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Factors Regulating Nitrogen Mineralization Rates of an Oak Pine and Northern
        Hardwood Forest Along an Elevation Gradient
(Under the Direction of DAVID C. COLEMAN)

Reaction rates typically decrease with decreasing temperature. Temperature decreases with increasing elevation. Thus, nitrogen (N) mineralization rates are predicted to decrease with increasing elevation. However, N mineralization rates are more than an order of magnitude greater at a high elevation northern hardwood (NH) stand than at a lower elevation Oak Pine stand (OP) at the Coweeta Hydrologic Laboratory in the southern Appalachian mountains, NC. A preliminary experiment tested whether a promoter substance existed in the leachate of the herbs, leaf litter or soils of the NH site, by treating soils with cold water extracts of these components. The extracts did not have significant effects on N mineralization rates. Nitrogen budgets were then constructed for both sites to compare the sizes of N pools and fluxes. Values from the N budgets were used to develop a STELLA model. Sensitivity analysis was performed for 200-yr simulations. The large N soil pool, finer textured soil, and higher soil moisture content at the NH seems to be the most important variables in explaining the N mineralization rate differences between these two sites.

INDEX WORDS: Nitrogen, Mineralization, Budgets, STELLA Model, Soil Texture,

                  Elevation Gradient, Mineralization Promoter

FACTORS REGULATING NITROGEN MINERALIZATION RATES OF AN OAK

PINE AND HARDWOOD FOREST ALONG AN ELEVATION GRADIENT

by

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DEDICATION

This thesis is dedicated to my parents for all their support and encouragement.

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CHAPTER 1

INTRODUCTION

1.1 Introduction

Nitrogen (N) is often cited as being the most limiting macronutrient to forest production, and therefore important in regulating ecosystem processes (Vitousek et al. 1997; Mitter et al. 1984; Pastor et al. 1984). Although organic N is often plentiful in soils, this form is not readily available to plants. Organic N must be mineralized into inorganic N since most plants obtain nutrients in inorganic mineral forms, the most important being nitrate (NO_3^-) and ammonium (NH_4^+) (Paul and Clark 1989). The rate of N mineralization is an important rate-limiting step of N availability in forests.

Soils are fundamental components of ecosystems and crucial in understanding ecosystem processes (Coleman and Crossley 1996). Both biotic and abiotic factors influence soil structure and function. Because the soil comprises the largest nutrient pool in a forest and is the medium through which all nutrients cycle, soils are central to studies concerning biogeochemical cycling.

Microorganisms are responsible for the mineralization process, consuming organic residues and releasing excess and waste N in inorganic forms (Paul and Clark 1989). However, despite large annual N fluxes in soils, mineral N pools in forest soils tend to be relatively small due to rapid transformation and N uptake by plant roots, fungi, and microorganisms (Schlesinger 1991). The rate of N mineralization is preferred over

the total mineral N pool size to estimate nutrient supply, because rates of N mineralization tell how much N becomes available in soils over time (Powers 1980).

Over the last few decades many studies have correlated environmental and site characteristics with rates of N mineralization. Temperature and moisture factors may be the two most important environmental factors influencing organic matter decomposition and mineralization rates (Murphy et al. 1998; Holmes and Zak 1994). Soil characteristics, such as texture and percent organic matter, have also been important in explaining different N mineralization rates across forests (Prescott et al. 2000, Reich et al. 1997).

Other reports have hypothesized that rates or N mineralization are mostly a function of the total N capital at any particular site (Hobbie 1992; Vitousek 1982; Gosz 1981). The size of the N pool may affect the quality of the organic debris and cause feedbacks within the N cycle of a particular site; high quality litter should indicate a lower N use efficiency, larger N pools and faster N cycling (Hobbie 2000). Plants do not influence N cycling by litter quality alone. Studies have shown root exudates, particularly sugars and amino acids, to be important in stimulating microbial growth in the rhizosphere, and increasing rates of nutrient turnover (Jaeger et al. 1999). Differences in microbial communities and their rates of turnover may also be important in understanding nutrient cycles. Studies using isotope tracers have shown that N released from microbial tissue may be mineralized in larger amounts than N in organic matter (Currie and Nadelhoffer 1999; Marumoto et al. 1982). Therefore soil fauna that feed on bacteria and fungi can increase rates of N turnover (Schesinger 1991; Anderson et al. 1983).

Rates of mineralization, as with other chemical and biological reactions, are temperature dependent, with warm temperatures favoring faster rates and colder temperatures slower rates (Ross and Bridger 1978). Temperatures typically decrease with increasing elevation, thus N mineralization rates are hypothesized to also decrease with increasing elevation. However, at Coweeta Hydrologic Lab in NC, N mineralization rates are highest at a colder high elevation northern hardwood forest and lowest at a warmer lower elevation oak pine forest (Knoepp and Swank 1998). Other studies have found similar trends, though this phenomenon has not been fully explained (Fernandez et al. 2000; Morecroft et al. 1992).

1.2 Purpose of Study

For my thesis, factors responsible for differences in N mineralization rates between a northern hardwood forest and an oak pine forest will be assessed in order to isolate those that are most important. The first experiment was designed to test if a mineralization promoter is present at the northern hardwood site, which may explain the higher rates of mineralization at this site. The next study synthesized long-term data from these two sites to construct N budgets, to examine how N pool sizes and fluxes correlate with N mineralization rates. The final study used STELLA 6.0 to build a model of these two sites using data from the N budgets to assess which variables have the most control over N mineralization rates for each site. The factors which best explain the nitrogen cycling and mineralization rates occurring at these two sites are discussed in the conclusion.

