AN ABSTRACT OF THE THESIS OF

Emily R. Sinkhorn for the degree of Master of Science in Forest Science presented on September 18, 2007.
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Abstract approved:

Steven S. Perakis

Understanding how N availability influences base cation stores is critical for long-term ecosystem sustainability. Indices of nitrogen (N) availability and the distribution of nutrients in plant biomass, soil, and soil water were examined across ten young, unpolluted Douglas-fir (*Pseudotsuga menziesii*) stands in the Oregon Coast Range spanning a three-fold soil N gradient (0-10 cm: 0.21 – 0.69% N, 0-100 cm: 9.2 – 28.8 Mg N · ha^{-1}) but having similar stand age and sandstone parent material. δ^{15}N in foliage and forest floor increased across the gradient and approached the isotopic signature of the atmosphere at high soil N stands, suggesting that variation in N accumulation across sites is related to historic site occupancy by N_2-fixing red alder (*Alnus rubra*). Although no longer present on these sites, red alder stands can add 100-200 kg N ha^{-1} yr^{-1} to an ecosystem for decades, a significantly higher N input than precipitation (0.65 kg N ha^{-1} yr^{-1}). Annual net N mineralization and litterfall N return displayed non-linear relationships with soil N, increasing initially, and then decreasing at more N-rich sites. In contrast, nitrate leaching from deep soils increased linearly across the soil

N gradient and ranged from 0.074 to 30 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1}. Nitrogen availability was negatively correlated with indices of Ca availability. Soil exchangeable Ca, Mg, and K pools to 1 m depth were negatively related to nitrate losses across sites. Calcium was the only base cation that decreased in both plant and soil pools across the soil N gradient, and a greater proportion of total available ecosystem Ca was sequestered in plant biomass at high N, low Ca sites. The preferential storage of Ca in aboveground biomass at high N and low Ca sites, while critical for sustaining plant productivity, may also predispose forests to Ca depletion in areas managed for intensive biomass removal. Our work supports a hierarchical model of coupled N-Ca cycles across gradients of soil N enrichment, with microbial production of mobile nitrate leading to depletion of readily available Ca at the ecosystem scale, and plant sequestration promoting Ca conservation as Ca supply diminishes. Long-term N enrichment of temperate forest soils appears capable of sustaining an open N cycle and key symptoms of N saturation for multiple decades after the cessation of elevated N inputs.

Non-Linear Nitrogen Dynamics and Calcium Depletion along a Temperate Forest Soil Nitrogen Gradient

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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.

Emily R. Sinkhorn, Author

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Non-Linear Nitrogen Dynamics and Calcium Depletion along a Temperate Forest Soil Nitrogen Gradient

CHAPTER 1: INTRODUCTION

Nitrogen (N) is a critical, limiting nutrient in many temperate forests (Vitousek and Howarth 1991) and has a strong influence on the productivity and community composition of plants and microbes (Pastor et al. 1984, DeForest et al. 2004), decomposition rates (Swanston et al. 2004), and cycling of other nutrients (Perakis et al. 2006, Gilliam et al. 2005). However, excessive N availability can have significant negative effects on ecosystems, including reduced plant productivity (Aber et al. 1989), elevated nitrate leaching (Tietema et al. 1998, Pregitzer et al. 2004), soil acidification (Reuss and Johnson 1986), and base cation depletion (Federer et al. 1989). Initially, plant and microbial communities may respond positively to increased N availability (Binkley and Högberg 1997) but may subsequently become limited by other nutrients (Sinsabaugh et al 1993) or hindered by high concentrations of N (Fog 1988). The N saturation concept, in which N availability exceeds plant and microbial demands (Aber et al. 1989), was developed considering the heavily N-polluted regions of the eastern US and Europe; however, its predictions have rarely been considered for ecosystems with naturally elevated soil N accumulation.

Base cation depletion in forested ecosystems, and that of calcium (Ca) in particular, has been a concern in recent decades as a consequence of both forest harvest (Federer et al. 1989) and N saturation (Aber et al. 1989). Accelerated N cycling resulting from excessive N availability may increase Ca mobilization in soil solution (Gilliam et al. 2005, Homann et al. 1994). When leaching losses are especially intense and/or prolonged, foliar nutrient imbalances and Ca deficiency can occur (McNulty et al. 1996, Schaberg et al. 1997, McLaughlin et al. 1991). However, studies of potential Ca depletion have been limited to relatively short-term increases in N supply by N deposition (Reuss and Johnson 1986, Gilliam et al. 2005), N fertilization (Currie et al. 1999), and biological N fixation (Homann et al. 1994). Additionally, few studies have examined whether reducing the source of N inputs to forest ecosystems ameliorates N saturation or if symptoms of N saturation may persist on account of long-term excessive soil N accumulation.

Biogeochemical couplings between N and base cations hinge on the microbially-mediated process of nitrification. Hydrogen ions (H^+) produced during nitrification can displace base cations from exchange sites, and base cations can subsequently leach with nitrate, the mobile anion product of nitrification, through ionic charge balance (Reuss and Johnson 1986). However, this depletion can also be balanced by the stimulation of bedrock weathering, improving ecosystem base cation availability. Plant and microbial demand for nitrate and the presence of other acid anions in solution will thus dictate potential base cation leaching losses. The balance of these complex interactions has not been fully explored in the context of a broad range of soil N availability.

Ca is rarely a limiting nutrient in temperate ecosystems, as inputs of Ca from atmospheric deposition and weathering generally exceed plant nutrient demands on an annual basis (Likens et al. 1967, Sollins et al. 1980, Trettin et al. 1999). Ca is essential for regulating physiological processes related to growth and stress response (McLaughlin and Wimmer 1999) and for strengthening cell walls and regulating membrane permeability (Marschner 2002). Plants are unable to exert direct, physiological control to conserve Ca, as Ca cannot be retranslocated from senescing foliage (McLaughlin and Wimmer 1999). Yet, some species are able to effectively sequester Ca in biomass after stand replacing disturbance and reduce leaching losses (Marks 1997). Although ecosystems have been noted to conserve Ca as stores of Ca decline (Huntington 2000), the mechanisms of this biotic conservation are not well understood.

Although not frequently applied, Ca fertilization may be able to improve stand productivity in areas of local Ca depletion. Many Ca fertilization studies have occurred in hardwood forests of the northeastern US where chronic acid-deposition has depleted soil Ca reserves. Ca fertilization of sugar maple led to increased survivorship, foliar Ca concentrations, and mycorrhizal colonization of seedlings (Juice et al. 2006). Additionally, different species within a community can be limited by either N or Ca (Bigelow and Canham 2007). Even in the Oregon Coast Range, Ca fertilization of N-rich Douglas-fir stands may be able to improve growth (Sinkhorn *personal observation*, unpublished study by Mark Gourley, Starker Forests, Inc). Ca fertilization may also be complicated with the often resultant increase in soil pH which can reduce the propensity for H^+ replacement of Ca on the exchange complex and decrease aluminum antagonism (Wilmot et al. 1996). Considering plant Ca content in forest nutrition analyses may aid in determining if Ca fertilization could improve stand health.

Although the Pacific Northwest overall has been far less impacted by chronic N deposition than many other temperate forest regions (Vanderbilt et al. 2003, Fenn et al. 2003), biological N_2-fixation associated with red alder can supply up to 200 kg $N \cdot ha^{-1} \cdot yr^{-1}$ into an ecosystem, and is particularly common throughout the Coast Range (Binkley et al. 1994). Red alder colonization often follows disturbance (Harrington et al. 1994) and can accelerate soil N enrichment (Binkley et al. 1992a, Tarrant et al. 1969, Cole et al. 1990), nitrification and soil acidification (Van Miegroet and Cole 1985), and nitrate and base cation leaching (Cole et al. 1990, Homann et al. 1994). After removal of overstory red alder and planting of Douglas-fir, exchangeable base cations may remain depleted even after nitrate leaching has decreased (Cole et al. 1990). Although speculative, historical patterns in red alder colonization could be responsible for the mosaic of soil N content seen in the Coast Range (Perakis et al. 2006). Less is known whether excessive soil N accumulation through N_2-fixation may lead to N saturation as seen in areas of chronic N deposition.

Forest fertilization in the Coast Range is often limited to N additions, and N fertilizers are applied to approximately 50,000 hectares in Oregon and Washington every year (Chappell et al. 1992). However, N appears to be naturally abundant in many parts of the Oregon Coast Range as nearly one third of forests do not respond to N fertilization (Peterson and Hazard 1990, Chappell et al. 1992). N fertilization in the range of 1,000 kg $N \cdot ha^{-1}$ does not seem to affect net N mineralization rates (Chappell et al. 2000); however, it remains unclear if naturally broad ranges in soil N capital may influence N cycling rates and associated base cation availability.

Gradient studies have often been utilized to identify the influence of a particular nutrient or climatic condition on ecosystem processes. Natural gradients provide a means to address long-term effects of the particular variable in question, as experimental manipulation may not address the appropriate time scales of nutrient interactions (Vitousek 2004). Additionally, in consideration of N gradients, the amount of N typically applied in forest fertilizations (200 - 1,000 kg $N \cdot ha^{-1}$) does not span the natural variation of soil N present in the Pacific Northwest (Prescott et al. 2000, Remillard 1999). Unfortunately, gradients can be confounded by variation in other controlling factors (Austin and Vitousek 1998); as many N availability gradients have been constructed across a shift in tree species composition (Pastor et al. 1984, Reich et al. 1997). Previous N gradient work in coastal Northwest Douglas-fir forest have found increasing litterfall inputs (Prescott et al. 2000) and decreasing foliar and soil exchangeable Ca (Perakis et al. 2006) with increasing soil N. Less is known whether extremely broad variations in soil N availability can influence the openness of the N cycle and the distribution of base cations within an ecosystem.

The impetus for this thesis stemmed from the identification of a wide surface soil N gradient in the Coast Range across which foliar and surface soil exchangeable Ca declined (Perakis et al. 2006). The objectives of this thesis were to thoroughly examine ecosystem N and base cation pools, N cycling rates and isotopic signatures, and N-Ca biogeochemical couplings across a wide gradient in soil N in ten young, unpolluted Douglas-fir plantations of the central Oregon Coast Range. Chapter 2 addresses how soil and plant N pools vary across the sites, the possible causes of the wide variation in soil N pools, whether N cycling rates respond linearly to increases in soil N availability, and if N leaching corresponds with an acceleration of N cycling. Chapter 2 also compares N dynamics across this gradient to predictions from N saturation theory (Aber et al. 1989) as a way to evaluate the generality of forest responses to long-term N enrichment. Chapter 3 examines the dynamics and distribution of base cations, particular Ca, in the ecosystem, whether base cation leaching is associated with nitrate loss, if exchangeable base cation pools are related to N availability, and how plants may respond to variations in base cation availability. Answers to these questions regarding potential couplings between N and Ca are of fundamental importance for understanding biogeochemical controls over the functioning of forests along N availability gradients, and have broader implications for forest management strategies seeking to recognize site fertility and maximize stand productivity and long-term sustainability.

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CHAPTER 2:
DEVELOPMENT AND DYNAMICS OF A BROAD TEMPERATE FOREST SOIL NITROGEN GRADIENT

Abstract

Indices of nitrogen (N) availability and the distribution of N in plant biomass, soil, and soil water were examined across ten Douglas-fir (*Pseudotsuga menziesii*) stands in the Oregon Coast Range. These sites span a wide gradient in soil N capital (9.2 – 28.7 Mg N $\cdot$ ha^{-1}) but have similar stand age and sandstone parent material. δ^{15}N in foliage and forest floor increased across the gradient and approached the isotopic signature of the atmosphere at high soil N stands, suggesting that variation in N accumulation across sites is related to historic site occupancy by N_2-fixing red alder (*Alnus rubra*). Net N mineralization increased with soil N up to 0.5% N, but then decreased at higher N levels. Litterfall N return displayed a similar non-linear relationship with soil N. Plants responded directly to the amount of N mineralized in mineral soil, as annual plant production and foliar N concentration increased linearly with net N mineralization. Nitrification as a percent of net N mineralization increased from 1 – 99% across the gradient, and annual leaching losses of nitrate-N from deep soils ranged from 0.074 to 30 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1}. These results are consistent with the idea that N is not a limiting nutrient in higher N stands, and that excessive soil N availability may negatively impact forest productivity. Long-term N enrichment of temperate forest soils appears capable of sustaining an open N cycle and key symptoms of N saturation for multiple decades after the cessation of elevated N inputs.

Introduction

Nitrogen (N) is a critical, limiting nutrient in many temperate forests (Vitousek and Howarth 1991). N has been noted to have a strong influence on decomposition (Swanston et al. 2004), the productivity and community composition of plants and microbes (Pastor et al. 1984, DeForest et al. 2004), and cycling of other nutrients (Perakis et al. 2006, Gilliam et al. 2005). However, excessive N availability can have significant negative effects on ecosystems, including reduced plant productivity (Aber et al. 1989), elevated N leaching (Tietema et al. 1998, Pregitzer et al. 2004), soil acidification (Reuss and Johnson 1986), and base cation depletion (Federer et al. 1989). The majority of our understanding of the effects of excess N comes from studies of chronic N deposition in polluted regions of eastern North America and Europe, with comparatively few tests of the generality of these ideas in unpolluted temperate forests (e.g. Perakis et al. 2005).

An ecosystem can approach N saturation if N availability exceeds plant and microbial demands (Aber et al. 1989). N saturated systems often experience elevated net nitrification and significant losses of nitrate, but N cycling processes may not increase linearly with further N input (Aber et al. 1998). Initially, plant and microbial communities may respond positively to increased N availability (Binkley and Högberg 1997) but may subsequently become limited by other nutrients (Sinsabaugh et al 1993) or hindered by high concentrations of N (Fog 1988, Rennenburg et al. 1998). Thus N mineralization rates may not increase indefinitely (Matson et al. 2002) to create a runaway N cycle. In N saturated systems where ecosystem N demands are fully met, additional inputs are often reflected in subsequent N losses (Aber et al. 1989). However, it remains unclear how systems presently receiving low N inputs but with high N availability can in theory approach limits to N mineralization yet continue to leach significant amounts of nitrate.

Artificial N additions can give insight into the effect of increasing N availability on ecosystem processes (Magill et al. 2004, McNulty and Aber 1993); however, less is known about how natural long-term soil N accumulation may influence N cycling rates and stand productivity. Long-term N accumulation in temperate forests may eventually result in accelerated N cycling and a relaxation of N limitation, with productivity ultimately controlled by other nutrients, as occurs in P-limited tropical forests on old soils (Vitousek 2004). Yet, examples of natural N saturation in temperate forests are rare, where N limitation is both widespread and strong (LeBauer and Treseder in press). Temperate forests may recover previous functioning and nutrient status after cessation of short-term N inputs (Gunderson et al. 1998, Binkley and Högberg 1997), but it is less clear whether symptoms of N saturation can persist in such systems as a consequence of long-term soil N accumulation.

The forests of the Pacific Northwest are often considered highly productive and N-limited (Sollins et al. 1980, Waring and Franklin 1979, Fenn et al. 2003), exhibiting little N loss through leaching (Vanderbilt et al. 2003) or denitrification (Binkley et al. 1992a). In particular, the productivity of the Oregon Coast Range exceeds that of most mature forests globally (Gholz 1982). Yet approximately one-third of Douglas-fir forests in the Coast Range exhibit declining or zero growth in response to N fertilization (Peterson and Hazard 1990), suggesting that these highly productive forests are not N limited. Although the Pacific Northwest generally has been far less impacted by chronic N deposition than many other temperate forest regions (Vanderbilt et al. 2003), biological N_2-fixation associated with red alder can supply up to 200 kg $N \cdot ha^{-1} \cdot yr^{-1}$ into an ecosystem, and is particularly common throughout the Coast Range (Binkley et al. 1994). Red alder colonization often follows disturbance (Harrington et al. 1994) and can impart greater soil N enrichment to a site (Tarrant et al. 1969, Binkley et al. 1992a, Cole et al. 1990). Consequently, Douglas-fir forests in the Coast Range are present across a range of N-poor and N-rich sites. Net N mineralization and nitrification in Coast Range Douglas-fir forests range from very low (Myrold et al. 1989) to relatively high (Binkley et al. 1992b), but N turnover under red alder is consistently elevated (Binkley et al. 1992b). Red alder also influences N outputs through leaching (Homann et al. 1992, Van Miegroet and Cole 1985, Homann et al. 1994), but only one study has previously found significant nitrate leaching in Coast Range Douglas-fir forests (Binkley et al. 1992a), although elevated streamwater nitrate concentrations in the Coast Range are relatively widespread (Compton et al. 2003, Wigington et al. 1998). Although Douglas-fir seedling biomass can increase when grown on a previous red alder site (Brozek 1990), less is known if N cycling patterns influenced by red alder N inputs will persist in the long-term after a shift to conifer dominance.

There is large variation and potential for substantial accumulation of soil N and C capital in forests across the Pacific Northwest (Homann et al. 1995, Remillard 1999, Edmonds and Chappell 1994, Cromack et al. 1999), but the factors responsible for this accumulation are not entirely understood. Soils in this region may store proportionally more C and N at depth than other soils globally (Homann et al. 2004); however, surface soil N pools appear indicative of total soil N capital when compared across Pacific Northwest subregions (Remillard 1999). Differences in climate (namely precipitation and temperature) and soil texture have been implicated as potential controls on soil N and C accumulation in the broader Northwest region (Homann et al. 1995, Remillard 1999), but climatic variables in the geographically constrained Coast Range have not been correlated with variations in soil N capital (Prescott et al. 2000). Variations in disturbance history and thus red alder colonization could be potential factors influencing soil N and C accumulation in the Coast Range (Perakis et al. 2006) but have yet to be fully examined.

Natural abundance N isotopes are often employed to examine the potential openness of N cycles (Amundson et al. 2003), as ecosystem δ^{15}N reflects the isotopic composition of both N inputs and losses (Högberg 1997). Foliar δ^{15}N often increases with soil N availability (Garten and Van Miegroet 1994), as losses of isotopically light nitrate and trace N gases cause residual soil N to become more enriched in ^{15}N (Högberg 1997). Examination of foliar δ^{15}N in the Coast Range has revealed high variability among individual Douglas-fir trees and sites, ranging both above and below the atmospheric standard of 0 per mil; whereas red alder foliage consistently shows -1 per mil, and $\delta^{15}N$ signatures of red alder soils average 2.2 per mil (Scott et al. in press). Because of the extremely high rate of N_2-fixation input by red alder, shifts in forest vegetation between the fixer (red alder) and non-fixer (Douglas-fir) across sites could be an additional important mechanism that shapes landscape level variations in both soil N content and isotopic composition. N isotopic fractionation within ecosystems can also occur through mycorrhizal influence upon plant uptake (Hobbie et al. 2000). Therefore, shifts in $\delta^{15}N$ across a range of soil N availability in the Coast Range may be a reflection of N cycling and leaching rates, mycorrhizal colonization, and the isotopic signature of previous N inputs.

Based on previous work in the Coast Range (Perakis et al. 2006), we were able to identify sites to represent a gradient of surface soil N. Gradient studies have often been utilized to identify the influence of a particular nutrient or climatic condition on ecosystem processes. Many N availability gradients have been constructed across a shift in tree species composition (Pastor et al. 1984, Reich et al. 1997); therefore, the creation of a soil N gradient with similar overstory cover and parent material is uniquely suited for isolating the effect of N availability on N cycling and plant responses. Previous N gradient work in coastal Oregon and Washington found increasing litterfall inputs with soil N capital (Prescott et al. 2000). Less is known whether extremely broad variations in soil N availability found within a common physiographic province can influence the openness of the N cycle and plant production.

In this study I examined N and C pools, N cycling and leaching, and $\delta^{15}N$ signatures across a wide gradient in surface soil N in ten young, unpolluted Douglas-fir plantations of the north-central Oregon Coast Range. Several research questions shaped the study: 1) How do soil and plant N pools vary across the sites? 2) What climatic and site characteristics are correlated with soil N capital? 3) How do indices of N cycling vary as soil N content increases? 4) Does the magnitude of N leaching correspond with an acceleration of N cycling? I also compare N dynamics across this gradient to predictions from N saturation theory (Aber et al. 1998) as a way to evaluate the generality of forest response to long-term N enrichment.

Methods

Study area

The study area was located in the north-central Oregon Coast Range from (43° 48'N, 123° 24'W) in the north to (44° 34'N, 123° 48'W) in the south (Figure 2.1). The Coast Range was formed from uplifted ocean floor during the tertiary period (Orr et al. 1992) and from the collision of a volcanic island chain with the North American continent (Duncan 1982). Consequently, bedrock in the Coast Range includes both marine sandstone, siltstone, and shale, and basaltic volcanic rock (Orr et al. 1992). Soils in this region range include Inceptisols, Alfisols, Ultisols, and Andisols. The climate in the study area is maritime and temperate with cool, wet winters and warm, dry summers. The study area receives most precipitation as rain from October-April, and rainfall varies approximately 180 to

300 cm · yr^{-1} across the area (National Atmospheric Deposition Program [NADP] OR02 watershed, averaged annual data from 1980-2004). N deposition through precipitation averages 0.65 kg N ha^{-1} yr^{-1} (NADP OR02). January mean minimum and July mean maximum temperatures range from –2 to +2°C and from 20 to 28°C, respectively (Maguire et al. 2002). The study area falls within the western hemlock (*Tsuga heterophylla*) vegetation zone, and has Douglas-fir (*Pseudotsuga menziesii*), western hemlock, western red cedar (*Thuja plicata*), red alder, big-leaf maple (*Acer macrophyllum*), as major forest tree species with Sitka spruce (*Picea sitchensis*) also found near the coast. However, many forest stands in these zones are often dominated solely by Douglas-fir because of preferential monoculture plantation planting.

Study sites

Ten study sites, selected to represent a surface soil N gradient, were chosen from Douglas-fir plantations being monitored to examine the effect of Swiss Needle Cast (SNC) on Douglas-fir growth (Maguire et al. 2002). The sites in this study were chosen based on similar tree age (~30 years), sedimentary parent material, and varying mean age of Douglas-fir needle retention. Eight of these ten sites were preliminarily sampled for plant and soil chemistry in summer 2002 (Perakis et al. 2006), and two additional sites with intermediate mean needle ages were added in 2004. The stands at these sites range from 23 to 31 years of age and vary in mean needle longevity from 1.4 to 4.0 years. Elevation ranges from 23 to 484 m, and all sites were located within 25 km of the Pacific Ocean with a north/south range of 137 km. Soil type among the sites included both alic Hapludands and andic Dystrudepts. The sites named Music Rd. and Juno Hill in Perakis et al. (2006) are here referred to as sites 20 and 6, respectively. Site characteristics are shown in Table 2.1.

Nine of the ten sites were dominated by planted Douglas-fir with occasional western hemlock, red alder, Sitka spruce, vine maple (*Acer circinatum* Pursh), and bigleaf maple (*Acer macrophyllum*) (Table 2.2). One of the ten sites, site 6, was co-dominated by western hemlock and Douglas-fir. The history of site 6 indicates that hemlock naturally regenerated into the stand. Volunteer red alder did not dominate any of the stands and represented less than 9% of total basal area at all sites. The study plots at each site covered 0.2 acre occurring within continuous plantation cover. Five sites were located between Newport and Corvallis, and the other five sites were scattered in the northern Coast Range around the communities of Tillamook, Grand Rhonde, and Nehalem. These sites were located on land owned by the Oregon Department of Forestry, Hampton Forests, and Green Diamond Resource Company.

Soil sampling and preparation

Soil and forest floor sampling occurred during summer 2003 and summer 2005. Forest floor was collected for both bulk density and nutrient analysis and included the entire O horizon. Four locations within each site were randomly selected for forest floor sampling. A 30 cm by 30 cm square sampling frame was placed on the surface of the forest floor, and material greater than 1 cm in diameter was discarded. A keyhole saw was used to cut along the inside of the grid to remove the forest floor solely contained within the grid. Five measurements were taken to estimate the depth of the forest floor. After sampling, the forest floor was returned to the lab, dried at 65°C for 48 hr, sorted again to remove any mineral soil, weighed, and a subsample ground in a Wiley mill.

Mineral soil, to a depth of 1 m, was sampled separately for bulk density and chemistry. One objective of mineral soil sampling was to determine the total mass of nitrogen (N) and carbon (C) in six mineral soil layers (0-10 cm, 10-20 cm, 20-30 cm, 30-50 cm, 50-70 cm, 70-100 cm). Soil bulk density, soil volume, layer depth, and nutrient concentrations were used to determine total soil chemistry. A pit excavation method was used for the first 10 cm and a 4 cm diameter corer was used for the lower soil depths. Four locations within each site were randomly selected for soil sampling. For the top 10 cm of mineral soil, a sampling frame was placed on the ground, and the forest floor was removed. A 10 cm deep pit was excavated within the frame, and the soil was removed and placed in Ziploc bags. To validate the depth of the pit, five measurements were taken from the surface to the bottom of the pit. Next, a 4 cm diameter corer, fitted with a core liner and hammering handle, was used to obtain soil from the 10-20 cm, 20-30 cm, 30-50 cm, 50-70 cm, and 70-100 cm depths. Soil layers exceeding 10 cm were sampled in the middle of their profile, with intervening soil excavated by an auger. Coring to 1 m depth was possible in 39 of 40 total sample locations.

Mineral soils were sieved to 2 mm to remove rocks and debris and to homogenize the soil. Soil bulk density was calculated for each soil layer as the total dry mass of < 2 mm soil divided by the volume of the entire soil core. Separate subsamples of fresh soil were dried at 105°C for 48 hr to determine moisture content and at 65°C for 48 hr prior to grinding by roller mill for chemical analysis. Soil solution pH (2 water: 1 soil) was assayed using fresh soil by an Accumet pH probe meter with a glass-body liquid-filled combination probe (Fisher Scientific, Hampton, NH, USA). Subsamples from the 0-10 cm and 10-20 cm were composited by depth within sites and analyzed for soil texture (% clay, silt, and sand) by the hydrometer method (Central Analytical Laboratory, Oregon State University, Corvallis, OR).

Vegetation sampling and preparation

Foliage sampling occurred during the summer of 2005. A pole pruner was used to clip the tip of the southern-most branch in the fifth whorl from the top of three randomly selected trees per site (Maguire et al. 2002). The clipped branches were immediately frozen, and needles were separated from the branches and kept frozen until analysis. Frozen needle samples were thawed and dried at 65°C for 48 hr. Dried needles were ground on a ball mill.

Sampling of Douglas-fir bolewood and branches occurred in winter 2007. Tree cores were taken from six Douglas-fir trees per site. Cores were taken at breast height on the uphill or north side of the tree. These cores were then bulked into two composite samples per site. At each site, three branches were cut with a pole pruner, or if live branches were not easily accessible, green branches were collected from the ground, having been knocked down after a recent storm event.

The branches were allowed to air dry for one week and then were defoliated and cut into representative pieces for analyses. Cores and branch subsamples were dried at 65^{o}C for 48 hr and ground in a Wiley mill.

In order to estimate annual litterfall inputs, litter traps were installed at each of the sites in August 2004. The traps were made by attaching mesh (1.4 mm) onto baskets covering an area of 0.26 m^2, and these traps captured litter falling vertically from a height of 0.33 m above the forest floor. Ten traps were randomly placed at each site by overlaying each site with a virtual numeric grid and selecting placement of the traps on the grid by random number generation. From September 2004 to June 2006, litter was collected each month by unclipping the mesh from the basket and folding the mesh into labeled paper bags. A new piece of mesh was then clipped to the basket to collect litterfall for the next month. If a basket was tipped over or a corner of the mesh had become unclipped, a note was made and litter from that basket was excluded from the collection.

Litter was characterized as total litter and Douglas-fir needle litter. The paper bags containing the mesh and litter were dried at 65^{o}C for 48 hr. The dried litter was then removed from the mesh and weighed. Each month litter from 3-4 different baskets at the same site was combined to form three composite samples per month per site. Each composite sample was then sorted, removing any insects, charcoal, and woody debris with a thickness >1 cm, and continually divided in half on a tray until one subsample weighed approximately 2 g. Each litterfall sample was then ground on a roller grinder and stored in scintillation bottles. Next, 1 g of

Douglas-fir needle litter was removed from the remaining litter in each composite sample and ground in a ball mill.

Nutrient analysis

Ground foliage, forest floor, litterfall, Douglas-fir needle litter, branches, wood tissue, and soil were re-dried at 65°C for 24 hr before chemical analysis. Approximately 3-5 mg of foliage, litterfall, and forest floor and 15-100 mg of soil were weighed into 5mm by 9mm tin capsules and analyzed for total carbon and nitrogen on a Costech ECS-4010 elemental combustion analyzer (Costech Analytical, Valencia, CA, USA) using atropine as the standard and apple leaf as the reference material. C and N capital of the soil and forest floor was calculated using forest floor or soil layer thickness, elemental concentrations, and bulk density. C and N pools within soil layers were then summed to a 1 m depth.

$\delta^{15}N$ analysis

Foliage, forest floor, Douglas-fir needle litter, and soil underwent δ^{15}N isotope analysis on a mass spectrometer (Finnigan MAT Delta Plus XP) at the Integrated Stable Isotope Research Facility at the Environmental Protection Agency (Corvallis, OR). Approximately 8-17 mg of forest floor, foliage, and Douglas-fir needle litter and 25-100 mg soil were weighed in tin capsules for analysis. Corn stalk, pine needle, and citrus leaf were used as isotopic standards. Isotope values are expressed in delta notation (δ):

$$\delta^{15}N = [(R_{sample} / R_{standard}) - 1]*1000$$

where R_{sample} is the ratio of the heavy isotope, ^{15}N, to the light isotope, ^{14}N, in the sample and $R_{standard}$ is the ratio of the heavy to light isotope of the standard (atmospheric N_2) (Martinelli et al. 1999). The precision of isotope analysis for replicate samples was within 0.3‰ for $\delta^{15}N$. An enrichment factor, ε, ($\varepsilon = \delta^{15}N_{soil} - \delta^{15}N_{foliage}$) was calculated to compare how isotopic differences among soil and plant pools may vary across sites (Garten and Van Miegroet 1994).

Site 6 was systematically omitted from all plant $\delta^{15}N$ analyses. Although this site fit most of the criteria for inclusion in this study, SNC severity in Douglas-fir is very high and 80% of the basal area is western hemlock. The $\delta^{15}N$ signatures of Douglas-fir foliage, needle litter, and forest floor from site 6 were significant outliers in regression analyses with large studentized residuals (< -2) and mild influence (Cook's distance ~ 0.50). As case-influence statistics indicated outlier status, site 6 was excluded from plant $\delta^{15}N$ analyses. Greater ^{15}N depletion than predicted from regression in plant pools at site 6 will be discussed later.

