at that site (meansN).

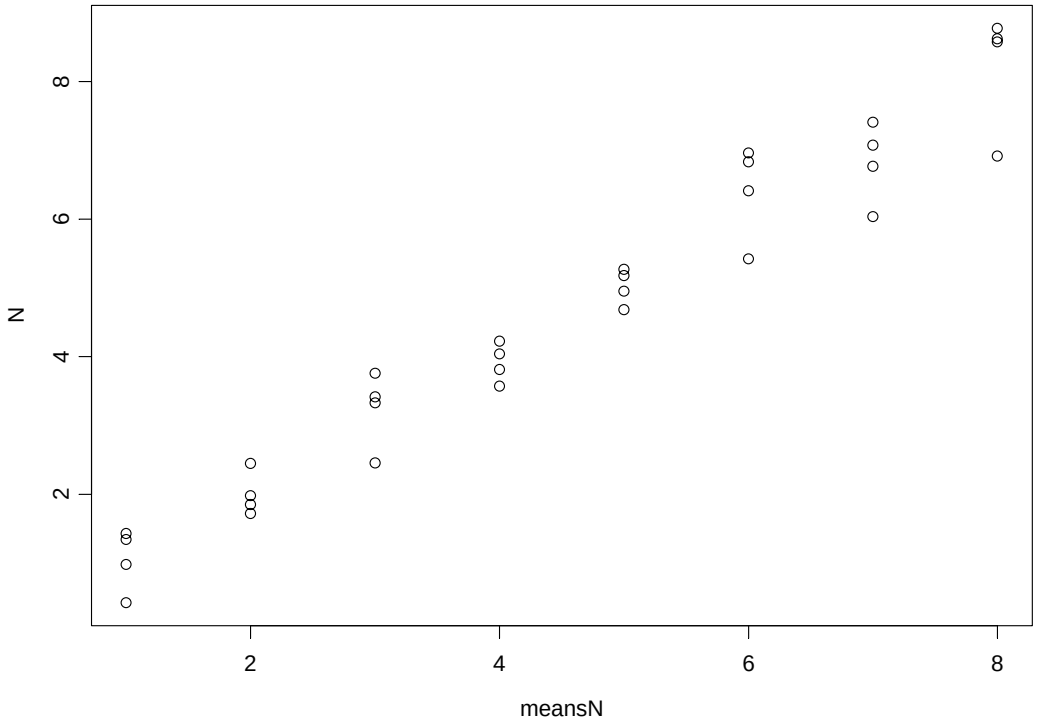

Figure A2. Mean for each species at a site (N) is autocorrelated with the mean of all species at that site (meansN).

Appendix B: Tables of Soil Properties by Field Site

Table B1. Organic Horizon Properties.