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CHAPTER 2

LITERATURE REVIEW – FACTORS THAT AFFECT NITROGEN

MINERALIZATION AND CYCLING IN FORESTS

2.0 Nitrogen Mineralization and Turnover

It has long been thought that the availability of ammonium (NH_4^+) and nitrate (NO_3^-) limits forest productivity because many forests show a growth response to mineral nitrogen (N) fertilizer (Pastor et al.1984). Large quantities of N exist in forest ecosystems, but most is bound in organic forms unavailable to plants. Only small quantities of N are in accessible mineral forms usable by plants in the system (Schlesinger 1991).

Nitrogen mineralization is the conversion of organic N in soil organic matter and decaying microbial biomass into ammonium. The rate of N mineralization is important since it is a major rate-limiting step in forest production. Jansson (1958) proposed an early model of N mineralization-immobilization transformation in soil. In this model, microbes mineralize organic N to inorganic N, which is then converted to organic N (immobilization) during growth and decay of microbial biomass (Jansson 1958). Nitrogen in excess of microbial requirements is released as NH_4^+ (Jansson 1958). Locations in the soil where N mineralization occurs can be physically and/or temporally separated from sites of N immobilization (Drury et al. 1991). Although Jansson's early

model does not account for direct organic N utilization by microbes, it serves as a useful conceptual framework for studying N mineralization.

Rates of soil N mineralization often differ with forest type, elevation, and topographic position, and are attributed to site variations in soil organic matter, temperature, and soil water availability (Knoepp and Swank 1998). It is the microbial activity in the bulk soil, controlled by the physical environment (soil water potential and temperature), that is responsible for N mineralization (Drury et al. 1991). Typical N mineralization rates among temperate forests range from 2 to 12 $g\text{-}N/m^2/yr$ (Zak et al.1993).

Most forest materials need to be weathered and processed by microbes before they are mineralized. Climate, edaphic properties, resource quality, and organism activity are the major determinants of decomposition, or mass loss of organic material (Heneghan et al.1998). During brief periods of microbial growth on carbon substrates, decomposition is controlled by the availability of inorganic N and the relative diffusion rates of NH_4^+ and NO_3^- from the sites of production to sites of immobilization (Drury et al. 1991). Under high mineral N levels, carbon may limit decomposition (Holmes and Zak 1994).

2.1 Nitrogen Availability

Procedures to determine rates of N mineralization under different conditions and the quantities of nitrogenous compounds involve extractions using salts and strong oxidants (Hart et al. 1994; Mahendrappa et al. 1986). Approaches such as site classification, soil and foliar analyses, and analyses of nutrient mineralization rates have

been adapted to determine nutrient availability and soil fertility (Mehendrappa et al. 1986). The accumulation and potential availability of mineral N is limited, in part, by the rates of N transformation and extractable inorganic forms of N (Mehendrappa et al. 1986). Nitrogen availability in forest soils may also be influenced by the decomposability of organic nitrogen compounds.

Nutrient cycling processes may occur in solid, liquid, or gaseous phases and are so dynamic that it is impossible to attempt to determine the availability of a nutrient based on analyses of soil samples collected at a specific point in time (Gobran et al. 1998; Mehendrappa et al. 1986). In addition to mineral soil horizons, forest floor materials should also be evaluated and considered independently in tree nutrition studies (Mahendrappa et al. 1986).

2.2 Amount of N Inputs and Exports

Nitrogen may enter an ecosystem through dry and wet deposition or by N fixation (Boring et al. 1988). The quantities of N measured as dry deposition in open areas may only be a small proportion of the quantities of N actually added to forests (Boring et al. 1988). Vitousek et al. (1997) reports that human activities have significantly altered the global N cycle, resulting in unprecedented rates of atmospheric N deposition in forests throughout the northeastern United States and Europe. The estimated total (wet + dry) quantities of N in bulk precipitation range from about 3 kg N ha-1 yr-1 in relatively unpolluted areas, to 20 kg N ha-1 yr-1 in polluted areas (Mahendrappa et al. 1986; Boring and Swank 1984). During the average rotation age of forests in the northern temperate region, even the lowest rates of annual N deposition recorded can represent a high

proportion of total N in the forest ecosystems (Mahendrappa et al. 1986). This abiotic mechanism of N incorporation into soil organic matter could be an important process influencing ecosystem N retention (Zogg et al. 2000).

The quantities of N entering the nutrient cycle of forest ecosystems through microbial N fixation are directly available to trees and appear to equal or exceed the quantities cycled as throughfall and litterfall (Mahendrappa et al. 1986). Estimates of annual rates of N fixation range from 0.22 to over 100 kg N/ha/yr for hardwood and conifer forests (Boring et al. 1988).

Throughfall and stemflow are also recognized as important pathways for nutrient transfer to the soil (Monk and Day 1985). Qualls and Haines (1991) reported substantial throughfall inputs of dissolved organic nutrients to the soil. Still, the uncertainty in estimating nutrient recycling by throughfall and stemflow is related to the difficulty in distinguishing nutrients derived from within the plant community (recycling) from those deposited on plant surfaces by wet and dry deposition (inputs into ecosystem).

A major mode of N export in many ecosystems is by leaching through the soil in dissolved organic or inorganic form (Goodale et al. 2000, Qualls and Haines 1991). Nitrate leaching is a major mode of N export in forests. Nitrate leaches through the soil, attaches with other nutrient cations, and may lead to soil acidification and declines in forest growth (Zogg et al. 2000). Qualls and Haines (1991) found most dissolved organic N (DON) in forest soil was in humic, hydrophilic acid, and hydrophilic neutral fractions. DON concentrations increased after passing through the forest floor and then declined 35-70 fold as water percolated through the soil profile (Qualls and Haines 1991). Free

proteins and amino acids appear to be a very small percentage of the DON in soil solution (Qualls and Haines 1991).

