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ECOSYSTEMS

Coupled Nitrogen and Calcium Cycles in Forests of the Oregon Coast Range

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ABSTRACT

Nitrogen (N) is a critical limiting nutrient that regulates plant productivity and the cycling of other essential elements in forests. We measured foliar and soil nutrients in 22 young Douglas-fir stands in the Oregon Coast Range to examine patterns of nutrient availability across a gradient of N-poor to N-rich soils. N in surface mineral soil ranged from 0.15 to 1.05% N, and was positively related to a doubling of foliar N across sites. Foliar N in half of the sites exceeded 1.4% N, which is considered above the threshold of N-limitation in coastal Oregon Douglas-fir. Available nitrate increased five-fold across this gradient, whereas exchangeable magnesium (Mg) and calcium (Ca) in soils declined, suggesting that nitrate leaching influences base cation availability more than soil parent material across our sites. Natural abundance strontium isotopes ($^{87}Sr/^{86}Sr$) of a single site indicated that 97% of available base cations can originate from atmospheric inputs of marine aerosols, with negligible contributions from weathering. Low annual inputs of Ca relative to Douglas-fir growth requirements may explain why foliar Ca concentrations are highly sensitive to variations in soil Ca across our sites. Natural abundance calcium isotopes ($\delta^{44}Ca$) in exchangeable and acid leachable pools of surface soil measured at a single site showed 1 per mil depletion relative to deep soil, suggesting strong Ca recycling to meet tree demands. Overall, the biogeochemical response of these Douglas-fir forests to gradients in soil N is similar to changes associated with chronic N deposition in more polluted temperate regions, and raises the possibility that Ca may be deficient on excessively N-rich sites. We conclude that wide gradients in soil N can drive non-linear changes in base-cation biogeochemistry, particularly as forests cross a threshold from N-limitation to N-saturation. The most acute changes may occur in forests where base cations are derived principally from atmospheric inputs.

Key words: nitrogen cycle; N-saturation; base cations; calcium; magnesium; strontium; stable isotopes; atmospheric deposition; marine seasalt aerosols; nutrient limitation; Douglas-fir.

INTRODUCTION

Biogeochemical couplings between nitrogen (N) and calcium (Ca) are an important suite of interactions that impact the long-term health and stability of forest ecosystems. Where plant growth is limited by N availability, moderate increases in N supply can stimulate both plant growth and Ca uptake from soil. More dramatic increases in N supply can overcome N limitation, drive forests towards N saturation, and accelerate coupled

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leaching of N and Ca. In this way, long-term increases in N supply have a dual effect of stimulating plant Ca demands and depleting Ca from soils. These opposing drivers are thought to cause progressively non-linear N–Ca interactions along gradients of ecosystem N status, yet such processes rarely are represented in forest biogeochemical models (McNulty and others 1996; Asner and others 2001).

There is broad recognition that chronic N deposition is causing many temperate forests to cross a critical threshold from N-limitation to N-saturation, with serious implications for plant-soil Ca cycling (Aber and others 1998; McLaughlin and Wimmer 1999). At the same time that N supply has increased, atmospheric Ca inputs have decreased in many areas (Hedin and others 1994). Preferential depletion of Ca relative to other elements by forest harvest is also of particular concern, especially in N-rich areas (Federer and others 1989). These changes, combined with long-standing impacts from acid deposition, are modifying ecosystem Ca balances and creating Ca deficiencies over large areas of temperate forest (Shortle and Smith 1988; Lawrence and others 1997; Adams and others 2000; Huntington 2000; Driscoll and others 2001; Bailey and others 2004). It remains unclear from these studies, however, whether changes in ecosystem Ca cycling can be traced primarily to effects of excess N alone, and whether such changes will intensify as long-term N inputs increase site N status.

Forests of the Pacific Northwest are far less impacted by chronic N and other air pollutants than many other temperate regions. These ecosystems are often considered N-poor and base-rich (for example, Sollins and others 1980; Cole and Gessel 1992; Fenn and others 2003). However, high rates of N input can occur in forests of the Pacific Northwest via biological N fixation associated with red alder (100–200 kg N ha^{-1} y^{-1}, Binkley and others 1994). Fixed N contributes to exceptionally high soil N capital (up to 30,000 kg N ha^{-1}, Remillard 2000), and can accelerate N cycling, nitrification, and Ca leaching in a manner similar to chronic N pollution (Van Miegroet and Cole 1984). These factors are thought to predispose coastal Douglas-fir forests to intensification of an endemic fungal needle cast disease, resulting in 22–53% reductions in tree growth over the past decade, particularly on N-rich sites (Waring and others 2000; Maguire and others 2002; El-Hajj and others 2004).

Exceptionally wide gradients of soil N in the Pacific Northwest provide a unique opportunity to examine the long-term consequences of elevated N on forest biogeochemistry. We here use a range of Douglas-fir forests in the Oregon Coast Range to ask the following questions: Do variations in soil N status translate to changes in N availability for vegetation? How does base cation availability, in particular Ca and Mg, change across a wide gradient in soil N? Are N–Ca interactions linear or non-linear across variations in N status? At a single study site, we also use natural abundance $^{87}Sr/^{86}Sr$ stable isotope ratios to identify long-term ecosystem sources of base cations, and introduce the use of novel $^{44}Ca/^{40}Ca$ stable isotopes to evaluate pathways of Ca recycling in the plant-soil system.

METHODS

Site Description

We conducted this research in young Douglas-fir forests in the north-central Coast Range of Oregon. Results from two collections are reported: (1) foliar and soil nutrient concentrations across 22 sites spanning a gradient of soil N availability, and (2) strontium and calcium isotope analyses from a single stand with high N availability. All stands studied were established as plantations, and none have been fertilized. Climate across the study area is temperate and maritime, with wet cool winters, dry warm summers, and approximately 170 cm annual precipitation.