Soil property	Units	Site			
		703	704	726	733
Oi					
Thickness	cm	3.0 (2.2, 3.9)	ND	1.9 (1.5, 2.4)	2.0 (1.5, 2.5)
Mass	g/m^2	9.0 (6.3, 11.7)	ND	6.9 (5.4, 8.4)	5.3 (3.8, 6.8)
Oe+Oa					
Thickness	cm	2.1 (1.4, 2.8)	ND	1.7 (1.2, 2.2)	1.1 (0.9, 1.4)
Mass	g/m^2	20.1 (14.0, 26.1)	ND	19.1 (13.8, 24.4)	14.2 (8.6, 19.8)
Nutrient Concentrations					
C	%	40.58 (37.42, 43.75)	35.74 (31.11, 40.37)	38.30 (34.50, 42.10)	36.68 (32.52, 40.84)
C:N	mol:mol	49.27 (43.25, 55.28)	45.45 (40.94, 49.96)	52.08 (46.59, 57.56)	46.01 (43.15, 48.88)
C:P	mol:mol	1358 (1074, 1642)	1075 (883, 1269)	1264 (1061, 1467)	1106 (931, 1252)
N:P	mol:mol	26.82 (23.94, 26.69)	22.85 (20.36, 25.35)	23.94 (22.20, 25.68)	23.96 (21.28, 26.63)
C:Ca	mol:mol	140.3 (122.9, 157.7)	132.0 (109.0, 155.0)	131.4 (115.6, 147.2)	138.8 (116.2, 161.3)
C:Mg	mol:mol	1155 (999, 1312)	741.6 (626.2, 857.0)	940 (765, 1115)	889 (759, 1020)
Ca:Mg	mol:mol	8.30 (7.63, 8.96)	5.82 (5.31, 6.33)	7.30 (6.37, 8.23)	6.67 (5.79, 7.55)
C:K	mol:mol	2651 (2287, 3014)	1649 (1334, 1964)	2221 (1850, 2592)	1700 (1353, 2048)
Nutrient Pools					
C	g/m^2	8.29 (5.80, 10.79)	ND	7.57 (5.07, 10.07)	5.48 (3.12, 7.85)
N	mg/m^2	199.33 (143.61, 255.05)	ND	165.66 (119.83, 211.50)	135.90 (80.23, 191.57)
P	mg/m^2	16.52 (11.47, 21.56)	ND	15.13 (11.27, 18.98)	12.19 (7.25, 17.13)
Ca	mg/m^2	202.69 (147.33, 258.05)	ND	190.03 (137.53, 242.52)	145.63 (67.97, 223.29)
Mg	mg/m^2	15.53 (10.23, 20.83)	ND	15.45 (11.85, 19.05)	11.28 (7.01, 15.56)
K	mg/m^2	10.03 (7.44, 12.62)	ND	10.43 (7.98, 12.88)	9.63 (6.29, 12.97)

Note: Values are means with 95 % confidence intervals in parentheses (n = 24).

Table B1, extended

Soil property	Units	Site			
		806	810	819	821
Oi					
Thickness	cm	2.1 (1.4, 2.7)	2.2 (1.8, 2.6)	3.3 (2.6, 4.0)	4.3 (3.2, 5.3)
Mass	g/m^2	7.8 (6.5, 9.1)	6.5 (5.4, 7.5)	6.9 (5.9, 8.0)	5.3 (3.9, 6.6)
Oe+Oa					
Thickness	cm	1.8 (1.3, 2.4)	2.04 (1.6, 2.5)	1.9 (1.4, 2.3)	1.7 (1.3, 2.0)
Mass	g/m^2	20.5 (13.0, 28.0)	15.1 (11.1, 19.1)	23.1 (17.7, 28.6)	27.9 (19.5, 36.3)
Nutrient Concentrations					
C	%	44.18 (41.49, 46.87)	42.15 (39.31, 44.99)	42.34 (39.34, 45.33)	41.33 (38.35, 44.31)
C:N	mol:mol	66.19 (60.37, 72.01)	60.66 (56.08, 65.24)	53.77 (48.09, 59.45)	51.71 (47.07, 56.35)
C:P	mol:mol	1765 (1475, 2055)	1605 (1398, 1812)	1378 (1149, 1608)	1476 (1284, 1669)
N:P	mol:mol	25.87 (23.45, 28.29)	26.02 (24.38, 27.67)	24.09 (20.94, 27.24)	28.21 (26.45, 29.98)
C:Ca	mol:mol	140.2 (123.8, 156.6)	132.11 (116.79, 147.42)	111.9 (95.3, 128.5)	144.31 (118.45, 170.18)
C:Mg	mol:mol	1159 (1012, 1306)	989 (870, 1109)	1020 (848, 1192)	1161 (1037, 1285)
Ca:Mg	mol:mol	8.40 (7.68, 9.12)	7.59 (6.89, 8.30)	9.30 (8.22, 10.38)	8.87 (7.53, 10.20)
C:K	mol:mol	2221 (1916, 2526)	2651 (2352, 2950)	2626 (2331, 2922)	2774 (2394, 3153)
Nutrient Pools					
C	g/m^2	8.95 (5.84, 12.06)	6.40 (4.52, 8.27)	10.02 (7.38, 12.65)	11.55 (8.06, 15.05)
N	mg/m^2	160.73 (100.44, 221.01)	121.43 (88.97, 153.89)	217.61 (165.11, 270.11)	280.10 (184.41, 375.80)
P	mg/m^2	13.60 (8.79, 18.41)	10.32 (7.77, 12.89)	19.20 (13.97, 24.42)	22.81 (14.36, 31.26)
Ca	mg/m^2	214.66 (142.89, 286.44)	161.09 (119.01, 203.17)	311.89 (225.59, 398.19)	303.08 (214.65, 391.15)
Mg	mg/m^2	15.73 (10.53, 20.93)	13.26 (9.88, 16.63)	20.47 (15.70, 25.24)	21.34 (14.80, 27.88)
K	mg/m^2	12.93 (8.82, 17.04)	7.86 (5.63, 10.08)	12.44 (9.38, 15.50)	14.76 (9.97, 19.55)