2.3 Nitrogen Use Efficiency

Forests appear to be more efficient in net production per unit of N at low levels of N availability (Vitousek 1982). Nitrogen-use efficiency (NUE) may be a reliable indicator of N availability in forests, since NUE of litter production varies as an inverse function of N availability (Vitousek 1982). Litter N concentration is positively correlated with soil N concentration (Hobbie 1992). Sites with symbiotic N-fixers ('increased N supply') tend to have high N circulation and low N efficiency (Vitousek 1982). Similarly, temperate forests with large amounts of litterfall N and low N efficiencies tend to be in regions receiving high levels of anthropogenic N input through rain and snow (N-availability is enhanced) (Vitousek 1982). This parallels studies of forest fertilization that show applied inorganic N increases foliar N concentrations, thus NUE of litter fall decreases (Magill et al. 2000). Nitrogen-use efficiency of below ground litter probably varies similarly with above ground litter production (Vitousek 1982). Still, there is no single method used widely enough to allow comparisons of apparent soil N availability and NUE in a wide range of sites (Vitousek 1982).

2.4 N-rich vs. N-poor Sites

Nitrogen cycling is generally considered to be more rapid on sites with high availability of N (Prescott et al. 2000b). In many studies changes in N cycling are associated with differences in tree species composition. However, Prescott et al. (2000b)

found that rates of N cycling and decomposition rates are faster on N-rich sites, even in the absence of changes in tree species composition. Increased soil N availability was associated with increased mass and concentrations of N in litterfall (Prescott et al. 2000b). The forest floor mass was smaller at N-rich sites, despite the greater litter inputs, indicating more rapid turnover (Prescott et al. 2000b). Pastor et al (1984) also report higher N return in litter at eight sites along a gradient in soil N mineralization. These results agree with Gosz (1981) who reported vegetation on N-rich sites produced litter with high N concentrations and low amounts of phenolics, leading to rapid decomposition and mineralization of N.

Studies of individual plants from low nutrient environments suggest plants allocate more C belowground than plants in high nutrient environments (Hobbie 1992). In nutrient-poor ecosystems, plants grow slowly, use nutrients efficiently and produce poor-quality litter that decomposes slowly and deters herbivory (Hobbie 1992). On N-poor sites, not only is decomposition slower, but also a smaller proportion of the N in litter is mineralized and removed from the forest floor (Hobbie 1992). This may be due to greater production of polyphenols on N-poor sites, which would cause more N to remain in the forest floor bound as polyphenol-protein complexes (Prescott et al. 2000b). This would act as positive feedback, increasing N availability on N-rich sites and decreasing N availability on N-poor sites (Prescott et al. 2000b).

2.5 N Mineralization in Relation to Total N Capital

There is indeed evidence that net N mineralization in the forest floor is much less in sites circulating small amounts of N annually (Vitousek 1982). Prescott et al. (2000a)

hypothesize that if N turnover is influenced by site N availability in the absence of changes in tree species composition, then rates of N input in litter, N turnover in the forest floor and net N mineralization would increase as soil N capital increased. Reich et al. (1997) report that soil properties had significant impacts on N mineralization and annual net primary production (ANPP), and their results support the paradigm that proximate control of productivity of temperate forests ecosystems is linked to their N status. The total amount of N returned in annual litterfall was also positively correlated with soil N capital (Reich et al. 1997). However, net N mineralization may be most affected by the N concentration in the forest floor and less tightly linked to soil N capital and associated site factors (Prescott et al. 2000b). Fernandez et al. (2000) concluded that forest floor N concentration was a better predictor of potential net N mineralization than was total C or C:N ratio.

Morecroft et al. (1992) suggests that a higher capital of mineralizable N, not necessarily reflected by the total N content accounts for the increase in N turnover at a site. Zak et al. (1993) found that mineralized N was only weakly correlated with total N among 154 forest stands. Similarly, Gower and Son (1992) did not observe a significant correlation between net N mineralization and previously measured soil characteristics such as total soil N content, mineral soil N concentration, soil organic C, or soil pH. Although the soil N pool is generally the largest N pool in a forest ecosystem, the majority of soil N occurs in fractions that are long-lived and resistant to microbial degradation (Zak et al.1993).

Nitrogen release from the forest floor often occurs at a faster rate than in the soil, even though the total pool size in the forest floor is much smaller than in the mineral soil

(Zak et al.1993). Poor relationships between net N mineralization and the soil N capital and rates of N turnover suggest that laboratory measures of net N mineralization in the forest floor may not provide a good indication of site N availability (Prescott et al. 2000b). Field measurements are preferred (Knoepp and Swank 1995). Differences observed in rate constants for forest floor and mineral soil also suggest that N is mineralized from different types of organic matter in these ecosystem components and should be modeled separately (Zak et al.1993).

2.6 Nutrient Reabsorption and Leaf Translocation

A considerable proportion of the nutrients, especially N and P, are withdrawn from the foliage and redistributed within the tree before leaf fall, tightening the N cycle in forests (Griffith 1993; Mahendrappa et al. 1986). Chapin (1980) reviewed the literature on nutrient reabsorption and found both an absolute and proportionally greater reabsorption of N in species with higher foliage N concentrations. Leaf translocation efficiencies vary inconsistently across gradients of nutrient availability and leaching losses show no pattern with nutrient availability (Hobbie 1992). Between 60 and 84% of the nutrients in the foliage can be retranslocated before abscission and litterfall (Chapin 1980). The quantity of a nutrient retranslocated within trees of a species is dependent on the availability of that nutrient from the soil and it appears that retranslocation is controlled by the sizes of sources and sinks. In sites with low nutrient availability trees retranslocate relatively more nutrients out of their leaves than species on rich sites (Mahendrappa et al. 1986). Hardwoods tend to retranslocate more N before leaffall than do conifers, and translocation seems to be species specific (Mehendrappa et al. 1986).