The 22 stands representing the N gradient were selected from a set being monitored to examine the effect of Swiss needle cast on Douglas-fir growth (Maguire and others 2002). Stands ranged from 11 to 25 years of age, and exhibited a range of needle longevity from 0.8 to 3.6 years (Table 1). Soils are derived from either sedimentary (that is, sandstones and siltstones) or basalt parent material, with Andic properties and silty to silty clay loam textures (NRCS, in press). Most study sites were relatively flat and located on broad upland topography, though a few sites may have received upland colluvial inputs. The stand sampled for strontium and calcium isotopes supported 45-year-old Douglas-fir along a ridgeline with sandstone-derived soils.

Sample Collection and Analysis

Samples of foliage and soil were collected across the N gradient in spring 2000. Sampling was based on five randomly selected target trees per site. Mineral soil (0–10 cm) at two locations within 5 m of each target tree was collected using a 2 cm diameter corer, and all samples were combined to yield one

Table 1. Site and Stand Characteristics of the Twenty-two Sites at the Time of Sampling in 2000

Site[†]	Soil suborder (USDA)*	Aspect	Elevation (m)	Slope (%)	Stand age (y)	Site index (m)	Mean needle age[¶] (y)	Standing volume (m^3/ha)	Annual increment[‡] (m^3 $ha^{-1}y^{-1}$)
Sedimentary									
Music road	Alic Hapludand	N	484	5	16	47	3.3	38	11.0
7	Andic Dystrudept	N	278	50	25	43	3.5	141	18.0
5	Andic Dystrudept	SW	322	55	23	40	3.0	176	23.7
77	Andic Dystrudept	W	235	10	22	45	3.0	221	25.9
58	Andic Dystrudept	E	80	15	17	45	3.1	102	22.1
85	Typic Fulvudand	SW	121	25	12	38	1.9	211	11.3
Juno Hill	Andic Dystrudept	S	86	10	18	36	1.1	61	4.5
16	Andic Dystrudept	SW	115	15	20	38	1.7	89	10.5
Smith Creek	Typic Fulvudand	S	167	20	17	34	1.9	77	16.3
39	Andic Dystrudept	S	23	10	21	45	1.8	123	16.3
Cloverdale	Typic Fulvudand	E	105	10	16	30	0.8	129	4.2
Basalt									
Steinburger	Andic Dystrudept	E	539	22	–	42	2.9	62	16.1
Jensen	Typic Palehumult	W	361	25	11	42	3.4	24	7.8
Hoag pass	Alic Hapludand	NW	755	20	12	30	3.6	27	
60	Typic Fulvudand	N	201	75	22	40	3.2	130	21.6
East Beaver	Typic Fulvudand	S	127	57	20	36	1.8	137	13.9
108	Alic Hapludand	W	269	40	16	42	2.9	98	16.7
Chopping block	Andic Dystrudept	W	76	5	19	35	1.7	88	8.4
Powerline road	Typic Fulvudand	NW	78	47	17	36	1.8	92	15.7
51	Typic Fulvudand	N	171	85	16	32	1.5	9	1.7
101	Typic Fulvudand	SW	262	15	24	31	1.8	31	3.3
119	Typic Fulvudand	S	366	30	18	13	0.9	2	0.5

[†] *Divided into sedimentary versus basalt soil parent material, ordered by increasing soil % N.*

**Provisional soil classifications based on ongoing revision of Tillamook and Benton County NRCS Soil Surveys.*

[¶] *Determined in 1999 from one branch in each third of the crown per tree, averaged over ten trees per site.*

[‡] *Average annual increment for the 4 year period 1998–2002, except for 2 year periods at Cloverdale (1995–1996) and Plot 108 (1998–1999).*

composite soil sample per site. The tip of the southmost branch in the fifth whorl of each tree was clipped off with a pole pruner, and all lateral 1999 shoots were clipped and combined into one composite foliage sample per site.

Soil and foliage samples were analyzed by the Central Analytical Laboratory at Oregon State University. Soil samples were sieved (2 mm) before analysis. Soil pH was determined in 1:2 mixture of soil:water, and a subsample of fresh soil was dried at 105°C for 48 h to determine moisture content. Available NH_4^+ and NO_3^- were assayed by extracting 20 g soil with 75 mL 2 M KCl for 1 h. Exchangeable Ca, Mg, and K were assayed by extracting 2 g soil with 40 mL of 1 N NH_4OAc. Available Bray-P was determined by extracting 2 g soil with 20 mL of 0.03 N NH_4F and 0.025 N HCl. All suspensions were filtered through Whatman 42 filters. Soil and foliage samples were dried at 80°C and ground to fine powder prior to total elemental analysis. Total C, N, and S in plant and soils were analyzed on a Leco-CNS 2000. Total elemental P, K, Ca, Fe, Mg, Mn, Cu, B, and Zn were determined by microwave digestion with HNO_3, followed by analysis on Perkin Elmer Optima 3000 DV ICP. NH_4^+, NO_3^-, and P in soil extracts were analyzed by Alpkem RFA 300 automated colorimetry.

The 45-year-old Douglas-fir stand was sampled in summer 2001 for natural abundance strontium and calcium isotopes in stemwood and soil. This stand was selected on the basis of displaying slow rates of stand growth determined as part of a regional tree growth survey (Maguire and others 2002). A single tree core taken to the pith at breast height (1.4 m) was dried and separated into 5 year growth increments using a dissecting scope. Samples were digested in 5 mL of concentrated Teflon-distilled HNO_3 for 24 h, followed by evaporation of HNO_3, treatment with concentrated HNO_3 and Ultrex H_2O_2 to remove organic compounds, redissolution in 3 mL of 2% HNO_3, and the final solution reserved for analysis. We collected litter and soil immediately beneath the target tree. Litter was collected to the surface of the mineral soil horizon. Mineral soil was collected incrementally to the depth of resistance using a 4 cm diameter corer (0–5, 5–10, 10–15, 15–25, 25–35, 35–45, 45–55, and 55–65 cm). These soils received a three-stage sequential treatment, yielding exchangeable, leachable, and digestible fractions (compare, Blum and others 2002; TD. Bullen and SW. Bailey, 2005). The exchangeable fraction was assayed by equilibrating 5 g of soil with 50 mL of 1 N NH_4OAc for 24 h. The leachable fraction was assayed by thoroughly rinsing 1 g of soil remaining from the exchange procedure with de-ionized water and combining with 10 mL of 1 N HNO_3 for 24 h at 30°C. The digestible fraction was determined by ashing at 650°C, digesting in a mixture of concentrated HF (5 mL) and HNO_3 (1 mL) at 30°C, evaporating, redissolving in 10 mL of 6 N HCl, and finally reevaporating and treating with HNO_3 and Ultrex H_2O_2 to eradicate organic compounds.