Estimation of stand biomass

Estimates of stand biomass (foliage, branches, stems, roots) at the ten study sites were produced using the Douglas-fir Hybrid Growth System Model (DF.HGS) (Weiskittel 2006), which was developed from previous biomass sampling at these sites (Maguire et al. 2002). If percent basal area of a species other than Douglas-fir was greater than 10% on a given site, biomass of that species was calculated and included in the stand budget. As 80% and 18% of the basal area at sites 6 and 39, respectively, was comprised of western hemlock, allometric equations were used to estimate western hemlock biomass pools (Ter-Mikaelian and Korzukhin 1997). Biomass estimates were multiplied by N concentration to determine N pools in each tissue type. N concentrations in hemlock tissue, and in Douglas-fir branch and stem tissues, were estimated from previous work in the Coast Range (Binkley et al. 1992a). Root biomass from the DF.HGS model included both coarse and fine roots, and root N concentration was adopted from N content data for fine and coarse roots in a Douglas-fir forest in western Oregon (Sollins et al. 1980). Annual N uptake was estimated as the sum of N in the annual production of branches and stems plus the N content of fine litterfall (Binkley et al. 1992a).

Lysimeter installation and soil water sampling

In order to monitor soil water nutrient concentrations, three pairs of low-tension lysimeters (Prenart, Denmark) were installed at 20 cm (shallow) and 1 m (deep) soil depth at each of the sites in August 2004. The locations for lysimeters were spread across each site and were selected to avoid hitting large roots or bedrock upon installation. In the field before installation, one part deionized water and one part soil were combined to make a slurry in which each lysimeter was conditioned under vacuum for 15 minutes. The soil for the slurry was sieved to 2 mm and came from the depth to which the lysimeter was being installed. After conditioning in the slurry, the lysimeter was coated in a thick soil film. Next, a heavy steel rod was pushed into the ground at a 60^{o} angle upslope with a twisting motion. The steel rod was removed, and the Tygon tubing of the conditioned lysimeter was threaded through a hollow plastic tube, causing the lysimeter to be at the end of the rod. The lysimeter-rod system was pushed through the hole, and the lysimeter was gently pressed into 10 cm of fresh soil at the end of the hole. The plastic tube was removed, and the hole was backfilled with soil using a wooden dowel to pack soil tightly. The lysimeter tubing was secured in 1 L sample collection bottles, and the collection bottles and excess tubing were housed in PVC piping 25 cm in diameter and with a removable lid. Lysimeters were allowed to equilibrate for several months before soil water nutrient analysis commenced.

Every month from December 2004 to June 2006, a 12 mm Hg vacuum was placed on the lysimeters for 48 hr. Approximately 5 mL of accumulated sample was used to rinse two 60 mL HDPE bottles, and the remaining soil water was collected. One of the bottles was immediately capped, and the other received approximately 0.2 mL of chloroform to stop microbial processes. Chloroformed and unchloroformed field blanks were also taken at each site during each collection period by rinsing bottles with deionized water. The bottles were kept on ice during transport back to the lab and were refrigerated until analysis, generally within 48 hr of collection.

Soil water analysis

Soil water was analyzed colorometrically for nitrate (NO_3^-)-N and ammonium (NH_4^+)-N with cadmium reduction and salicylate methods, respectively, on a Lachat QuikChem 8000 flow-injection autoanalyzer (Lachat

Instruments, Milwaukee, WI, USA). Samples were run against known standards, duplicates were run every ten samples, and field blanks were used to account for any effects of transferring collected water in the field. Soil water was then analyzed for total nitrogen (TN) and dissolved organic carbon (DOC) 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) was calculated as TN minus ammonium-N and nitrate-N. DON could not be calculated in 25 % of samples because measured TN concentrations were below total inorganic-N concentrations, typically when nitrate-N exceeded 1 ppm, so that the acceptable 5% analytical error on total inorganic-N exceeded 0.050 ppm. Occasionally TN values less than 1 ppm were also below measured nitrate-N concentrations.

Water yield was estimated by using estimates of evapotranspiration and precipitation to convert nutrient concentrations to fluxes (Binkley et al. 1992a). Estimates of annual precipitation and mean minimum and maximum temperature for each of the sites were gained from GIS layers generated by PRISM (Precipitation-elevation Regressions on independent Slopes Model) (PRISM Group, Oregon State University, http://www.prismclimate.org, created 4 Feb 2004). PRISM is a unique climate database because it accounts for rain shadows, temperature inversions, coastal effects in the climate mapping process, and it uses a digital elevation model to account for grid cell and weather station location (Daly et al. 1994). Precipitation and temperature layers coincided with sampling dates

(September 2004 – June 2006) and had a grid size of 4 km. Annual mean minimum and maximum temperatures for each site were averaged to provide an estimate of mean annual temperature. Site coordinates were used to obtain annual data from the precipitation and temperature layers.

Estimates of evapotranspiration were obtained from the 3-PG (Physiological Processes for Predicting Growth) forest process model. 3-PG is a process-based stand growth model and was designed to predict forest growth variables of interest to both foresters and ecologists (Lansberg and Waring 1997). As forest growth is strongly related to water availability, 3-PG also predicts evapotranspiration using the Penman-Monteith equation which sets limits on evaporative demand (Waring et al. 1980). 3-PG uses a monthly time step and requires climatic data and additional input data such as latitude, site fertility rating, initial stocking density (trees per hectare), soil class, leaf area index, and maximum and minimum available soil water. Unknown parameters (initial foliage, root, and stem biomass, quantum efficiency, and climatic data) were used from a previous modeling of a similar high fertility site in the Oregon Coast Range. Maximum canopy conductance was constrained at 0.013 m/s by running a sensitivity analysis with 3-PG to find the conductance that produced the most reasonable maximum leaf area index and maximum annual increment for a site II Douglas-fir forest in the Oregon Coast Range (Waring et al. 2006, Waring et al. 2002). Ranges of planting density, LAI, latitude, and fertility of the ten study sites did not vary greatly, so an average of these parameters across all sites was used to give one estimate of evapotranspiration for all ten sites. Lysimeters at all ten sites ran dry during the middle of the summer, so the available soil water in August was manually set to zero in the model. The model was run for 30 years, the mean stand age of these sites, to estimate current water demands.

The difference between precipitation and evapotranspiration was taken to be the volume of water that leached past 1 m, because nearly all transpiration occurs within the top 1 m of soil. A fine root profile from a nearby Coast Range site (Lee et al. 2007) was used to estimate the percentage of fine roots in the top 20 cm of soil, as fine roots are largely responsible for transpiration. The percentage of fine roots in the top 20 cm was applied to the transpiration value estimated by 3-PG and added to the volume of water lost by evaporation to obtain the volume of water leaching past the 20 cm lysimeters. A significant percentage of soil water is transpired in the top 20 cm of mineral soil, so a greater volume of water leaches past the 20 cm depth than the 1 m depth. Soil water nutrient fluxes were calculated as nutrient concentration times the volume of water leaching past each lysimeter depth.

Buried bag procedure for net N cycling rates

Net mineralization and nitrification rates in 0-10 cm mineral soil were assessed each month with a buried bag technique (Eno 1960). The buried bag method involves placing soil cores in plastic bags in the field and measuring inorganic-N accumulation. The bags are impermeable to water but permit gas exchange, so mineralization and nitrification can occur but N cannot leach out of the bag.

From September 2004 to December 2005, six replicate pairs (initial and final) of buried bags were taken every month at each site, for a total of sixteen collection periods. Within each site, coring location was randomly selected every collection period. Soil cores were taken in plastic core liners, which were pushed 10 cm into mineral soil. For initial buried bags, soil inside the core was pushed out and placed in 1.5 mil low-density flat poly bags and secured with a twist tie. The final core was taken within 4 cm of the initial core, and the soil was retained in the core liner and placed within a plastic bag and mesh wrapping and secured with a twist tie. The final cores were placed back into the coring holes and retrieved and extracted a month later during the next collection period. All soil samples were transported back to the lab on ice.

Nitrate-N concentrations in initial buried bags can increase sevenfold if extractions are delayed 24 hr (Van Miegroet 1995); therefore, the initial cores from the current collection month and final cores from the previous month were extracted back at the lab the same day as they were collected. All soil was sieved to 2 mm to remove rocks and roots, and a 10 g subsample was weighed and dried at 105^{o}C for 48 hr to determine moisture content. Next, 7 g of each soil was weighed into snap-cap bottles and extracted with 35 mL 2 M potassium chloride (KCl) for one hour on a shaker table. The extract solution was allowed to settle for 30 min before the supernatant was poured into funnels lined with filter paper (Whatman #40) that had been leached twice with KCl. The filtered solutions were collected into labeled scintillation bottles and frozen until analysis.

Buried bag extracts were thawed and analyzed colorometrically for NO_3^--N and NH_4^+-N with 2 M KCl as the carrier as described above on a Lachat QuikChem 8000 flow-injection autoanalyzer (Lachat Instruments, Milwaukee, WI, USA). Net mineralization and nitrification rates ($\mu g\ N \cdot g\ soil^{-1} \cdot day^{-1}$) were determined as follows:

$$\text{Mineralization} = (\text{Final}_{NH4+ + NO3-} - \text{Initial}_{NH4+ + NO3-}) / t$$

$$\text{Nitrification} = (\text{Final}_{NO3-} - \text{Initial}_{NO3-}) / t$$

where t = number of days between initial and final sampling dates and $\text{Final}_{NH4+ + NO3-}$ and $\text{Initial}_{NH4+ + NO3-}$ = the sum of NH_4^+-N and NO_3^--N (expressed as $\mu g\ N \cdot g\ soil^{-1}$) for the final and initial cores, respectively. Soil bulk density was used to convert net N mineralization and nitrification rates from $\mu g\ N \cdot g\ soil^{-1} \cdot day^{-1}$ to $kg\ N \cdot ha^{-1} \cdot yr^{-1}$.

Gross N cycling rates and microbial biomass N uptake

The buried bag method addresses the net change in inorganic-N concentration, so gross mineralization and nitrification rates were also determined to isolate the competing microbial processes of production and consumption of inorganic-N. ^{15}N pool dilution (Davidson et al. 1991) was conducted at all ten sites on three occasions, October 2004, February 2005, and June 2005.

On each date, four locations were randomly selected within each site. At each location, the forest floor was removed, and four cores of 0-10 cm mineral soil were taken within 10 cm of each other. Cores were collected in 10 cm long plastic core liners, 5 cm in diameter, with six 0.5 cm diameter holes cut into each. The cores were labeled with either $^{15}NH_4Cl$ or $Na^{15}NO_3$, creating an approximate concentration of 20 μg N · g dry soil at 99.9 atom % ^{15}N (Perakis and Hedin 2001). Into each core, six 6 mL injections of the 60 μg N · mL ^{15}N solution were made through the holes in the plastic core liner with an 18-gauge side-port spinal needle and syringe (Hamilton Company, Reno, NV). At each labeling location, two cores received injections of $^{15}NH_4Cl$, and the other two cores were injected with $Na^{15}NO_3$. One $^{15}NH_4Cl$ labeled core and one $Na^{15}NO_3$ core were extracted 15 min after labeling to determine initial ^{15}N enrichment, and the remaining two cores were capped, placed in a 1.5 mil low-density flat polyethylene bag secured with a twist tie, and put back into the coring holes for final extraction after 24 hr.

Initial and final ^{15}N labeled soil cores were extracted with 0.5 M potassium sulfate (K_2SO_4) in the field. The soil cores were uncapped and the soil pushed out of the core liner into a Ziploc bag. The soil was homogenized in the Ziploc bag for one minute and then 60 g was weighed out and placed in a container pre-filled with 300 mL 0.5 M K_2SO_4. The remaining soil was kept in the Ziploc bag, and moisture content was determined back at the lab. The extraction containers were lightly shaken six times during the one hour extraction and then were allowed to settle for 30 min. The supernatant was then filtered through funnels lined with rinsed Whatman number 1 filters and kept frozen until analysis.

Microbial biomass N and the relative microbial uptake of ammonium-N and nitrate-N were determined by chloroform fumigation (Davidson et al. 1989). A 7 g subsample of each 24 hr incubated ^{15}N labeled soil was chloroform fumigated for 48 hr and subsequently extracted with 35 mL 0.5 M K_2SO_4.

Persulfate digests were performed on the chloroform fumigated samples and the unfumigated 24 hr soil extracts in order to determine total N (organic-N plus inorganic-N) and microbial biomass N shifts across the gradient. 1:1 solutions of K_2SO_4 extracts and persulfate oxidizing solution were autoclaved for 50 min at ~ 120°C. Glycine was used as a standard and was oxidized by the same method as the samples (D'Elia et al. 1977). Microbial biomass N was estimated as the difference in N content of the digested fumigated minus unfumigated soils.

The pool dilution and persulfate digest extracts were analyzed colorometrically for inorganic-N on a Lachat QuikChem 8000 flow-injection autoanalyzer (Lachat Instruments, Milwaukee, WI, USA). Persulfate digest extracts were analyzed for nitrate-N while pool dilution extracts were analyzed for their target labeled N species, ammonium-N or nitrate-N. The oxidized glycine standards were used as analytical standards for the persultate digest extracts, and nitrate-N or ammonium-N in 0.5 M K_2SO_4 were used as standards for the pool dilution extracts. Initial soil extracts were only analyzed for their target inorganic-N species. A 6-day teflon (PTFE) tape diffusion procedure (Stark and Hart 1996) was used to prepare all samples for ^{15}N analysis. Ammonium-N and nitrate-N concentrations were used to determine the correct volume of soil extract to diffuse in order to volatilize approximately 50 μg N. Filter paper discs on which the volatilized N is trapped during the diffusion were pre-rinsed with deionized water, acidified with 2.5M $KHSO_4$, and completely sealed in PTFE tape to create acid traps. Soil extracts were poured into 120 mL specimen cups, and acid traps were placed on the surface of the solutions. NaCl was added to prevent water accumulation around the discs. For the nitrate-N soil extracts, Devardas alloy was added to reduce NO_3^- to NH_4^+, and next the addition of MgO increased the pH of the solution in order to volatilize ammonia (NH_3) onto the acidified discs. For solutions containing ammonium-N as the target species, MgO was the only reagent added. A 5 μg N standard ($^{15}NH_4Cl$, 99.9 atom %) was diffused in varying volumes of 0.5 M K_2SO_4 (20 mL, 60 mL, and 100 mL) to test the effect of salt solution volume on ^{15}N contamination delivered to the acid traps. Three non-diffused standards were also made for every 80 diffused samples by applying 5 μg N of the $^{15}NH_4Cl$, 99.9 atom % standard solution directly onto unacidified filter paper discs and sealing the discs in PTFE tape.

After the 6-day period, the acid traps were removed from the solution and the discs were dried for 4 hr in a desiccator with an open container of sulfuric acid, included to draw any ambient NH_3 in the air away from the discs. The discs were then wrapped in tin capsules and analyzed for their $^{15}N/^{14}N$ ratio with continuous-flow direct combustion and mass spectrometry using a Europa Scientific SL-2020 system (Europa Scientific, Crewe, UK) at the Utah State University Stable Isotope Laboratory. Analytical precision for $^{15}N/^{14}N$ was better than 0.004 atom %.

Gross mineralization, nitrification, and consumption rates were determined from equations developed by Kirkham and Bartholomew (1954) and cited elsewhere (Davidson et al. 1991). Gross ammonium consumption in this pool dilution model includes both microbial immobilization of ammonium and nitrification, and nitrate consumption includes microbial immobilization of nitrate and denitrification. Although not acknowledged in the calculation method, abiotic ammonium and nitrate immobilization may also be consumptive processes (Davidson et al. 2003). Annual gross cycling rates were estimated by averaging rates from the three labeling dates.

Data analysis

Regression was used to explore relationships between response variables of interest and indices of soil N availability. A correlation matrix was performed to identify potential site characteristic correlates with soil N capital. Several comparisons of data averaged across all sites were made using two-tailed t-tests. The statistical software package, SAS 9.1 (SAS Institute Inc. 2003), was used for all statistical procedures. Given the small number of sites (ten), the accepted level of significance for regressions was $\alpha < 0.10$. Prior to observing analysis results, normal probability plots were used to check data distributions for normality, and residuals were checked to ensure equal variance, applying a log transformation when necessary.

Results

Soil N and C pools

The gradient in 0-10 cm mineral soil N varied three-fold from 0.21 to 0.69% N (Table 2.1). Across the ten sites, total mineral soil N capital to 1 m depth varied from 9.2 to 28.7 Mg N $\cdot$ ha^{-1} and total soil C capital ranged from 166.6 to 413.2 Mg C $\cdot$ ha^{-1} (Table 2.3 and 2.4). Soil N and C capital were significantly correlated ($r = 0.93$, $p < 0.0001$, $n = 10$). For all analyses, soil N and C capital were log transformed to meet model assumptions. Surface soil N and C pools (0-10 cm) were correlated with N and C capital at depth (10-100 cm) (N: $r = 0.87$, $p = 0.001$, $n = 10$; C: $r = 0.71$, $p = 0.02$, $n = 10$). The proportion of soil N or C located in any specific depth did not vary with total soil pools (Tables 2.3 and 2.4). Forest floor pools of N and C were not correlated with either soil N and C capital or the surface soil N gradient (Tables 2.3 and 2.4).

Site correlations with soil N capital

Correlations between soil N capital and potential explanatory variables are shown in Table 2.5. Sample size was low, $n = 10$, as one mean value represented each site, so model selection criteria could not be employed to identify the best fitting model to predict soil N capital. Therefore, a correlation matrix of soil N capital and potential explanatory variables was performed. Soil N capital was log transformed to meet normality assumptions. I did not seek to identify the best fitting model but rather to eliminate variables which did not have a relationship with soil N capital. Soil N capital did not possess a relationship with the climatic variables, mean annual precipitation and mean annual temperature. Additionally, soil texture, as defined by % clay, did not describe the variation in soil N capital. Slope, aspect, and soil moisture were not correlated with soil N capital. Two geographic variables, elevation and distance from the coast, were significant correlates with the soil N pool. Foliar δ^{15}N exhibited a relationship with soil N capital; however, the δ^{15}N enrichment between foliage and soil and soil δ^{15}N were not significant correlates. Mean soil profile pH was also a potential correlate.

Although multicollinearity did not prohibit the exploratory nature of these correlations, many of these variables were indeed correlated. Elevation and distance from the coast were correlated with each other (r = 0.82, p = 0.004) and also with foliar δ^{15}N (elevation: r = -0.63, p = 0.07; distance from coast: r = -0.78, p = 0.01) and mean pH (elevation: r = -0.81, p = 0.004; distance from coast: r = 0.68, p = 0.03). MAP and MAT were correlated (r = -0.81, p = 0.005) but not with elevation (MAP: p = 0.41; MAT: p = 0.27) or distance from the coast (MAP: p = 0.33; MAT: p = 0. 17). The range in values of potential correlates is shown in Table 2.6.

δ^{15}N of soil and plant pools

Douglas-fir foliage, needle litter, and forest floor became more enriched in the ^{15}N isotope with increasing soil N capital (Figure 2.2). In all plant biomass pools, δ^{15}N became more positive with greater soil N capital and trended towards the atmospheric isotopic signature of 0 $^{o}/_{oo}$. δ^{15}N and N content were linearly related in both foliage and Douglas-fir needle litter (foliage: r = 0.57, p = 0.003, litter: r = 0.83, p = 0.0001, n = 9). Douglas-fir needle litter was significantly more depleted in ^{15}N than foliage (t_{16} = 3.35, p < 0.002). Mean foliar and needle litter δ^{15}N signatures were -1.28 $^{o}/_{oo}$ (95% CI: -1.33, -1.23) and -2.23 $^{o}/_{oo}$ (95% CI: -2.29, -2.17), respectively. Forest floor N concentration did not influence its δ^{15}N signature. Although plant pools showed a distinct pattern in δ^{15}N, the δ^{15}N enrichment span between soil (0-10 cm) and foliage did not vary with soil N capital (p = 0.21). For each individual depth, soil δ^{15}N did not display a pattern with N content, and the $\delta^{15}N$ enrichment span between deep (70-100 cm) and shallow (0-10 cm) soil at each site also did not vary with soil N ($p = 0.57$). Combining data from all sites, soils at depth were significantly more enriched in ^{15}N than surface soils ($t_{55} = 5.57$, $p < 0.001$). Soils from the 0-10 cm and 70-100 cm depths had mean $\delta^{15}N$ signatures of 2.85 $^{o}/_{oo}$ (95% CI: 2.80, 2.90) and 4.02 $^{o}/_{oo}$ (95% CI: 3.96, 4.08), respectively. Ecosystem $\delta^{15}N$, as defined by the isotopic signatures of soil to 1m, forest floor, and aboveground biomass, weighted by the size of each N pool, did not possess a significant relationship with ecosystem N capital; however, ecosystem $\delta^{15}N$ displayed a curvilinear relationship with mean soil profile %N (Figure 2.3). $\delta^{15}N$ in plants and soil were uncorrelated with net N mineralization.

Indices of N cycling

Two potential indices of N cycling rates, net N mineralization in surface soil and litterfall N input rate, exhibited non-linear relationships with the surface soil N gradient. Net N mineralization in the top 10 cm of mineral soil varied over four-fold and displayed a curvilinear relationship with soil N, increasing along the first half of the gradient and then tapering off with additional soil N (Figure 2.4a). Percent nitrification was 1.4% and 21% of total mineralized N at the two sites of lowest surface soil N, yet often approached 100% (range = 57.9%-94.7%, average = 82.2%, n=8) at more N rich sites across the gradient (Figure 2.4b).

Annual litterfall N inputs ranged from 15.3 – 29.2 kg $N \cdot ha^{-1} \cdot yr^{-1}$ and also displayed a curvilinear relationship with surface soil N (Figure 2.5). Litterfall N inputs increased until around 0.50% surface soil N, and then decreased further across the gradient. Annual N production, calculated as litterfall N return plus woody N uptake, also displayed a curvilinear relationship with surface soil N ($y = -151.5x^2 + 150.0x - 6.9$, $p < 0.0001$, $r^2 = 0.96$). Annual mineralized N and annual litterfall N return were correlated ($p < 0.05$, $r = 0.66$), suggesting these two indices of ecosystem N cycling are linked.

In contrast to the patterns found in net N cycling rates, gross N production and consumption rates did not vary systematically across the soil N gradient (Table 2.7). Neither the gross production nor consumption of ammonium and nitrate were related to net N mineralization, nitrification, or soil moisture. Seasonality was not an important factor in gross cycling rates, as only June gross ammonium consumption was significantly different from that in October ($t_{18} = -2.54$, $p = 0.01$) (Appendix Table A1.1). Seasonal N cycling rate and nitrate-N fluxes are shown in Table A1.1 of the Appendix.

Microbial uptake of both $^{15}NH_4^+$ and $^{15}NO_3^-$ after 24 hr in pool dilution incubations was highly variable, and uptake preference was inconclusive (Table 2.8). The raw data consistently yielded positive microbial biomass N values, but atom percent ^{15}N was often higher in the unfumigated samples, creating artificially negative microbial ^{15}N uptake values.

Plant response to N availability

Plant N pools across the sites are displayed in Table 2.9. The amount of N stored in aboveground biomass was minor in comparison to soil N pools. Total plant N pools were not correlated with soil N availability but qualitatively appeared to increase across the first half of the gradient. The proportion of total plant N stored in any tissue type was unrelated to soil N capital. N uptake into each tissue type is shown in Table 2.10. Annual plant N production, calculated as woody N production plus litterfall N flux, increased linearly with net N mineralization (Figure 2.6). Annual N flux into foliage was highly variable across the sites, with some sites gaining foliar biomass and others decreasing canopy N. For example, sites 6 and 16 had very similar N mineralization and total soil N values, yet displayed extremes in the annual loss (-5 kg $N \cdot ha^{-1} \cdot yr^{-1}$) and accretion ($+14$ kg $N \cdot ha^{-1} \cdot yr^{-1}$) of canopy N among sites.

Foliar N ranged from 1.21 to 1.91% (Table 2.11) and increased with net N mineralization (Figure 2.7). Foliar and litterfall N concentration also displayed logarithmic increases along the surface soil N gradient (foliage: $p < 0.001$, $r^2 = 0.65$; litterfall: $p < 0.05$, $r^2 = 0.51$). N concentration in the forest floor did not vary significantly with any index of N availability (Table 2.11). N resorption efficiency, calculated as the percent reduction of N between green and senesced foliage, decreased linearly with net N mineralization (Figure 2.8).

Soil water nutrients

Leaching of nitrate-N from both the 20 cm and 1 m depths increased significantly across the gradient (Figure 2.9). Annual leaching losses of nitrate-N from deep soils at these sites ranged from 0.074 to 30 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (Table 2.7). Nitrate-N leaching from shallow and deep lysimeters were significantly related near 1:1 (slope = 1.02 [95% CI: 0.7, 1.34], $p = 0.0002$, $r^2 = 0.84$, $n = 10$), suggesting high downward mobility of nitrate through the soil profile. Nitrate-N leaching did not possess a significant relationship with net nitrification rate (Figure 2.10); however, an increasing trend was interrupted by one site possessing elevated rates of nitrate production but insignificant nitrate loss. pH at both sampling depths decreased significantly with increasing nitrate (deep: $p < 0.01$, $r^2 = 0.84$; shallow: $p < 0.01$, $r^2 = 0.74$). Nitrate leaching was variable across the seasons but was lowest in late summer when soils were dry (Appendix Table A1.1). In contrast to the pattern found for nitrate-N, fluxes of ammonium-N, DON, and were relatively constant across the gradient (Figure 2.11). DOC flux at both depths was uncorrelated with soil N or C (Table 2.12).

Discussion

Soil N and C pools

Soil N capital varied over three-fold across the ten sites (Table 2.3), illustrating the broad variations in soil N stores that can occur over a relatively small geographic area in coastal Oregon. Soil N and C capital fell within the range of values reported for western Oregon and Washington Douglas-fir forests (Cromack et al. 1999, Homann et al. 1995, Edmonds and Chappell 1994), and several sites possess among the highest soil C and N capital found in the Pacific Northwest, and indeed, among forested sites worldwide (Cole and Rapp 1981, Batjes 1996). Yet, soil N stores at two sites were lower than what is often found in the Coast Range (~ 10,000 $\text{kg} \cdot \text{ha}^{-1}$) (Binkley et al. 1992a, Remillard 1999). Soil

C storage at several sites exceeded mean soil C pools in tropical (210 kg $\cdot$ ha^{-1}) and boreal rain forests (256 kg $\cdot$ ha^{-1}) (Post et al. 1982). I determined soil N and C capital on only the < 2mm size fraction, which represents ~ 75% of the N and C stored in Coast Range soils (Remillard 1999). Total soil N and C capital across these sites may be even higher than my estimates if large soil fractions are considered. The potential for such high N accumulation in a temperate forest soil, coupled with wide site-to-site differences in soil N stocks, defies most conventional explanations of regional-to-global controls over soil N content. These explanations are evaluated below, and by deduction, point to a likely causal factor for unusually high soil N that may be unique to the Oregon Coast Range among temperate forest regions globally: a legacy of N_2-fixation by an early successional tree species, red alder.

Low atmospheric N deposition and significant N loss processes are likely to constrain N accumulation in the Pacific Northwest similar to their role in temperate forest N budgets in general. Atmospheric deposition of N to Pacific Northwest forests is among the lowest globally (1.6 kg $\cdot$ ha^{-1} $\cdot$ yr^{-1}, Vanderbilt et al. 2003). Greater potential inputs are possible via epiphytic N_2-fixation in mature forests (~ 5 kg N ha^{-1} yr^{-1}, Sollins et al. 1980), yet these rates are also not particularly high compared to the suite of N_2-fixation fluxes in temperate forests globally (Cleveland et al. 1999). N losses both hydrologically as DON (Vanderbilt et al. 2003, Edmonds et al. 1995) and via periodic stand replacing wildfires (Giesen 2005) also are likely to restrict N accumulation in ways similar to many other forest ecosystems worldwide.

Soil N and C content of forest soils has been correlated with geographic and site variations in climate in the Pacific Northwest and elsewhere (Homann et al. 1995, Remillard 1999, Burke et al. 1989). However, the sites here span a much narrower climate range (Table 2.6) than other sites where climate correlates with soil N and C differences (Homann et al. 1995). It is therefore not surprising that climate does not directly explain inter-site variations in N and C capital reported here (Table 2.5). Perhaps the climatic ranges across Coast Range sites are not broad enough for climate to have an appreciable effect on the variation in soil N storage. Furthermore, Homann et al. (2004) note that the global pattern of increasing C storage in 0-20 mineral soil with decreasing temperature and increasing precipitation would predict that Pacific Northwest soils store at least 50% of soil C in the top 20 cm. The mean proportion of total soil C in 0-20 cm, 20-50 cm, and 50-100 cm pools across all sites studied here was more evenly distributed across depths than average C depth distributions globally (Jobbagy and Jackson 2000). Roughly a third of total soil C was stored in each of these three depths, in contrast to global C storage patterns in which half of soil C is often located in the top 20 cm of mineral soil and less C is stored at depth. These depth distribution anomalies, and the lack of climatic correlation to site N and C capital, suggest that other factors besides climatic variation may be influencing organic N and C storage in the Coast Range.

Soil texture, and specifically % clay, is frequently identified as a key control of soil N and C accumulation in the Pacific Northwest (Homann et al. 1995, Remillard 1999, Prescott et al. 2000) and elsewhere (Burke et al 1989).

Clay minerals, with their diffuse positive charge, can assist in aggregating SOM. Finer textured soils have been correlated with faster N cycling (Reich et al. 1997) and often have higher water holding capacity promoting the formation of organic matter complexes (Brady and Weil, 1996). Although there was a wide range in clay content at these sites of approximately 25 to 50%, soil texture was not correlated with N accumulation. Slope angle has previously been negatively correlated with soil N (Cromack et al. 1999), but slope and aspect in this study did not correlate with soil N storage, suggesting erosion on steeper slopes or sun exposure is not responsible for limiting N accumulation at these sites. Likewise, soil $\delta^{15}N$ is often found to increase with soil age as more time allows for the removal of lighter mineralized N (Brenner et al. 2001), but such a relationship was not observed at these sites. While low statistical power ($n = 10$) may have limited detecting significant climate, textural, and slope influences over N and C capital in this study, the exceptionally wide (three-fold) range in soil N and C under investigation makes this less likely.

Significant correlations with soil N capital were observed for the variables: distance from the coast, elevation, mean soil profile pH, and foliar $\delta^{15}N$ (Table 2.5), which were highly correlated with each other as well. The association of pH and soil N capital may reflect soil acidification driven by increased nitrate leaching as soil N availability increases (Chapter 3). Elevation could influence ecosystem processes by shaping locally important micro-climatic and geomorphologic features that affect the spatial distribution of plant species and fire disturbance across the landscape. Distance from the coast may be associated with other factors which in turn may influence soil N storage. Sea salt inputs decrease further from the ocean (Bockheim and Langley-Turnbaugh 1997), and the fog belt, which stretches several miles inland, provides additional moisture inputs close to the coast (Franklin and Dyrness 1973). The strong relationship between soil N capital and foliar $\delta^{15}N$ (Figure 2.2) suggests that as soil N increases the isotopic signature of plant-available N in the soil trends toward that of the atmosphere. A common theme may influence the correlation of these four site characteristics - distance from the coast, elevation, mean soil profile pH, and foliar $\delta^{15}N$ - with soil N capital.