Table B2. Mineral Soil Moisture and C and N Concentrations.

Soil property	Units	Site			
		703	704	726	733
0-10 cm					
Moisture	%	17.7 (13.6, 15.8)	25.8 (24.2, 27.3)	24.9 (24.0, 25.8)	15.7 (14.7, 16.7)
Total C	%	4.89 (4.40, 5.38)	10.39 (8.27, 12.50)	7.94 (6.62, 9.27)	5.30 (4.71, 5.90)
Total N	%	0.22 (0.21, 0.24)	0.51 (0.43, 0.59)	0.36 (0.31, 0.41)	0.25 (0.23, 0.27)
C:N	mol:mol	21.66 (20.52, 22.80)	19.77 (18.55, 20.99)	21.91 (20.13, 23.69)	21.20 (19.84, 22.57)
NH_4^+-N	mg/kg	3.0 (2.3, 3.7)	4.3 (3.4, 5.2)	5.1 (4.0, 6.2)	2.2 (1.7, 2.7)
NO_3^--N	mg/kg	1.5 (1.2, 1.8)	4.7 (3.4, 5.9)	2.3 (1.7, 2.9)	0.4 (0.3, 0.6)
NH_4^+-N:NO_3^--N	mol:mol	3.8 (0, 7.8)	1.3 (0.9, 1.6)	2.7 (2.0, 3.4)	6.3 (4.6, 8.0)
Exch. DOC	mg/kg	140.8 (87.9, 121.7)	156.0 (121.1, 190.8)	101.2 (85.7, 116.8)	94.7 (80.8, 108.6)
Exch. DON	mg/kg	6.2 (4.9, 7.4)	8.3 (5.9, 10.7)	5.5 (4.1, 6.8)	6.1 (5.3, 7.0)
DON:DOC	mol:mol	0.059 (0.053, 0.064)	0.053 (0.048, 0.057)	0.055 (0.044, 0.067)	0.068 (0.057, 0.078)
Microbial C	mg/kg	293.2 (268.3, 318.1)	455.4 (377.9, 533.0)	389.4 (337.9, 441.0)	241.3 (216.8, 265.8)
Microbial N	mg/kg	45.1 (41.2, 48.9)	67.6 (54.6, 80.6)	68.8 (58.8, 78.8)	30.6 (27.2, 33.9)
Microbial C:N	mol:mol	6.6 (6.1, 7.1)	6.8 (6.2, 7.4)	5.8 (5.5, 6.1)	8.0 (7.4, 8.5)
10-20 cm					
Moisture	%	15.3 (14.4, 16.2)	24.8 (23.7, 26.0)	23.4 (22.5, 24.3)	16.6 (15.3, 17.8)
Total C	%	3.44 (3.04, 3.84)	5.62 (4.64, 6.60)	4.25 (3.55, 4.94)	3.00 (2.24, 3.77)
Total N	%	0.17 (0.16, 0.18)	0.30 (0.26, 0.33)	0.23 (0.20, 0.25)	0.17 (0.13, 0.20)
C:N	mol:mol	20.07 (18.64, 21.50)	18.38 (16.84, 19.92)	18.58 (17.31, 19.84)	17.48 (16.04, 18.93)
NH_4^+-N	mg/kg	2.6 (2.0, 3.1)	3.2 (2.6, 3.9)	3.7 (3.1, 4.3)	1.5 (1.2, 1.8)
NO_3^--N	mg/kg	1.7 (1.6, 1.8)	3.0 (2.3, 3.6)	2.1 (1.9, 2.3)	0.7 (0.4, 1.0)
NH_4^+-N:NO_3^--N	mol:mol	1.5 (1.2, 1.8)	1.3 (1.0, 1.6)	1.8 (1.5, 2.2)	4.3 (2.9, 5.6)
Exch. DOC	mg/kg	104.8 (82.4, 127.2)	151.9 (121.8, 182.0)	152.6 (131.1, 174.2)	72.0 (59.8, 84.1)
Exch. DON	mg/kg	5.0 (4.0, 6.1)	7.9 (6.2, 9.5)	6.7 (5.7, 7.7)	3.3 (2.7, 3.9)
DON:DOC	mol:mol	0.048 (0.044, 0.052)	0.053 (0.042, 0.063)	0.046 (0.040, 0.053)	0.047 (0.041, 0.052)
Microbial C	mg/kg	201.5 (175.8, 277.1)	204.8 (168.6, 241.0)	199.8 (168.8, 230.8)	140.6 (124.0, 157.3)
Microbial N	mg/kg	33.0 (30.0, 36.0)	36.0 (29.5, 42.5)	32.9 (27.0, 38.8)	18.7 (16.5, 20.9)
Microbial C:N	mol:mol	6.0 (5.6, 6.5)	5.7 (5.4, 6.0)	6.3 (5.9, 6.8)	7.7 (6.9, 8.4)