Solutions were analyzed for major and trace elements on a Perkin Elmer Elan 6000 inductively-coupled plasma mass spectrometer. All tree and soil samples were analyzed for Mg, Ca, Sr and Ba. Digestible fractions were analyzed for Nb, an immobile trace element used here to estimate the isotopic composition of weathered $^{87}Sr/^{86}Sr$. Sr and Ca were separated for isotopic analysis from sample digests using AG50X8 cation resin with 2 N HCl eluant. Prior to Ca purification, an aliquot of each sample sufficient to provide 750 ng of Ca was mixed with a calibrated ^{42}Ca–^{48}Ca double spike solution. The double spike allows correction for both instrumental mass discrimination and possible isotope fractionation associated with non-quantitative recovery during column chemistry. Both Sr and Ca isotopic compositions were measured on a Finnigan MAT 261 thermal-ionization mass spectrometer. Internal precision of $^{87}Sr/^{86}Sr$ measurements was ±0.00003 or better at the 95% confidence level (2σ). For the Ca isotope measurements, the double spike procedure allows $^{44}Ca/^{40}Ca$ to be determined with an internal precision of ±0.15‰ or better at the 2σ level. Here we report the Ca isotopes as $\delta^{44}Ca$, calculated as the per mil difference of $^{44}Ca/^{40}Ca$ in the sample from that of modern seawater. Seawater analyzed in our laboratory has $^{44}Ca/^{40}Ca$ of 0.021713. Further details of column chemistry, mass spectrometric techniques and data reduction procedures for the Ca isotope measurements are available elsewhere (Skulan and others 1997; Skulan and DePaolo 1999).

Calculations and Statistics

The $^{87}Sr/^{86}Sr$ isotopic composition of weathering was calculated by plotting $^{87}Sr/^{86}Sr$ of the digestible fraction in the two deepest soil samples against Nb/Sr, with weathered $^{87}Sr/^{86}Sr$ estimated by linear extrapolation to the Nb-free end-member (Bullen and others 1999). Relationships between nutrient concentrations in soils and foliage were examined using Pearson correlations with Bonferroni adjusted *P*-values. To illustrate graphically the response patterns for Ca and Mg in foliage and soil samples as a function of soil N, we also developed non-linear regressions of the general form $y = a + b/x$. However, we do not evaluate the statistical properties of these regressions, because low values of X in equations of this form correspond to a wide range of possible Y values, resulting in intrinsically poor fit between X and Y variables. All statistical tests were performed using SYSTAT 10.2 (SPSS, Chicago, IL), and were considered significant at $\alpha = 0.05$.

RESULTS

Soil Nutrients

Chemical properties of 0–10 cm mineral soil for 22 sites across the N gradient are listed in Table 2. Soil N ranged from 0.15 to 1.05% N across sites and correlated with soil C ($r = 0.96$). Extractable NH_4^+ and NO_3^- exhibited saturating log-normal relationships with soil N (Figure 1, bottom). Exchangeable calcium ($r = -0.53$) and magnesium ($r = -0.42$) displayed significant inverse variations with soil N (Figure 2, bottom). Total S and N in soils were positively correlated ($r = 0.95$). Soil N was negatively related to pH ($r = -0.73$) and available K ($r = -0.45$), and was unrelated to available P ($r = 0.04$).

There were no significant differences in pH, C, or soil nutrient concentrations between soils derived from basalt versus sedimentary parent materials (*t*-tests, $P = 0.12$ for pH, $P > 0.26$ for all nutrients, $n = 11$ for each parent material). Average soil C and N concentrations, C:N ratio, and pH were within 5% when comparing across parent material. Soils derived from basalt contained on average 63% more extractable Ca and Mg, and 72% more Bray-P, but none of these differences were significant.

Plant Nutrients

Nutrient concentrations in Douglas-fir foliage across the N gradient are listed in Table 3. Foliar N

Table 2. Soil Chemistry across 22 Douglas-fir Stands

Site	pH	C (%)	N (%)	S (%)	C:N	NH_4^+–N (µg/g)	NO_3^-–N (µg/g)	P (µg/g)	K (µg/g)	Ca (meq/100 g)	Mg (meq/100 g)
Sedimentary											
Music road	5.4	5.84	0.21	0.02	28	4.1	0.9	5	137	1.4	0.5
7	5.8	5.94	0.24	0.01	25	4.3	0.8	7	335	4.9	2.8
5	5.7	5.67	0.26	0.02	22	5.1	1.8	8	296	5.6	3.8
77	5.5	5.14	0.30	0.01	17	6.2	3.2	19	328	5.1	3.2
58	5.0	7.40	0.37	0.03	20	8.5	5.0	7	218	1.3	0.9
85	5.2	8.81	0.48	0.05	18	10.4	3.7	7	207	0.8	1.0
Juno Hill	4.5	7.31	0.51	0.04	14	4.6	11.5	4	133	0.4	0.4
16	4.8	8.85	0.56	0.05	16	8.9	4.7	9	285	0.9	1.0
Smith Creek	5.0	11.70	0.61	0.06	19	7.2	8.7	3	149	1.3	1.3
39	4.3	16.50	0.69	0.06	24	10.2	9.5	6	218	1.7	1.6
Cloverdale	4.8	14.60	0.76	0.08	19	7.1	6.8	10	140	0.5	0.7
Basalt											
Steinburger	5.6	3.80	0.15	0.01	25	4.0	0.7	5	192	2.7	1.3
Jensen	6.1	4.93	0.18	0.01	27	4.4	0.5	7	386	6.2	3.3
Hoag pass	5.5	4.52	0.18	0.01	25	3.8	0.7	34	188	2.4	1.0
60	5.6	4.72	0.25	0.02	19	4.8	4.4	5	125	10.4	10.0
East Beaver	5.4	4.77	0.30	0.03	16	6.5	3.7	15	261	3.9	3.6
108	5.6	7.36	0.39	0.02	19	5.1	4.6	7	250	8.4	4.8
Chopping block	5.0	7.93	0.48	0.06	17	7.8	8.2	13	140	1.3	1.1
Powerline road	4.9	9.86	0.52	0.07	19	5.4	9.9	6	137	1.1	0.8
51	5.0	10.60	0.66	0.07	16	9.0	10.3	28	179	0.8	1.0
101	4.7	19.30	1.05	0.09	18	13.4	9.9	20	133	0.6	0.4
119	5.0	18.70	1.05	0.11	18	6.9	6.7	6	152	1.3	0.7