The correlation between soil N capital and these four variables may suggest a possible influence of historical red alder colonization. Red alder presence can impart greater soil organic matter accumulation (Franklin et al. 1968, Tarrant and Miller 1963) and soil N enrichment (Binkley et al. 1992a, Tarrant et al. 1969, Cole et al. 1990) to a site. Previous stand composition data were only available immediately before current plantation initiation, and red alder was present on all but one of the N-rich sites prior to planting (Table 2.6). Although historical stand composition cannot be reconstructed for the small scale of our study sites, the likelihood of historical red alder presence can be determined by examining site characteristics and broad scale disturbance history of the Coast Range. Red alder occurs most prevalently below 450 m (Harrington et al. 1994) and its site index has been found to decrease with elevation (Harrington and Courtin 1994). The percent cover of red alder in Coast Range watersheds may also increase with proximity to the coast (Compton et al. 2003). Thus, historical red alder presence may have been more probable in warmer, lower-elevation areas, which are often found closer to the coast than the crest of the Coast Range.

Correlations of foliar δ^{15}N and mean soil profile pH with soil N capital may also indicate the role of varying red alder N inputs to soil. The trend in foliar δ^{15}N with soil N capital may reflect increasing plant uptake of N with an isotopic signature near to that of the atmosphere (a trend described more fully in the next section). Similarly, the decrease in soil pH with elevated nitrification and nitrate leaching across the N gradient is characteristic of red alder effects on soils (Cole et al. 1990, Van Miegroet and Cole 1985, Binkley and Sollins 1990, Van Miegroet and Cole 1984). Although red alder does not currently dominate any of these stands, residual red alder N inputs could be providing the opportunity for high rates of nitrification and soil acidification. A similar legacy of elevated soil inorganic-N availability has been observed for a decade after cessation of inorganic-N fertilization of Douglas-fir in the region (Homann et al. 2001).

Historical patterns of disturbance could also affect soil N storage. Although fire effects on the stand scale are not known, fire appears to have occurred in either the 19th or 20th centuries in the landscapes of nine of the ten sites (Zybach 1993). Interestingly, site 39, which was the only site located in a landscape that did not experience fire in the last two centuries, was the only site that did not have red alder in its previous stand composition. Differing disturbance histories across these sites could influence soil N storage, as red alder is a pioneering species that often colonizes recently disturbed landscapes (Harrington et al. 1994). Greater red alder coverage may be indicative of frequent disturbance, as pollen records from lake sediments indicate a historical peak in abundance of red alder that corresponded to periods of increased fire frequency (Long et al 1998). Increased human disturbance of forested landscapes after European settlement may also have promoted more recent red alder colonization (Carlton 1989, Kennedy and Spies 2005). Time since intense disturbance and subsequent soil formation could also affect soil N accumulation, but the impact of soil age may be complicated by the probability of red alder colonization increasing with landscape age. Although stand-replacing wildfire may cause short-term loss of N (approximately 1000 kg $N \cdot ha^{-1}$, Giesen 2005), the long-term effect of such disturbance may be N accumulation by the promotion of red alder, with the potential to fix over 10,000 kg $N \cdot ha^{-1}$ during the 75-100 year lifetime of a stand.

Across these sites, soil N capital was correlated with site characteristics that may either indicate red alder habitat suitability or the effect of red alder N inputs. Other studies have posited that the heterogeneity of alder presence may be responsible for the variability of nitrate seen in Coast Range and Alaskan streams (Wigington et al. 1998, Compton et al. 2003, Stottlemyer 1992), and here I suggest that historic forest vegetation may also be responsible for the range in soil N capital in the Coast Range.

Natural abundance $\delta^{15}N$

Foliage, needle litter, and forest floor became more $\delta^{15}N$ enriched with greater soil N capital (Figure 2.2). Plant $\delta^{15}N$ signatures suggest a trend toward the atmospheric $\delta^{15}N$ of 0 $^{o}/_{oo}$ as sites become more N-rich. Foliar $\delta^{15}N$ fell within the range of values from one study of Coast Range Douglas-fir (Scott et al. in press). Foliar $\delta^{15}N$ was significantly depleted relative to that reported by Binkley et al. (1985), whose values are globally inexplicable by virtue of being enriched relative to soil $\delta^{15}N$ (Peter Högberg and Dan Binkley, *personal communication*). Soil $\delta^{15}N$ signatures did not exhibit a linear trend with N capital, suggesting that many competing processes may be operative. Surface soil $\delta^{15}N$ values were comparable to previous natural abundance $\delta^{15}N$ work in the Coast Range (Scott et al. in press, Binkley et al. 1985). The elevated $\delta^{15}N$ signature at depth in relation to surface soils is consistent with the hypothesis that recalcitrant organic matter, containing residual heavy N after the loss of light mineralized N, may accumulate at depth (Nadelhoffer and Fry 1994, Martinelli et al. 1999).

There are several factors that influence the isotopic signature of plant N: rooting zone depth, N availability, timing and form of N uptake, mycorrhizal fractionation, and soil organic matter $\delta^{15}N$ (Robinson 2001). Greater plant uptake of N from shallow depths could lead to an incorporation of relatively isotopically light N. Although rooting depth was not evaluated in this study, root biomass N as estimated by the DF.HGS model did not vary significantly across the sites (Table 2.9). Foliar $\delta^{15}N$ has been seen to increase with net N mineralization as plants take up more isotopically light N made available through mineralization (Garten and Van Miegroet 1994). In particular, greater plant uptake of nitrate could lead to ^{15}N depleted biomass as nitrate-N is often lighter in relation to ammonium-N due to further microbial processing. Microbial preference of nitrate-N or ammonium-N was inconclusive, and although nitrate-N fluxes were higher at N-rich sites (Figure

2.9), plant $\delta^{15}N$ was elevated in relation to N-poor sites. N availability can also influence mycorrhizal growth, as N fertilization has been noted to decrease mycorrhizal biomass (Wallenda and Kottke 1998). Indeed, mycorrhizal mats were found only at the three lowest soil N sites (personal observation), suggesting plant N at N-poor sites could be more depleted in ^{15}N through mycorrhizal processing (Hobbie et al. 2000). The correlation between foliar $\delta^{15}N$ and %N may also be brought about by decreasing mycorrhizal influence as soil N increases (Hobbie et al. 2000). Although reduced mycorrhizal influence as soil N increases may be partly responsible for plant $\delta^{15}N$ patterns, foliage – soil $\delta^{15}N$ enrichment was not related to soil N capital, suggesting differences in the fractionation between soil and foliage cannot fully explain the plant $\delta^{15}N$ pattern across these sites. Ecosystem N stocks that influence N cycling rates may also influence rooting depth shifts and the potential for mycorrhizal colonization and thus plant $\delta^{15}N$ patterns.

Variations in isotopic signatures of soil organic matter across the sites could also account for the increasing trend in plant $\delta^{15}N$ with soil N capital. Red alder is a N_2-fixing species possessing root nodules in which bacteria of the genus *Frankia* fix N from the atmosphere with little discrimination between isotopes. Red alder litter N content is far greater than that of other tree species in the region (Swanston and Myrold 1997), and red alder tissues have an isotopic signature near to that of the atmosphere, with an average of $-1^{o}/_{oo}$ for the Coast Range (Scott et al. in press). Thus litter inputs and root N exudation by red alder could lead to the incorporation of isotopically light, N-rich organic matter in soil. Longer periods of historical red alder colonization on a site could lead to a greater accumulation of soil N capital (Binkley et al. 1992a), with the current stand reflecting the isotopic signature of historical N inputs. The trees at N-rich sites may therefore be gaining access to N imparted by a legacy of red alder colonization.

The curvilinear relationship of ecosystem δ^{15}N and weighted soil N concentration (Figure 2.3) suggests competing influences of N inputs and losses on ecosystem δ^{15}N. The initial decreasing trend in δ^{15}N is consistent with an increasing influence of isotopically depleted red alder N inputs as soil N increases. This decreasing trend is disrupted, however, at the most N-rich sites, consistent with accelerated losses of isotopically depleted N (Högberg and Johannisson 1993). Nitrification fractionates in favor of the lighter N isotope, resulting in production of nitrate that is depleted in ^{15}N relative to soil organic matter (Högberg 1997). An increase in nitrate leaching across the gradient (Figure 2.9) is likely associated with ^{15}N depleted losses, and would account for the increased soil δ^{15}N at N-rich sites. In this way, inputs of fixed N from red alder may be a dominant mechanism responsible for declining ecosystem δ^{15}N signatures initially across the N gradient, followed by enrichment in ecosystem δ^{15}N at particularly N-rich sites due to losses of isotopically light N (Högberg 1990). Ecosystem δ^{15}N did not possess a relationship with soil N capital, suggesting the complexity of these δ^{15}N signatures is not solely due to the variation in the soil N pool. Plant δ^{15}N seems to reflect the isotopic signature of the plant available soil N pool which is more heavily influenced by atmospheric N influence as soil N capital increases, but total ecosystem $\delta^{15}N$ may also indicate increasing losses of isotopically light nitrate at N-rich sites.

Across all sites, Douglas-fir needle litter N was lighter than foliar N. Before senescence, trees actively resorb many nutrients as a conservation strategy. My data suggest that resorption may be a fractionating process in favor of the heavier N isotope, making a needle more ^{15}N depleted before senescence. Metabolic compounds, which are more easily resorbed than structural compounds, may be enriched in ^{15}N because they are composed of reduced amino acids. Protein within a cell tends to be more enriched relative to whole cell composition, as amination can form amino groups that are heavier than the compounds from which they originate (Macko et al. 1987). An increased proportion of enriched metabolic amino N may also explain why foliage from the top of Douglas-fir canopies (exposed to light) is more $\delta^{15}N$ enriched than foliage from lower canopy positions (Scott 2004). Following the resorption of isotopically heavy metabolic compounds, senescing needle N may be light relative to that of green foliage, suggesting that structural N compounds in needles are depleted relative to metabolic N compounds.

The outlying ^{15}N depletion in plant pools at site 6 suggests that severe SNC infection of Douglas-fir and western hemlock dominance may be influencing $\delta^{15}N$ isotopic signatures. Western hemlock has greater mycorrhizal colonization than Douglas-fir (Hobbie et al. 2000), suggesting greater isotopic fractionation upon uptake of N from the soil. Additionally, western hemlock has a greater percentage of roots in surface soil than Douglas-fir (Bennet et al. 2002). Here, surface soils are more depleted in ^{15}N than soil deeper in the profile, and N flux through western hemlock biomass may be partly responsible for the ^{15}N depleted signature of the forest floor which through uptake may also be reflected in Douglas-fir foliage. Also Douglas-fir at site 6 have experienced the highest SNC infestation, and mean needle retention is the shortest of all ten sites. Although undocumented, if SNC affected uptake; then mycorrhizal associations could become more critical to tree survival. Whereas soil $\delta^{15}N$ at site 6 fit the pattern exhibited by the entire gradient of sites, the anomalous behavior of foliage at this single site suggests that unusual mycorrhizal processing may have transferred disproportionately more depleted N to trees. The pool and residence time of N are much larger in soils than plants, so long-term patterns would be expected to be exhibited in soil $\delta^{15}N$; therefore the anomalous nature of plant $\delta^{15}N$ signatures is likely to be a more recent phenomenon.

Non-linear feedback of N status on N cycling

Most N biogeochemistry studies evaluate soil N dynamics primarily at the soil surface and pay less attention to deep soils. This approach is justified by the disproportionate accumulation of N in shallow vs. deep soils, a higher fraction of “active” N and greater biological (plant, microbial) activity in surface soils, as well as logistical difficulties associated with studying deep soils. Across our sites, soil N (and C) pools in 0-10 cm surface soils were significantly linearly correlated with total soil stocks, which indicates that (1) sampling of surface soil can be predictive of total soil N and C capital variations across sites similar to ours, and (2) intensive measurements of N cycling processes focused on surface soils across our sites can provide a reasonably unbiased view of site level N dynamics. Below I focus on a series of N biogeochemical dynamics in relation to the gradient in surface soil N.

Soil N mineralization rates and the N returned through litterfall are indicative of N availability (Pastor et al. 1984, Vitousek 1982). However, N cycling may not always be linearly related to N status. Here, two indices of N cycling, litterfall N inputs and net N mineralization, exhibited non-linear relationships with the surface soil N gradient (Figures 2.4 and 2.5). Prescott et al. (2000) found a linear increase in litterfall N inputs along a similarly constructed soil N gradient in the Oregon and Washington Coast Range, although the N gradient in that study spanned only half the range of surface soil N reported here. Indeed litterfall N inputs observed in the current study increase linearly within the span of soil N explored in Prescott et al. (2000). Thus, a tapering off of litterfall N inputs in Coast Range Douglas-fir forests may only be apparent under highly elevated soil N. Under high N conditions, the uptake of nitrate may also be inhibited at the root surface by the accumulation of organic amino compounds in order to avoid N over-nutrition (Rennenburg et al. 1998). If N uptake and productivity decrease at high N sites, litterfall N inputs and N cycling rate may also diminish.

Net N mineralization rates in mineral soil in this study also expressed a non-linear relationship with surface soil N; whereas, Prescott (2000) did not find a significant correlation between mineralization in the forest floor and soil N. Based on the data, I estimate that an N saturation point near 0.50 % surface soil N may be present, above which further increases in soil N may not positively affect N cycling rates. Although the paucity of data at the high N end of the gradient prohibits determination of the direction of the trend, the data do suggest a limit to inorganic-N production. Net N mineralization rates across the ten sites spanned the range of values reported globally, and rates from site 22 in particular exceeded all others globally excepted for several sites in eastern North American forests (Mladenoff 1987, Strader et al. 1989, Nadelhoffer et al. 1983, Gilliam et al. 2001, Sasser and Binkley 1989). The average 0-10 cm soil N pool in the seven sites with net N mineralization exceeding 60 kg N · ha^{-1} · yr^{-1}, was over twice that found in glacial soils with similar mineralization rates (Nadelhoffer et al. 1983), suggesting that greater soil N storage alone does not increase N mineralization rates. The high intersite variability in N cycling rates in the small geographic area of this study is astounding, as the low mineralization rates at my N-poor sites compare with previous work in Coast Range Douglas-fir forests (Myrold et al. 1989). Prescott et al. (2000) suggest that increasing N availability may continue to have a positive feedback on N-rich sites; however, our study shows that there may be a limit to the development of positive feedbacks and a “runaway” N cycle in forests. Variability in N cycling rates and N loss mechanisms may increase as an ecosystem approaches N saturation (Aber et al. 1998). The leveling off of N mineralization at the high N end of the gradient suggests that microbial enzymatic systems may no longer be N limited and additional inputs of N may not increase N mineralization. Patterns in net nitrification across the gradient likely reflect changes in autotrophic nitrifier function because Douglas-fir dominated sites have not been observed to have appreciable heterotrophic nitrification (Stark and Hart 1997).

Other studies have noted a limitation to N mineralization as N availability increases (Aber et al. 1998, Matson et al. 2002, Tietema et al. 1998). The non-linearity in N mineralization may arise through either a change in microbial enzymatic function with increased N availability, a limitation in an available carbon source, or a decrease in aboveground litter inputs. Microbial production of humus degrading enzymes may be suppressed at high levels of N (Fog 1988). For example, several years of heavy N additions resulted in no discernible increase in N mineralization from the soil organic matter pool under Corsican pine (Miller et al. 1976). Additionally, elevated N additions could lead to a non-linear response in mineralization due to changes in the chemistry of soil organic matter, causing reduced efficiency of extracellular enzymes in the decomposition process (Aber et al. 1998). Increased N inputs can even facilitate the stabilization of organic matter, causing less mineralized N to be produced (Swanston et al. 2004). If sites at the high N end of the gradient historically received a higher quantity and quality (lower C:N ratios) of organic matter inputs, as could arise from extended periods of red alder colonization, an increase in the relative amount of N in litter could reduce the efficiency of microbial enzymatic processes involved in decomposition. The microbial breakdown of lignin requires both N and phosphorus (P); if N additions increase above critical levels, microbes can become P limited and decomposition will not increase (Sinsabaugh et al. 1993). The tapering of net N mineralization rates suggests further N availability will not cause a runaway N cycle.

The limit to net nitrification rates in the later half of the gradient most likely arises from the near total consumption of ammonium-N by nitrifying bacteria. Only the two lowest N sites exhibited nitrification of less than half the mineralized N. Nitrification can often be the dominant fate of most mineralized N in N-polluted forests (Jussy et al. 2000, Gilliam et al. 2001). The elevated percent nitrification found in eight of these sites exceeds that of many eastern US forests (Gilliam et al. 2001). Our net nitrification rates span a similar range found by Pastor et al. (1984) in Wisconsin; and net nitrification rates were very high in several sites, in contrast to the net nitrate immobilization observed in previous work in Coast Range sites (Myrold et al. 1989). The general conception of western Oregon Douglas-fir forests as systems without the appropriate site conditions for nitrification and high nitrate mobility (Sollins et al. 1980, Myrold et al. 1989) should be revised to acknowledge the wide variability in N availability and nitrification potential in the Coast Range. These elevated nitrification rates along with increased nitrate leaching suggest the possibility of N production beyond biological demand in some of these systems.

The correlation between annual litterfall N inputs and annual mineralized N suggests that the increased delivery of N to the forest floor has a positive effect on the degree of inorganic-N production in surface mineral soil, and increased N availability in mineral soil positively affects plant productivity. Although not all studies report a significant relationship between litterfall N inputs and net N mineralization (Prescott et al. 2000, Scott and Binkley 1997), linear relationships between N returned in litterfall and mineralization rates have been observed across several forest types (Vitousek et al. 1982, Pastor et al. 1994, Reich et al. 1997). Perhaps the broad range of net N mineralization rates across these sites enabled the elucidation of this relationship.

Gross rates of N production and consumption fell within the range of values reported for undisturbed forests of the Pacific Northwest (Stark and Hart 1996); however, both gross N mineralization and nitrification rates were at the low end of values reported for terrestrial ecosystems globally (Booth et al. 2005). Gross N mineralization was uncorrelated with soil N content and soil moisture in contrast to many previous findings (Booth et al. 2005). Although differences in gross nitrification were not apparent across the gradient, microbial production of nitrate-N was consistently greater than annual N inputs from litterfall (Tables 2.7 and 2.10). The magnitude of nitrate-N cycled through microbial biomass may thus be much greater than that which is taken up by plants.

Microbial uptake of the ^{15}N label was highly variable, and microbial preference for $^{15}NH_4^+$ or $^{15}NO_3^-$ was inconclusive. The raw data indicate greater concentrations of the label in some of the unfumigated samples; therefore, microbes may not have taken up much of the label, but after fumigation lighter N released from the lysed cells could have decreased the ^{15}N concentration. Two standard errors of the diffusion samples were applied to data values to conclude if the negative values were just a factor of mass spectrometer error. Although some microbial ^{15}N uptake values became positive after this correction, other differences in unfumigated and fumigated samples appeared to be beyond this reasonable error. Sites with the highest soil C:N had consistently positive microbial uptake ^{15}N values, indicating higher C:N ratios may encourage microbial immobilization of the added ^{15}N label. In contrast, low C:N sites possessed microbial ^{15}N uptake values near to and less than zero, qualitatively suggesting microbes at these sites may not be limited by N and did not take up much of the label. Microbial nitrate-^{15}N uptake values were often less negative than ammonium-^{15}N uptake values. The addition of the ammonium-^{15}N label effectively doubled the extractable ammonium pool in the soil across all sites, but the variability in ambient extractable nitrate across these sites caused the nitrate label to increase the extractable nitrate-N pool nearly 100-fold in some sites. Therefore, greater recovery of nitrate-^{15}N in microbial biomass could be caused by flooding the soil system with nitrate high above ambient levels (Stark and Hart 1997).

The disparity between net and gross N mineralization rates possibly suggest differing pathways of inorganic-N consumption across the sites. Two sites, 20 and 7, with the highest gross nitrate consumption exhibited the lowest rates of net nitrification. Site 20 exhibited virtually no net nitrification and low net N mineralization but possessed highly elevated gross production and consumption of ammonium-N. Microbial ^{15}N uptake at site 20 was also consistently positive, suggesting this low N site may experience high microbial immobilization of inorganic-N. The significant pattern in net N cycling rates across the soil N gradient cannot be explained by either the gross production or microbial consumption of inorganic-N. Re-immobilization of mineralized-N by microbial biomass can lead to this lack of correlation between gross and net N mineralization rates (Davidson et al. 1992). Net rates were determined from values averaged over an entire year, while gross rates were averaged from just three dates. Perhaps seasonal variation missed in the gross rate measurement is partly responsible for the lack of relationship between gross and net rates.

Plant response to N availability

Aboveground N production increased linearly with mineralization (Figure 2.6) yet displayed a curvilinear relationship with surface soil N. Aboveground N production has previously been observed to increase with mineralization (Pastor et al. 1994, Reich et al. 1997). As mineralization rates also possessed a non-linear relationship with soil N (Figure 2.4), further increases in soil N capital beyond a critical level do not appear to feedback positively on microbial enzymatic systems and plant productivity. Annual plant N production decreased at very N-rich sites, suggesting a decline in productivity at N-rich sites. If soil N capital exceeds a pool size above which N mineralization no longer increases, plant productivity may be limited by the availability of other nutrients (Chapter 3).

The linear relationship between net N mineralization and foliar N concentration (Figure 2.7) suggests plants may be responding directly to inorganic-N being made available by microbial processes. Increases in N mineralization have previously been associated with increases in foliar N (Scott and Binkley 1997). Foliar N in all but the two lowest soil N sites exceeded 1.4% N, which is considered above the threshold of N-limitation in coastal Oregon Douglas-fir

(Hopmans and Chappell 1994). Photosynthetic capacity displays a curvilinear relationship with foliar N (Manter et al. 2005), reaching a max around this same critical N level, above which N accumulates in soluble proteins (Bauer et al. 2004). Previous work has suggested that foliar N could be utilized as an indicator for the likely success of stand fertilization (Peterson and Hazard 1990, Hopmans and Chappell 1994). If soil N increases to a level above which it no longer stimulates N mineralization, positive effects on growth may not be seen.

Douglas-fir at low N sites resorbed close to 40% of N from foliage and may have more efficient resorption than at high N sites because the N supply in the soil is relatively limited (Killingbeck 1996). Efficient nutrient resorption can be considered an adaptation to nutrient poor sites (Chapin 1980). Additionally, reduced resorption of N has been seen in response to increasing ecosystem N availability through fertilization (Flanagan and Van Cleve 1983). The decrease in N resorption efficiency with mineralization (Figure 2.8) suggests that as more N becomes available to plants, less foliar N is retained before senescence. As N availability increases, plants may facilitate continued development of this elevated N availability by dropping more N-rich litter. Increased nutrient availability by fertilization has been found to initially increase needle retention, but long-term effects appear to be elevated litterfall and decreased retention of needles (Gower et al. 1992). Additionally, N resorption could be decreasing at N-rich sites because of the influence of SNC. Mean needle retention in these stands explained the largest amount of variation in SNC severity (Maguire et al 2002). Site 6 in particular has a high SNC infection rate (Oregon Department of Forestry *personal* *communication*), and mean needle age is only 1.1 years (Perakis et al. 2006). This short retention time perhaps does not allow trees to resorb adequate N before senescence. High mineralization rates or an increase in environmental stressors may facilitate a decrease in N resorption efficiency.

The amount of N stored in living aboveground biomass was small compared to that in soil, ranging from 0.53 to 1.80% of total ecosystem N. The distribution of N in aboveground compartments was highly variable and not correlated with soil N (Table 2.9), suggesting the rate of plant N uptake may vary across the gradient but the relative distribution of N in plant tissue types is not strongly influenced by N availability. Forest floor N concentration and pools decreased along the gradient presented in Prescott et al. (2000), suggesting more rapid decomposition with increasing N availability. Forest floor N concentrations and pool sizes were conservative across this soil N gradient, suggesting degradation of organic matter in the forest floor may not be responding to increases in N availability in mineral soil. Indeed, N fertilization in Coast Range forests reduces decay rates of Douglas-fir litter across a wide range of initial litter N content (Matkins and Perakis, unpublished data). Forest floor decomposition patterns across the gradient could also be obscured by the curvilinear increase in litterfall N inputs.

N leaching

Nitrate-N leaching spanned a wide range and generally increased across the soil N gradient (Table 2.7 and Figure 2.9). High variability of nitrate across watersheds is a characteristic feature of Coast Range streams (Wigington et al. 1998). The loss of nitrate-N was exceptionally high at several N-rich sites; nitrate leaching from site 16 in particular approaches that found in pure alder stands in the Oregon Coast Range (Binkley et al. 1992a) and watersheds with a high proportion of red alder (Compton et al. 2003). Nitrate concentrations in Oregon Coast Range streams are often elevated relative to other forested watersheds in the Pacific Northwest due to red alder cover (Compton et al. 2003). Although red alder does not dominate any sites reported here, previous cover by red alder could have imparted significant N legacies in the soil that continue to influence nitrate leaching. Rates of nitrate leaching at the low end of the soil N gradient (0.07 – 0.09 kg $N \cdot ha^{-1} \cdot yr^{-1}$) were similar to other studies in Douglas-fir forests in the Pacific Northwest (Sollins et al. 1980, Binkley et al. 1992a) although not as low as some loss rates from the Cascades (Vanderbilt et al. 2003); however, nitrate-N at several high N sites was not tightly conserved, suggesting nitrate production above biological demands. Elevated net nitrification in the summer months (Appendix Table A1.1) and reduced nitrate leaching due to the drying out of soils could lead to summer accumulation of nitrate in soils. The flush of nutrients seen during autumn rain events (Wigington et al. 1998) could be a result of mobilizing nitrate that accumulated during summer.

The variation in nitrate-N was responsible for the differences in soil water N speciation observed across the gradient (Figure 2.11). The elevated leaching of nitrate at high N sites not only increased the quantity of inorganic-N leaving the system but also the relative abundance of different N species in soil water. As the rooting zone is concentrated in the top 20 cm of soil, concentrations of nutrients in soil solutions from the shallow lysimeters may reflect what species are available for plant uptake and/or leaching. The lowest N sites exhibited ammonium-N leaching as high as nitrate-N. Previous watershed analyses have found correlated nitrate-N and ammonium-N leaching fluxes (Lewis et al. 1999); however, increases in nitrate-N leaching across this soil N gradient were not tracked by either ammonium-N or DON. The varying speciation of N in soil solution, driven by differences in nitrate-N leaching, may have the effect of supporting different microbial communities adapted to taking up specific forms of inorganic-N. The relative microbial uptake of inorganic-N species was supposed to be elucidated by ^{15}N pool dilution; however, no conclusions of inorganic-N preference could be made as there was low uptake of ^{15}N into microbial biomass. Additionally, DON export from a nearby Coast Range watershed was found to increase with nitrate export (Compton et al. 2003); however, soil water DON did not vary with either soil N or nitrate leaching in my study. Land cover in the Compton et al. (2003) study included a high percentage of red alder, which can directly impart greater quantities of organic matter to an ecosystem through higher litterfall and production rates than a pure conifer stand. Additionally, my study may have had an insufficient sample size to detect the shallow slope of a DON increase. DON did comprise a smaller proportion of total N in soil solution after N additions in the Harvard Forest (Currie et al. 1996) and in Chile (Perakis et al. 2005). When N accumulates in soil, non-linear increases in nitrate leaching can occur once a threshold N retention is attained (Perakis et al. 2005). The wide range in nitrate loss and the conservation of DON across this gradient is likely caused by variations in nitrification potential due to differences in soil N pools.

Despite the apparent leveling-off of inorganic-N production, nitrate leaching at some high N sites was highly elevated. A connection between nitrate production and leaching would be expected as most nitrate exported in streamwater has been cycled through microbes (Pardo et al. 2004). However, a decoupling between nitrate production and leaching may appear to be happening at several sites (Figure 2.10). One site in particular, 22, displayed the highest net nitrification rates, nearly 100 kg $N \cdot ha^{-1} \cdot yr^{-1}$, yet nitrate-N leaching was consistently less than 5 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (Table 2.7). This imbalance between nitrate production and leaching suggests differing N loss mechanisms or rates of uptake. Additionally, base cation stores at site 22 were higher than those found at other sites with elevated nitrification (Chapter 3). The acidifying potential of elevated nitrification should in theory be followed by depleted base cation reserves and high rates of nitrate leaching, both of which are not seen at site 22. Perhaps the combination of a high pH buffering capacity and elevated biological demand for nitrate keep leaching rates low at site 22. Previous work in the Coast Range also failed to find a correlation between N mineralization rates and N leaching (Binkley et al. 1992a).

Variation in microbial uptake of nitrate-N does not seem to account for leaching differences between two high N sites, 16 and 22. Gross nitrate production and consumption, microbial biomass N pools, and microbial uptake of nitrate-N were not significantly different between sites 22 and 16 (Tables 2.7 and

2.8). Inorganic-N uptake preference between the microbial communities at the two sites also does not seem to be significantly different between the two sites. Plant N uptake, defined here as fine litterfall N return plus N in annual wood production (Binkley et al. 1992a) and calculated using a stand growth model (Weiskittel 2006), was actually higher at site 16 than 22 (Table 2.10). Although litterfall rates were similar between the two sites, modeled wood production at site 16 is greater. Therefore, differences in plant and microbial N uptake cannot account for the discrepancy in nitrate leaching between sites 16 and 22. Other factors may be responsible for the imbalance between nitrate production and leaching at site 22.

Denitrification capacity was not measured in this study, and denitrification rates previously measured in the Coast Range suggest only a minimal loss of N through this pathway (Binkley et al. 1992a, Myrold et al. 1989). Ecosystem $\delta^{15}N$ at site 22 is elevated compared to that of the high nitrate-N leaching site 16 (Figure 2.3). Greater losses of isotopically light trace N gases from the system could account for more positive ecosystem $\delta^{15}N$ values at site 22. In tropical forests with similar precipitation as these sites, estimates of trace N gas loss reach 8-10 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1}(Houlton et al. 2006), an amount which could partially account for the disparity between nitrate production and leaching at site 22. Therefore, elevated denitrification could potentially be a loss pathway for isotopically light N from site 22 that would not be detected by our sampling.