2.7 Vegetation Influence on N Mineralization

Plant species create positive feedbacks to patterns of nutrient cycling in natural ecosystems (Hobbie 1992). Many studies have shown N mineralization rate differences among plant species (Hobbie 1992). The annual contribution of herbs and shrubs to total nutrient content is much greater than their contribution to litterfall biomass because of the high nutrient concentrations of herb and shrub litter relative to tree litter (Mahendrappa et al. 1986).

Knoepp and Swank (1998) suggest that vegetation type is the overriding regulator of net N mineralization rates in southern Appalachian forests. Other studies have reported that substrate quality regulates N mineralization rates (Knoepp and Swank 1998; Nadelhoffer et al. 1984). Studying the differences in soil and leaf litterfall N dynamics in five forest plantations Gower and Son (1992) demonstrated that tree species can modify soil N mineralization rates in a relatively short time relative to rates of soil development. Thus, species effects may be more important than abiotic factors such as climate, in controlling ecosystem fertility (Hobbie 1992).

2.8 N Mineralization in Conifer and Hardwood Forests

When comparing the total amounts and distribution of N and organic matter in deciduous and conifer forests, Foster et al. (1985) found that the deciduous ecosystem contained twice as much organic matter and three times as much N as the conifer ecosystem. Fernandez et al. (2000) found both conifer and hardwood forests had nearly identical concentrations of N in the forest floor (1.6 %) but the mean C:N ratio under softwoods was significantly higher. These results are similar to those of Hu et al. (1997)

who surveyed a number of sites and found the highest C:N ratio under pine trees. The lowest N mineralization rate constants are found in coniferous forests, where inputs of lignified litter generally lead to slow rates of decomposition and N mineralization (Zak et al.1993).

Data on annual rates of in-situ net N mineralization compiled by Reich et al. (1997) for 16 conifer and 34 hardwood forests show that ANPP increased linearly with annual net N mineralization rates. In this study hardwood and conifer stands did not differ significantly in ANPP or N mineralization on comparable soils and stand origin. They suggest that observed average differences among natural forest types in ANPP and N mineralization resulted largely from variation in their distribution on differing soils, and not from feedback effects on N mineralization or differing productivity per available N (Reich et al.1997).

2.9 Foliar Nutrients and Litter Quality

Litter quality has been stated as an explanatory variable of N mineralization and decomposition. Pastor et al. (1984) report net aboveground production, its allocation to woody increment or litter, nutrient return in litter, NUE in litter production, and litter quality were all strongly related to mineralization as measured by the buried bag technique. Heneghan et al. (1998) found a negative linear relationship between initial %N and mass of litter remaining after 250 days. However, increased availability of N alone (in the absence of climate or vegetation differences) may not increase rates of litter decay. Prescott (1995) found no evidence that greater N availability resulted in more rapid litter decomposition. Similarly, Murphy et al. (1998) found no correlation between

initial litter N content and the rate of decomposition suggesting that decomposition is limited by easily decomposable carbon substrates rather than nutrients. Griffith (1993) found no association between foliar nutrient concentrations and soil mineralization rates along an elevational gradient in the southern Appalachians. Limits in soil moisture may have a more significant influence on the rate of decomposition and mineralization than the litter N content (Murphy et al.1998).

Contrary to the above, Pastor et al. (1984) demonstrated that in-situ N mineralization was well correlated with N in aboveground litter. In this study, mineralized N in forest floor was approximately equal to that contained in the annual litterfall of jack pine (Pastor et al. 1984).

Within a species, Vitousek (1982) suggests low foliar concentration can be used as a standard indicator of low nutrient availability in a site. Mahendrappa et al. (1986) disagree, stating that the status of foliar nutrient concentrations to tree growth or nutrients in the soil does not appear to be a good index of soil nutrient availability. Prescott et al. (2000a) also report that nutrient concentrations in forest floors correlated poorly with litter nutrient concentrations.

Scott and Binkley (1997) found no significant relationship between litterfall N and net N mineralization, and Prescott et al. (2000b) report that rates of N mineralization in the forest floors do not seem to be related to rates of decomposition of foliage litter. Contrary results by Pastor et al. (1984) report that NUE in litter production declined with increasing N mineralization (except in Hemlock stands).

One characteristic of vegetation that can ultimately influence soil processes is how long trees retain their foliage (leaf lifespan) because there are intrinsic relationships

between biochemical characteristics of foliage and leaf lifespan (Gower and Son 1992). Foliage N concentration is inversely related to leaf lifespan for tree species in natural forests (Gower and Son 1992). There tends to be a strong positive correlation between concentrations of immobile defense compounds, such as lignin and tannins, and leaf lifespan (Gower and Son. 1992; Coley 1988). There seems to be support for the idea that decomposition is controlled somewhat by initial litter chemistry and litter quality (Murphy et al. 1998).