ranged from 0.85 to 1.74% N across sites, and increased with soil N (Figure 1, top). Foliar C:N (average = 39, range = 30–61) was negatively related to soil N ($r = -0.78$). Significant correlations between foliar N and other nutrients were observed for Ca ($r = -0.67$), S ($r = 0.78$), Mn ($r = -0.60$), B ($r = -0.62$), and Zn ($r = -0.46$). Foliar Mg (Figure 2, top) and foliar P, K, Fe, Cu did not vary significantly with foliar N.

Strontium and Calcium Isotopes

Exchangeable $^{87}Sr/^{86}Sr$ in soil at the 45-year-old Douglas-fir site exhibited a narrow range of values (Figure 3). Exchangeable $^{87}Sr/^{86}Sr$ ranged from 0.7094 to 0.7096, with the exception of one value at 35–45 cm depth ($^{87}Sr/^{86}Sr = 0.7086$). $^{87}Sr/^{86}Sr$ of soil HF digests ranged from 0.7148 at the surface to 0.7165 at depth. Based on a plot of $^{87}Sr/^{86}Sr$ against Nb/Sr for HF digests of the two deepest samples, we calculate $^{87}Sr/^{86}Sr$ of weathering as 0.7217 (Bullen and others 1999). From two-end member mixing calculations that set atmospheric inputs to seawater values (0.7092) and set weathering to our calculated $^{87}Sr/^{86}Sr$ (0.7217), we estimate that exchangeable Sr to 65 cm depth originates almost exclusively (>97%) from atmospheric sources. A limited number of Ca isotope analyses show progressive depletion in $\delta^{44}Ca$ of exchangeable and leachable pools towards shallow soils, with values in 0–5 cm soil depth approximately 1‰ depleted relative to Ca in HF digested residue (Figure 4).

$^{87}Sr/^{86}Sr$ in Douglas-fir stemwood displayed a narrow range of values (range: 0.70923–0.70946, mean = 0.70934, $n = 8$) similar to soil exchangeable pools (Figure 5, triangles). Using Sr atmospheric and weathering end-members as above, we estimate that more than 99% of $^{87}Sr/^{86}Sr$ in wood is derived from atmospheric inputs over stand development (Figure 5). Ca/Sr of stemwood increases steadily from 48 to 121 over the growth history of the tree, compared to Ca/Sr equal to 120 for the exchangeable fraction of 0–5 cm soil, and Ca/Sr equal to 162 for current leaf litter. Sr/Ba of all stemwood age classes (mean = 0.33, range 0.27–0.38, $n = 8$) was similar to that of the exchangeable fraction of 0–5 cm soil (Sr/Ba = 0.34). Sr/Ba declined logarithmically ($r^2 = 0.93$, $P < 0.001$) in deeper soil samples to a value of 0.02 at 60 cm.

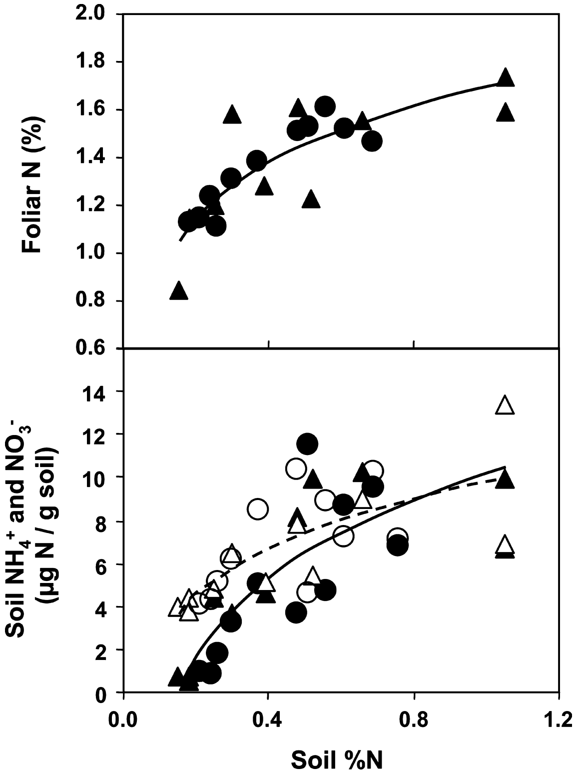

Figure 1. *Top Panel* Foliar N plotted against soil N in 0–10 cm mineral soil for 22 Douglas-fir forests. *Circles* indicate soils derived from sedimentary parent materials, *triangles* indicate basalt derived soils. *Line* includes all points, $y = 0.34 \ln(x) + 1.69$, $r^2 = 0.73$, $P < 0.001$. *Bottom Panel* Extractable NH_4^+ (*hollow symbols*) and NO_3^- (*solid symbols*) plotted against soil N. *Regression lines* include both bedrock types for $NH_4^+ = 3.3 \ln(x) + 9.7$ (*dashed line,* $r^2 = 0.55$, $P < 0.001$), and $NO_3^- = 5.3 \ln(x) + 10.1$ (*solid line,* $r^2 = 0.69$, $P < 0.001$).