Note: Values are means with 95 % confidence intervals in parentheses (n = 24).

Table B2, extended

Soil property	Units	Site			
		806	810	819	821
0-10 cm					
Moisture	%	21.3 (20.2, 22.4)	25.1 (23.8, 26.4)	15.0 (13.4, 16.2)	20.1 (18.9, 21.3)
Total C	%	6.55 (5.48, 7.61)	6.89 (5.69, 8.09)	4.79 (4.07, 5.52)	5.25 (4.24, 6.27)
Total N	%	0.29 (0.26, 0.32)	0.32 (0.28, 0.37)	0.019 (0.16, 0.21)	0.20 (0.18, 0.22)
C:N	mol:mol	22.42 (20.91, 23.92)	21.01 (19.52, 22.49)	25.53 (23.98, 27.08)	25.35 (23.05, 27.64)
NH_4^+-N	mg/kg	2.4 (2.0, 2.8)	3.6 (3.0, 4.3)	1.5 (0.9, 2.1)	2.4 (1.8, 3.1)
NO_3^--N	mg/kg	1.9 (1.8, 2.0)	3.0 (2.3, 3.8)	1.6 (1.5, 1.6)	1.9 (1.7, 2.0)
NH_4^+-N:NO_3^--N	mol:mol	1.3 (1.1, 1.5)	1.3 (1.1, 1.6)	1.0 (0.6, 1.4)	1.3 (1.0, 1.6)
Exch. DOC	mg/kg	141.2 (119.0, 163.4)	127.2 (107.8, 146.7)	33.7 (25.7, 41.6)	80.9 (56.3, 105.5)
Exch. DON	mg/kg	7.0 (6.2, 7.9)	8.3 (6.8, 9.8)	2.4 (1.8, 3.0)	3.6 (2.7, 4.5)
DON:DOC	mol:mol	0.052 (0.048, 0.057)	0.064 (0.059, 0.069)	0.066 (0.059, 0.073)	0.046 (0.040, 0.050)
Microbial C	mg/kg	365.6 (315.3, 415.7)	362.9 (300.3, 425.4)	289.2 (259.9, 318.5)	432.7 (381.8, 483.7)
Microbial N	mg/kg	55.1 (50.0, 60.3)	57.5 (47.4, 67.6)	44.0 (39.0, 49.1)	57.1 (52.3, 61.9)
Microbial C:N	mol:mol	6.6 (6.1, 7.1)	6.4 (6.1, 6.7)	6.7 (6.2, 7.3)	7.6 (7.0, 8.2)
10-20 cm					
Moisture	%	21.6 (20.7, 22.4)	26.5 (25.5, 27.5)	14.9 (13.9, 15.8)	19.9 (19.0, 20.8)
Total C	%	4.54 (4.05, 5.03)	4.69 (3.91, 5.48)	3.61 (3.03, 4.19)	3.98 (3.59, 4.37)
Total N	%	0.22 (0.20, 0.24)	0.25 (0.22, 0.28)	0.15 (0.13, 0.16)	0.17 (0.15, 0.18)
C:N	mol:mol	20.63 (19.26, 22.01)	18.02 (16.76, 19.28)	24.33 (22.961, 26.06)	23.62 (22.35, 24.89)
NH_4^+-N	mg/kg	2.2 (1.6, 2.9)	4.6 (3.5, 5.7)	0.9 (0.7, 1.1)	1.9 (1.3, 2.5)
NO_3^--N	mg/kg	1.8 (1.7, 1.8)	2.9 (2.3, 3.5)	1.6 (1.6, 1.6)	1.9 (1.8, 2.0)
NH_4^+-N:NO_3^--N	mol:mol	1.2 (0.9, 1.6)	1.7 (1.3, 2.1)	0.6 (0.4, 0.7)	1.0 (0.7, 1.3)
Exch. DOC	mg/kg	153.5 (126.6, 180.4)	139.9 (125.3, 154.5)	35.5 (23.3, 47.7)	60.6 (50.7, 70.4)
Exch. DON	mg/kg	6.7 (5.8, 7.7)	7.9 (6.7, 9.0)	1.8 (1.2, 2.5)	3.0 (2.5, 3.5)
DON:DOC	mol:mol	0.046 (0.042, 0.050)	0.055 (0.051, 0.059)	0.048 (0.043, 0.053)	0.048 (0.044, 0.052)
Microbial C	mg/kg	266.5 (240.4, 292.6)	262.1 (221.6, 302.6)	210.8 (187.2, 234.4)	363.3 (337.2, 389.3)
Microbial N	mg/kg	39.6 (35.0, 44.3)	46.0 (38.9, 53.1)	34.1 (29.7, 38.4)	45.3 (41.7, 49.0)
Microbial C:N	mol:mol	6.9 (6.4, 7.4)	5.7 (5.5, 6.0)	6.3 (5.8, 6.8)	8.1 (7.5, 8.7)