2.10 C:N Ratio as an Indicator of Potential Mineralizable N

The carbon to nitrogen ratio (C:N) of litter and soils is often used as a predictor of decomposition and mineralization. The critical C:N ratio below which net N mineralization occurs is commonly quoted as being in the range of 12 to 20:1, or 1.7 to 2.5 % N (Prescott et al. 2000b; Vitousek 1982). Prescott et al. (2000b) report strong correlations between C:N and N mineralization of the forest floor, in laboratory incubations. Rates of net N mineralization in forest floors were highest at the two sites with the lowest forest floor C:N ratios, and mineralization was generally low above a C:N ratio of 35 (Prescott et al. 2000b).

Woody plants in low-N sites produce litterfall with a much higher C:N ratio than those in high-N sites (Vitousek 1982). Litter fall with high C:N should favor N retention by decomposers and reduce N availability in the soil, which would then lead to high NUE and production of litter with a higher C:N ratio (Vitousek 1982). Qualls and Haines (1991) report a consistent decrease in the C:N ratio moving from the forest floor to the C-horizon.

2.11 Lignin Content on Decomposition and N Mineralization

Many decomposition studies have identified the lignin concentration and the lignin:N ratio as the most reliable predictors of decomposition rates (Murphy et al. 1998). When the litter N concentration is low, litter lignin concentrations are generally higher, and litter lignin:N is also high (Murphy et al. 1998). Lignin content is also important in mineralization rates (Hobbie 1992). When the N concentration is high, litter lignin concentrations tend to be lower, litter lignin:N is low, and net N mineralization is high (Scott and Binkley 1997). The relationship between litter lignin:N and net N mineralization can best be described by a negative logarithmic function (Scott and Binkley 1997).

In a comparison between 11 studies, Scott and Binkley (1997) found litter lignin:N ratio explained more net N mineralization variation for forest ecosystems (r2=.74) than any other litter quantity or quality parameter (lignin concentration, litterfall mass, litterfall N%). They suggest that litter quality (lignin:N) may exert more than a proximal control over net N mineralization by influencing soil organic matter quality throughout the soil profile independent of climate (Scott and Binkley 1997).

2.12 Soil Rhizosphere and Soil Microbes

It has been estimated that 70 to 80 % of the annual net primary production may be allocated below ground creating a habitat known as the rhizosphere (Gobran et al.1998; Vogt et al. 1982). The total rhizosphere environment is determined by interactions between soil, plant and organisms associated with the roots (Gobran et al. 1998). The rhizosphere is an important zone in the soil where mineralization rates are often double

that of the bulk soil (Jaeger et al. 1999). Due to root turnover, sloughed cells, exudates and secretions, the rhizosphere strongly influences heterotrophic microbes that depend on C as an energy source (Hobbie 1992). The rhizosphere tends to support higher microbial biomass, a more active population of microbes, and a higher ratio of bacteria to fungi than the bulk soil (Hobbie 1992). An enhanced C availability in the rhizosphere has been suggested to increase N immobilization by heterotrophic soil microbes, attract microbial grazers that in turn increase N mineralization rates (Hobbie 1992). During the breakdown of substrates rich in N, microbes tend to immobilize N until sufficient C has been respired to a point where C or some element other than N is limiting catabolism (Mitter et al. 1984). Microbes are the most important labile C pool since they are vital for soil organic C dynamics and nutrient cycling (Hu et al.1997).

Rates of gross N mineralization are correlated with rates of C mineralization, but a very substantial proportion of the mineralized N is re-immobilized into microbial biomass (Prescott et al. 2000a). Results by Zak et al. (1993) also show mineralized N to be well correlated with respired C among stands.

About 30 to 50 % of organic C in temperate soils is contained in highly recalcitrant organic-mineral complexes with a turnover time of thousand years in temperate soils (Hu et al.1997; Trumbore 1993). Low percentages of C present as carbohydrates and low mineralized carbon:organic carbon ratios in forest soils indicate that substrate availability for soil microorganisms is relatively low (Zak et al. 1993). This may explain why only a small fraction of soil organic matter is metabolized by soil microorganisms although the forest floor and mineral soils may contain 60 % of the C and 95 % of N within the forests (Zak et al.1993).

The concept that soil fauna regulates the decomposition process has become increasingly popular in spite of the fact that the amount of soil metabolism (CO_2 production) that can be attributed to all soil animals is 10 % or less of the total amount (Mitter et al. 1984). Fungi and bacteria are directly responsible for most of the organic matter breakdown, but a diverse assemblage of protozoans, nematodes, annelids, and arthropods greatly influence the functioning of the decomposer flora as a direct and indirect result of their feeding activities (Hunt et al. 1987; Coleman et al. 1983). Mycorrhizal fungi are also important as they allow plants access to organic nitrogen forms nutrients, bypassing the mineralization step (Chalot and Brun 1998; Abuzinadah and Read 1986). They also represent a sizable nutrient reservoir themselves and are important in translocating nutrient resources through the soil column (Mitter et al. 1984).

Microarthropod feeding activities on microflora probably result in rapid recycling of most N within the system (Mitter et al. 1984). Nitrogen may be mineralized even at relatively high C:N ratios by the grazing and excretory activities of protozoans, nematodes, and perhaps, microarthropods (Mitter et al. 1984). Currie and Nadelhoffer (1999) stress the importance of direct assimilation of inorganic N to humus and microbial biomass, as compared to N flux due to litter humification. Microarthropods appear to have direct and indirect effects of internal pool sizes and patterns of N cycling, as constrained by external environmental factors such as temperature and moisture (Sulkava et al. 1996; Mitter et al. 1984). Microarthropods are also important in immobilizing inorganic N. The main N immobilizing mechanisms, both in the N-poor and N-rich humus layers, tend to be direct microbial N assimilation followed by incorporation of N in soil organic matter (SOM) (Sjoberg and Persson 1998).