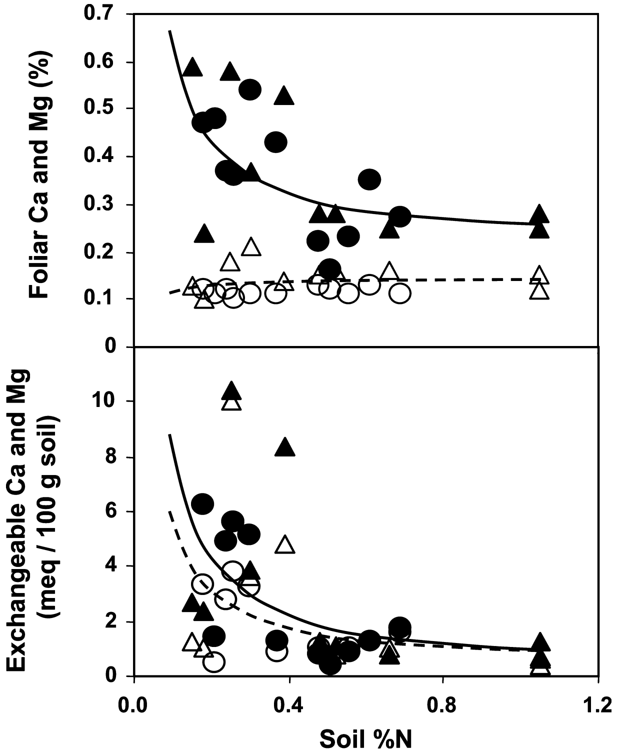

Figure 2. *Top Panel* Foliar Ca (*solid symbols*) and Mg (*hollow symbols*) plotted against soil N across 22 Douglas-fir forests. *Circles* indicate soils derived from sedimentary parent materials, *triangles* indicate basalt derived soils. *Bottom Panel* Soil exchangeable Ca and Mg, symbols as above. For both panels, we show *regression lines* of the general form $y = a + b/x$ to illustrate response patterns. Significant Pearson's correlations ($P < 0.05$) with soil N are calculated for foliar Ca ($r = -0.61$), soil Ca ($r = -0.53$), and soil Mg ($r = -0.42$).

DISCUSSION

Gradient of Nitrogen Biogeochemistry

We found an approximately ten fold gradient in surface soil N concentrations across the Oregon Coast Range, ranging from low values (0.15% N) typical of N-poor temperate forests to very high values (1.05% N) characteristic of N-rich tropical forests. Soil inorganic N ($NH_4^+ + NO_3^-$) and foliar N increased markedly across this soil N gradient, consistent with a positive feedback cycle of plant nutrient use that reinforces local patterns of nutrient availability (Vitousek 1982; Prescott and others 2000). Foliar N in half of the sites exceeded 1.4% N, which is considered above the threshold of N-limitation in coastal Oregon Douglas-fir (Hopmans and Chappell 1994). This suggests that positive reinforcement of plant-soil N cycling feedbacks can persist beyond the point at which N is no longer limiting. However, this feedback does not continue indefinitely to create a "runaway" N cycle, as indicated by the asymptotic behavior of both foliar and soil inorganic N in very N-rich sites (Figure 1). Selection against luxury N uptake in plants to minimize herbivore and pathogen risks (Chapin and others 2002), or acceleration of N losses to limit inorganic N accumulation in soils (Perakis 2002; Perakis and others 2005), may constrain plant-soil feedbacks when N is not limiting.

Coupled leaching losses of NO_3^- and base cations are likely to explain the inverse relationship we observed between soil N and exchangeable Ca and Mg in soils (Figure 2). This conclusion is supported by watershed-level patterns of nutrient export across our study area. NO_3^- dominates anion fluxes in most Coast Range streams, and is closely correlated with Ca and Mg levels, which together account for more than 75% of total cation export in

Table 3. Foliar Chemistry across 22 Douglas-fir Stands

Site	C (%)	N (%)	S (%)	C:N	P (%)	K (%)	Ca (%)	Mg (%)	Mn (µg/g)	Fe (µg/g)	Cu (µg/g)	B (µg/g)	Zn (µg/g)
Sedimentary													
Music road	51.60	1.15	0.10	45	0.18	0.49	0.48	0.11	423	66	4	21	16
7	52.10	1.24	0.10	42	0.20	0.58	0.37	0.12	478	54	5	20	17
5	52.30	1.11	0.08	47	0.11	0.59	0.36	0.10	129	43	15	11	16
77	51.00	1.31	0.10	39	0.15	0.48	0.54	0.11	351	334	5	15	15
58	52.00	1.38	0.10	38	0.14	0.67	0.43	0.11	289	102	5	17	15
85	52.90	1.51	0.11	35	0.16	0.73	0.22	0.13	142	241	5	15	13
Juno Hill	53.30	1.53	0.11	35	0.14	0.57	0.16	0.12	226	79	4	14	12
16	52.70	1.61	0.11	33	0.14	0.73	0.23	0.11	197	384	5	13	13
Smith Creek	52.10	1.52	0.11	34	0.18	0.58	0.35	0.13	274	125	5	15	13
39	52.30	1.46	0.11	36	0.14	0.73	0.27	0.11	548	77	6	18	16
Cloverdale	53.10	1.59	0.12	33	0.13	0.52	0.17	0.17	328	79	5	10	16
Basalt													
Steinburger	51.50	0.85	0.09	61	0.23	0.65	0.59	0.13	810	62	4	23	16
Jensen	51.60	1.13	0.11	46	0.12	0.54	0.47	0.12	682	88	3	19	19
Hoag pass	51.20	1.15	0.09	45	0.21	0.48	0.24	0.10	382	68	3	11	13
60	52.00	1.20	0.10	43	0.14	0.49	0.58	0.18	215	83	4	11	11
East Beaver	52.80	1.58	0.11	33	0.19	0.67	0.37	0.21	168	112	4	11	11
108	51.60	1.28	0.10	40	0.20	0.77	0.53	0.14	211	428	6	16	16
Chopping block	53.40	1.61	0.11	33	0.17	0.66	0.28	0.15	118	284	5	12	13
Powerline road	52.10	1.23	0.10	42	0.14	0.64	0.28	0.16	202	134	4	15	14
51	53.30	1.55	0.11	34	0.20	0.73	0.25	0.16	202	219	5	13	13
101	53.70	1.59	0.10	34	0.17	0.54	0.25	0.15	190	120	4	11	14
119	52.70	1.74	0.12	30	0.15	0.41	0.28	0.12	248	64	4	7	14