Table B3. Mineral Soil pH (H_2O), P, and Base Cation Concentrations.

Soil property	Units	Site			
		703	704	726	733
0-10 cm					
pH (H_2O)		5.82 (5.66, 5.98)	5.58 (5.38, 5.78)	5.58 (5.41, 5.76)	5.82 (5.68, 5.96)
Exch. P	mg/kg	103.9 (74.7, 133.1)	34.3 (21.1, 47.6)	65.5 (49.9, 81.1)	57.8 (40.3, 75.4)
Exch. Ca^{2+}	$cmol_c/kg$	11.18 (9.42, 12.93)	20.73 (16.97, 24.49)	18.19 (15.23, 21.15)	18.46 (16.47, 20.44)
Exch. Mg^{2+}	$cmol_c/kg$	2.13 (1.75, 2.50)	5.08 (4.32, 5.84)	3.94 (3.39, 4.49)	4.68 (4.13, 5.24)
Exch. K^+	$cmol_c/kg$	0.98 (0.78, 1.18)	1.38 (1.06, 1.70)	1.34 (1.11, 1.58)	1.44 (1.21, 1.68)
∑Base Cations	$cmol_c/kg$	14.32 (12.14, 16.49)	27.36 (22.82, 31.89)	23.59 (20.07, 27.11)	24.66 (22.29, 27.04)
Ca^{2+}: Mg^{2+}	mol:mol	5.48 (4.79, 6.16)	4.05 (3.51, 4.60)	4.62 (4.03, 5.21)	4.17 (3.53, 4.81)
10-20 cm					
pH (H_2O)		5.84 (5.69, 6.00)	5.65 (5.48, 5.82)	5.65 (5.52, 5.78)	5.99 (5.88, 6.10)
Exch. P	mg/kg	92.7 (66.3, 119.0)	33.7 (19.2, 48.3)	58.2 (37.6, 78.8)	59.1 (42.7, 75.5)
Exch. Ca^{2+}	$cmol_c/kg$	6.93 (5.74, 8.13)	14.09 (11.030, 16.87)	9.83 (7.53, 78.83)	13.61 (12.11, 15.12)
Exch. Mg^{2+}	$cmol_c/kg$	1.56 (1.23, 1.88)	4.11 (3.46, 4.76)	2.62 (2.13, 3.11)	4.26 (3.73, 4.80)
Exch. K^+	$cmol_c/kg$	0.85 (0.65, 1.05)	1.22 (0.90, 1.55)	0.86 (0.67, 1.06)	1.13 (0.95, 1.32)
∑Base Cations	$cmol_c/kg$	9.39 (7.82, 10.97)	19.58 (16.07, 23.09)	13.44 (10.65, 16.23)	19.09 (17.27, 20.91)
Ca^{2+}: Mg^{2+}	mol:mol	4.71 (4.09, 5.33)	3.41 (2.89, 3.94)	3.78 (3.12, 4.43)	3.45 (2.79, 4.10)