Soil texture may also play a role in the residence time of soil water moving through ecosystems. Flow path lengths can be a potential influence on nitrate leaching, and longer contact time may provide more time for nitrification and nitrate leaching to occur (Asano et al. 2007). Although lysimeters were installed at random at each site, the soil environment into which they were inserted is uncertain. Differences in microbial and plant uptake of nitrate between sites 16 and 22 cannot fully account for the appreciable disparity in nitrate leaching; therefore, differing soil water flow paths could be causing the apparent disconnect between nitrate production and leaching at site 22. Lysimeters at both site 16 and 22 consistently held vacuum and collected appreciable amounts of water, although the volume of water collected was not recorded. The soil environment is naturally heterogeneous, and lysimeter placement may miss the importance of macropores and other soil profile features that may accelerate the bulk flow of soil solution (Sollins et al. 1980). Randomized lysimeter placement may not have given an adequate survey of soil solution chemistry, and nitrate leaching at site 22 may have gone undetected. Therefore, the imbalance between nitrate production and leaching at site 22 could be a combination of trace N gas loss and variation in the subsurface environment for which our sampling methods were unable to account.

N budget of N-rich sites

Paradoxically, N losses appear to exceed N inputs at several N-rich sites. N inputs are relatively low, as inorganic-N in precipitation is approximately 0.65 kg $N \cdot ha^{-1} \cdot yr^{-1}$ in a nearby Coast Range watershed (NADP OR02) and asymbiotic N_2-fixation in the forest floor can attain up to 1 kg $N \cdot ha^{-1} \cdot yr^{-1}$ (Heath et al. 1988). Nitrate-N losses exceeding 8 kg $N \cdot ha^{-1} \cdot yr^{-1}$ were observed at sites 58, 6, and 39 with even greater nitrate leaching at site 16 (30 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1}). I did not quantify N_2-fixation from occasional red alder (5.1% and 8.2% of total basal area) at sites 58 and 16, respectively. The absence of N_2-fixation estimates could mislead the N budget interpretation for these two sites, but red alder was not present at sites 6 and 39. Forests respond variably to N inputs, but systems receiving < 4 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1} typically do not leach significant amounts of N (Peterjohn et al. 1996). Yet, N losses from these sites may exceed inputs by at least 7 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1}.

Some forests have been observed to have greater N losses than inputs (Johnson et al. 1991, Turner and Singer 1976), but little is known how long these N budget imbalances may persist. Ammonium-bearing bedrock can be an overlooked source of N in rare geographic locations such as the Klamath Mountains in northern California (Dahlgren 1994). Typically watersheds considered to be N saturated do not experience greater N losses than inputs in the northeastern US (Campbell et al. 2004), Europe (Gunderson 1995, Dise and Wright 1995), and Asia (Ohrui and Mitchell 1997). Fernow Experimental Forest in West Virgina has an N output that nearly matches inputs (Peterjohn et al. 1996), and one watershed in Japan displayed N leaching above inputs, attributed to high mineralization rates and low woody N uptake (Ohrui and Mitchell 1997). Although the N budget at my N-rich sites appears to be relatively unique to temperate forest systems, the apparent limitation to net N mineralization rates suggests that losses will not be sustained in the long-term. However, if elevated nitrate leaching at site 16 continued at the present rate, the soil N pool would not be depleted to levels seen at N-poor sites for nearly 300 years. The persistence of greater N output than input is rarely found in aggrading forests and would not be expected to promote ecosystem sustainability.

Conclusions and management Implications

The Coast Range possesses an astounding and globally unique range in soil N capital, N cycling rates, and nitrate leaching. N-rich sites can have net N mineralization rates which exceed those in chronically N-polluted regions of the eastern United States and Europe. Plant δ^{15}N and soil pH patterns, as well as site characteristics (elevation, proximity to the coast) that may promote red alder colonization, were correlated with soil N capital. The range in soil N capital across these ten sites could be a result of many factors, but red alder seems most likely to have imparted a mosaic of N-rich inputs into these soils. Soil N availability appears to feedback positively on N cycling to a point, but not indefinitely, as N stocks do not seem to increase N cycling rates in perpetuity. Plant N uptake appears to respond directly to the amount of N being mineralized, as plant N uptake increased linearly with net N mineralization but possessed a curvilinear relationship with soil N. N availability beyond biological demand may also lead to symptoms of ecosystem N saturation, such as elevated nitrate leaching.

This study demonstrates that some Douglas-fir dominated sites in the Coast Range may indeed be exhibiting signs of excess N availability beyond which N is no longer being tightly retained in the ecosystem. Several N-rich sites even exhibit symptoms of N saturated systems, namely high rates of nitrification and nitrate leaching and reduced aboveground production. Although the concept of N saturation has drawn primarily from studies examining N fertilization or chronic N deposition, systems with high soil N accumulation through N_2-fixation may also become N saturated. Atmospherically-derived N inputs have been thought to leach easily from systems and not accumulate in soils (Johnson 1992); however, the source of N inputs may not be essential in determining the propensity of an ecosystem to accumulate N.

As elevated nitrate-N losses were observed in several of these intact stands, reducing plant uptake through harvesting could cause given greater N losses. A long-term pulse of N release is often not observed following stand harvest in western Oregon (Brown et al. 1973, Martin and Harr 1989) perhaps because of high microbial immobilization (Sollins and McCorison 1981). However, elevated nitrate losses have occurred following clearcutting (Sollins and McCorison 1981, Brown 1972, Harr and Fredriksen 1988). These systems have the potential for high nitrate production and mobility as elevated nitrate losses have been observed following trenching in Pacific Northwest soils (Vitousek et al. 1982). The high mineralization rates and nitrate mobility observed in N-rich sites of this study suggest that the reduction of plant uptake may significantly increase N loss. As the storage of N in aboveground pools is minuscule compared to that in the soil, management activities that negatively impact soil N cycling may be detrimental to ecosystem function. Additionally, some stands may not be N limited and fertilization may not positively affect stand productivity, as many of the sites in this study have large nitrate losses and possess high foliar N concentrations. A cursory observation of an individual Douglas-fir site in the Coast Range may not yield significant insight into the nutrient balance required for forest productivity. The establishment of this soil N gradient provided the chance to study fundamental biogeochemical processes of N cycling across a range of N availability. Even though the Pacific Northwest has not experienced chronic N deposition, elevated N accumulation in the Coast Range can produce areas of local N saturation.

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Figures

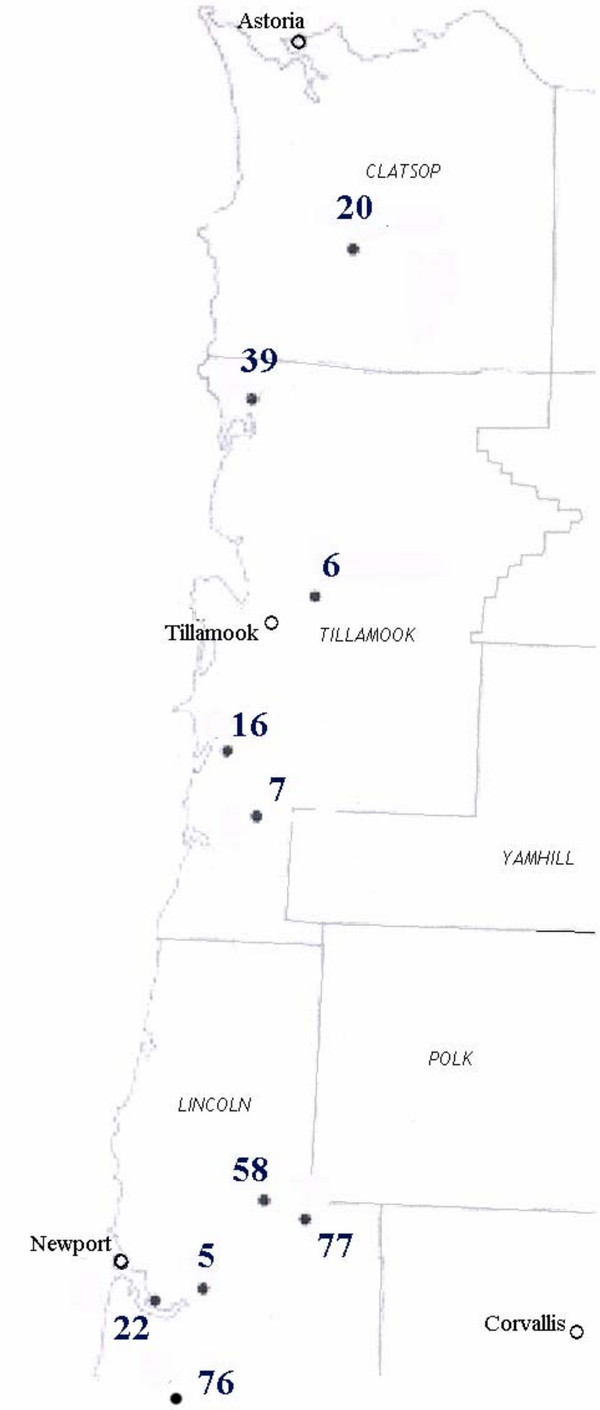

Figure 2.1. Location of study area and sites in western Oregon.

Figure 2.2. Plant $\delta^{15}N$ vs. log soil N capital. Soil N capital was log transformed for normality. Regressions: Foliage, $y = 3.09x - 4.92$, $F_8 = 15.53$, $p = 0.006$; Douglas-fir needle litter, $y = 4.33x - 7.31$, $F_8 = 45.22$, $p = 0.0003$; FF, $y = 2.17x - 4.16$, $F_8 = 24.66$, $p = 0.002$.

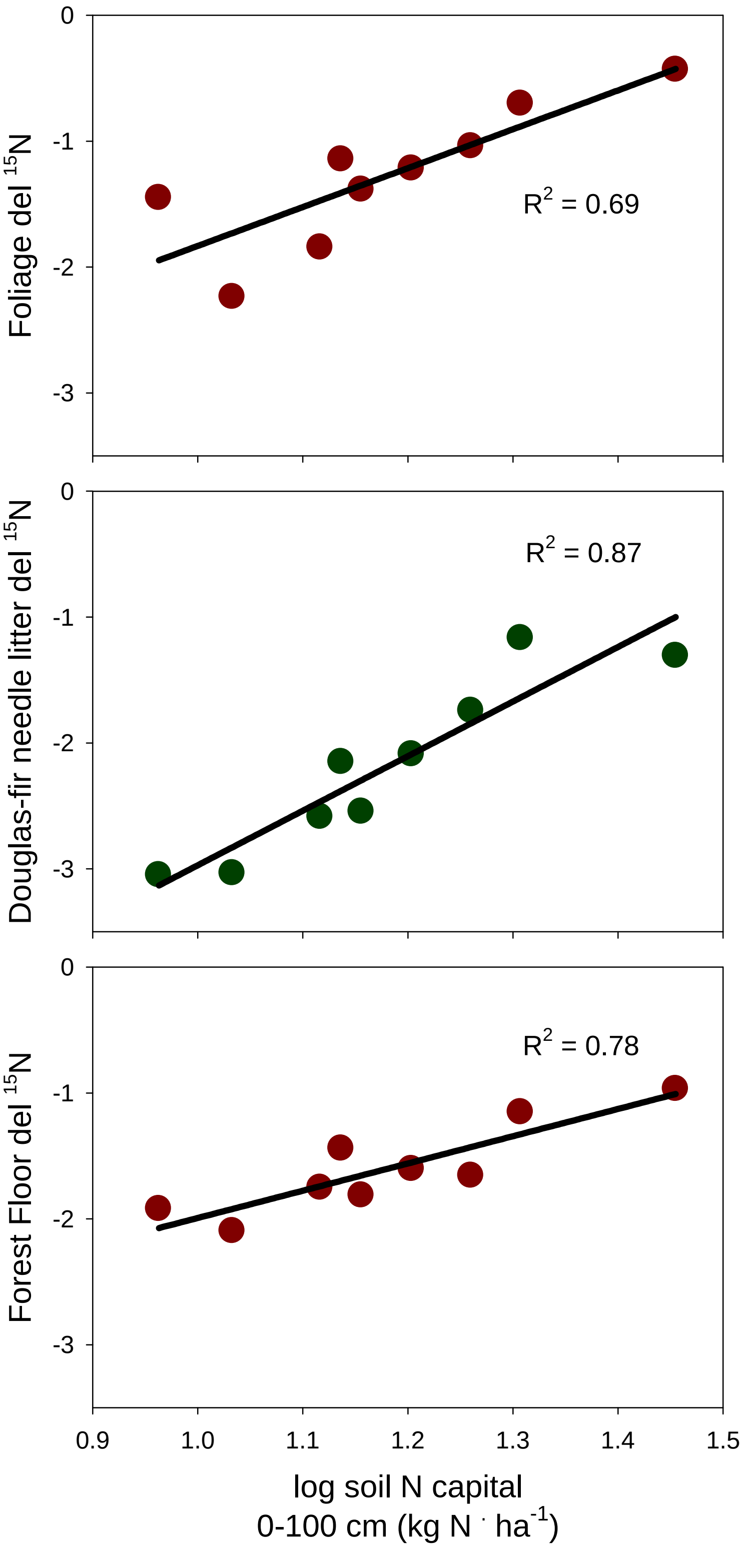
0
-1
-2
-3
Foliage del ^{15}N
R^2 = 0.69
0
-1
-2
-3
Douglas-fir needle litter del ^{15}N
R^2 = 0.87
0
-1
-2
-3
Forest Floor del ^{15}N
R^2 = 0.78
0.9
1.0
1.1
1.2
1.3
1.4
1.5
log soil N capital
0-100 cm (kg N · ha^{-1})

Figure 2.2.

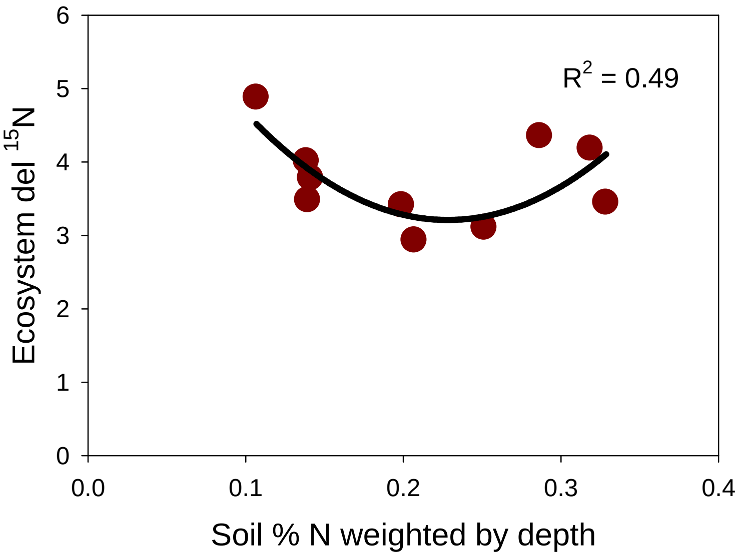

Figure 2.3. Ecosystem δ^{15}N, weighted by the mass of N in ecosystem pools, versus the weighted soil profile %N. Weighted soil %N calculated as the average soil %N of each sampling depth weighted by the contribution of that depth (10cm, 20cm, or 30cm) to the total profile (1m). Regression: $y = 88.69x^2 - 40.49x + 7.93$, $F_9 = 3.32$, $p = 0.097$.

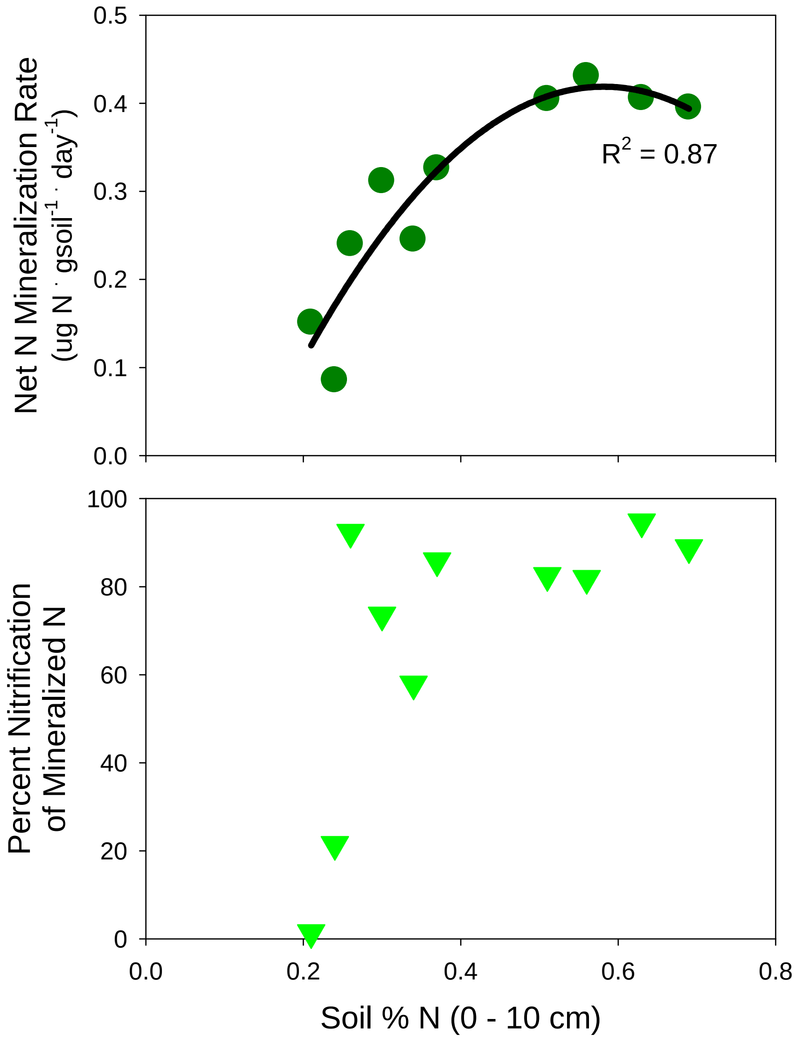

Figure 2.4. Net N mineralization and percent nitrification in 0-10 cm mineral soil across the gradient. Top panel regression: $y = -2.13x^2 + 2.48x - 0.301$, $F_9 = 23.49$, $p = 0.0008$.

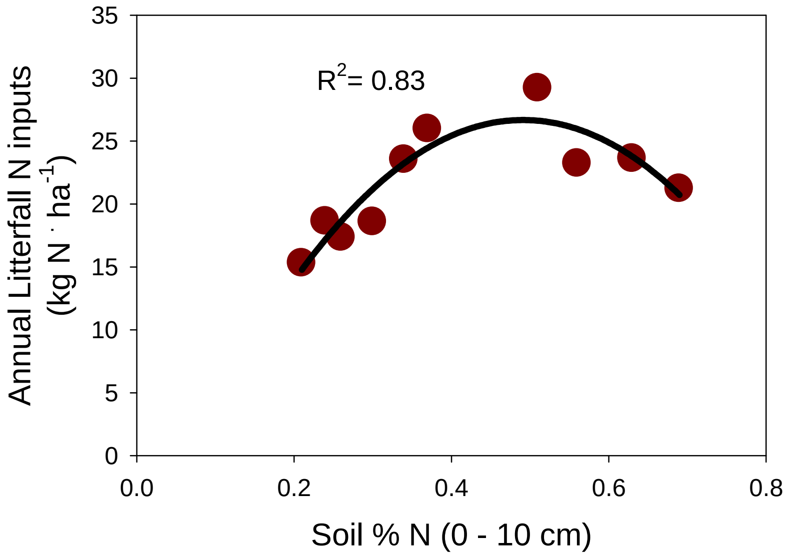

Figure 2.5. Annual inputs of litterfall N across the gradient. Regression: $y = -150.49x^2 + 147.82 - 9.63$, $F_9 = 17.25$, $p = 0.002$.

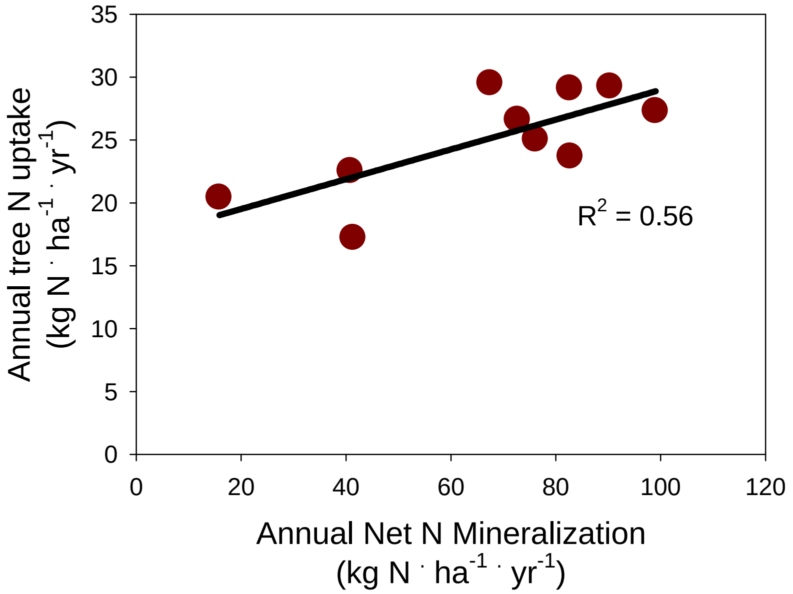

Figure 2.6. Annual tree N uptake increases linearly with net N mineralization in 0-10 cm mineral soil. Regression: $y = 0.12x + 17.1$, $F_9 = 10.35$, $p = 0.01$.

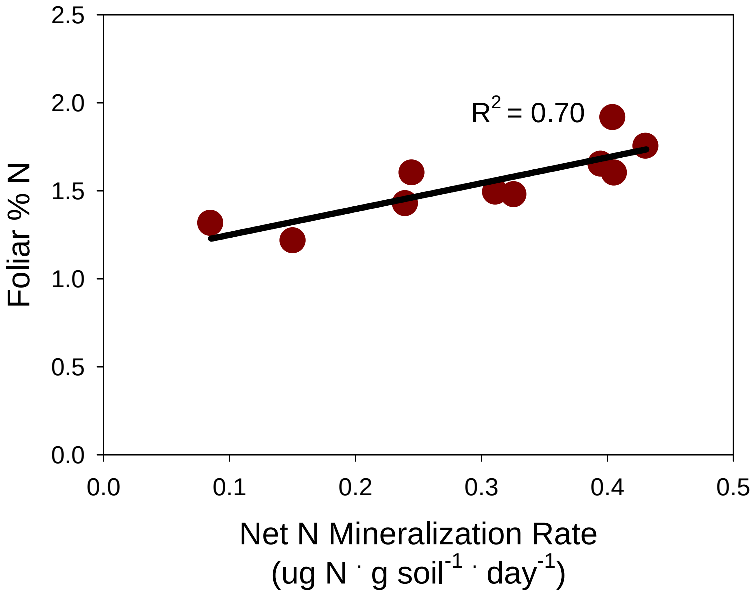

Figure 2.7. Foliar N concentration increases linearly with net N mineralization in 0-10 cm mineral soil. Regression: $y = 1.47x + 1.10$, $F_9 = 18.83$, $p = 0.003$.

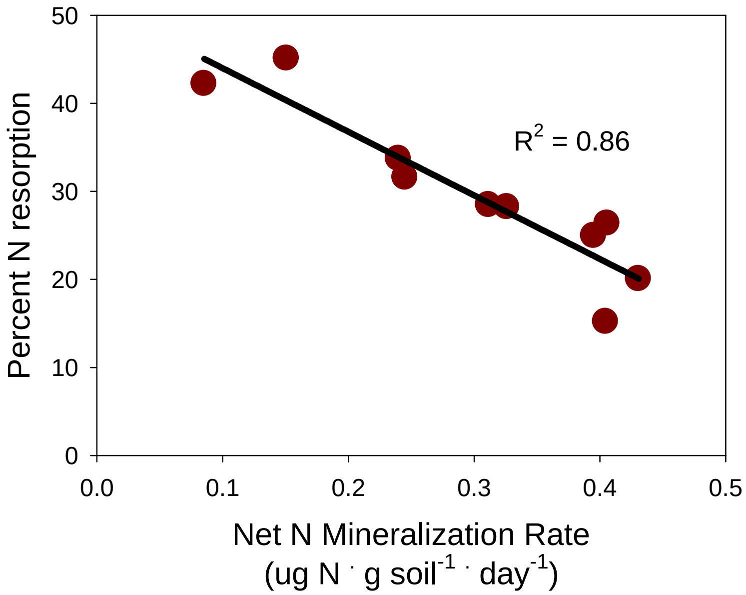

Figure 2.8. % N resorption in foliage decreases linearly with net N mineralization in 0-10 cm mineral soil. Regression: $y = -72.3x + 51.2$, $F_9 = 48.78$, $p = 0.0001$.

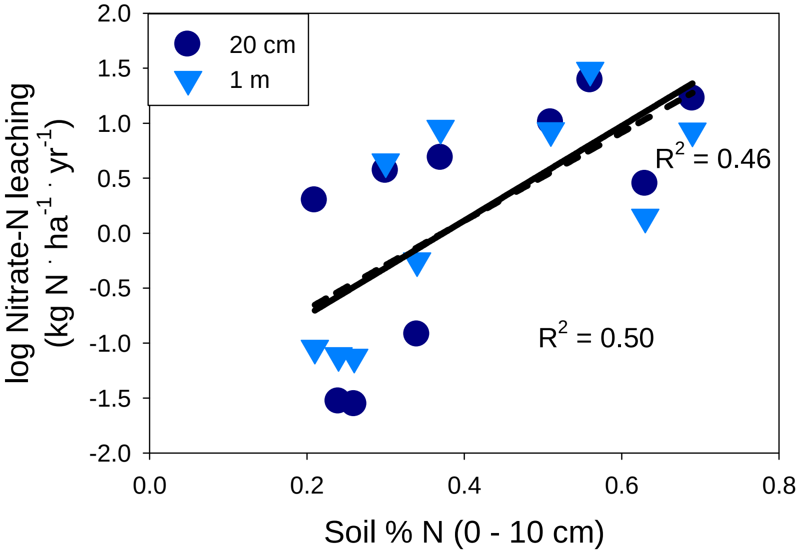

Figure 2.9. Nitrate-N leaching across the gradient. Nitrate-N leaching log transformed for normality. Regressions: solid line 20 cm, log y = 4.30x – 1.61, $F_9 = 6.75$, p = 0.03, $r^2 = 0.46$; dotted line 1m, log y = 4.02x – 1.50, $F_9 = 7.98$, p = 0.02, $r^2 = 0.50$.

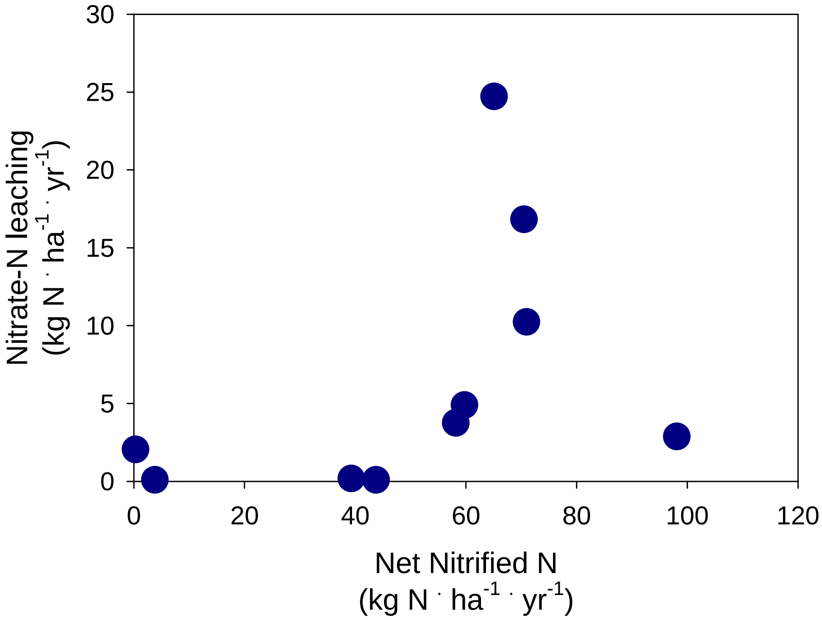

Figure 2.10. Annual nitrate production in 0-10 cm soil vs. leaching at 20 cm.

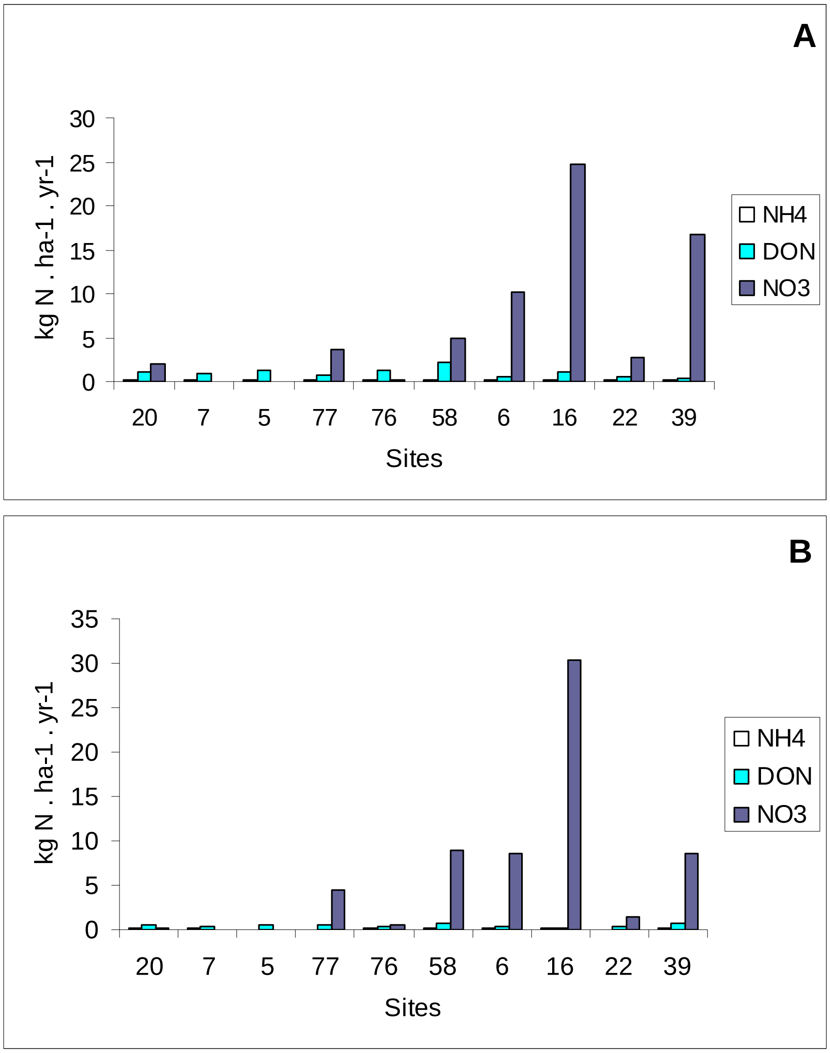

Figure 2.11. Speciation of N leaching at 20 cm (a) and 1 m (b). Sites organized left to right with respect to increasing N in 0-10 cm mineral soil.