excess of marine seasalt inputs (Compton and others 2003). The strong inverse relationship that we observed between soil N and base cations was surprisingly robust to variations in soil parent material across the study area, which raises the possibility that excess NO_3^- leaching – not geology – is a primary control of surface soil Ca and Mg in these forests.

How do such wide gradients in soil N develop in a region of low N deposition? Large areas of the Oregon Coast Range that currently support conifer forests, including our study area, were dominated historically by the N-fixing tree red alder (*Alnus rubra*) (RSH. Kennedy and TA. Spies, 2005). This aggressive pioneer can fix 150 kg N ha^{-1} y^{-1} for many years before succession to more shade-tolerant conifers (Binkley and others 1994). Prior to European settlement in the 1800's, stand replacing fires occurred at an average return interval of 200 years (Long and others 1998), and were the most likely control over red alder distribution across the landscape. Variation in the extent and intensity of Coast Range fires could thus shape local N balances by controlling both the distribution of red alder N-fixation, as well as fire induced N-losses from organic N combustion.

Atmospheric Constraints on Calcium Availability

$^{87}Sr/^{86}Sr$ ratios provide insight into long-term sources of base cations for forest ecosystems, particularly Ca (Capo and others 1998). Using $^{87}Sr/^{86}Sr$ ratios measured at a single study site, we found that more than 97% of base cations in plants and soil could be traced to atmospheric inputs of marine sea-salt aerosols (Figures 3,5). Atmospheric deposition dominates ecosystem Sr pools in other humid tropical and temperate coastal forests (Kennnedy and others 1998, 2002; Poszwa and others 2002), yet we were surprised to reproduce this result in the Oregon Coast Range, which is considered geologically dynamic, with active soil turnover by uplift, erosion, and landslides (Lancaster and others 2001). In addition, high watershed fluxes of base cations to streams suggest ample supplies of weatherable minerals in soils (Compton and others 2003). On the other hand, the old age of Coast Range parent materials (>30 m.y.b.p.) creates opportunities for long-term weathering and local depletion of surface soil minerals, particularly on sites with low potential for erosion or colluvial inputs, where soils can be

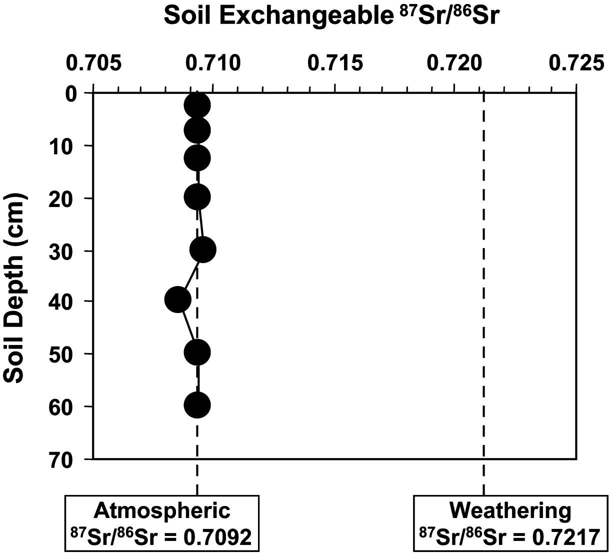

Figure 3. Strontium isotope ($^{87}Sr/^{86}Sr$) composition of exchangeable soil pools to 65 cm depth in a 45-year-old Douglas-fir forest. *Dashed lines* indicate expected Sr isotope composition of atmospheric versus weathering inputs, as described in text.

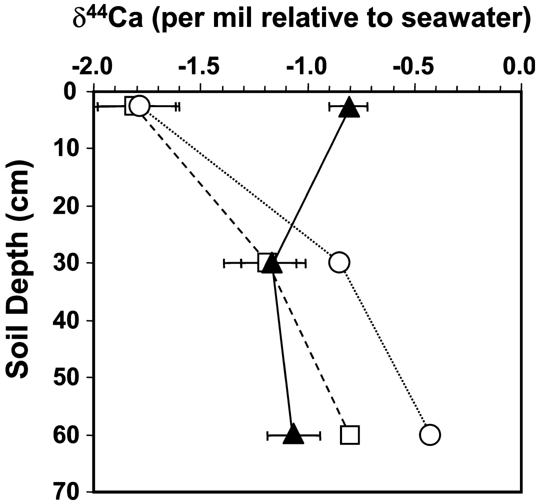

Figure 4. Calcium isotopes reported as δ^{44}Ca relative to seawater in soil pools from three depths, same site as Figure 3. Squares denote NH_4OAc fraction, circles denote HNO_3 leachable fraction, and triangles denote residual HF digest fraction. The standard error of two laboratory replicates is shown for all samples. *Error bars* are smaller than symbols when not visible.

several meters deep atop a thick (>5 m) mantle of weathered sandstone (Anderson and Dietrich 2001; Heimsath and others 2001). The ridgeline where our study site was sampled for Sr isotopes may represent a stable landform with greater depletion of weatherable minerals relative to lower slope positions. We expect that a broader survey of sites and landscape positions might reveal a range of atmospheric versus weathering source contributions of Sr (for example, Vitousek and others 2003). Nevertheless, the narrow range of Sr isotope values that we measured in vegetation and soils (range = 0.7092–0.7096, with a single value 0.7086) so closely resembles seawater sources of marine aerosols (0.7092) that we are confident of a dominant role for atmospheric inputs in supplying base cations to our sample site.