Note: Values are means with 95 % confidence intervals in parentheses (n = 24).

Table B3, extended

Soil property	Units	Site			
		806	810	819	821
0-10 cm					
pH (H_2O)		5.88 (5.72, 6.04)	6.09 (6.03, 6.16)	6.18 (6.06, 6.30)	5.71 (5.53, 5.89)
Exch. P	mg/kg	85.1 (67.3, 102.9)	15.3 (11.3, 19.2)	133.2 (100.2, 166.3)	17.8 (10.1, 25.5)
Exch. Ca^{2+}	$cmol_c/kg$	19.14 (17.34, 20.95)	28.51 (26.10, 30.91)	11.87 (9.80, 13.93)	9.94 (8.31, 11.57)
Exch. Mg^{2+}	$cmol_c/kg$	5.52 (5.04, 6.00)	7.51 (6.44, 8.59)	2.14 (1.89, 2.38)	1.98 (1.66, 2.30)
Exch. K^+	$cmol_c/kg$	1.76 (1.42, 2.10)	1.82 (1.67, 1.98)	0.95 (0.86, 1.04)	0.84 (0.70, 0.97)
∑Base Cations	$cmol_c/kg$	26.56 (24.26, 28.87)	37.97 (34.73, 41.21)	15.02 (12.72, 17.32)	12.82 (10.82, 14.82)
Ca^{2+}: Mg^{2+}	mol:mol	3.52 (3.23, 3.81)	4.07 (3.59, 4.54)	5.55 (4.98, 6.12)	5.09 (4.63, 5.56)
10-20 cm					
pH (H_2O)		5.78 (5.64, 5.92)	6.06 (5.99, 6.13)	6.21 (6.10, 6.32)	5.69 (5.55, 5.82)
Exch. P	mg/kg	73.8 (50.5, 97.2)	15.2 (10.1, 20.3)	108.1 (76.6, 139.6)	10.17 (7.29, 13.06)
Exch. Ca^{2+}	$cmol_c/kg$	13.78 (11.68, 15.87)	23.99 (21.15, 26.82)	8.94 (7.55, 10.32)	6.94 (5.62, 8.26)
Exch. Mg^{2+}	$cmol_c/kg$	4.72 (4.19, 5.24)	7.15 (5.99, 8.30)	1.77 (1.59, 1.95)	1.64 (1.38, 1.90)
Exch. K^+	$cmol_c/kg$	1.44 (1.12, 1.76)	1.54 (1.37, 1.71)	0.91 (0.79, 1.03)	0.68 (0.58, 0.78)
∑Base Cations	$cmol_c/kg$	20.09 (17.36, 22.82)	32.82 (29.04, 36.61)	11.69 (10.11, 13.27)	9.33 (7.76, 10.89)
Ca^{2+}: Mg^{2+}	mol:mol	2.92 (2.60, 3.25)	3.61 (3.14, 4.07)	5.07 (4.55, 5.58)	4.23 (3.69, 4.78)

Table B4. Mineral Soil Bulk Density and Nutrient Pools.