Tables

Table 2.1. Site characteristics, arranged in order from low to high soil N.

Site	**Location**	**Soil N (0-10 cm)**	**Soil subgroups[*]**	**Elevation[#]**	**Slope[#]**	**Aspect[#]**
		(%)	**(USDA)**	**(m)**	**(%)**	**(°)**
20	45° 48’ N, 123° 24’ W	0.21	Alic Hapludands	484	5	20
7	45° 8’ N, 123° 39’ W	0.24	Andic Dystrudepts	278	50	8
5	44° 38’ N, 123° 48’ W	0.26	Andic Dystrudepts	322	55	220
77	44° 42’ N, 123° 40’ W	0.30	Andic Dystrudepts	235	10	250
76	44° 35’ N, 123° 48’ W	0.34	Andic Dystrudepts	187	55	90
58	44° 43’ N, 123° 49’ W	0.37	Andic Dystrudepts	80	15	75
6	45° 29’ N, 123° 49’ W	0.51	Andic Dystrudepts	86	10	180
16	45° 10’ N, 123° 55’ W	0.56	Andic Dystrudepts	115	15	240
22	44° 36’ N, 123° 55’ W	0.63	Andic Dystrudepts	155	25	100
39	45° 44’ N, 123° 53’ W	0.69	Andic Dystrudepts	23	10	160

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

[#] Maguire et al. (2002) unpublished data.

Table 2.2. Percent basal area of tree species and total basal area on the ten sites[*].

Site	Douglas-fir	Western Hemlock	Hardwoods[#]	Other conifers[¶]	Total basal area
	% basal area				$m^2 \cdot ha^{-1}$
20	98.4	1.6	0	0	17.21
7	95.8	0.0	4.2	0	25.46
5	100.0	0	0	0	33.85
77	93.9	0.0	6.1	0	42.71
76	98.7	0.0	1.3	0	36.03
58	94.9	0.0	5.1	0	33.58
6	14.8	80.4	2.3	2.5	78.41
16	82.7	1.3	8.2	7.8	29.19
22	98.7	0.0	1.3	0	33.65
39	82.0	18.0	0	0	34.29

[*] Basal area measured in 2004 (all tree stems measured, no minimum dbh), Maguire et al. (2002) unpublished data.

[#] Hardwood species include: red alder, big-leaf maple, and vine maple (*Acer circinatum*).

[¶] Other conifer species include: Sitka spruce and Pacific Silver fir (*Abies amabilis*).

Table 2.3. Soil and forest floor N capital and N distributions by soil depth as percent of total mineral soil N capital in parentheses.

Site	0-10 cm	10-20 cm	20-30 cm	30-50 cm	50-70 cm	70-100 cm	Total¶	Weighted soil %N#	Forest Floor
				kg N $\cdot$ ha^{-1}					
20	1784 (16%)	1592 (15%)	1700 (16%)	2378 (22%)	1264 (12%)	2020 (19%)	10737	0.107	149
7	1426 (16%)	1137 (12%)	900 (10%)	1965 (21%)	1959 (21%)	1787 (20%)	9175	0.139	144
5	1579 (11%)	1919 (13%)	1866 (13%)	4337 (30%)	1826 (13%)	2822 (20%)	14349	0.207	162
77	2323 (16%)	2045 (14%)	1705 (12%)	4350 (30%)	1101 (8%)	2876 (20%)	14399	0.141	108
76	2684 (17%)	2905 (18%)	1892 (12%)	3869 (24%)	2264 (14%)	2366 (15%)	15981	0.140	165
58	2330 (15%)	1569 (10%)	1650 (10%)	3482 (22%)	4441 (28%)	2335 (15%)	15808	0.199	168
6	3156 (17%)	2278 (12%)	2067 (11%)	2429 (13%)	4183 (22%)	4815 (25%)	18928	0.251	181
16	2746 (15%)	2283 (13%)	1695 (9%)	4591 (25%)	4686 (26%)	2243 (12%)	18244	0.329	209
22	3669 (13%)	4695 (16%)	4573 (16%)	6995 (24%)	5026 (18%)	3783 (13%)	28741	0.287	123
39	3688 (17%)	2706 (13%)	2448 (12%)	3300 (16%)	4441 (21%)	4500 (21%)	21083	0.319	163
slope*	-0.00007	0.00009	0.0001	-0.0002	0.0003	-0.0002			
p value*	0.58	0.55	0.43	0.60	0.55	0.45			

* Significance and slope of regressions between the proportion of total mineral soil N in each depth and total soil N capital. ¶ Total mineral soil N capital to 1m. # Weighted soil %N calculated as average soil %N of each sampling depth weighted by the contribution of that depth (10cm, 20cm, or 30cm) to the total profile (1m).

Table 2.4. Soil and forest floor C capital and C distributions by soil depth as percent of total mineral soil C capital in parentheses.

Site	**0-10 cm**	**10-20 cm**	**20-30 cm**	**30-50 cm**	**50-70 cm**	**70-100 cm**	**Total**¶	**Forest Floor**
				Mg C · ha^{-1}				
20	38.26 (21%)	37.13 (20%)	31.37 (17%)	38.92 (21%)	16.98 (9%)	20.89 (12%)	183.54	5.56
7	29.84 (19%)	24.12 (14%)	15.26 (9%)	39.88 (24%)	29.60 (18%)	27.90 (17%)	166.60	6.22
5	31.72 (12%)	36.05 (13%)	36.99 (14%)	81.93 (30%)	33.62 (12%)	52.30 (19%)	272.60	5.81
77	37.47 (18%)	33.23 (16%)	25.34 (12%)	59.50 (29%)	13.23 (7%)	34.71 (17%)	203.47	3.48
76	43.54 (19%)	45.58 (20%)	27.46 (12%)	60.67 (26%)	29.24 (13%)	26.10 (11%)	232.57	6.86
58	40.87 (15%)	26.05 (10%)	27.36 (10%)	58.51 (22%)	75.98 (29%)	35.86 (13%)	264.63	5.89
6	46.34 (17%)	33.24 (12%)	32.97 (12%)	33.49 (12%)	59.48 (22%)	65.59 (24%)	271.12	4.68
16	44.23 (14%)	35.69 (13%)	29.43 (10%)	78.35 (26%)	78.31 (26%)	39.25 (13%)	305.26	4.85
22	53.53 (13%)	72.57 (17%)	68.64 (17%)	100.28 (24%)	73.27 (18%)	44.89 (11%)	413.18	4.80
39	77.40 (20%)	56.97 (15%)	47.10 (12%)	56.79 (15%)	75.98 (20%)	70.75 (18%)	384.99	7.29
slope*	-0.015	-0.007	0.008	-0.02	0.04	-0.002		
p value*	0.24	0.65	0.52	0.45	0.24	0.92		

* Significance and slope of regressions between the proportion of total mineral soil C in each depth and total soil C capital. ¶ Total mineral soil C capital to 1m.

Table 2.5. Correlations between soil N capital and site characteristics.

Potential Correlates	**log Soil N Capital (1m)[©]**	
	r	**p-value[*]**
Elevation (m)	**-0.61**	**0.06**
Distance from coast (miles)	**-0.76**	**0.01**
Slope (%)	NS	0.57
Aspect (°)	NS	0.24
Clay (%)	NS	0.88
Soil moisture (%)	NS	0.16
MAT (°)	NS	0.54
MAP (mm)	NS	0.42
pH[$]	**-0.71**	**0.02**
Foliar δ^{15}N[#]	**0.78**	**0.01**
Foliage to soil δ^{15}N enrichment[#][¶]	NS	0.19
Soil δ^{15}N[¶]	NS	0.76
Stand Age	NS	0.85

[©] Soil N capital log transformed for normality.
[*] Correlations significant at $p < 0.1$ denoted by bold type.
[$] Mean soil profile pH.
[#] Site 6 not included.
[¶] 0-10 cm mineral soil.
NS, correlation not significant.

Table 2.6. Climatic and site characteristic variables.

Site	MAP[©]	MAT[©]	Clay (0-20 cm)	Soil Moisture[¥] (0-10 cm)	Stand Age[¶]	Previous stand composition[#]	Soil pH[*]	Distance from Coast
	(cm)	(°C)	(%)		(yr)			(miles)
20	231	9.1	26.25	36.16	23	DF, Brush, RA	5.42	27.8
7	180	10.7	47.50	33.85	32	DF,RA	5.65	15.8
5	173	11.2	25.00	33.31	30	RA,DF	5.61	10
77	158	10.8	40.00	32.23	29	RA,DF	5.21	19.8
76	172	11.4	32.50	31.19	27	RA,DF	4.94	10.2
58	175	10.8	36.25	36.31	24	RA,DF	5.03	12.4
6	209	10.3	32.50	40.35	25	MC, RA	4.49	6.5
16	169	10.7	38.75	38.99	27	RA,SS	4.70	2.8
22	155	10.6	28.75	37.60	30	RA,DF	4.96	5
39	200	10.3	38.75	49.01	28	WH	4.55	2.8

[#] Abbreviations: DF = Douglas-fir, Brush = mixed shrubs, RA = red alder, MC = mixed conifer, WH = western hemlock, SS = Sitka spruce. [*] Soil profile pH calculated as arithmetic mean of all depths. [¶] Maguire et al. (2002) unpublished data. [©] MAP and MAT estimated from the PRISM digital elevation model (PRISM Group, Oregon State University, http://www.prismclimate.org, created 4 Feb 2004). [¥] Soil moisture values are average annual moisture in 0-10 cm mineral soil.

Table 2.7. N cycling rates and nitrate leaching.

Site	**Net N Mineralization**	**Net Nitrification**	**Litterfall N inputs**	**Wood N uptake**[#]	**Nitrate-N flux (20 cm)**	**Nitrate-N flux (1 m)**
			kg N · ha^{-1} · yr^{-1}			
20	41.38	0.48	15.30	1.92	1.984	0.090
7	15.86	3.97	18.62	1.80	0.029	0.077
5	40.85	43.92	17.34	5.20	0.028	0.074
77	82.79	58.33	19.49	4.19	3.695	4.449
76	72.72	39.47	23.52	3.10	0.120	0.561
58	67.50	59.91	25.96	3.56	4.838	8.981
6	90.37	71.13	29.19	5.06	10.181	8.543
16	82.66	65.27	23.22	5.89	24.656	30.321
22	99.05	98.26	23.61	3.69	2.812	1.398
39	76.17	70.66	21.21	3.69	16.760	8.496

[#] Woody N production includes production in stems and branches.

Table 2.7. Continued.

Site	**Gross N Mineralization**[*]	**Gross Nitrification**[*]	**Gross NH_4^+ Consumption**[*]	**Gross NO_3^- Consumption**[*]
	kg N · ha^{-1} · yr^{-1}			
20	597.20	136.49	870.37	346.16
7	245.58	203.18	386.32	292.17
5	199.19	133.92	264.40	134.98
77	164.28	141.72	316.90	82.44
76	98.72	105.25	213.27	69.85
58	124.13	86.45	226.64	44.41
6	117.36	143.83	243.19	106.03
16	120.91	121.69	98.32	89.36
22	180.40	181.56	264.59	164.82
39	202.34	43.24	333.31	28.46

[*] Annual gross cycling rates calculated as the average rates from the three labeling dates, extrapolated to annual rates.

Table 2.8. Microbial biomass N in ^{15}N labeled cores and microbial uptake of the ^{15}N label.

Site	**Microbial biomass N in $^{15}NH_4^+$ labeled cores**[*]	**Microbial biomass N in $^{15}NO_3^-$ labeled cores**[*]	**Microbial uptake of $^{15}NH_4^{+}$**[#]	**Microbial uptake of $^{15}N0_3^{-}$**[#]
	kg N · ha^{-1}		**µg N · g soil^{-1}**	
20	39.97	23.23	1.349	0.825
7	17.56	14.14	0.033	0.749
5	13.23	11.90	-0.130	0.453
77	13.06	7.34	-0.043	0.241
76	7.54	7.64	-0.059	-0.025
58	13.89	12.71	-0.365	-0.306
6	14.85	15.38	-0.311	0.352
16	8.69	8.04	-0.177	0.325
22	18.68	20.94	-0.029	0.038
39	27.50	17.31	0.227	0.613

[*] Calculated as microbial biomass N 24 hr after addition of label.

[#] Negative uptake values when greater 15N concentration in unfumigated samples than fumigated samples.

Table 2.9. Plant N pools in each tissue type for trees of species comprising at least 10% of total basal area.

Component	**Plant N pools**[*]									
Sites	**20**	**7**	**5**	**77**	**76**	**58**	**6**	**16**	**22**	**39**
	kg N · ha^{-1}									
Foliage	71	69	95	99	104	123	79	124	87	98
Branches	19	14	26	22	20	19	9	16	17	21
Stems	13	29	37	45	40	28	13	19	39	27
Roots[#]	17	32	42	49	44	33	36	23	41	31
Total	120	144	200	216	208	203	138	182	184	177

[*] Pool sizes calculated from Douglas-fir Hybrid Growth System Model (Weiskittel 2006).

[#] Root estimates are for combined coarse and fine roots and based on root N content estimated from data in Sollins et al. (1980).

Table 2.10. Annual N production and flux through tree biomass.

Component	**N flux (kg N · ha^{-1} · yr^{-1})**									
	Sites									
	20	**7**	**5**	**77**	**76**	**58**	**6**	**16**	**22**	**39**
Litterfall	15.30	18.62	17.34	19.49	23.52	25.96	29.19	23.22	23.61	21.21
Production[*]										
Foliage	1.57	1.40	1.78	-0.07	-0.72	-2.36	-4.49	14.00	-1.68	2.61
Branches	0.07	0.15	0.00	-0.29	-0.24	-0.45	-0.35	3.89	-0.62	1.00
Stems	1.73	1.77	5.20	4.49	3.34	4.00	0.41	2.00	4.30	2.83
Roots[©]	3.88	2.00	4.63	4.57	3.49	3.29	-0.84	2.69	4.47	2.85
Woody N production[#]	1.92	1.8	5.2	4.19	3.1	3.56	0.06	5.89	3.69	3.83
Plant N uptake[¶]	17.22	20.42	22.54	23.68	26.62	29.52	29.25	29.11	27.30	25.04

[*] Production calculated in each tissue type using Douglas-fir Hybrid Growth System Model (Weiskittel 2006).

[#] Woody N production includes production in stems and branches.

[¶] Plant N uptake calculated as litterfall N flux plus production in branches, stems, and roots.

[©] Root estimates are for combined coarse and fine roots and based on root N content data in Sollins et al. (1980).

Table 2.11. Douglas-fir foliage, total litterfall, and forest floor N concentrations.

Site	**Foliage**	**Litterfall**	**Forest Floor**
		(%)	
20	1.21	0.89	1.24
7	1.31	1.10	1.06
5	1.42	1.07	1.33
77	1.49	1.22	1.22
76	1.60	1.16	1.17
58	1.48	1.21	1.33
6	1.91	1.20	1.64
16	1.75	1.45	1.67
22	1.60	1.18	1.18
39	1.65	1.24	1.10

Table 2.12. DOC soil water flux.

Site	**DOC (20 cm)**	**DOC (1m)**
	kg C · ha^{-1} · yr^{-1}	
20	25.331	6.302
7	21.490	3.995
5	19.046	10.775
77	12.625	6.526
76	12.159	5.266
58	16.179	3.462
6	21.447	6.381
16	16.776	4.468
22	17.828	6.106
39	12.436	7.832

CHAPTER 3:
CALCIUM DEPLETION ALONG A FOREST SOIL NITROGEN GRADIENT

Abstract

Understanding the interaction between N availability and the relative distribution and magnitude of ecosystem base cation stores is critical for long-term ecosystem sustainability. Biogeochemical couplings between nitrogen (N) and base cations (calcium [Ca], magnesium [Mg], and potassium [K]) were examined across ten Douglas-fir (*Pseudotsuga menziesii*) sites in the Oregon Coast Range. Sites were all located on sandstone parent materials in this region of low atmospheric N deposition, and spanned a three-fold soil N gradient (0-10 cm: 0.21 – 0.69% N, 0-100 cm: 9.2 – 28.8 Mg N $\cdot$ ha^{-1}). Nitrate-N leaching ranged from 0.074 to 30 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1} across sites and was negatively related to soil exchangeable Ca, Mg, and K pools, but not to base cation leaching. These results suggest that soil base cation depletion resulted from long-term N enrichment and nitrate leaching prior to establishment of the current 30 year old stands. Ca was the only base cation exhibiting concentration decreases in both plant and soil pools across the surface soil N gradient, with a greater proportion of total available Ca sequestered in plant biomass at high N, low Ca sites. This work supports a hierarchical model of coupled N-Ca cycles across gradients of soil N enrichment, with microbial production of mobile nitrate anions leading to depletion of readily available soil Ca, and plant uptake promoting ecosystem Ca conservation as Ca supply diminishes. The sequestration of Ca in aboveground biomass at high N and

low Ca sites, while critical for sustaining plant productivity, may also predispose forests to Ca depletion in areas managed for intensive biomass removal.

Introduction

Ca is an essential plant nutrient that is relatively abundant in most forest ecosystems. Inputs of Ca from atmospheric deposition and weathering generally exceed plant nutrient demands on an annual basis, usually resulting in net export of Ca that far exceeds biological Ca demands (Likens et al. 1967, Sollins et al. 1980, Trettin et al. 1999). As a result, instances of Ca limitation of natural ecosystems that lack disturbance from logging and/or air pollution are rare (but can occur, Cuevas and Medina 1986), and instead nitrogen (N) or phosphorus (P) are most often considered limiting to tree growth (Vitousek and Howarth 1991). Variations in soil Ca status among forest ecosystems most often reflect effects of tree species recycling (Stone and Gibson 1975) or uptake during stand growth (Johnson et al. 1994), as well as differences in soil age (Kennedy et al. 1998), parent material (Anderson 1988), and soil organic matter content (Zarin et al. 1998). Likewise, variations in Ca status can have other important ecosystem effects, as Ca availability is important for organic matter stability (Oades 1988), and can have effects on higher trophic levels such as snail populations (Gardenfors et al. 1995) and avian reproduction and eggshell strength (Graveland et al. 1994, Mand et al. 2002).

In recent decades, forest Ca depletion has emerged as an issue of concern in many forests impacted by human activities, particularly in eastern North

America and Europe. Forest harvest has been implicated to promote Ca depletion in some areas (Federer et al. 1989, Huntington et al. 2000) by direct removal of Ca in biomass, as well as accelerated Ca leaching in the years immediately following forest removal. The effects of air pollution on forest Ca depletion can also be significant in some regions, and have been linked both to increases in the deposition of strong acid anions of sulphur (S) and N and to decreases in atmospheric Ca inputs (Hedin et al. 1994). Accelerated N deposition effects on Ca cycling and depletion have received particular attention as components of the N saturation hypotheses (Aber et al. 1989). These changes occur as a result of both accelerated nitrification (which produces competing H^+ ions) and nitrate leaching (which provides a mobile anion carrier), which depletes Ca from soil exchange sites and promotes Ca leaching loss.

There is strong evidence from a range of different temperate forest ecosystems that accelerated N cycling leads to accelerated Ca leaching and loss from soils. Much of this evidence comes from transient increases in N supply over one to several decades, which suggests that ecosystem Ca cycles can be very dynamic in response to N supply variations. Relatively short-term (multi-decadal) increases in N supply by N deposition (Reuss and Johnson 1986, Gilliam et al. 2005), N fertilization (Currie et al. 1999), and biological N fixation (Homann et al. 1994) can all result in coupled increases in N and Ca leaching. The commonality of these responses highlights a fundamental influence of N biogeochemistry on Ca dynamics. When leaching losses are especially intense and/or prolonged, foliar nutrient imbalances and Ca deficiency can occur (McNulty et al. 1996, Schaberg et al. 1997, McLaughlin et al. 1991). Over longer time scales, it is less clear whether Ca mobilization and loss is replenished via atmospheric inputs and weathering, or whether chronic Ca deficiency occurs (Likens et al. 1998).

Few studies have examined whether reducing the source of N inputs to forest ecosystems promotes a reduction in coupled N and Ca leaching, or if N saturation effects on Ca supply and depletion may persist due to excessive soil N accumulation. Removing the source of acid inputs through a "clean rain" experiment led to base cation accumulation in soil solution in less than a decade (Beier et al. 1998); however, changes in exchangeable soil pools were not examined. Nutrient differences in aboveground biomass and 0-10 mineral soil were not seen in Norway spruce subjected to varying levels of N additions 13 years after the cessation of fertilization (Jacobsen et al. 2000, Nohrstedt et al. 2000). As percolating acid anions can redistribute surface base cations to deeper in the soil profile (Homann et al. 1992), examining deeper soil base pools would help to more fully assess effects of N loading. While nitrate leaching decreased one year after overstory red alder (*Alnus rubra*) harvest and planting of Douglas-fir, ecosystem recovery from depleted base cation stores and soil acidification were not observed (Cole et al. 1990). If N deposition or fertilization does not lead to substantial N accumulation in soil, then removal of the N source may restore nutrient balances, but elevated soil N accumulation (e.g. resulting from long-term red alder N inputs) may continue to impact base cation availability in the long term.

Nutrient conservation through uptake and storage in plant biomass (Vitousek and Reiners 1975) prevents the loss of essential nutrients from ecosystems. After stand replacing disturbance, early successional species are able to incorporate nutrients into biomass and subsequently reduce nutrient leaching (Marks 1974). Ca is often not a limiting nutrient in temperate ecosystems, but as plants are unable to retranslocate Ca from senescing foliage, adequate soil supply of this nutrient for plant uptake is critical. Ca is essential for regulating physiological processes related to growth and stress response (McLaughlin and Wimmer 1999) and for strengthening cell walls and regulating membrane permeability (Marschner 2002). As Ca levels decline, ecosystems often respond by conserving calcium (Huntington 2000). The annual cycling of calcium through aboveground biomass may be an order of magnitude greater than the rate of weathering in some forests (Watmough and Dillon 2003), so Ca dropped in litterfall may be taken up again and incorporated into biomass. Reductions in soil available Ca pools may, therefore, increase the tightness of Ca recycling through litterfall and uptake pathways.

Base cation depletion may also hinder the resilience of an ecosystem to changes in soil acidity. As exchangeable bases become depleted, a soil will have less buffering capacity to offset hydrogen ion (H^+) inputs by acid deposition or nitrification. Additionally, the mobilization of aluminum (Al) has also been observed in soils with low pH (Berden et al. 1997) and high rates of nitrification (Johnson et al. 1987, Gilliam et al. 2005). Al mobilization can interfere with plant uptake of base cations (McLaughlin and Wimmer 1999), inhibit nitrification

(Gilliam et al. 2005), and decrease plant resistance to disease as Ca:Al ratios in plant tissue decline (Högberg and Jenson 1994). As pH declines and Al mobilization increases, the relative abundance of base cations in solution may decrease (McLaughlin and Wimmer 1999). However, as bases in solution decline and Al becomes mobilized, it is unknown if nitrate and base cation leaching may become decoupled and nitrate leaching more frequently associated with Al.

Douglas-fir forests of the Pacific Northwest are widely considered N-limited and base-rich (Sollins et al. 1980, Fenn et al. 2003), and without excessive N leaching losses (Vanderbilt et al. 2003, Sollins and McCorison 1981, Martin and Harr 1989, Edmonds and Blew 1997). Although the Pacific Northwest overall has been less impacted by chronic N deposition than many other temperate forest regions (Vanderbilt et al. 2003), biological N-fixation associated with red alder can supply up to 200 kg $N \cdot ha^{-1} \cdot yr^{-1}$ into an ecosystem (Binkley et al. 1994). Ecosystem N accumulation resulting from red alder colonization can often increase the potential for nitrification and base cation leaching (Van Miegroet and Cole 1984). Soil pools of exchangeable base cations are often depleted under red alder relative to Douglas-fir stands (Homann et al. 1992, Binkley and Sollins 1990), with redistribution of exchangeable bases deeper in the soil profile under red alder (Homann et al. 1992). Dissolved concentrations of Ca and magnesium (Mg) have been positively related to nitrate under red alder in both soil lysimeter water at the level of individual stands (Homman et al. 1994), and in streamwaters across entire coastal watersheds (Compton et al. 2003). However, decreasing concentrations of calcium (Ca) in both plants and surface soil have been observed in Douglas-fir forests across a gradient in surface soil N (Perakis et al. 2006). Although Douglas-fir seedling biomass can increase when grown on a previous red alder site (Brozek 1990), less is known if N cycling and base cation distribution patterns brought about by red alder N inputs will persist after stand composition changes. While many Pacific Northwest forests may be N limited, a legacy of red alder inputs may have imparted a mosaic of high N accumulation in the Coast Range (Chapter 2) which may influence base cation availability.

Although other base cations are susceptible to depletion in coastal Oregon, Ca may be of greatest concern as plant demands may not be fully met by atmospheric inputs (Perakis et al. 2006, Bockheim and Langley-Turnbaugh 1997). Many studies examining base cation stores in the Pacific Northwest have been located on relatively N-poor sites underlain by base-rich glacial till (Homann et al. 1992) or basalt (Binkley et al. 1992, Sollins et al. 1980), where Ca depletion was not identified as a potential problem. Ca depletion may be more prevalent on base-poor Coast Range sandstones (Bockheim and Langley-Turnbaugh 1997), or N-rich sites underlain by sandstone or basalt (Perakis et al. 2006). Under these conditions, stands may be more dependent on atmospheric inputs of Ca (Perakis et al. 2006).

The objective of this study was to examine base cation pools and dynamics in plants, soil, and soil water across a gradient in surface soil N and nitrate leaching in ten young Douglas-fir plantations of the central Oregon Coast Range. Several research questions shaped the study: 1) Is base cation leaching associated with nitrate leaching? 2) Do the size and depth distribution of soil exchangeable base cation pools vary with N availability? 3) Is there evidence of plant conservation of base cations in response to variations in soil availability?

Methods

Study area

The study area was located in the north-central Oregon Coast Range from (43° 48'N, 123° 24'W) in the north to (44° 34'N, 123° 48'W) in the south (Figure 3.1). The Coast Range was formed from uplifted ocean floor during the tertiary period (Orr et al. 1992) and from the collision of a volcanic island chain with the North American continent (Duncan 1982). Consequently, bedrock in the Coast Range includes both marine sandstone, siltstone, and shale, and basaltic volcanic rock (Orr et al. 1992). Soils in this region range include Inceptisols, Alfisols, Ultisols, and Andisols. The climate in the study area is maritime and temperate with cool, wet winters and warm, dry summers. The study area receives most precipitation as rain from October-April, and rainfall varies approximately 180 to 300 $\mathrm{cm} \cdot \mathrm{yr}^{-1}$ across the area (National Atmospheric Deposition Program [NADP] OR02 watershed, averaged annual data from 1980-2004). January mean minimum and July mean maximum temperatures range from -2 to $+2^{o}$C and from 20 to 28^{o}C, respectively (Maguire et al. 2002). The study area falls within the western hemlock (*Tsuga heterophylla*) vegetation zone, and has Douglas-fir (*Pseudotsuga menziesii*), western hemlock, western red cedar (*Thuja plicata*), red alder, big-leaf maple (*Acer macrophyllum*), as major forest tree species with Sitka spruce (*Picea sitchensis*) also found near the coast. However, many forest stands in these zones are often dominated solely by Douglas-fir because of preferential monoculture plantation planting.

Study sites

Ten study sites, selected to represent a surface soil N gradient, were chosen from Douglas-fir plantations being monitored to examine the effect of Swiss needle cast on Douglas-fir growth (Maguire et al. 2002). The sites in this study were chosen based on similar tree age (~30 years), sedimentary parent material, and varying mean age of Douglas-fir needle retention. Eight of these ten sites were preliminarily sampled for plant and soil chemistry in summer 2002 (Perakis et al. 2006), and two additional sites with intermediate mean needle ages were added in 2004. The stands at these sites range from 23 to 31 years of age and vary in mean needle longevity from 1.4 to 4.0 years. Elevation ranges from 23 to 484 m, and all sites were located within 25 km of the Pacific Ocean with a north/south range of 137 km. Soil type among the sites included both alic Hapludands and andic Dystrudepts. The sites named Music Rd. and Juno Hill in Perakis et al. (2006) are here referred to as sites 20 and 6, respectively. Site characteristics are shown in Table 3.1.

Nine of the ten sites were dominated by planted Douglas-fir with occasional western hemlock, red alder, Sitka spruce, vine maple (*Acer circinatum* Pursh), and bigleaf maple (*Acer macrophyllum*) (Table 3.2). One of the ten sites, site 6, was co-dominated by western hemlock and Douglas-fir. The history of site 6 indicates that hemlock naturally regenerated into the stand. Volunteer red alder did not dominate any of the stands and represented less than 9% of total basal area at all sites. The study plots at each site covered 0.2 acre occurring within continuous plantation cover. Five sites were located between Newport and Corvallis, and the other five sites were scattered in the northern Coast Range around the communities of Tillamook, Grand Rhonde, and Nehalem. These sites were located on land owned by the Oregon Department of Forestry, Hampton Forests, and Green Diamond Resource Company. All sites were located within 25 km of the Pacific Ocean with a north/south range of 137 km.

Soil sampling and preparation

Soil and forest floor sampling occurred during summer 2003 and summer 2005. Forest floor was collected for both bulk density and nutrient analysis and included the entire O horizon. Four locations within each site were randomly selected for forest floor sampling. A sampling frame was placed on the surface of the forest floor, and material greater than 1 cm in diameter was discarded. A keyhole saw was used to cut along the inside of the grid to remove the forest floor solely contained within the grid. Five measurements were taken to estimate the depth of the forest floor. Forest floor samples were dried at 65°C for 48 hr, sorted again to remove any mineral soil, weighed, and a subsample ground in a Wiley mill.

Mineral soil, to a depth of 1 m, was sampled separately for bulk density and chemistry. One objective of mineral soil sampling was to determine the total mass of base cations in six mineral soil layers (0-10 cm, 10-20 cm, 20-30 cm, 30-

50 cm, 50-70 cm, 70-100 cm). Soil bulk density, soil volume, layer depth, and nutrient concentrations were used to determine total soil chemistry. A pit excavation method was used for the first 10 cm and a 4 cm diameter corer was used for the lower soil depths. Four locations within each site were randomly selected for soil sampling. For the top 10 cm of mineral soil, a sampling frame was placed on the ground, and the forest floor was removed. A 10 cm deep pit was excavated within the frame, and the soil was removed and placed in Ziploc bags. To validate the depth of the pit, five measurements were taken from the surface to the bottom of the pit. Next, a 4 cm diameter corer, fitted with a core liner and hammering handle, was used to obtain soil from the 10-20 cm, 20-30 cm, 30-50 cm, 50-70 cm, and 70-100 cm depths. Soil layers exceeding 10 cm were sampled in the middle of their profile, with intervening soil excavated by an auger. Samples below 50 cm depth were frequently obtained by impact coring through intact weathered sandstone. Coring to 1 m depth was possible in 39 of 40 total sample locations.