$^{87}Sr/^{86}Sr$ ratios preserved in Douglas-fir stemwood provide a retrospective record of Sr sources to vegetation, and confirm an important long-term role for atmospheric inputs. $^{87}Sr/^{86}Sr$ in 5-year radial increments of our sample tree indicates consistent reliance (99–100%) on marine aerosol Sr throughout 45 years of growth (Figure 5). A progressive increase in Ca/Sr of stemwood over this same period, plus elevated Ca/Sr in leaf litter, are consistent with preferential biological cycling of Ca relative to Sr (Poszwa and others 2000, 2002; Watmough and Dillon 2003), particularly because a large fraction of annual Ca uptake by trees occurs through recycled nutrients from detritus. Alternative explanations for directional changes in Ca/Sr ratios, such as shifts in tree foraging among different soil minerals (Blum and others 2002) or depths (Poszwa and others 2002) over time, are unlikely given constant Sr/Ba ratios recorded in stemwood over this same period (data not shown). Overall, the remarkable similarity between $^{87}Sr/^{86}Sr$ in marine aerosols (0.7092), stemwood (0.7093), and depth-integrated soil (0.7094) suggests strong reliance on a pool of accumulated atmospheric Sr, and by inference Ca.

Our data suggests that Ca is far more susceptible than Mg to depletion at high soil N. Both exchangeable Ca and Mg declined at high soil N, yet only foliar Ca tracked these changes (Figure 2). Foliar and soil base cations across sites were closely correlated for Ca ($r = 0.73$, $P < 0.001$), but not for Mg ($r = 0.32$, $P = 0.86$). Foliar Ca concentrations were at the low-end of values reported for field grown Douglas-fir in the Pacific Northwest, whereas foliar Mg was well within regional averages (Walker and Gessel 1991). Ratios of Ca:Mg in foliage from our sites declined from 5:1 to 1:1 as soil N increased, yet ratios less than 2 are extremely uncommon regionally (calculated from Walker and Gessel 1991). Ca–Mg antagonism cannot explain the pattern of declining foliar Ca at high N, because both elements were present at similar concentrations in exchangeable soil pools.

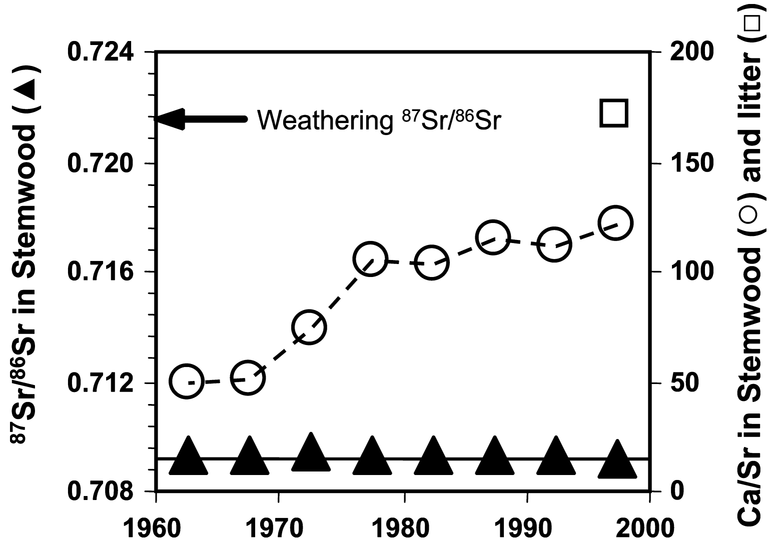

Figure 5. Strontium isotopes (*triangles*) and Ca/Sr ratios (*circles*) in 5-year annual increments of stemwood of a 45 year-old Douglas-fir, same site as Figure 3. *Square* denotes Ca/Sr ratio of litter. *Solid line* is atmospheric end-member, set to $^{87}Sr/^{86}Sr$ of sea water (0.7092). *Arrow* indicates calculated $^{87}Sr/^{86}Sr$ weathering end-member (see text for details).

Disparities in rates of atmospheric deposition relative to plant demands may explain why foliar Ca is more sensitive than foliar Mg to patterns of availability in soil. We compared annual Ca and Mg inputs from wet deposition (NADP Site OR02, average of 1983–2002 data, http://nadp.sws.uiuc.edu) plus cloud deposition (Weathers and others 1988) against net annual demands for bole and branch construction in coastal Oregon Douglas-fir (Binkley and others 1992). We estimate that Mg deposition (2.1 kg ha^{-1} y^{-1}) can supply 300% of Mg uptake by growing Douglas-fir (0.7 kg ha^{-1} y^{-1}). In contrast, Ca deposition (1.6 kg ha^{-1} y^{-1}) can supply only about 12% of plant demands (Table 4). Consequently, trees must derive a significant fraction of annual Ca demands from soil reserves, which accounts for the close dependency of foliar Ca on available soil Ca across our study sites (Figure 2). Given the low rate of atmospheric Ca input relative to annual plant demands, efficient long-term retention and recycling of Ca between plants and soils is needed to support the high rates of primary productivity that are characteristic of this region.

Ca retention in these forests may be promoted by recycling through sparingly soluble Ca-oxalate precipitates. The pool of Ca-oxalate in Coast Range soils is roughly equivalent to exchangeable Ca (Cromack and others 1979), and a host of soil invertebrates facilitate Ca-oxalate turnover to available forms (Cromack and others 1977). Oxalate levels are typically highest in surface soils of forests (Certini and others 2000) coincident with oxalate production by roots and fungi. Ionic Ca bonding (such as occurs with Ca-oxalate) yields characteristically depleted δ^{44}Ca (<1–3‰) relative to source pools, yet dissolution of solid phase Ca does not exhibit fractionation (Skulan and DePaolo 1999; Gussone and others 2003). We expect that our nitric acid leaching procedure would dissolve Ca bound by oxalate and other organic compounds, and we observed 1‰ δ^{44}Ca fractionation in both acid leachable and exchangeable pools relative to HF-digests at the soil surface. Such fractionation is consistent with the idea that depleted δ^{44}Ca may have cycled through oxalate to exchangeable pools in surface soils (Figure 4). The enhanced solubility of Ca-oxalate at low pH has been invoked to explain long-term increases in Ca export following harvest of northern hardwood forests (Bailey and others 2003). We consider that increased nitrification and lower pH that characterize N-rich soils (Table 2) may liberate oxalate bound Ca in similar fashion, resulting in the potential for enhanced uptake by plants or accelerated loss via coupled NO_3^- and Ca leaching.