Soil property	Units	Site			
		703	704	726	733
0-10 cm					
Bulk density	g/cm^3	0.82 (0.71, 0.92)	0.77 (0.66, 0.88)	0.87 (0.76, 0.99)	0.98 (0.85, 1.11)
Total C	kg/m^2	3.85 (3.46, 4.25)	7.12 (6.17, 8.08)	6.43 (5.72, 7.15)	5.05 (4.33, 5.76)
Total N	kg/m^2	0.18 (0.16, 0.20)	0.36 (0.32, 0.39)	0.30 (0.27, 0.34)	0.24 (0.21, 0.27)
NH_4^+-N	g/m^2	0.24 (0.17, 0.32)	0.32 (0.24, 0.40)	0.42 (0.34, 0.50)	0.23 (0.15, 0.30)
NO_3^--N	g/m^2	0.12 (0.09, 0.14)	0.32 (0.25, 0.40)	0.19 (0.14, 0.23)	0.04 (0.03, 0.06)
Microbial C	g/m^2	24.1 (20.1, 28.1)	31.6 (28.1, 35.1)	33.4 (28.2, 38.6)	23.0 (20.0, 26.1)
Microbial N	g/m^2	3.7 (3.0, 4.4)	4.7 (4.1, 5.3)	5.9 (4.9, 7.0)	2.9 (2.5, 3.3)
Exch. P	g/m^2	8.4 (6.1, 10.8)	2.4 (1.5, 3.4)	5.3 (4.1, 6.5)	5.6 (3.7, 7.6)
Exch. Ca^{2+}	mg/m^2	180.0 (146.8, 213.3)	306.6 (242.1, 371.1)	308.4 (255.2, 361.6)	357.6 (305.1, 410.2)
Exch. Mg^{2+}	mg/m^2	21.1 (16.7, 25.5)	45.9 (38.2, 53.7)	40.3 (34.5, 46.2)	53.8 (46.5, 61.2)
Exch. K^+	mg/m^2	30.9 (23.4, 38.3)	40.9 (30.0, 51.8)	44.5 (35.8, 53.3)	54.3 (43.5, 65.1)
10-20 cm					
Bulk density	g/cm^3	1.60 (1.43, 1.77)	1.17 (1.05, 1.29)	1.57 (1.34, 1.80)	1.66 (1.52, 1.81)
Total C	kg/m^2	5.29 (4.61, 5.96)	6.41 (5.15, 7.67)	6.54 (5.19, 7.89)	5.04 (3.38, 6.69)
Total N	kg/m^2	0.26 (0.23, 0.30)	0.34 (0.29, 0.40)	0.34 (0.28, 0.40)	0.29 (0.21, 0.37)
NH_4^+-N	g/m^2	0.41 (0.29, 0.53)	0.37 (0.29, 0.46)	0.55 (0.46, 0.64)	0.25 (0.18, 0.31)
NO_3^--N	g/m^2	0.27 (0.23, 0.30)	0.35 (0.27, 0.43)	0.33 (0.27, 0.39)	0.13 (0.07, 0.19)
Microbial C	g/m^2	32.8 (26.7, 38.9)	23.7 (18.4, 29.0)	30.1 (34.9, 35.3)	23.2 (20.6, 25.7)
Microbial N	g/m^2	5.3 (4.5, 6.1)	4.2 (3.2, 5.2)	4.9 (3.9, 5.9)	3.1 (2.7, 3.5)
Exch. P	g/m^2	14.5 (10.7, 18.2)	3.8 (2.1, 5.5)	8.2 (5.5, 11.0)	9.8 (6.9, 12.8)
Exch. Ca^{2+}	mg/m^2	214.5 (173.0, 256.1)	324.4 (245.5, 403.3)	290.8 (218.3, 363.3)	464.0 (407.8, 520.3)
Exch. Mg^{2+}	mg/m^2	29.4 (23.1, 35.8)	56.9 (47.1, 66.6)	46.3 (38.9, 53.7)	87.9 (74.7, 101.1)
Exch. K^+	mg/m^2	51.7 (38.8, 64.6)	56.5 (38.9, 74.2)	49.6 (39.8, 59.3)	71.3 (60.0, 82.5)

Note: Values are means with 95 % confidence intervals in parentheses (n = 24).