Mineral soils were sieved to 2 mm to remove rocks and debris and to homogenize the soil. Soil bulk density was calculated for each soil layer as the total dry mass of < 2 mm soil divided by the volume of the entire soil core. Separate subsamples of fresh soil were dried at 105^{o}C for 48 hr to determine moisture content, and at 65^{o}C for 48 hr prior to grinding by roller mill for chemical analysis. In addition, subsamples from the 0-10 cm and 10-20 cm were composited by depth within sites and analyzed for soil texture (% clay, silt, and sand) by the hydrometer method (Central Analytical Laboratory, Oregon State University, Corvallis, OR).

Vegetation sampling and preparation

Foliage sampling occurred during the summer of 2005. A pole pruner was used to clip the tip of the southern-most branch in the fifth whorl from the top of three randomly selected trees per site (Maguire et al. 2002). The clipped branches were immediately frozen, and needles were separated from the branches and kept frozen until analysis. Frozen needle samples were thawed and dried at 65°C for 48 hr. Dried needles were ground on a ball mill.

Sampling of Douglas-fir bolewood and branches occurred in winter 2007. Tree cores were taken from six Douglas-fir trees per site. Cores were taken at breast height on the uphill or north side of the tree. These cores were then bulked into two composite samples per site. At each site, three branches were cut with a pole pruner, or if live branches were not easily accessible, green branches were collected from the ground, having been knocked down after a recent storm event. The branches were allowed to air dry for one week and then were defoliated and cut into representative pieces for analyses. Cores and branch subsamples were dried at 65°C for 48 hr and ground in a Wiley mill.

In order to estimate annual litterfall inputs, litter traps were installed at each of the sites in August 2004. The traps were made by attaching mesh (1.4 mm) onto baskets covering an area of 0.26 m^2, and these traps captured litter falling vertically from a height of 0.33 m above the forest floor. Ten traps were randomly placed at each site by overlaying each site with a virtual numeric grid and selecting placement of the traps on the grid by random number generation. From September 2004 to June 2006, litter was collected each month by unclipping the mesh from the basket and folding the mesh into labeled paper bags. A new piece of mesh was then clipped to the basket to collect litterfall for the next month. If a basket was tipped over or a corner of the mesh had become unclipped, a note was made and litter from that basket was excluded from the collection.

Litter was characterized as total litter and Douglas-fir needle litter. The paper bags containing the mesh and litter were dried at 65^{o}C for 48 hr. The dried litter was then removed from the mesh and weighed. Each month litter from 3-4 different baskets at the same site was combined to form three composite samples per month per site. Each composite sample was then sorted, removing any insects, charcoal, and woody debris with a thickness >1 cm, and continually divided in half on a tray until one subsample weighed approximately 2 g. Each litterfall sample was then ground on a roller grinder and stored in scintillation bottles.

Nutrient analysis

Exchangeable soil cations, calcium (Ca), magnesium (Mg), potassium (K), were determined on moist subsamples of soil by ammonium acetate extraction (Bullen and Bailey 2005) and analysis by inductively-coupled plasma optical emission spectrometer (ICP), Perkin Elmer Optima 3000DV, (Norwalk, CT, USA) at the USGS Metal Isotope Laboratory (Menlo Park, CA). Soil solution pH (2 water: 1 soil) was assayed using fresh soil by an Accumet pH probe meter with a glass-body liquid-filled combination probe (Fisher Scientific, Hampton, NH, USA). Other analyses of ground foliage, forest floor, litterfall, Douglas-fir needle litter, branches, wood tissue, and soil were conducted after re-drying samples at 65^{o}C for 24 hr. Plant biomass base cations (Ca, Mg, K) were determined by nitric acid microwave digestion and analysis with an ICP at the Oregon State University Central Analytical Laboratory (Corvallis, OR). Nutrient capital of the soil and forest floor was calculated using forest floor or soil layer thickness, nutrient concentrations, and bulk density. Nutrient pools within soil layers were then summed to a 1 m depth.

Estimation of aboveground Ca pools

In order to determine aboveground Ca pools, estimates of stand biomass (foliage, branches, stems) at the ten study sites were produced using the Douglas-fir Hybrid Growth System Model (DF.HGS) (Weiskittel 2006), which was developed from previous biomass sampling at these sites (Maguire et al. 2002). If percent basal area of a species other than Douglas-fir was greater than 10% on a given site, biomass of that species was calculated and included in the stand budget. As 80% and 18% of the basal area at sites 6 and 39, respectively, was comprised of western hemlock, allometric equations were used to estimate western hemlock biomass pools (Ter-Mikaelian and Korzukhin, 1997). Biomass estimates were multiplied by Ca concentration to determine Ca pools in each tissue type. Ca concentrations in hemlock tissue were estimated from previous work in the Coast Range (Binkley et al. 1992a).

Lysimeter installation and soil water sampling

In order to monitor soil water nutrient concentrations, three pairs of low-tension lysimeters (Prenart, Denmark) were installed at 20 cm (shallow) and 1 m (deep) soil depth at each of the sites in August 2004. The locations for lysimeters were spread across each site and were selected to avoid hitting large roots or bedrock upon installation. During installation, one part deionized water and one part soil were combined to make a slurry in which each lysimeter was conditioned under vacuum for 15 minutes. The soil for the slurry was sieved to 2 mm and came from the depth to which the lysimeter was being installed. After conditioning in the slurry, the lysimeter was coated in a thick soil film. Next, a heavy steel rod was pushed into the ground at a 60^{o} angle upslope with a twisting motion. The steel rod was removed, and the Tygon tubing of the conditioned lysimeter was threaded through a hollow plastic tube, causing the lysimeter to be at the end of the rod. The lysimeter-rod system was pushed through the hole, and the lysimeter was gently pressed into 10 cm of fresh soil at the end of the hole. The plastic tube was removed, and the hole was backfilled with soil using a wooden dowel to pack soil tightly. The lysimeter tubing was secured in 1 L sample collection bottles, and the collection bottles and excess tubing were housed in PVC piping 25 cm in diameter and with a removable lid. Lysimeters were allowed to equilibrate for several months before soil water nutrient analysis commenced.

Every month from December 2004 to June 2006, a 12 mm Hg vacuum was placed on the lysimeters for 48 hr. Approximately 5 mL of accumulated sample was used to rinse two 60 mL HDPE bottles, and the remaining soil water was collected. One of the bottles was immediately capped, and the other received approximately 0.2 mL of chloroform to stop microbial processes. Chloroformed and unchloroformed field blanks were also taken at each site during each collection period by rinsing bottles with deionized water. The bottles were kept on ice during transport back to the lab and were refrigerated until analysis, generally within 48 hr of collection.

Soil water analysis

Soil water was analyzed colorometrically for nitrate (NO_3^-)-N with cadmium reduction on a Lachat QuikChem 8000 flow-injection autoanalyzer (Lachat Instruments, Milwaukee, WI, USA). Samples were run against known standards, duplicates were run every ten samples, and field blanks were used to account for any effects of transferring collected water in the field. Soil water was then analyzed for dissolved organic carbon (DOC) by catalytic oxidation combustion using a Shimadzu TOC-V CSH total organic carbon analyzer (Shimadzu Scientific Instruments, Columbia, MD, USA). Lysimeter waters were analyzed for Ca, Mg, K, sodium (Na), aluminum (Al), iron (Fe), and manganese (Mn) with an ICP, Perkin Elmer Optima 3000DV (Norwalk, CT, USA) at the USGS Metal Isotope Laboratory (Menlo Park, CA). Chloride (Cl), sulfate (SO_4^{2-}), and bromide (Br) in soil waters were analyzed by ion chromatography using a Dionex-600 IC system (Dionex Corporation, Sunnyvale, CA). To better isolate weathering and deposition sources, all base cation concentrations and fluxes in soil water were normalized to remove sea-salt inputs (Keene et al. 1986) using Cl:ion ratios in precipitation in a nearby Coast Range watershed (NADP OR02 watershed, averaged annual data from 1980-2004). Cl:ion ratios precipitation from this watershed were elevated with respect to seawater concentrations for Ca and sulfate and to a lesser extent K and Na; thus reported fluxes are lower than if seawater ratios were used. Cl was used as a measure of sea-salt input as it is both abundant in seawater and not biologically essential to plants (Hedin et al. 1995). Sea-salt derived fluxes assume Cl is conservative, and the system does not preferentially retain sea-salt ions. The leaching of base cations is reported both in absolute flux and non sea-salt flux.

Water yield was estimated by using estimates of evapotranspiration and precipitation to convert nutrient concentrations to fluxes (Binkley et al. 1992). Estimates of annual precipitation for each of the sites were gained from precipitation layers generated by PRISM (Precipitation-elevation Regressions on independent Slopes Model) (PRISM Group, Oregon State University, http://www.prismclimate.org, created 4 Feb 2004). PRISM is a unique climate database because it accounts for rain shadows, temperature inversions, coastal effects in the climate mapping process, and it uses a digital elevation model to account for grid cell and weather station location (Daly et al. 1994). Precipitation layers coincided with sampling dates (September 2004 – June 2006) and had a grid size of 4 km. Site coordinates were used to obtain annual data from the precipitation layers.

Estimates of evapotranspiration were obtained from the 3-PG (Physiological Processes for Predicting Growth) forest process model. 3-PG is a process-based stand growth model and was designed to predict forest growth variables of interest to both foresters and ecologists (Lansberg and Waring 1997). As forest growth is strongly related to water use, 3-PG also predicts evapotranspiration using the Penman-Monteith equation which sets limits on evaporative demand (Waring et al. 1980). 3-PG uses a monthly time step and requires climatic data and additional input data such as latitude, site fertility rating, initial stocking density (trees per hectare), soil class, leaf area index, and maximum and minimum available soil water. Unknown parameters (initial foliage, root, and stem biomass, quantum efficiency, and climatic data) were used from a previous modeling of a similar high fertility site in the Oregon Coast Range. Maximum canopy conductance was constrained at 0.013 m/s by running a sensitivity analysis with 3-PG to find the conductance that produced the most reasonable maximum leaf area index and maximum annual increment for a site II Douglas-fir forest in the Oregon Coast Range (Waring et al. 2006, Waring et al. 2002). Ranges of planting density, LAI, latitude, and fertility of the ten study sites did not vary greatly, so an average of these parameters across all sites was used to give one estimate of evapotranspiration for all ten sites. Lysimeters at all ten sites ran dry during the middle of the summer, so the available soil water in August was manually set to zero in the model. The model was run for 30 years, the mean stand age of these sites, to estimate current water demands.

The difference between precipitation and evapotranspiration was taken to be the volume of water that leached past 1 m, because nearly all transpiration occurs within the top 1 m of soil. A fine root profile from a nearby Coast Range site (Lee et al. 2007) was used to estimate the percentage of fine roots in the top 20 cm of soil, as fine roots are largely responsible for transpiration. The percentage of fine roots in the top 20 cm was applied to the transpiration value estimated by 3-PG and added to the volume of water lost by evaporation to obtain the volume of water leaching past the 20 cm lysimeters. A significant percentage of soil water is transpired in the top 20 cm of mineral soil, so a greater volume of water leaches past the 20 cm depth than the 1 m depth. Soil water nutrient fluxes were calculated as nutrient concentration times the volume of water leaching past each lysimeter depth. Volume-weighted nutrient concentrations were also computed to remove the influence of the quantity of water leaching past the lysimeters and were calculated as nutrient concentrations divided by the volume of water leaching past each lysimeter depth.

Data analysis

Regression and correlation were used to explore relationships between response variables of interest and indices of soil N availability. The statistical software package, SAS 9.1 (SAS Institute Inc. 2003), was used for all statistical procedures. Given the small number of sites (ten), the accepted level of significance for analyses was $\alpha < 0.10$. Prior to observing analysis results, normal probability plots were used to check data distributions for normality, and residuals were checked to ensure equal variance, applying transformations when necessary.

Results

Soil water nutrients and exchangeable soil pools

Leaching of both absolute and non-sea salt (NSS) Ca, Mg, K, and Na (corrected for cation contributions in precipitation, see Methods) was highly variable (Tables 3.3 and 3.4) and did not possess a relationship with nitrate-N leaching (Figure 3.2) or the surface soil (0-10 cm) N gradient. The surface soil N gradient ranged from 0.21 – 0.69 %N, and annual leaching losses of nitrate-N from deep soils at these sites ranged from 0.074 to 30 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1} (Chapter 2). The NSS proportion of absolute base cation leaching was not related to any index of N availability (Table 3.3), but soil pH at 20 cm increased with increasing NSS proportion of Ca and K (Ca: $p < 0.05$, $r^2 = 0.40$; K: $p = 0.02$, $r^2 = 0.51$, $n = 10$). Soil water anions, chloride, bromide, and sulfate (Table 3.5), also did not show a pattern with either nitrate-N or 0-10 cm soil N. A full charge balance was not constructed for these sites because bicarbonate was not measured.

Volume weighted absolute Cl, Na, and Mg soil water concentrations from the 1 m depth (but not 20 cm) decreased with miles from the coast (Cl: $y = -0.43\ln x + 3.17$, $p = 0.008$, $r^2 = 0.60$; Na: $y = -1.70\ln x + 7.78$, $p = 0.03$, $r^2 = 0.47$; Mg: $y = -0.30\ln x + 1.38$, $p = 0.09$, $r^2 = 0.31$), but this pattern was not seen for Ca or K (Appendix Table A1.4). Cl leaching at both the 20 cm and 1 m depths was elevated compared to the sixteen year mean deposition rate from the nearby Alsea

River watershed (23.5 kg $\cdot$ ha^{-1} $\cdot$ yr^{-}1, NADP OR02 watershed, averaged annual data from 1980-2004).

Variations in nitrate leaching influenced the range of total N losses across the soil N gradient (range of total N leaching at 1 m: 0.58 – 30.63 kg N $\cdot$ ha^{-1} $\cdot$ yr^{-1}), as both ammonium-N and dissolved organic N losses did not vary with soil N (Chapter 2). Nitrate-N losses from shallow and deep lysimeters were significantly related near 1:1 (slope = 1.02 [95% CI: 0.7, 1.34], p = 0.0002, r^2 = 0.84), suggesting high downward mobility of nitrate through these soils. The regression of shallow versus deep leaching for Ca and Mg yielded a slope significantly less than 1, indicating greater leaching of these nutrients at 20 cm than at 1m (Ca: slope = 0.19 [95% CI: 0.03, 0.25], p = 0.05, r^2 = 0.40, n = 10; Mg: slope = 0.50 [95% CI: 0.36, 0.64], p = 0.0001, r^2 = 0.86, n = 10). K and Na leaching between depths were not significantly different (K: slope = 0.53 [95% CI: -0.01, 1.07], p = 0.08, r^2 = 0.34, n = 10; Na: slope = 0.76 [95% CI: 0.42, 1.10], p = 0.002, r^2 = 0.72, n = 10).

Soil exchangeable pools of base cations to 1 m depth varied considerably across sites, but the distribution by depth was relatively unbiased across this range. Soil exchangeable Ca to 1 m varied 35-fold across sites, compared to 24-fold for Mg and 5-fold for K (Tables 3.6, 3.7, 3.8). Surface soil exchangeable base cation pools (0-10 cm) were highly correlated with exchangeable pools at depth (10-100 cm) (Ca: r = 0.98, $p < 0.0001$, n = 10; Mg: r = 0.81, p = 0.004, n = 10; K: r = 0.84, p = 0.002, n = 10). The proportion of total exchangeable bases located at any specific depth was most often not related to the total exchangeable pool (Tables 3.6, 3.7, 3.8). Although several correlations were found between the proportion stored at a specific depth and the total pool, the slopes were very shallow. Charge equivalent concentrations of exchangeable base cations are shown in the appendix, Table A1.3.

Exchangeable Ca, Mg, and K at both 0-20 cm and 0-100 cm depths decreased significantly with nitrate leaching (Figure 3.3 and Tables 3.6, 3.7, 3.8). Concentrations of exchangeable Ca and K in 0-10 cm soil also decreased with increasing soil N (0-10 cm) (log transformed: Ca, $p = 0.03$, $r^2 = 0.46$; K, $p < 0.01$, $r^2 = 0.37$). Mg soil concentrations displayed a similar but insignificant pattern. However, the proportion of total exchangeable Ca and Mg stored in 0-10 cm soil was positively correlated with 0-10 cm soil N (Ca: $p = 0.07$, $r = 0.59$; Mg: $p = 0.05$, $r = 0.62$). Measured leaching of absolute and non sea-salt base cations was unrelated to exchangeable pools at either 0-20 cm or 0-100 cm depths. Mean soil profile pH ranged over 1 unit across the sites (Table 3.9). The sum of Ca, Mg, and K soil pools to 1 m depth was correlated with average soil profile pH ($r = 0.86$, $p = 0.001$), and soil pH increased also increased linearly with the concentration of base cations (Ca + Mg + K) in 0-10 cm soil (Figure 3.4). The sum of exchangeable Ca, Mg, and K pools to 20 cm was uncorrelated with both soil organic carbon (SOC) ($r = -0.46$, $p = 0.18$) and percent clay ($r = 0.04$, $p = 0.92$).

Although base cation leaching was not related to nitrate leaching, nitrate and Al flux were correlated at both the shallow ($r = 0.86$, $p = 0.001$) and deep depths ($r = 0.91$, $p = 0.0002$). Nitrate and Mn flux were also correlated at the shallow depth ($r = 0.67$, $p = 0.03$) but not at depth ($p = 0.27$). Fe flux was not correlated with either nitrate leaching or the soil N gradient. Al and Mn were only elevated at sites with soil $\text{pH} < 5$. Additionally, pH at both sampling depths decreased significantly with increasing nitrate (deep: $p < 0.01$, $r^2 = 0.84$; shallow: $p < 0.01$, $r^2 = 0.74$). Al and DOC were not correlated at either lysimeter depth (shallow $p = 0.81$, deep $p = 0.50$). DOC flux was also unrelated to soil pH or soil %C.

Biomass nutrients

Ca was the only cation to display decreasing concentration trends in biomass along the surface soil N gradient. Ca concentrations systematically decreased in foliage, litter, branches, and forest floor across the gradient; whereas, Mg and K increased in the litter and branch pools, respectively (Figure 3.5). No cations in wood tissue displayed a pattern across the gradient (Table 3.10); however, concentrations were near detection limits. Foliar Ca was also negatively correlated with foliar N ($r = -0.58$, $p = 0.08$, $n = 10$). Integrated annual plant uptake of Ca (calculated as the current aboveground Ca pool divided by stand age) averaged 4.8 Ca $\text{kg} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$ and decreased with 0-10 cm soil N ($p = 0.04$, $r^2 = 0.44$, $n = 10$) (Table 3.11). Although Ca concentrations decreased in both soil and plant biomass pools across the surface soil N gradient, a greater proportion of the total ecosystem Ca and K pools was stored in plant biomass at the high N end of the gradient (Figure 3.6).

Discussion

Cation and nitrate leaching

The absolute leaching fluxes of base cations observed in this study (Table 3.3) are within the range reported for soil water of Douglas-fir dominated forests located on sandstone parent material (Bockheim and Langley-Turnbaugh 1997) and glacial till (Homann et al. 1992, Homann et al. 1994, Van Miegroet and Cole 1984). Ca concentrations from this study are lower than those reported from a basalt bedrock site in the Oregon Cascades but Mg and K concentrations were similar (Sollins et al. 1980). Although the sites in this study may be located on relatively base-poor sandstone, base cation leaching is similar to sites located on more base-rich parent material.

Volume weighted absolute Cl, Na, and Mg concentrations decreased further from the coast, a pattern which has been previously observed in precipitation (Blew and Edmonds 1989), streamwater (Compton et al. 2003, Hedin et al. 1995) and soil water (Bockheim and Langley-Turnbaugh 1997). Ca and K concentrations were not as closely linked to distance from the coast or Cl concentrations, suggesting greater biotic control or internal generation of these elements relative to Mg and Na. Cl leaching (range: 27.1 – 103.9 kg Cl $\cdot$ ha^{-1} $\cdot$ yr^{-1}) was greater than annual deposition measured at the Alsea NADP site located 24 miles from the coast (23.3 kg Cl $\cdot$ ha^{-1} $\cdot$ yr^{-1}); however, nine of the ten sites are located closer to the coast and likely receive greater sea-salt deposition.

Nitrate is a strongly acid anion; and as electroneutrality in soil solution must be maintained, anion leaching occurs in conjunction with the mobilization of exchangeable cations in the soil (Johnson and Cole 1980). Positive correlations between nitrate-N and base cation concentrations have been observed in soil and streamwaters of the Pacific Northwest (Homann et al. 1994, Compton et al. 2003) and elsewhere (Poss and Saragoni 1992, Gilliam et al. 2005, Jussy et al. 2000). Where coupled leaching losses of these elements are substantial, adequate supplies of readily mobilized base cations must exist in soil exchangeable and/or weatherable pools to sustain leaching losses. However, I did not observe a clear relationship between base cation and nitrate leaching losses across my sites. This suggests either differences in availability of readily mobilized base cations across sites and/or confounding effects of other mobile anions (e.g. bicarbonate, sulfate) on base cation leaching. I did not measure bicarbonate anion concentrations in lysimeter samples, but the higher soil pH at sites with low nitrate leaching raises the possibility that bicarbonate may have been a relatively more important counter ion for base cation leaching at low N sites. Bicarbonate has been observed to dominate anion leaching in Pacific Northwest soils even following disturbance (Johnson and Cole 1980). Although soil pH at all my sites are below the pKa of carbonic acid (pKa = 6.4), bicarbonate may still be present in sufficient quantities at sites with pH > 5 to couple with cation leaching. Sulfate leaching did not vary across the gradient, and sulfate concentrations at all sites were below what would be expected from sea-salt inputs, suggesting net ecosystem sulfate retention and negligible effects on base cation leaching.

Nutrient leaching is controlled by the competing processes of atmospheric inputs, internal generation, and plant demand. Although the non sea-salt proportion of base cation loss was not directly related to nitrate leaching, a greater proportion of leaching appears to be due to internal generation at high pH sites, potentially balanced in solution by bicarbonate (which was not measured). Non sea-salt proportion of Ca and K leaching decreased significantly at lower pH, suggesting greater relative importance of atmospherically derived bases in the base cation dynamics of more acidic sites.

The internal generation of bases can be due to many processes, including primary mineral weathering, oxalate or other secondary mineral dissolution, and the release of Ca from decomposing organic matter. Analysis of Ca mass balance in a northern hardwood forest watershed suggests that calcium oxalate, a rarely considered pool of Ca, could be providing inputs of Ca upon dissolution of oxalate crystals when pH decreases (Bailey et al. 2003). Significant stores of oxalate exist in Coast Range soils and may be an unaccounted for source of calcium at low N, high pH sites (Cromack et al. 1979). Preliminary measurements indicate that extractable oxalate in 0-10 cm soil decreases across the soil N gradient studied here, suggesting likely depletion of Ca-oxalate forms at low pH sites as well (data not shown). Greater leaching of Ca and Mg in shallow soil than at depth indicates that these nutrients are being preferentially retained in the biologically active upper regions of the soil profile. Plant uptake demands appear to influence further percolation of these bases and limit excessive loss. Soil water concentrations of Na and K were similar to stream chemistry from the nearby Salmon River watershed (Compton et al. 2003), but Ca and Mg concentrations were often less than that reported in streamwater. Basalt parent material in the Salmon River watershed could be responsible for some high Ca and Mg concentrations, or the bulk of internal generation of Ca and Mg may be occurring deeper in the soil profile and bedrock (Anderson et al. 2002). Differences in the proportion of leaching bases from internal generation (i.e. from non sea-salt base cations), while not related to nitrate-N loss or exchangeable bases, may still reflect differences in weatherable soil components.

My results raise the possibility that pool size variations in soil base cations across sites may reflect historic depletion patterns influenced in part by long-term nitrate leaching. Soil base cation stores were negatively related to nitrate leaching variations across sites (Figure 3.3), yet significant N inputs have not occurred at these sites for at least three decades. In addition, nitrate and base cation leaching losses were unrelated (Figure 3.2) even though couplings of these ions are common among temperate forests displaying transient increases in nitrate leaching (Homann et al. 1994, Ruess and Johnson 1986). In Oregon sandstone soils, low net cation losses can reflect low levels of exchangeable bases driven by long-term weathering (Bockheim and Langley-Turnbaugh 1997). The strong association of nitrate leaching and exchangeable pools of Ca, Mg, and K in this study suggests that base cation depletion may also be influenced by long-term nitrate leaching. Declines in soil base cations and reduced plant available calcium sources has occurred within a half century of acid deposition in the eastern US (Likens et al. 1996), and shorter-term experimental N additions can also significantly reduce soil exchangeable Ca and Mg (Fernandez et al. 2003). Although elevated N inputs are not currently impacting these sites, the correlation between exchangeable base pools and pH is consistent with nitrate leaching as the mechanism for base depletion (Van Miegroet and Cole 1985). Because sites in this study were selected to have similar stand age, species cover, and bedrock, the range in nitrate leaching and soil cation pools likely reflect long-term processes that commenced before current stand initiation. The globally high soil N pools and nitrate leaching that characterizes these sites relative to other unpolluted coniferous temperate forests (Chapter 2) further indicates that differences in soil age alone is unlikely to explain the strong N – cation relationship observed here.

Calcium storage and conservation

Although the logging history of these sites prior to establishment of the current plantation forests is not known, a competing hypothesis for differences in base cation stores is that that stands growing on more productive N-rich sites would store greater quantities of nutrients above ground than less productive sites and could be preferentially logged. One whole-tree harvest rotation in these stands would result in the average removal of 128 kg $Ca \cdot ha^{-1}$ (range 59 – 184 kg $Ca \cdot ha^{-1}$, n = 10), far less than the > 5000 kg $Ca \cdot ha^{-1}$ disparity in exchangeable Ca between some of these sites. Generic nutrient removal through harvesting does not seem to be the dominant mechanism for nutrient loss as soil P did not vary with N availability across many of these sites (Perakis et al. 2006). Differences in SOC and percent clay can often influence exchangeable base cation retention (Zarin et al. 1998); however, I found no relationships of cations with SOC and clay, suggesting these factors are not dominant mechanisms influencing exchangeable base cation reserves. In light of these analyses, variations in nitrate leaching across these sites are a likely mechanism for exchangeable base cation depletion in coastal Oregon forests.

Whether by harvesting or leaching loss, base cations may be susceptible to depletion. Stand-level mass balance calculations indicate that plant demands for Mg and K can be met by atmospheric inputs in coastal Oregon; whereas Ca deposition may only supply a fraction of plant demands (Perakis et al. 2006). If leaching of Ca continues at present rates at N-rich sites without resupply from weathering, exchangeable Ca reserves could be depleted in less than 100 years (Tables 3.3 and 3.6). This depletion rate is greater than inputs of Ca through internal generation (non sea-salt leaching, Table 3.4) and atmospheric deposition ($0.87 \text{ kg Ca} \cdot \text{ha}^{-1} \cdot \text{yr}^{-1}$) (NADP).

Nutrient uptake and storage in living and dead biomass (Vitousek and Reiners 1975) and the recycling between these two pools (Jobaggy and Jackson 2000) aids in nutrient conservation and prevents nutrient loss from ecosystems. Although Ca, Mg, and K all decreased in soils with high N leaching, Ca was the only base cation that also decreased in vegetation (Figure 3.5). Concomitant with this decrease in overall Ca availability, the proportion of total ecosystem Ca (and K) stored in above-ground biomass increased with surface soil N (Figure 3.6). Total ecosystem Ca was defined as the sum of Ca in aboveground biomass, forest floor, and the soil exchangeable pool. The greater proportional storage of Ca in aboveground biomass at high N sites results in a smaller fraction of ecosystem Ca susceptible to leaching loss. Additionally, the proportion of total exchangeable Ca (and Mg) located in the top 20 cm of mineral soil was positively correlated with the soil N gradient. These patterns suggest increased plant-soil recycling of Ca at high N sites. The localization of Ca in aboveground biomass and surface soil suggests plants may be more dependent on surface pools, and that weathering inputs at depth may not be able to counteract the impact of nitrate leaching.

As Ca levels decline, ecosystems will respond by conserving Ca (Huntington 2000). Plants can also adapt to this limitation by slowing growth or becoming more efficient in Ca uptake (McLaughlin and Wimmer 1999). Calcium uptake in Douglas-fir is thought to be an active metabolic process, suggesting potential for acclimation to variations in Ca availability (Bledsoe and Rains 1981). Yet plants cannot retranslocate Ca before leaf senescence (Van den Driessche 1985), and therefore are less able to control cycling of Ca than other nutrients such as N or P. However, biotic control of ecosystem Ca cycles can still occur. For example, after stand replacing disturbance, species involved in primary succession are able to incorporate nutrients into biomass and reduce nutrient leaching (Marks 1974). Likewise, at N-rich, low Ca sites, plant nutrient uptake may be important for preventing further losses of already depleted base cation stores. At Walker Branch watershed, the net accumulation of Ca in vegetation over an eleven-year period was directly related to a decrease in soil exchangeable Ca (Johnson et al. 1988). Perhaps a proportional shift in nutrient distribution to plant pools enables an ecosystem to maintain functioning when soil pools are reduced. The annual cycling of calcium through aboveground biomass can be an order of magnitude greater than the rate of weathering in some forests (Watmough and Dillon 2003), highlighting the potential importance of biotic control over ecosystem Ca cycling. Assuming soil and forest floor pools of Ca are at steady state (Bormann and Likens 1994) and Cl is a conservative tracer of atmospheric Ca inputs (Hedin et al. 1995), the cycling of Ca through aboveground biomass (integrated annual tree uptake + litterfall) did indeed exceed weathering estimates (non sea-salt leaching at 1 m + integrated annual tree uptake) for all sites. Previous Ca isotopic work at one of these sites has also suggested that strong Ca recycling may occur to meet plant demands (Perakis et al. 2006). As soil N increases and base cation stores decline, plants may be taking up more nutrients at the soil surface which have previously cycled through biomass.

In this study, plants do not appear to passively reflect the nutrient availabilities in the soil environment. As soil exchangeable Ca varied over 35-fold across the gradient, total Ca stored in aboveground biomass and foliar Ca concentration varied approximately 3-fold. Although plant Ca pools are relatively constrained across the sites given the wide range of exchangeable Ca pools, plants may not have access to much of the Ca mobilized into soil solution. Even though exchangeable Ca pools are low at N-rich sites, Ca is present in relatively high quantities in soil solution. At N-rich sites plant uptake of Ca in soil solution may be hindered by either the rapid export of Ca from the system through charge balance association with nitrate and/or inadequate root densities to forage for sufficient quantities of Ca. Root growth can be induced when N is limiting, but Ca deficiencies have not been seen to affect the shoot:root ratio in silver birch (Ericsson 1995). At N-rich sites in which N is in abundance, plants may allocate more biomass aboveground, reducing relative root densities which may prohibit adequate uptake of Ca.