Implications for Management of Coastal Douglas-fir Forests

Highly productive coastal Douglas-fir forests of the Pacific Northwest are capable of storing more C (Mg/ha) than any other biome, anywhere on Earth (Smithwick and others 2002). High soil N availability is at least partially responsible for such high productivity, and N is so abundant that fully one-third of coastal Douglas-fir forests are not N-limited (Peterson and Hazard 1990). Foliar N can be used to identify Douglas-fir stands that are unlikely to respond to N fertilization (Hopmans and Chappell 1994), yet N fertilization and interplanting with N_2-fixing red alder remain common practices across

Table 4. Estimated Ca Fluxes and Long-term Supply under Stemwood-only and Whole-tree Harvest

Calcium pool or flux	Stemwood harvest	Whole-tree harvest
Total Inputs (kg / ha-y)	1.55	1.55
Wet deposition[*]	0.9	0.9
Cloud deposition[¢]	0.6	0.6
Weathering[ω]	0.05	0.05
Net Uptake and Harvest Removal (kg / ha-y[†])	−3.2	−13.8
Stemwood only	−3.2	−3.2
Branches, twigs, and foliage	–	−10.6
Net Annual balance (kg / ha-y)	−1.65	−12.25
Soil Ca reserves (kg / ha)[§]	663	663
Years of available Ca supply[‡]	402	54

[*] *Average wet deposition recorded at NADP-OR2 for the period 1980–2002.*

[¢] *Cloudwater concentrations from Weathers and others 1988, assuming 50 cm/y fog inputs.*

[ω] *Plant-available weathering, set to 3% of total Ca inputs, inferred from* ^{87}*Sr/*^{86}*Sr in Figure 3.*

[†] *Data from Binkley and others 1992. Negative sign denotes eventual Ca removal by harvest.*

[§] *This study, exchangeable Ca 0–65 cm depth.*

[‡] *Soil Ca reserves divided by annual losses. Assumes zero Ca leaching loss and storage in non-harvestable pools. Inclusion of these terms would further diminish Ca supply.*

the region, intended to increase forest productivity. However, excessive N additions to N-rich forests have the potential to create nutritional imbalances in vegetation, accelerate greenhouse gas (for example, CH_4, N_2O) emissions from soils, and impair downstream water quality (Vitousek and others 1997). In Oregon Coast Range forests, excess N has been implicated in the intensification of Swiss needle cast, an endemic fungal disease that impairs stomatal conductance and reduces Douglas-fir productivity by 22–53% (Waring and others 2000; Maguire and others 2002; El-Hajj and others 2004). There is great potential to use remote sensing of foliar and ecosystem N status (for example, Ollinger and others 2002) as a way to identify N sufficient stands in the Oregon Coast Range, thus maximizing returns on fertilization while minimize deleterious impacts associated with excess N.

Rates of nutrient supply from atmospheric deposition and weathering are an important constraint on the long-term sustainability of managed forests. We estimate in Table 4 the number of years of Ca supply that are available to support Douglas-fir growth under two harvest scenarios for conditions when atmospheric inputs dominate over weathering as a nutrient source. Under stemwood-only harvest in which leaves and branches are left on site, we estimate sufficient Ca is available for approximately 400 years of tree growth. Under whole-tree harvest, we estimate only about 50 years of Ca supply for tree growth. We expect that real-world harvest operations would remove Ca at an intermediate rate due to piling and burning of logging slash. We emphasize that our calculations rest on the assumption that 97% of plant-available Ca is derived from atmospheric inputs, as occurred in the site we sampled for Sr isotopes (Figures 3, 5). Although limited in scope, these results support earlier speculation that weathering may be insufficient to support long-term Ca demands of intensive forest harvest in the Oregon Coast Range (Bockheim and Langley-Turnbaugh 1997).

Whereas the majority of Coast Range forests are managed by private landowners for timber production, many federally owned forests are managed primarily for the provision and restoration of old-growth characteristics within Late-Successional Reserves. Dense young stands of Douglas-fir currently dominate Late-Successional Reserves, yet Douglas-fir requires approximately 275 years (range = 200–350 years) to develop old-growth characteristics (Franklin and others 2002). Thinning of young dense stands to levels that are typical of unmanaged forests (for example, Tappeiner and others 1997) is being implemented widely in the Pacific Northwest as one way to accelerate restoration of old-growth forests. Typically, thinned stems are removed and sold to cover the cost of thinning operations. On excessively N-rich sites, leaving felled stems onsite could provide benefits by providing a high C:N substrate for N immobilization, thus reducing nitrate leaching and mitigating the potentially deleterious impacts of further ecosystem Ca loss. Remedial lime additions can also restore Ca pools and increase tree growth in young stands (M. Gourley, Starker Forest Products, personal communication), and approaches that promote tree species capable of enhancing Ca cycling (for example, western red cedar and big leaf maple; Tarrant and Issac 1951; Kiilsgaard and others 1987;

Fried and others 1990) may provide a more sustainable long-term alternative to fertilization. On sites that are N-rich and Ca-poor (for example, Figure 2), we suggests that fire may also benefit site nutrient balances by promoting N loss through combustion, while returning Ca and other mineral nutrients to soils in ash. These benefits may not be fully realized in areas where N-fixing red-alder is permitted to reestablish following fire.

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