Mites and collembolans usually account for about 95 % of the total microarthropod numbers (Mitter et al. 1984). Most oribatid mites, collembolans, and free-living astigmatid mites have well-developed mouthparts capable of fragmenting organic matter while feeding on the microflora adhering to this detritus (Coleman and Crossley 1996). Fragmentation and comminution (the reduction to small, particles) have very important consequences to decomposition and mineralization processes, particularly by creating new surface area for microbial colonization (Coleman and Crossley 1996). The absolute amount of N in litter often greatly increases during the initial stages of decay of more recalcitrant substrates, indicating considerable input of N by microbes (Blair et al. 1992). This is a reminder that the nutrient content of microbes may comprise a large percentage of the total amounts found in detrital systems. An important step in nutrient cycling processes, is the release of N and other nutrients from microbial tissue (Schlesinger 1991). It seems that most micro-arthropod densities are substrate limited, as microbial biomass C is significantly correlated with soil organic C on a stand basis (Holmes and Zak 1994; Mitter et al. 1984). Net N mineralization is probably driven by the turnover of microbial biomass rather than by changes in the size of the microbial pool (Holmes and Zak 1994).

2.13 Roots

The soil root system can be considered as a multiple-phase system with each soil compartment comprised of a gas phase, a solution phase, and a surface phase (Gobran et al. 1998). Plant roots help maintain microbial communities and increase weathering of minerals due to processes such as exudation of organic acids and enzymes to the

rhizosphere (Jaeger et al. 1999). The organic layers of forest soils have higher root densities than deeper mineral soil, allowing trees to efficiently recycle nutrients from litter and throughfall (Gobran et al.1998). Hendrick and Pregitzer (1993) reported that in a mixed deciduous forest fine roots, those smaller than 2-mm, made up over 70 % of the root mass and total root N, most of which was in the <0.5-mm root size class. Vogt et al. (1982) estimate that in a silver fir forest 3 to10 times more macronutrients are returned to the soil annually from fine root turnover (including mycorrhiza) than from aboveground litterfall.

2.14 Influence of Abiotic Soil Properties on N Mineralization Rates

The physical and chemical properties of soils are essential to ecosystem functioning. Organic matter is important in increasing soil water holding capacity, increasing soil cation exchange capacity (CEC) and providing substrate for soil microbes. Typically soils with low water holding capacity favor species with poor quality litter that further reduces N availability, while soils with high water-holding capacity favor species with high-quality litter that enhances N availability (Hobbie 1992). Finer textured soils have a higher water holding capacity, promote plant growth and organic matter production compared to sandier soils (Prescott et al. 2000b). Reich et al. (1997) report higher ANPP at any given N mineralizaton level in finer textured Alfisol soils. On coarser textured soils, accumulation of organic matter, C and N is slower, and is further constrained by slower N cycling in litter (Prescott et al. 2000b).

Intrinsic soil properties also exert a large influence on N mineralization. Soil texture along with mean annual temperature and litterfall N explained 81 % of the

variance in annual soil N mineralization in the 31 natural stands (Prescott et al. 2000a). Only percentage clay and percentage sand were significantly correlated with soil N and C capitals, suggesting soil N capital is associated with differences in soil texture among the nine sites (Prescott et al. 2000a). Differences in soil texture may lead to measurable differences in N cycling by influencing the build up of soil N. On coarser textured soils, accumulation of organic matter, C and N is slower, and is further constrained by slower N cycling in litter (Prescott et al. 2000a).

Soil pH has also been cited as being a limiting factor on the activity of soil microbes which may inhibit N mineralization (Reich et al.1997). There may be a pH threshold for soil microbes, which vary depending on species. However, Tietema et al. (1992) found no relationship between net mineralization and pH.

2.15 Temperature, Moisture, and Seasonality

As temperature and moisture availability regulate many ecosystem functions, including microbial activity and nutrient storage, they are considered the most critical driving forces in ecosystems, and have the greatest control over decomposition and mineralization rates (Murphy et al. 1998; Holmes and Zak 1994). In temperate forests of the North America there are strong seasonal trends in N mineralization. Higher rates occur in spring and summer when soil moisture is high and temperatures warm, and negligible activity occurs in the winter (Knoepp and Swank 1998; Zak et al. 1993; Gower and Son 1992; Morecroft et al. 1992). Temperature and soil moisture were used to explain more than 90% of the variation in laboratory N mineralization measurements made by Gonsalves and Carlyle (1994).

Separating the effect of moisture on mineralization from that of temperature is a difficult task. Intrinsic properties of soils may exert a significant effect on mineralization rate which can override the tendency of mineralization rate to decrease with decreasing temperature (Morecroft et al. 1992). For instance, Murphy et al. (1998) found decomposition rates were significantly greater at mesic upper elevation sites, which were colder and wetter. Fernandez et al. found that warmer sites had lower rates of N cycling, suggesting the sites were moisture limited (2000). Amundson et al. (1989) found that microbial activity (measured as CO2 evolved) was greater at the upper, colder and more mesic sites and that litter mass loss was correlated with precipitation events. Knoepp and Swank (1998) report that mesophytic sites had greater rates of N mineralization than more xeric sites despite altitudinal and temperature gradients. The importance of increasing temperature may be constrained by moisture availability (Murphy et al. 1998). Knoepp and Swank (1998) suggest that when N mineralized is expressed as a percent of total N, a positive correlation with soil temperature may be significant.