Table B4, extended

Soil property	Units	Site			
		806	810	819	821
0-10 cm					
Bulk density	g/cm^3	0.70 (0.56, 0.83)	0.72 (0.58, 0.86)	0.73 (0.62, 0.85)	0.81 (0.70, 0.92)
Total C	kg/m^2	4.31 (3.55, 5.07)	4.28 (3.69, 4.88)	3.41 (2.74, 4.07)	4.10 (3.34, 4.85)
Total N	kg/m^2	0.19 (0.16, 0.23)	0.20 (0.18, 0.23)	0.13 (0.11, 0.16)	0.16 (0.14, 0.18)
NH_4^+-N	g/m^2	0.16 (0.13, 0.20)	0.25 (0.18, 0.32)	0.09 (0.06, 0.12)	0.19 (0.14, 0.25)
NO_3^--N	g/m^2	0.13 (0.11, 0.16)	0.20 (0.16, 0.24)	0.11 (0.10, 0.13)	0.15 (0.13, 0.17)
Microbial C	g/m^2	24.4 (19.9, 28.9)	22.8 (20.1, 25.6)	20.8 (17.4, 24.2)	34.7 (29.0, 40.4)
Microbial N	g/m^2	3.7 (3.0, 4.4)	3.6 (3.2, 4.0)	3.1 (2.6, 3.7)	4.6 (3.9, 5.4)
Exch. P	g/m^2	5.8 (4.1, 7.6)	1.0 (0.7, 1.2)	9.2 (6.5, 12.0)	1.5 (0.7, 2.3)
Exch. Ca^{2+}	mg/m^2	263.1 (213.4, 312.7)	411.1 (315.4, 506.8)	163.3 (127.7, 198.8)	167.8 (129.9, 205.6)
Exch. Mg^{2+}	mg/m^2	46.1 (37.7, 54.5)	70.9 (49.0, 92.8)	18.2 (14.7, 21.8)	20.5 (15.6, 25.3)
Exch. K^+	mg/m^2	48.9 (35.3, 65.5)	52.4 (40.7, 64.0)	26.1 (21.2, 31.1)	27.8 (21.0, 34.5)
10-20 cm					
Bulk density	g/cm^3	1.50 (1.35, 1.64)	1.30 (1.10, 1.49)	1.84 (1.63, 2.06)	1.86 (1.68, 2.04)
Total C	kg/m^2	6.72 (5.84, 7.60)	5.41 (4.84, 5.98)	6.47 (5.36, 7.59)	7.27 (6.41, 8.13)
Total N	kg/m^2	0.33 (0.29, 0.37)	0.30 (0.27, 0.34)	0.27 (0.22, 0.31)	0.31 (0.28, 0.34)
NH_4^+-N	g/m^2	0.36 (0.23, 0.49)	0.58 (0.38, 0.78)	0.17 (0.13, 0.21)	0.38 (0.23, 0.52)
NO_3^--N	g/m^2	0.27 (0.23, 0.29)	0.36 (0.28, 0.44)	0.29 (0.26, 0.33)	0.35 (0.31, 0.39)
Microbial C	g/m^2	40.0 (34.5, 45.5)	32.2 (27.3, 37.2)	39.3 (31.6, 47.0)	66.5 (60.0, 72.9)
Microbial N	g/m^2	6.0 (5.1, 6.9)	5.6 (4.8, 6.4)	6.4 (5.0, 7.8)	8.3 (7.4, 9.3)
Exch. P	g/m^2	10.6 (7.0, 14.1)	1.82 (1.16, 2.48)	20.4 (13.8, 27.1)	1.8 (1.3, 2.4)
Exch. Ca^{2+}	mg/m^2	398.1 (325.4, 470.9)	619.8 (491.6, 747.9)	329.2 (251.6, 406.8)	258.8 (204.5, 313.1)
Exch. Mg^{2+}	mg/m^2	82.5 (72.4, 92.6)	115.7 (84.2, 147.2)	39.7 (32.2, 47.2)	37.7 (30.5, 44.8)
Exch. K^+	mg/m^2	84.1 (63.6, 104.6)	77.0 (62.5, 91.5)	66.4 (51.8, 80.9)	49.3 (40.8, 57.7)