Foliar and bolewood Ca concentrations across the sites were at the low-end of reported values for Douglas-fir in the Pacific Northwest (Walker and Gessel 1991, Binkley et al. 1992, Homann et al. 1992, Cross 2006), and the three highest soil N sites possessed foliar Ca concentrations at or below deficiency levels (Walker and Gessel 1991). Reduced foliar Ca concentrations have been observed in red spruce subjected to N fertilization and increased acid deposition (Schaberg et al. 1997, McLaughlin et al. 1991), and my results show Douglas-fir foliar Ca appears to respond similarly to natural soil N accumulation. The increasing trend of Mg and K in the litter and branch pools, respectively, across the gradient suggests plant demand for these nutrients are being met. Plants could be taking up excess quantities of these other base cations for charge balance purposes if Ca demands cannot be met. Douglas-fir branch concentrations of Ca, Mg, and K exceeded those reported from previous Pacific Northwest studies even though my sites are less base-rich (Binkley et al. 1992, Homann et al. 1992). Douglas-fir in this study were ~30 years whereas the previous studies sampled older trees (>50 years) and younger woody tissues are often more nutrient rich that of older wood. Bedrock type may have less influence on plant base cation concentrations, as sandstone versus basalt parent material had no effect on foliar cation concentrations in the Coast Range (Perakis et al. 2006).

Increased N availability can redistribute base cations to deeper in the soil profile (Van Miegroet and Cole 1984); however, my results indicate base cations at N-rich sites are consistently more depleted throughout the soil profile in comparison to N-poor sites. Surface soil exchangeable base pools were significantly correlated with pools at depth, suggesting not only that surface soil sampling may give a good estimate of base cation stores, but also depletion has occurred in both surface and deep soils. Additionally, nitrate leaching was similar for the shallow and deep depths; therefore, at sites with high leaching rates, nitrate does not appear to be taken up readily by plant roots at depth. As high nitrate leaching may be a symptom of N saturation (Chapter 2), the N cycle at N-rich sites may be more open and bring about base cation depletion as excess nitrate cannot be retained by plant or microbial uptake. One exception to the lack of base redistribution was site 6 which stored > 50% of total exchangeable Ca and Mg in the 70-100 cm depth. Although the size of the Ca and Mg pools at depth was not as high as that of N-poor sites, a higher proportion of total exchangeable Ca and Mg was stored deeper in the soil at site 6. Site 6 is dominated by western hemlock which tends to have shallower rooting systems than Douglas-fir (Bennet et al. 2002). Perhaps the combination of nitrate leaching and greater uptake of exchangeable bases in surface soil by western hemlock has led to greater relative accumulation of bases at depth. Interplanting or rotating species with differing rooting depths may be one way to maintain site productivity in areas with low base cation supplies, although such approaches will not necessarily increase long-term supplies in soils overall.

The results of this study raise the possibility that base cation depletion due to long-term high N inputs is not reversible on decadal time scales. These sites have not experienced elevated N inputs from red alder in at least 50 years (Chapter 2), but soil and foliar base cation levels at many sites remain low. Much soil Ca depletion literature has focused on eastern hardwood forests with acid deposition impacts (Huntington 2000, Hamburg et al. 2003, Federer et al. 1989) or on the influence of red alder in the Pacific Northwest (Homann et al. 1992, Binkley et al. 1992, Van Miegroet and Cole 1984, Homann et al. 1994). The conditions present in some of these N-rich Douglas-fir sites (low pH, depleted soil Ca pool, high nitrification and nitrate leaching rates) appear to sustain characteristics of N saturation in the absence of significant continued N input. In contrast, logging of red alder and conversion to Douglas-fir at a site in Washington resulted in decreased nitrate leaching within one year (Cole et al. 1990). Likewise, a "clean rain" experiment in acid rain impacted northern Europe revealed that reducing acid inputs promoted the accumulation of base cations within one year (Beier et al. 1998). Clearly not all temperate forests that receive highly elevated N inputs exhibit decreased productivity and losses of base cations (Jacobsen et al. 2000). Even in cases where decades of elevated input have reduced base cations, many forests continue to respond positively to additional N (Binkley and Högberg 1997). Yet, soil N pools across my sites spanned a vast range of 20,000 kg N $\cdot$ ha^{-1}, far more that is typically applied during forest fertilization (200 - 1,000 kg N $\cdot$ ha^{-1}) or even a half century of highly elevated N deposition (ca. 500 - 2 ,500 kg N $\cdot$ ha^{-1}). At a minimum, one conifer planting rotation does not seem able to restore cation pools and N retention at my sites. If chronic N inputs accumulate excessively, the effects cannot be immediately reversed and ecosystem sustainability will be jeopardized.

High accumulation of foliar N in coastal Oregon Douglas-fir has been linked observationally (Waring et al. 2000) and experimentally (El-Hajj et al. 2004) with a significant outbreak of Swiss needle cast (SNC), a native fungal pathogen (*Phaeocryptous gaeumannii*), that is jeopardizing forest health and reducing tree growth in the region. Although speculative, foliar Ca nutrition may also play a role in SNC susceptibility, as my results indicate foliar Ca was negatively correlated with foliar N. Low Ca causes a loss of cell wall and membrane integrity (McLaughlin and Wimmer 1999), which may facilitate amino acid leakage from cells (Fujji 1994), increasing fungal access to nutrients (Soloman and Oliver 2002) and in turn SNC infection of foliage. Although no research has yet been published on the response of SNC to Ca fertilization, some trials have begun (Maguire *personal communication*). Reductions in wood Ca also have the potential to impact structural and growth properties (McLaughlin and Wimmer 1999). Ca availability is essential for the structural integrity of wood, as reduced lignification has been observed with low Ca availability in acidic soils (Eklund and Eliasson 1990). To the degree that some sites do exhibit severe nutrient imbalances characteristic of Ca depletion, other potential ecological indicators observed in forests elsewhere (e.g. declining snail populations in acidified soils [Gardenfors et al. 1995] and bird egg shell thinning [Mand et al. 2002]) may also warrant attention in the Oregon Coast Range.

Aluminum and soil acidification

Aluminum and manganese leaching were elevated at high N, low pH sites. Although analytical limitations prevented the determination of a thorough soil water charge balance, the disparity between base cation and nitrate-N soil water flux suggests other positively charged ions are being mobilized and leached. At low pH, some metal cations, specifically Al and Mn, can be mobilized and exist predominately as soluble species. Although the chemical form of Al was not determined, at pH levels below 4.7, Al^{3+} predominates with the hydrox-Al species, $Al(OH)^{2+}$and $Al(OH)_2^+$, present in smaller amounts. Al can also exist as a chelate with DOC, but as DOC fluxes were conservative across the gradient, the variation in Al flux is likely not due to organo-Al complexes.

Elevated fluxes of Al were only observed at sites with both high nitrate leaching and soil pH below 4.7. Many studies have observed elevated Al leaching in conjunction with nitrate and low pH, in the Smoky Mountains (Johnson et al. 1987), Sweden (Berden et al. 1997), and the Pacific Northwest (Homann et al. 1994, Cole et al. 1990). Strong relationships exist between labile Al and mobile anions when base saturation is low (Cronan and Schofield 1990). Therefore, if the pool of readily exchangeable base cations is diminished or if soil solution pH drops, nitrate leaching may be accompanied by the mobilization of Al. Because of its higher ionic potential, Al will be mobilized after base cations go into solution; but below pH 5, the relative concentration of Al in solution, with respect to Ca, will increase (Reuss and Johnson 1986). Therefore, the relative availability of Ca for plant uptake will decrease as more Al ions populate the soil solution.

The mobilization of Al in soil water could potentially impact plant health, as Al can interfere with plant uptake of base cations even at concentrations that do not directly inhibit root growth (McLaughlin and Wimmer 1999). As Ca:Al ratios decrease, plant growth and resistance to disease may also decrease (Högberg and Jenson 1994). Absolute soil solution Ca:Al ratios approached equality at several high N sites, which are thought to represent a 50:50 risk of adverse impacts on tree growth (Cronan and Grigal 1995). Yet, the growth of Douglas-fir seedlings can be unhindered by relatively high soil solution Al concentrations (Ryan et al. 1986), perhaps because of Al immobilization in roots, preventing further transfer of Al to other plant tissues (Vogt et al. 1987). Additionally, increases in soil extractable Al have been shown to inhibit nitrification (Gilliam et al. 2005), suggesting a consequence of further Al mobilization for soil microbial communities. The mobilization of Al into a water soluble form can also have a continuing influence on soil acidity through the hydrolysis of water (Sparks 2000). High N availability with its affects on Al mobilization may be detrimental to ecosystem function.

Mn is involved in redox reactions in soil solution, and Mn^{2+} is the product resulting from reducing manganese oxides (Sparks 1995). Mn toxicity is usually associated with highly reducing waterlogged soils (Marschner 2002), but reducing capacity and Mn^{2+} presence does increase with decreasing pH. In the Pacific Northwest, Douglas-fir foliar Mn has been found to increase dramatically as pH decreases below 5.0 (Rollwagen and Zasoski 1988); however, Douglas-fir may be tolerant to high levels of Mn (Radwan et al. 1979). The potential for synergistic toxic or antagonistic effects of elevated Mn and Al occurring in combination is one area that clearly warrants more research in strongly acid Douglas-fir forest soils of the Pacific Northwest.

Across the gradient, the average pH of the soil profile varied over 1 unit (Table 3.9). These soil pH differences are even more pronounced than those observed in several paired red alder/conifer plot studies (Homann et al 1992, Cole et al. 1990). Soil type was very similar across the gradient, so this range in soil acidity suggests that *in situ* processes could be actively influencing the soil environment. High rates of nitrification under red alder can accelerate cation leaching and soil acidification (Cole et al. 1990, Van Miegroet and Cole 1985, Binkley and Sollins 1990, Van Miegroet and Cole 1984). The internal production of H^+ by nitrification can be over ten times greater than atmospheric inputs of H^+ (Van Miegroet and Cole 1985). Nitrification is a naturally acidifying oxidation process, releasing into soil solution two moles of H^+ for every mole of nitrate. H^+ in soil solution will readily exchange binding sites with base cations, and can also increase primary mineral weathering; therefore, the size of the exchangeable base cation pool and availability of weatherable minerals will dictate the buffering capacity of a soil and the degree to which soil pH may be affected by increased nitrification (McFee et al. 1977). Changes in the strength of soil acids can also have a role in soil acidification (Binkley and Sollins 1990). Nitrification rates were not directly correlated with soil pH changes across the ten sites, suggesting some but not all sites are able to buffer against pH changes wrought by nitrification. Elevated nitrate production and leaching is indeed occurring at several N-rich sites and may be driving down soil pH and mobilizing metal (e.g. Al and Mn) cations.

Conclusions and management Implications

This study examined a wide range of variation in plant and soil base cation pools in the Oregon Coast Range that has generally been overlooked in analyses of forest biogeochemistry in the Pacific Northwest. The strongly negative relationships observed between soil extractable Ca, Mg, and K versus nitrate leaching highlights a key role for elevated nitrate leaching in promoting depletion of available soil base cations. The linkage between low base cations stores and high N leaching rates suggest further increases in N availability through fertilization or interplanting with red alder may negatively affect stand health at sites nearing N saturation. Paradoxically, contemporary nitrate and base cation leaching rates were uncoupled across the sites, which raises the possibility that base cation depletion occurred as a result long-term N enrichment from red alder prior to establishment of the current conifer stands. Such soil biogeochemical changes do not appear to be reversible on the time scale of one conifer rotation, even in the absence of substantial N inputs.

Ca appears most sensitive to depletion at N-rich sites studied here. Ca was the only base cation that displayed concentration decreases in both plants and soil with increasing site N fertility. Nevertheless, biotic uptake and recycling of Ca appears important for retaining Ca in sites with excessive N availability. Observed patterns of Ca distribution between plants, surface soil, and deep soil indicate that plant biomass and surface soils were proportionally most important in retaining ecosystem Ca at sites with high N availability. At these sites, Ca in litterfall may be quickly taken up and incorporated into biomass to meet plant growth demands and avoid leaching losses.

Overall, our results support a hierarchical model of coupled N-Ca cycles across gradients of soil N enrichment, with excess nitrate leaching leading to depletion of readily available soil Ca at high N sites, and plant uptake promoting ecosystem Ca conservation as Ca supply diminishes. Multiple time scales and biogeochemical interactions have been involved in reducing Ca availability at N-rich sites. Historical soil N accumulation through N_2-fixation by red alder creates favorable conditions for microbes to produce significant quantities of nitrate, which, after N availability exceeds ecosystem demands, leaches from the system with cations (Ca) for charge balance. The subsequent depletion of the exchangeable Ca pool promotes tight recycling of Ca between plants and surface soil. This complex suite of biotic and abiotic interactions is important to consider for long-term ecosystem sustainability.

Greater accumulation of base cations in aboveground biomass has considerable implications for management, as decreases in soil cation reserves may threaten long-term forest productivity. Harvest may significantly decrease Ca pools at N-rich sites which store a significant portion of ecosystem Ca aboveground. Perakis et al. (2006) noted that removal of nutrient rich foliage and twigs through whole-tree harvest could deplete soil exchangeable Ca in 350 years. The percent of aboveground Ca located in foliage and branches averaged 76%

across the sites (range 69 – 89%, n = 10). Removal of these nutrient-rich pools may be even more detrimental for ecosystem health at the high N sites, where soil cation pools have been depleted by long-term leaching.

Given that current base cation leaching was not associated with nitrate leaching, the mobilization of aluminum and other metals may be contributing to soil water cation balance. Elevated nitrification can release large quantities of H^+ leading to depleted soil exchangeable base pools, soil acidification, and Al mobilization which may be detrimental to plant health and ecosystem buffering capacity. Reduced Ca:Al ratios in soil solution may reduce the relative availability of Ca for uptake, and Al may also directly interfere with plant uptake of essential nutrients. While these sites are not currently receiving elevated N inputs, the long-term accumulation of soil N may lead to continued soil acidification and mobilization of metal cations. Forest N fertilization and intensive harvesting would be expected to intensify Ca loss and exacerbate soil acidification and metal cation cycling.

N availability beyond biological demand can lead to symptoms of N saturation in an ecosystem, such as elevated nitrate leaching and depleted base cation soil reserves (Aber et al. 1998). Previous work in the Pacific Northwest has attributed differences in nitrate and cation leaching, nitrification rates, and soil pH to differences in overstory vegetation (Homann et al. 1992, Binkley et al. 1992, Van Miegroet and Cole 1985, Van Miegroet and Cole 1984, Cole et al. 1990). These studies found higher Ca loss with increased nitrate-N leaching, reflecting the influence of current N inputs, whereas my data suggest a long-term base depletion by chronic N accumulation. This study demonstrates that some N-rich Douglas-fir forests in the Coast Range may indeed be exhibiting signs of base cation depletion and excessive N availability. The establishment of this soil N gradient provided the chance to study the fundamental biogeochemical processes of N cycling and base cation leaching without these being coupled to overstory differences. As elevated nitrate leaching continues to occur in some parts of the Coast Range with already depleted base cation reserves, ecosystem base cation status may become increasingly important to forest managers and ecologists.

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Figures

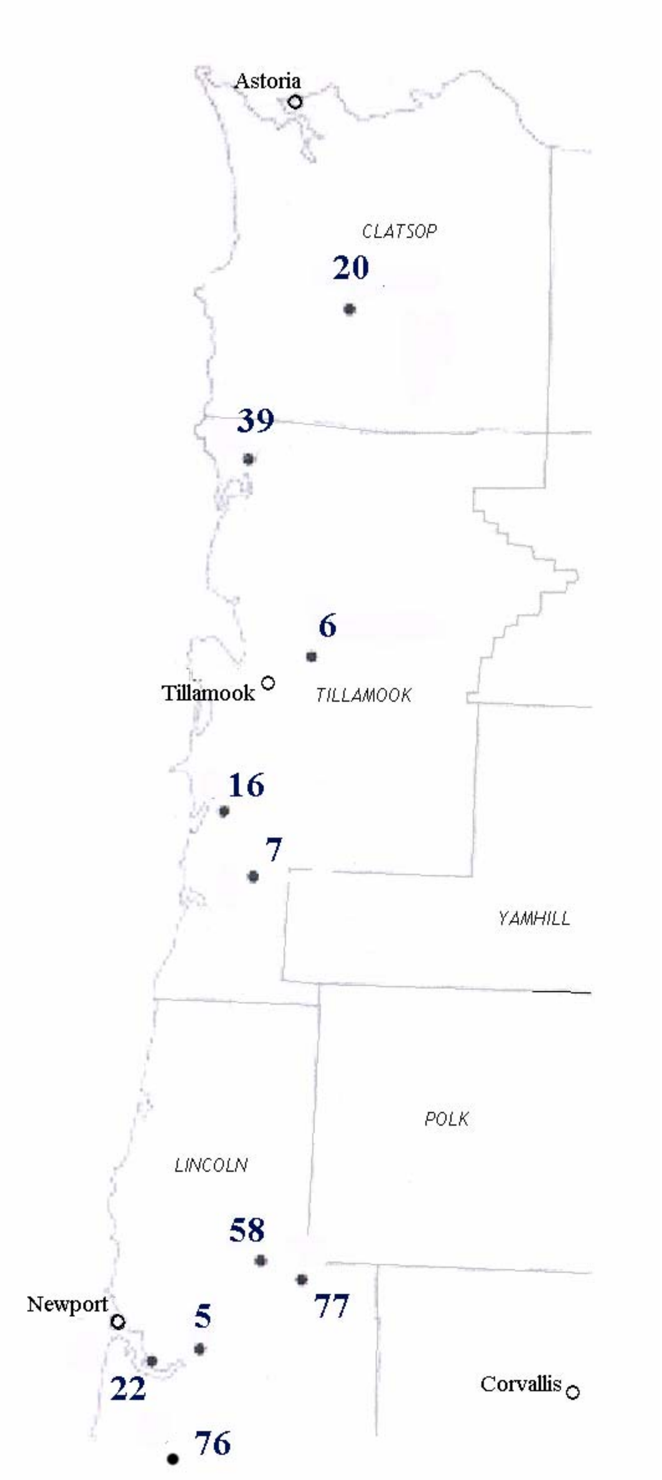

Figure 3.1. Location of study area and sites in western Oregon.

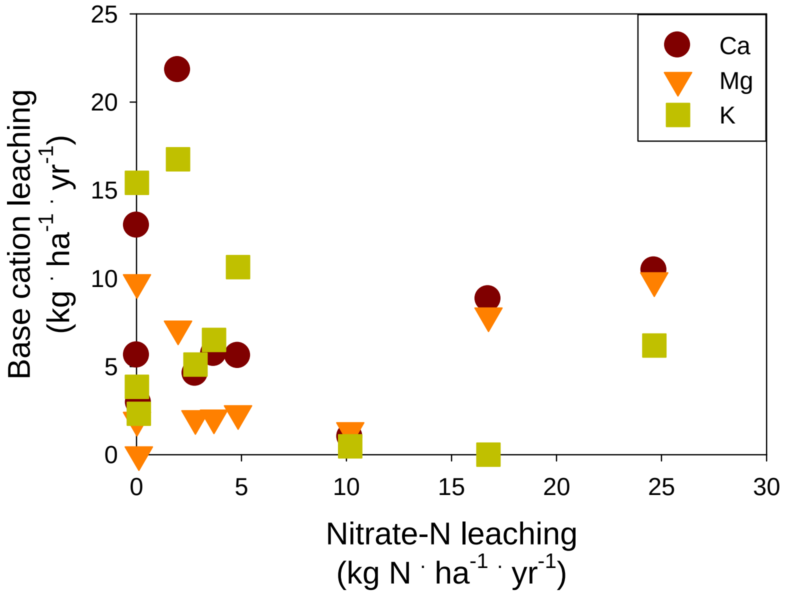

Figure 3.2. Non sea-salt base cation and nitrate-N leaching were not related at either the 20 cm (above) or 1 m (not shown) soil depths.

Figure 3.3. Exchangeable Ca and Mg (a) and K (b) pools at 20 cm and 1 m decreased with increasing nitrate-N leaching. (a) Regressions: 20cm solid line Ca, $y = -521.85 \log x + 798.38$, $F_9 = 28.14$, $p = 0.0007$; 20cm dotted line Mg, $y = -186.26 \log x + 340.95$, $F_9 = 30.3$, $p = 0.0006$; 1m solid line Ca, $y = -1755 \log x + 2575.02$, $F_9 = 14.42$, $p = 0.005$; 1m dotted line Mg, $y = -949.69 \log x + 1427.15$, $F_9 = 14.48$, $p = 0.005$. (b) Regression: 20 cm K, $\log y = -0.14 \log x + 2.44$, $F_9 = 9.49$, $p = 0.02$; 1m K, $\log y = -0.11 \log x + 3.05$, $F_9 = 3.86$, $p = 0.085$.

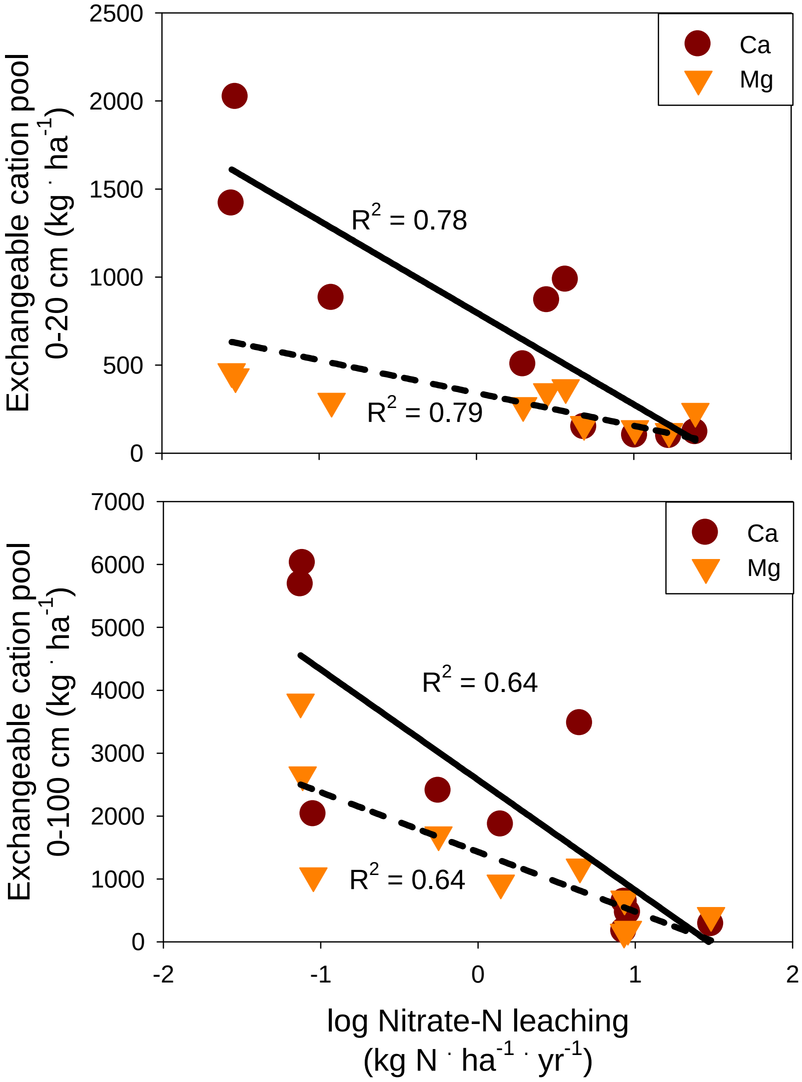
2500
2000
1500
1000
500
0
Exchangeable cation pool
0-20 cm (kg · ha-1)
Ca
Mg
R2 = 0.78
R2 = 0.79
7000
6000
5000
4000
3000
2000
1000
0
Exchangeable cation pool
0-100 cm (kg · ha-1)
R2 = 0.64
R2 = 0.64
-2
-1
0
1
2
log Nitrate-N leaching
(kg N · ha-1 · yr-1)

Figure 3.3a.

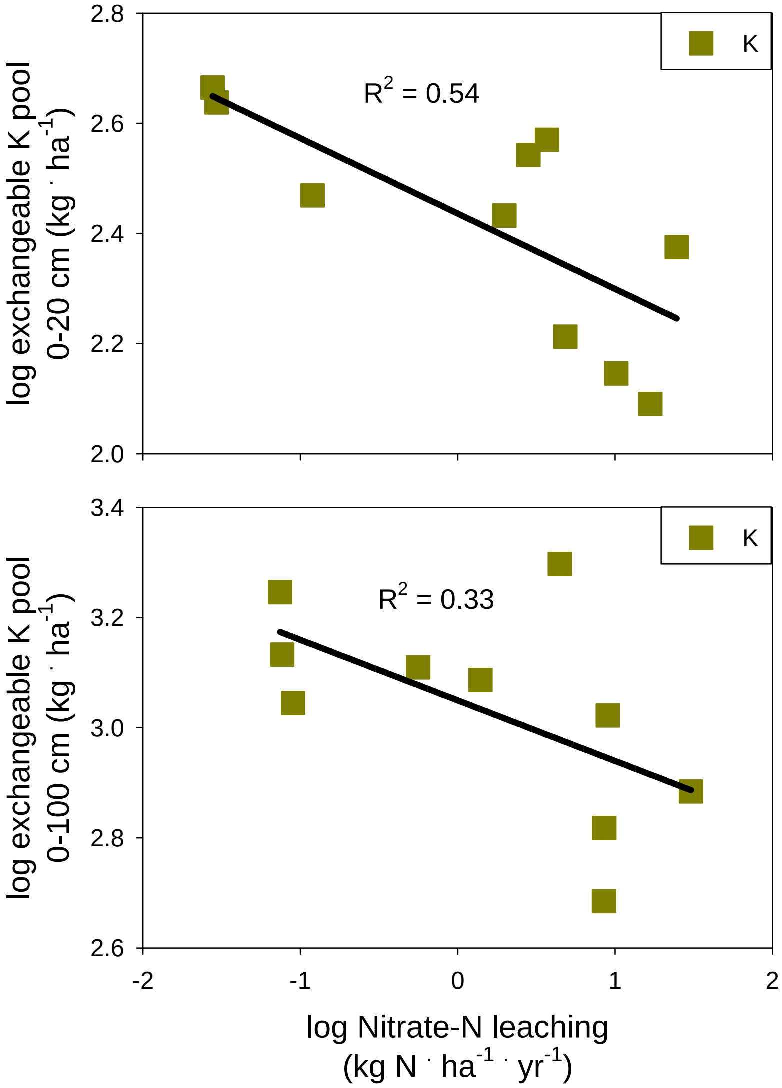
2.8
2.6
2.4
2.2
2.0
K
R2 = 0.54
log exchangeable K pool
0-20 cm (kg · ha-1)
3.4
3.2
3.0
2.8
2.6
K
R2 = 0.33
log exchangeable K pool
0-100 cm (kg · ha-1)
-2
-1
0
1
2
log Nitrate-N leaching
(kg N · ha-1 · yr-1)

Figure 3.3b.

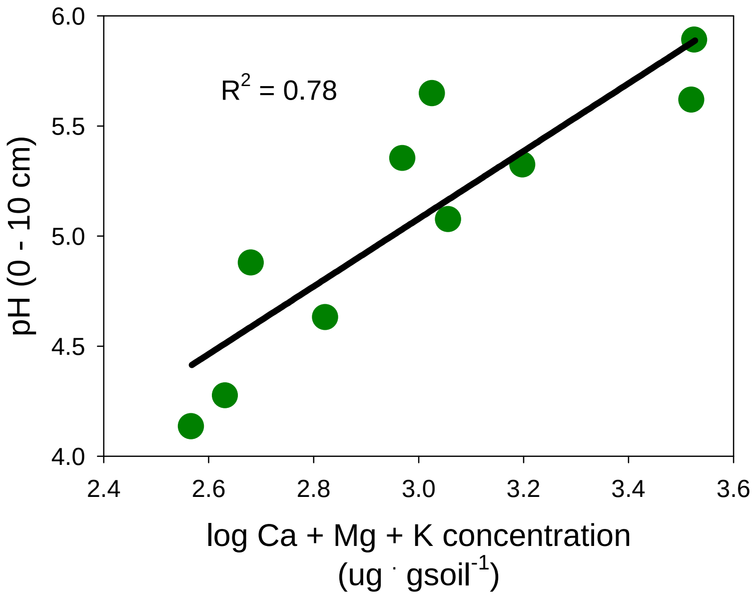

Figure 3.4. pH of 0-10 cm mineral soil increases with exchangeable soil cation concentration. Sum of exchangeable base cations was log transformed data for normality. Regression: $y = 0.51x + 0.43$, $F_9 = 27.85$, $p = 0.0007$.

Figure 3.5. Concentrations of base cations in plant tissue and forest floor across the soil N gradient. Regressions: (a) solid line Ca, $\log y = -0.61\log x + 0.15$, $F_9 = 6.31$, $p = 0.04$; dotted line Mg, $y = 0.07x + 0.09$, $F_9 = 4.63$, $p = 0.07$. (b) solid line Ca, $y = -0.45x + 0.75$, $F_9 = 13.65$, $p = 0.006$; dotted line K, $y = 0.22x + 0.13$, $F_9 = 7.91$, $p = 0.02$. (c) Ca, $y = -0.49x + 0.58$, $F_9 = 4.45$, $p = 0.07$. (d) Ca, $y = -1.09x + 1.26$, $F_9 = 11.29$, $p = 0.01$.