Quemada and Cabrera (1997) state that the effect of increased water potential on N mineralization was enhanced as temperature increased, indicating an interaction effect between both factors. They also report that volatilization losses in the form of N_2O and NH_3 increased with moisture at every temperature (Quemada and Cabrera 1997). Relative nitrification also seems to be a linear function of moisture content except at higher moisture contents when net mineralization and nitrification become independent of moisture (Tietema et al. 1992).

2.16 Influence of Altitude on N Mineralization

Results by Morecroft et al. (1992) show that a site at the top of a mountain in the Scottish highlands (920 m) had higher rates of mineralization than a low-altitude site (320 m) despite the altitudinal decline in temperature. Nitrification rates followed the same pattern (Morecroft et al. 1992). Total N concentration, C:N ratio, organic matter content, water content and pH can all influence mineralization rates; however none of them showed any altitudinal trend that could explain the increasing field and laboratory mineralization rate with altitude (Morecroft et al. 1992). Knoepp and Swank (1998) found the same trend of greater N mineralization rates at the high elevation site in the Southern Appalachians and attribute vegetation type to be the controlling factor. The highest elevation site, which had the highest Nmin:Ntot ratio, also had the highest N mineralization rate (Knoepp and Swank 1998).

2.17 Conclusions

Nitrogen mineralization rates are an important estimate of N turnover and soil N available for plant growth. The instantaneously available N in soil is generally present as a relatively small pool which turns over rapidly via microbial breakdown of organic N compounds, is lost from the system via leaching, or immobilized via plant and microbial uptake. Jansson (1958) proposed an early conceptual model of N cycling. The assumption that organic N must be mineralized before it is assimilated into microbial biomass should be revised (Chalot and Brun 1998). Recent evidence shows that some forms of organic N are available to microbes and plants (Chalot and Brun 1998; Drury et

al. 1991), and revised models should aim to demonstrate the importance of microbial assimilation of soil organic N directly.

Biotic factors that affect N mineralization rates include microbes in the soil and their turnover rates. Micro-arthropods, such as oribatid mites and collembola, are important in processing organic matter in the detritus layers (Coleman and Crossley 1996). They also manage the turnover of fungal and bacterial tissue. Macroarthropods are important at regulating population sizes of microarthropods, and help decompose organic matter (Coleman and Crossley 1996).

Abiotic factors seem to be particularly important in determining N mineralization rates. In general, litter decay rate is inversely related to C:N ratio and lignin:N ratio and positively related to N content (Hobbie 1992). It seems that N-poor sites produce longer-lived leaves, which have higher lignin contents and C:N ratios (Gower and Son 1992). Thus, the litter from these trees decomposes slower and N-turnover is much slower on these sites (Vitousek 1982). The total amount of N in the soil and forest floor are well correlated to the rate of N mineralization. However, it is difficult to determine cause from effect with these correlations (Scott and Binkley 1997).

Soil texture is also an important determinant of soil N mineralization. Typically, the finer soils (%clay, %silt) have better water holding capacities and a larger cation exchange capacity so are better at accumulating and turning over organic matter (Prescott et al. 2000b). Sandier soils typically have higher C:N ratios, less organic matter, and mineralize N at slower rates.

Temperature and moisture are both important in influencing rates of N mineralization (Sulkava et al. 1996). Increasing temperature increases reaction rates.

However, moisture tends to limit N mineralization more significantly than does temperature at most sites (Murphy et al. 1998). There are also interactions among these factors, and they all play a role in the N turnover in forests

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CHAPTER 3

IS THERE A NITROGEN MINERALIZATION PROMOTER THAT CAN ACCOUNT

FOR HIGHER NITROGEN MINERALIZATION RATES AT A HIGH ELEVATION

FOREST STAND COMPARED TO A LOWER ELVATION STAND?

3.1.0 Introduction

Nitrogen (N) is an important element in plant growth and processes. Although most of the N in the soil environment is in organic forms, most of the N taken up by plants from the soil is in simple inorganic forms i.e. nitrate (NO_3^-) and ammonium (NH_4^+). The conversion of organic-N to ammonium-N (mineralization/ammonification) is accomplished by a wide group of organisms, including decomposer microorganisms such as bacteria and fungi. Nitrification is typically associated with certain chemoautotrophic bacteria in the genera *Nitrosomonas*, *Nitrosospira*, *Nitrosococcus*, and *Nitrosovibrio*, which can oxidize ammonia (NH_3) to nitrite (NO_2-) (Paul and Clark 1989). Species in the genera *Nitrobacter*, *Nitrosospira*, and *Nitrococcus*, are able to oxidize NO_2^- to NO_3^- (Paul and Clark 1989).

Nitrogen mineralization rates typically decrease with decreasing temperature. Temperature and growing season decrease with increasing elevation. Thus N mineralization rates are predicted to decrease with increasing altitude. Contrary to this prediction, N mineralization rates measured at Coweeta Hydrologic Lab, N.C. are higher

at the highest elevations, and lowest at the lower elevations (Knoepp and Swank, 1998). Causes of higher N mineralization rates at the higher elevation have yet to be explained. Possible explanations of the highest N mineralization rates at the highest elevation include site differences in 1) plant and microbial communities, 2) temperature, 3) moisture availability, 4) soil pH, 5) the total N pools, or 6) chemical composition of plant, leaf litter, or soil matter.

Recent evidence has supported the notion that root exudates, particularly simple sugars and amino acids, stimulate microbial action and mineralization (Jaeger et al.1999). Similar substances may be found in decomposing litter or soil solutions. This study tested the hypothesis that there is a chemical promoter in the decomposing herbs, leaf litter, or soil of the high elevation site. If this is true, the rate of OP soil N mineralization should be stimulated when treated with cold water extracts made from NH leaf litter, herbs, or soil.