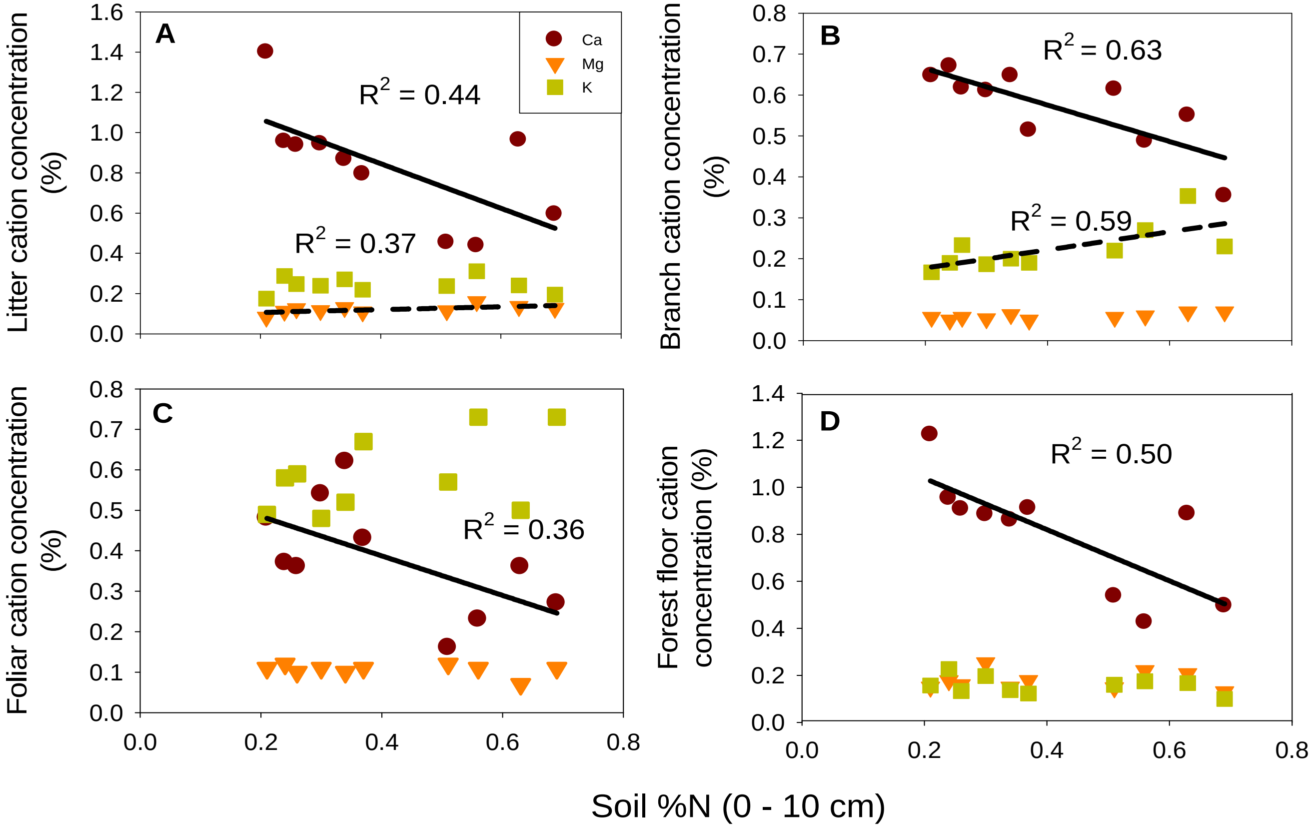
A
B
C
D
Ca
Mg
K
Litter cation concentration (%)
Branch cation concentration (%)
Foliar cation concentration (%)
Forest floor cation concentration (%)
Soil %N (0 - 10 cm)
R^2 = 0.44
R^2 = 0.37
R^2 = 0.63
R^2 = 0.59
R^2 = 0.36
R^2 = 0.50
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
0.1
0.3
0.5
0.7

Figure 3.5.

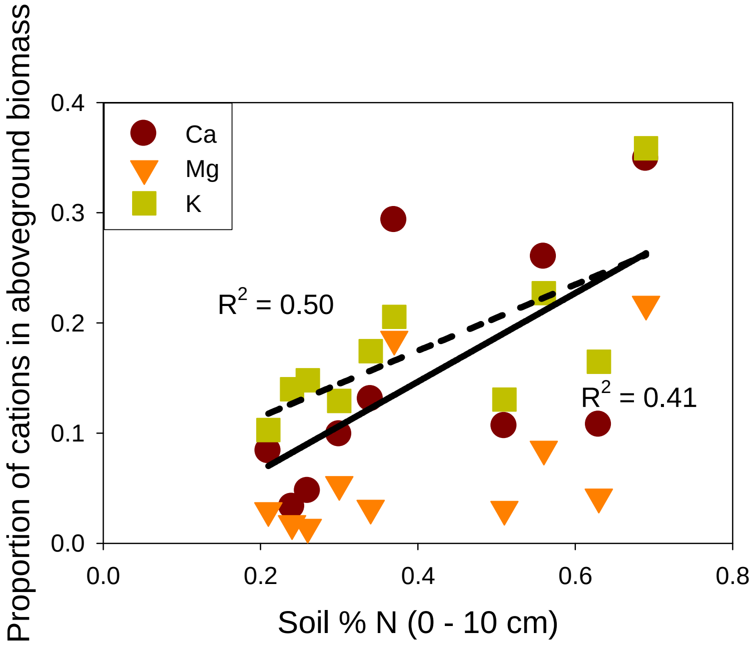

Figure 3.6. Proportion of the total ecosystem base cation pool in aboveground biomass vs. 0-10 cm mineral soil N. Regressions: black line Ca, $y = 0.40x - 0.014$, $F_9 = 5.45$, $p = 0.048$, $r^2 = 0.41$; dotted line K, $y = 0.30x + 0.055$, $F_9 = 7.97$, $p = 0.02$, $r^2 = 0.50$. No significant relationship for Mg.

Tables

Table 3.1. Site characteristics, arranged in order from low to high soil N.

Site	Location	Soil N (0-10 cm)	Soil subgroups[*]	Elevation[#]	Slope[#]	Aspect[#]
		(%)	(USDA)	(m)	(%)	(°)
20	45° 48’ N, 123° 24’ W	0.21	Alic Hapludands	484	5	20
7	45° 8’ N, 123° 39’ W	0.24	Andic Dystrudepts	278	50	8
5	44° 38’ N, 123° 48’ W	0.26	Andic Dystrudepts	322	55	220
77	44° 42’ N, 123° 40’ W	0.30	Andic Dystrudepts	235	10	250
76	44° 35’ N, 123° 48’ W	0.34	Andic Dystrudepts	187	55	90
58	44° 43’ N, 123° 49’ W	0.37	Andic Dystrudepts	80	15	75
6	45° 29’ N, 123° 49’ W	0.51	Andic Dystrudepts	86	10	180
16	45° 10’ N, 123° 55’ W	0.56	Andic Dystrudepts	115	15	240
22	44° 36’ N, 123° 55’ W	0.63	Andic Dystrudepts	155	25	100
39	45° 44’ N, 123° 53’ W	0.69	Andic Dystrudepts	23	10	160

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

[#] Maguire et al. (2002) unpublished data.

Table 3.2. Percent basal area of tree species and total basal area on the ten sites[*].

Site	**Douglas-fir**	**Western Hemlock**	**Hardwoods**[#]	**Other conifers**[¶]	**Total basal area**
	% basal area				**$m^2 \cdot ha^{-1}$**
20	98.4	1.6	0	0	17.21
7	95.8	0.0	4.2	0	25.46
5	100.0	0	0	0	33.85
77	93.9	0.0	6.1	0	42.71
76	98.7	0.0	1.3	0	36.03
58	94.9	0.0	5.1	0	33.58
6	14.8	80.4	2.3	2.5	78.41
16	82.7	1.3	8.2	7.8	29.19
22	98.7	0.0	1.3	0	33.65
39	82.0	18.0	0	0	34.29

[*] Basal area measured in 2004 (all tree stems measured, no minimum dbh), Maguire et al. (2002) unpublished data.
[#] Hardwood species include: red alder, big-leaf maple, and vine maple (*Acer circinatum*).
[¶] Other conifer species include: Sitka spruce and Pacific Silver fir (*Abies amabilis*).

Table 3.3. Absolute cation fluxes in soil water at 20 cm and 1 m and the non sea-salt (NSS) proportion of absolute flux in parentheses[#].

Site	**Ca**	**Mg**	**K**	**Na**	**Al[*]**	**Mn[*]**
				20 cm		
				kg · ha^{-1} · yr^{-1}		
20	23.297 (94%)	9.317 (77%)	13.400 (100%)	19.944 (0%)	0.394	0.052
7	7.620 (74%)	5.497 (35%)	5.079 (76%)	27.140 (0%)	0.480	0.035
5	18.032 (72%)	19.235 (51%)	17.111 (90%)	74.902 (0%)	0.336	0.051
77	7.860 (73%)	5.298 (39%)	7.572 (86%)	26.131 (1%)	0.062	0.104
76	6.537 (45%)	5.399 (0%)	4.336 (54%)	31.176 (0%)	0.245	0.100
58	8.669 (65%)	5.253 (44%)	11.382 (93%)	22.893 (20%)	0.000	0.066
6	3.758 (26%)	7.156 (19%)	2.285 (21%)	45.977 (1%)	2.908	0.527
16	13.461 (78%)	14.949 (66%)	7.953 (78%)	55.887 (30%)	3.460	0.261
22	6.386 (72%)	5.258 (39%)	6.228 (82%)	25.595 (0%)	0.206	0.100
39	14.292 (62%)	16.667 (47%)	2.070 (0%)	71.674 (1%)	1.654	0.388

[*] Al and Mn speciation not determined but mobilized species are most likely in monomeric (Al^{3+}, Mn^{2+}) or hydrolyzed form based on soil pH at 20 cm and 1 m. [#] NSS proportion of absolute flux determined by NSS leaching (calculation outlined in Methods) divided by absolute leaching.

Table 3.3. Continued.

Site	**Ca**	**Mg**	**K**	**Na**	**Al***	**Mn***
	1 m					
	kg · ha^{-1} · yr^{-1}					
20	10.474 (75%)	7.923 (59%)	4.089 (75%)	29.231 (28%)	0.440	0.072
7	4.126 (50%)	4.153 (20%)	1.381 (18%)	19.887 (0%)	0.065	0.029
5	6.319 (58%)	10.242 (53%)	14.196 (88%)	54.874 (26%)	0.139	0.027
77	7.705 (79%)	2.727 (23%)	13.310 (94%)	17.675 (2%)	0.153	0.051
76	5.500 (61%)	3.844 (9%)	3.607 (74%)	26.563 (0%)	0.032	0.206
58	9.031 (84%)	4.912 (47%)	7.171 (87%)	24.585 (10%)	0.231	0.151
6	5.260 (15%)	4.565 (0%)	6.592 (61%)	65.521 (8%)	1.773	0.385
16	7.007 (63%)	10.742 (54%)	8.318 (81%)	53.546 (27%)	4.086	0.193
22	6.031 (66%)	5.219 (34%)	4.227 (76%)	24.022 (0%)	0.058	0.123
39	7.160 (51%)	9.621 (35%)	1.735 (0%)	60.725 (17%)	0.183	0.301

Table 3.4. Non sea-salt[#] (NSS) soil water flux of base cations at 20 cm and 1 m

Site	**Ca**	**Mg**	**K**	**Na**	**Ca**	**Mg**	**K**	**Na**
	20 cm				**1 m**			
	kg · ha^{-1} · yr^{-1}							
20	21.814	7.132	16.755	-9.782	7.820	4.670	3.063	8.066
7	5.635	1.950	3.845	-3.020	2.056	0.845	0.244	-8.500[*]
5	12.989	9.769	15.417	-0.252[*]	3.651	5.474	12.538	14.360
77	5.710	2.08	6.509	0.148	6.091	0.626	12.570	0.358
76	2.929	-0.375[*]	2.321	-18.080[*]	3.330	0.365	2.663	-2.788[*]
58	5.602	2.331	10.636	4.672	7.577	2.314	6.267	2.498
6	0.995	1.369	0.473	0.421	0.787	-2.566[*]	4.020	4.925
16	10.453	9.866	6.186	16.709	4.416	5.841	6.747	14.294
22	4.587	2.043	5.110	-1.743[*]	3.969	1.781	3.217	-3.213[*]
39	8.816	7.876	-0.973[*]	0.380	3.664	3.350	-0.632[*]	10.606

[#] Sea-salt correction ratio from NADP OR02 watershed (1980 – 2004): Ca/Cl = 0.037, Mg/Cl = 0.065, K/Cl = 0.021, Na/Cl = 0.566.

[*] Negative values are a result of absolute flux being less than would be expected from sea salt inputs.

Table 3.5. Absolute anion and DOC fluxes in soil water

Site	**Cl**	**Br**	**SO_4^{2-}**[#]	**DOC**[*]	**Cl**	**Br**	**SO_4^{2-}**[#]	**DOC**[*]
	20 cm				**1 m**			
	kg · ha^{-1} · yr^{-1}							
20	35.490	0.287	4.934	25.331	29.490	0.420	6.998	6.302
7	47.618	0.140	13.248	21.490	35.508	0.289	7.753	3.995
5	135.116	0.180	17.518	19.046	103.879	0.325	11.302	10.775
77	41.049	0.069	4.003	12.625	27.114	0.088	2.701	6.526
76	72.196	0.321	3.048	12.159	60.137	0.379	2.936	5.266
58	41.664	0.149	2.169	16.179	34.627	0.145	3.620	3.462
6	95.661	0.163	13.321	21.447	96.911	0.324	8.746	6.381
16	82.533	0.234	5.848	16.776	74.062	0.272	7.913	4.468
22	40.733	0.156	3.648	17.828	44.399	0.186	3.999	6.106
39	126.049	0.715	2.595	12.436	88.974	0.779	3.257	7.832

[#] Sulfate ion fluxes reported in absolute flux since all fluxes were less than expected through sea-salt inputs. (Sea-salt correction ratio from NADP OR02, Alsea watershed (1980 – 2004): $SO_4^{2-}/Cl = 0.260$).

[*] DOC fluxes in kg C · ha^{-1} · yr^{-1}.

Table 3.6. Exchangeable Ca depth profile with % distribution by depth shown in parentheses.

Site	**0-10 cm**	**10-20 cm**	**20-30 cm**	**30-50 cm**	**50-70 cm**	**70-100 cm**	**Total**[¶]
				kg · ha^{-1}			
20	322 (16%)	182 (9%)	144 (7%)	271 (13%)	234 (12%)	877 (43%)	2030
7	1084 (18%)	938 (16%)	673 (11%)	1648 (27%)	961 (16%)	719 (12%)	6020
5	853 (15%)	564 (10%)	407 (7%)	1231 (13%)	672 (12%)	1955 (34%)	5680
77	638 (18%)	347 (10%)	148 (4%)	308 (9%)	258 (7%)	1778 (51%)	3480
76	481 (20%)	400 (17%)	287 (12%)	560 (23%)	298 (12%)	373 (16%)	2400
58	111 (24%)	37 (8%)	24 (5%)	59 (13%)	75 (16%)	158 (34%)	460
6	57 (9%)	43 (7%)	28 (4%)	67 (11%)	114 (18%)	327 (51%)	640
16	93 (33%)	26 (9%)	11 (8%)	47 (17%)	61 (22%)	42 (15%)	280
22	359 (19%)	509 (27%)	377 (8%)	265 (14%)	148 (8%)	206 (11%)	1860
39	72 (42%)	25 (14%)	15 (14%)	21 (12%)	15 (9%)	23 (13%)	170
slope[*]				0.00002			
p value[*]	0.17	0.73	0.61	**0.04**	0.53	0.99	

[*] Significance and slope of regressions between the proportion of exchangeable Ca in each depth and total exchangeable Ca to 1m.

[¶] Total exchangeable Ca to 1m.

Table 3.7. Exchangeable Mg depth profile with % distribution by depth shown in parentheses.

Site	**0-10 cm**	**10-20 cm**	**20-30 cm**	**30-50 cm**	**50-70 cm**	**70-100 cm**	**Total[¶]**
	kg · ha^{-1}						
20	88 (8%)	49 (5%)	37 (4%)	121 (12%)	181 (17%)	573 (55%)	1050
7	340 (13%)	313 (12%)	244 (9%)	639 (24%)	523 (20%)	597 (22%)	2660
5	303 (8%)	261 (7%)	209 (5%)	761 (20%)	548 (14%)	1731 (45%)	3810
77	225 (19%)	152 (13%)	71 (6%)	158 (13%)	106 (9%)	478 (40%)	1190
76	306 (18%)	269 (16%)	195 (11%)	395 (23%)	268 (16%)	266 (16%)	1700
58	61 (31%)	15 (7%)	10 (5%)	23 (11%)	46 (23%)	46 (23%)	200
6	63 (9%)	34 (5%)	29 (4%)	76 (11%)	136 (20%)	344 (50%)	680
16	93 (22%)	38 (9%)	16 (4%)	56 (13%)	90 (21%)	126 (30%)	420
22	183 (20%)	227 (24%)	150 (16%)	122 (13%)	89 (9%)	164 (18%)	940
39	62 (40%)	27 (18%)	14 (9%)	18 (12%)	13 (8%)	21 (14%)	160
slope[*]	-0.00006			0.00003			
p value[*]	**0.052**	0.71	0.87	**0.008**	0.92	0.56	

[*] Significance and slope of regressions between the proportion of exchangeable Mg in each depth and total exchangeable Mg to 1m.

[¶] Total exchangeable Mg to 1m.

Table 3.8. Exchangeable K depth profile with % distribution by depth shown in parentheses.

Site	**0-10 cm**	**10-20 cm**	**20-30 cm**	**30-50 cm**	**50-70 cm**	**70-100 cm**	**Total**[¶]
				kg · ha^{-1}			
20	155 (14%)	115 (10%)	144 (13%)	264 (24%)	178 (16%)	252 (23%)	1110
7	238 (17%)	197 (14%)	138 (10%)	259 (19%)	303 (22%)	223 (16%)	1360
5	239 (14%)	224 (13%)	144 (8%)	462 (26%)	196 (11%)	498 (28%)	1760
77	218 (11%)	154 (8%)	151 (8%)	479 (24%)	288 (15%)	693 (35%)	1980
76	142 (11%)	152 (12%)	121 (9%)	275 (21%)	245 (19%)	352 (27%)	1290
58	108 (10%)	55 (5%)	73 (7%)	303 (29%)	219 (21%)	295 (28%)	1050
6	83 (13%)	57 (9%)	61 (9%)	126 (19%)	169 (26%)	162 (25%)	660
16	133 (17%)	104 (14%)	67 (9%)	185 (24%)	181 (24%)	96 (13%)	770
22	148 (12%)	201 (16%)	156 (13%)	211 (17%)	208 (17%)	297 (24%)	1220
39	68 (14%)	55 (11%)	41 (8%)	68 (14%)	114 (24%)	138 (28%)	480
slope[*]					-0.00008		
p value[*]	0.47	1.00	0.80	0.19	**0.003**	0.23	

[*] Significance and slope of regressions between the proportion of exchangeable K in each depth and total exchangeable K to 1m.
[¶] Total exchangeable K to 1m.

Table 3.9. Soil pH (2:1 H_2O:soil) at 20 cm, 1 m, and mean soil profile pH.

Site	**Soil pH (20 cm)**	**Soil pH (100 cm)**	**Mean soil profile pH***
20	5.56	5.26	5.42
7	5.87	5.43	5.65
5	5.64	5.43	5.61
77	5.17	5.27	5.21
76	4.97	4.95	4.94
58	4.82	5.24	5.03
6	4.23	4.76	4.49
16	4.62	4.70	4.70
22	5.29	4.78	4.96
39	4.36	4.62	4.55

* Mean soil profile pH calculated across all 6 sampling depths.

Table 3.10. Stemwood cation concentrations.

Site	**Ca**	**Mg**	**K**
		%	
20	0.03	0.005	0.025
7	0.03	0.006	0.03
5	0.025	NA	0.025
77	0.03	0.006	0.03
76	0.025	NA	0.025
58	0.025	0.005	0.025
6	0.02	0.006	0.015
16	0.035	0.0075	0.025
22	0.025	NA	0.01
39	0.03	0.0065	0.03

NA, concentrations below detection limits.

Table 3.11. Ca storage in aboveground pools, annual litterfall Ca return, and integrated net annual Ca uptake[#].

Component	**Plant Ca pools[*]**									
Sites	**20**	**7**	**5**	**77**	**76**	**58**	**6**	**16**	**22**	**39**
	kg Ca · ha^{-1}									
Foliage	28	20	24	36	40	36	22	16	20	16
Branches	89	69	113	98	93	70	31	57	66	52
Stems	14	32	35	50	37	26	29	24	36	31
Total	131	120	172	184	171	132	75	98	121	99
Stand Age	23	32	30	29	27	24	25	27	30	28
Annual Uptake[#]	5.71	3.76	5.72	6.35	6.33	5.50	2.99	3.63	4.03	3.55
Annual Litterfall	23	19	16	25	18	15	8	10	22	13

[*] Pool sizes calculated from Douglas-fir Hybrid Growth System Model (Weiskittel 2006).

[#] Integrated net annual Ca uptake calculated as the total aboveground Ca pool divided the age of the stand.

CHAPTER 4: CONCLUSION

The objectives of this thesis were to determine N cycling patterns and potential biogeochemical couplings between N and base cations across a broad soil N gradient. The utility of the soil N gradient employed in this study permitted observation of fundamental biogeochemical processes without the competing influence of parent material, climate, or overstory species differences. Thesis objectives were addressed by examining soil, soil water, and plant nutrient pools, concentrations, and fluxes across a range of soil N availability. Chapter 2 examined the potential drivers and range of soil N pools and how N cycling patterns vary with soil N availability. Chapter 3 addressed the influence of N cycling patterns on Ca availability and distribution in the ecosystem. Overall this thesis has highlighted the wide range of nutrient availabilities present in the Coast Range, and the potential for localized N saturation and Ca limitation in some forests.

The Oregon Coast Range possesses a globally unique range in soil N, the spatial heterogeneity of which has influenced the variability in N cycling rates and base cation availabilities across the region. The range in soil N capital across these ten sites could be a result of many factors, but variations in historic N_2-fixing red alder colonization seems most likely to have imparted a mosaic of N-rich inputs across the Coast Range. Although red alder is absent from these ten sites, the effects of high soil N accumulation do not appear to be reversible during one conifer rotation. Soil N availability appears to feedback positively on N cycling and productivity to a point, but not indefinitely, as N stocks do not seem to increase microbial N processing rates and plant productivity in perpetuity. Paradoxically, a limitation in N cycling rates was also coupled with nitrate leaching losses in excess of current N inputs at several N-rich sites. Soil N availability also influenced exchangeable base cation stores, as exchangeable Ca in particular varied over 35-fold across the sites. The strongly negative relationships observed between soil extractable Ca, Mg, and K versus nitrate leaching highlights a key role for elevated nitrate leaching in promoting depletion of available soil base cations. At base-depleted, N-rich sites biotic uptake and tight recycling of Ca through aboveground biomass and surface soil appears important for retaining Ca in the ecosystem. Examining the complex suite of biotic and abiotic interactions involved in the N-Ca biogeochemical coupling is essential for understanding ecosystem function and achieving long-term sustainability in these managed systems.

Without consideration of ecosystem nutrient status, forest management practices may be detrimental to stand productivity and ecosystem resilience. Elevated nitrate leaching occurring at several N-rich sites suggests N availability exceeds ecosystem demands and would be exacerbated by N fertilization or a reduction in plant uptake by harvesting. As the storage of N in these soils far exceeds that in aboveground plant pools, management activities that impact soil N cycling may be detrimental to ecosystem function. Many of the sites in this study also possess high foliar N concentrations, suggesting these stands may not be N limited and fertilization may not positively affect stand productivity. Additionally, the substantial sequestration of Ca in aboveground plant pools at N-rich sites suggests harvesting, particularly whole-tree harvest, may further deplete Ca stores. Forest N fertilization and intensive harvesting would be expected to intensify Ca loss and exacerbate soil acidification and metal cation cycling. The heterogeneity of nutrient availability in the Coast Range may pose a challenge for the sustainability of future forest management.

The utility of this soil N gradient and results from this study and Perakis et al. (2006) have raised several issues for further consideration and ongoing research including: the N budget imbalance at several N-rich sites, the relative contribution of atmospheric and weathering Ca inputs across the gradient, the importance of calcium oxalate as a Ca source, and the effectiveness of Ca fertilization to mitigate depleted soil reserves and tree nutrition. The N budget at several N-rich sites yielded higher N outputs than N inputs. Although nitrate leaching increased across the gradient, the tapering in net N mineralization rates, suggests N cycling rates will eventually limit N outputs and restore the balance of N in the ecosystem. As few watersheds globally exhibit greater N losses than inputs, an in-depth determination of N inputs may provide a more accurate assessment of the N budget. Other researchers are currently investigating trace N gas efflux from these sites which will contribute to further understanding of how N cycling patterns vary with soil N availability. Additionally, my results preliminarily suggested greater internal generation of Ca may be occurring at high pH sites; however, present research employing strontium and Ca isotopes will determine if atmospheric inputs of Ca are relatively more important than inputs from weathering as soil N increases. Our lab is also investigating whether calcium oxalate contributes to the plant-available Ca pool and how the importance of calcium oxalate may shift across the soil N gradient. Lastly, plant conservation of Ca at N-rich sites, begs the question of possible Ca limitation which could be investigated with a Ca fertilization experiment. Long-term monitoring of N cycling and nutrient leaching could aid in determining the duration of N budget imbalances and biogeochemical couplings across the gradient.

This work emphasizes the variability in site fertility in the Oregon Coast Range. Some sites in the Coast Range exhibit excessive N availability with elevated nitrate loss and depleted base cation reserves, while other sites have very little N loss and substantial base cation stores. As the Northwest Forest Plan has effectively promoted an intensification of timber management within a smaller land area in western Oregon, a thorough examination of the complex biogeochemical interactions across the region may help to increase forest productivity and encourage sustainable forest management.

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APPENDIX

Table A1.1. N cycling seasonality in the 2005 season.

Site	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Net N Min. Gross N Min.* Nitrate-N flux						kg N · ha^{-1} · yr^{-1}						
20	1.94	0.36	0.52	1.37	1.69	1.54	2.43	3.98	3.43	2.10	7.12	14.89
	-	58.61	-	-	-	65.23	-	-	-	19.87	-	-
	-	0.11	0.05	0.03	0.03	0.03	0.04	-	-	-	-	0.02
7	0.07	0.74	1.09	0.83	1.80	1.89	1.91	1.22	3.03	0.65	1.52	1.14
	-	17.77	-	-	-	23.20	-	-	-	18.93	-	-
	0.12	0.04	0.02	0.16	-	0.04	-	-	-	-	-	0.04
5	2.11	2.72	1.29	2.89	6.23	6.63	8.51	2.01	1.99	2.39	2.75	1.34
	-	16.31	-	-	-	17.17	-	-	-	14.95	-	-
	0.21	0.12	0.00	0.00	0.01	0.01	0.02	0.22	-	-	-	0.02
77	3.18	1.07	4.11	3.25	7.53	8.61	12.77	9.75	12.47	12.87	4.71	2.47
	-	8.65	-	-	-	15.73	-	-	-	16.03	-	-
	3.38	4.51	2.03	1.30	4.00	5.93	7.44	-	-	-	17.84	2.90
76	3.20	1.54	2.49	1.56	6.01	6.96	15.46	8.90	7.63	9.26	5.73	3.99
	-	15.73	-	-	-	9.47	-	-	-	7.76	-	-
	1.76	0.89	0.02	0.01	0.04	0.13	-	-	-	-	-	0.02

*Gross N mineralization only determined in February, June, and October.

- Dashes indicate no soil water was collected to determine nitrate-N flux or gross N mineralization rates were not determined that month.

Table A1.1. Continued.

Site	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Net N Min. Gross N Min.* Nitrate-N flux	**kg N · ha^{-1} · yr^{-1}**											
58	1.07	1.79	4.67	3.88	6.09	8.27	11.45	5.95	5.79	6.50	7.01	5.03
	-	10.07	-	-	-	7.45	-	-	-	12.79	-	-
	11.64	7.24	0.09	3.54	0.04	0.06	0.15	-	-	-	-	10.76
6	3.00	2.26	3.71	7.32	7.56	5.36	10.69	9.00	18.72	14.89	3.41	4.47
	-	10.13	-	-	-	10.62	-	-	-	7.72	-	-
	14.55	9.55	4.23	9.62	4.02	3.59	0.06	7.59	-	-	3.72	5.95
16	1.93	3.07	4.97	2.33	7.10	13.37	12.84	10.23	11.23	8.32	4.27	3.00
	-	7.85	-	-	-	7.18	-	-	-	14.70	-	-
	23.64	21.71	28.26	29.69	14.39	36.16	38.60	23.29	-	-	55.75	23.52
22	3.66	3.57	2.94	6.36	7.17	12.96	19.06	8.39	10.91	13.80	6.28	3.96
	-	6.60	-	-	-	27.74	-	-	-	10.00	-	-
	1.06	0.73	1.45	0.67	0.58	0.09	0.12	-	-	-	-	0.38
39	5.91	1.47	3.29	3.17	5.80	8.96	10.63	11.57	4.77	12.27	4.21	4.13
	-	11.23	-	-	-	20.48	-	-	-	16.92	-	-
	11.44	12.17	9.31	8.10	9.97	12.44	11.56	-	-	-	4.84	8.42

Table A1.2. Surface (0-10 cm) soil N chemistry.

Site	**Surface soil N**	**Surface soil C:N**	**Extractable nitrate-N**	**Extractable ammonium-N**
	(0-10 cm)			
	%		**kg N · ha^{-1} · yr^{-1}**	
20	0.21	21.36	0.02	1.35
7	0.24	20.84	0.07	1.32
5	0.26	19.85	0.02	1.10
77	0.30	16.01	0.47	3.20
76	0.34	16.28	1.08	3.29
58	0.37	17.47	0.40	2.03
6	0.51	14.47	1.36	1.80
16	0.56	16.24	2.46	1.62
22	0.63	14.62	1.14	2.22
39	0.69	20.94	0.43	1.41

Table A1.3. Exchangeable base cation concentrations and pH to 1m[#].

Site	**Exchangeable Ca**	**Exchangeable Mg**	**Exchangeable K**	**Soil profile pH**
		$\mathrm{mmol_c \cdot kg^{-1}}$		
20	39	39	6	5.42
7	4	6	2	5.65
5	48	33	5	5.61
77	3	6	4	5.21
76	9	6	3	4.94
58	10	8	3	5.03
6	1	2	2	4.49
16	3	2	3	4.70
22	11	12	3	4.96
39	17	10	5	4.55

[#] Calculated as arithmetic mean of all depths

Table A1.4. Volume-weighted base cation and chloride soil water concentrations at 1m*.

Site	**Ca**	**Mg**	**K**	**Na**	**Cl**
	1 m				
	$\mu g \cdot L^{-1} \cdot mm^{-1}$				
20	0.490	0.371	0.191	1.514	1.936
7	0.454	0.457	0.152	2.190	1.494
5	0.812	1.317	1.825	7.054	2.028
77	1.442	0.510	2.491	3.308	2.086
76	0.723	0.506	0.508	3.493	2.003
58	1.115	0.606	0.885	3.035	2.019
6	0.235	0.232	0.334	3.324	2.901
16	0.979	1.501	1.162	7.481	2.765
22	1.206	1.044	0.879	4.806	2.326
39	0.561	0.724	0.111	4.568	2.673

* Calculated above dividing absolute leaching by estimated volume of water moving past lysimeters (see Methods for water volume estimation using 3PG).