3.2.0 Materials and Methods

3.2.1 *Site Description*

This study took place at the Coweeta Hydrologic Lab (CHL), a USDA Forest Service facility and a Long Term Ecological site (LTER) located within the Blue Ridge physiographic province of the southern Appalachians of North Carolina, USA, latitude 35°03'N, longitude 83°25'W (Swift et al 1988). The climate is characterized by 1900 mm of annual precipitation, and with the highest mean monthly temperatures in late summer (20° C) and the lowest in early winter (5° C) (Knoepp and Swank 1998). A series of 5 – 80 x 80 m elevation gradient plots has been set up on reference watersheds

as part of the LTER project. Many studies comparing vegetation and ecosystem processes along this elevation gradient have been done and there are much data gathered at these sites including soil carbon and N mineralization rates, decomposition rates, throughfall chemistry, soil solution chemistry, forest floor mass and chemistry, above ground productivity, and root productivity (Knoepp and Swank 2000, 1998). In this study I am comparing the lowest gradient plot (WS 1-18), a south facing xeric Oak Pine (OP) stand at 702 m in altitude which has the lowest N mineralization rate (1.9 mg-N/ kg soil/ 28 days) of the gradient plots, to the gradient plot highest in altitude (WS 5-27), a mesic north facing Northern Hardwood (NH) stand at 1347 m (Table 3.1). The NH stand has the highest N mineralization rate (33.1 mg-N/ kg soil/ 28 days) of the 5 gradient plots (Knoepp and Swank 1998).

The OP stand is dominated by tree species including *Pinus rigida*, *Quercus prinus*, *Quercus rubra*, and woody understories such as *Kalmia latifolia* (Knoepp et al. 2000). There is no an annual herb layer at this site. The NH stand is dominated by hardwood tree species including *Betula alleghaniensis*, *Liriodendron tulipifera*, and *Quercus rubra*, and has a patchy understory of *Rhododendron maximum*, a woody perennial, and annual herbs including non-woody composites and ferns. The soil at the OP stand is an Evard-Cowee gravelly loam that is well drained and poor in organic matter (Knoepp et al. 2000). The soil at the NH stand is of the Cullasaja-Tuckasegee complex, a fine sandy loam that is moderately well drained. The NH soil has a finer texture (less sand) and more organic matter than does the OP soil. The slope of the OP site (34 degrees) is comparable to that at the NH site (33 degrees).

Table 3.1 - Characteristics of an Oak Pine (WS 1-18) and northern Hardwood forest (WS 5-27) at the Coweeta Hydrologic Laboratory, NC.

Properties	Oak Pine (OP)	Northern Hardwoods (NH)
Elevation (m)[a]	782 m	1347 (m)
Annual Degree Days[a]	4621 ^{o}C	3438 ^{o}C
N mineralization rates (annual average)[b]	1.9 mg-N/kg soil/28 d	33.07 mg-N/kg soil/28 d
Precipitation (1990-1995 avg)[a]	204.0 cm/yr	260.7 cm/yr

[a] Data compiled from Coweeta Long-term Ecological Research Program records.
[b] From Knoepp and Swank 2000.
[c] From Hoover and Crossley 1995.

3.2.2 *Sampling Regime*

Samples used in this study were collected from the NH (WS 5-27) and OP (WS 1-18) gradient plots at Coweeta on September 24, 1999 and July 1, 2000. At both the NH and OP site 10 - 50 x 50 cm plots randomly selected along a 40-m transect were marked, and leaf litter and understory herbage was removed, bagged, dated and labeled (there was no understory herbage for the OP site). Three soil cores, 9.5-cm deep with a 4.5-cm diameter, were also taken from each of the 10 plots at each site. Samples were stored in polyethylene bags in a cold room at 4^oC before processing to reduce biological activity.

3.2.3 *Treatment Extracts*

Five concentrated cold water extracts were prepared using field samples. These extracts were made from: OP soil, OP leaf litter, NH soil, NH leaf litter, and NH herbs. Each was prepared by combining in a Nalgene plastic (36cm x 27cm x 15cm) container an equivalent mass of herbage, leaf litter, or soil, collected from each of the 10 plots at both sites. De-ionized (DI) water was added to each container at the ratio of 1:3 for the leaf litter and herbs (428 g:1290 ml), and 1:1 for the soil (1 kg:1 L) to encourage strong

extraction. Lead bricks (sealed in two zip lock bags to prevent contamination) were placed on top of leaf litter and herbs to keep the organic matter submerged. The five containers were then stored at 4° C for 1 month, after which the liquid was pressed out of the organic matter and collected in one-liter polypropylene bottles. These liquid-extracts were stored at 4° C, and represent the five treatment extracts: OP soil, OP leaf litter, NH soil, NH leaf litter, NH herbs. A control of de-ionized water represents the sixth treatment used in this experiment.

3.2.4 *Adjusting Soil Water Potential*

Soil water potentials were adjusted to 0.01 MPa to maximize microbial activity (Quemada and Cabrera 1997). Using a tension plate (Topp et al. 1993), connected by a 102.2 cm drain tube, three soil rings were filled with each soil type, saturated with water, and gravitationally equilibrated to a soil tension of 0.01 MPa. Field weight, 0.01 MPa tension equalibrium weight, and dry weight of each of the two soil types were used to calculate how many grams of extract should be added to 5 g samples of each soil type to bring the water potential to 0.01 MPa.

3.2.5 *Incubations*

The experimental procedures were carried out at room temperature (23° C). For both OP and NH soils, an equal mass of soil from each of the 10 plots was combined and sieved through a 2-mm sieve. Five-gram samples of each sieved soil type was added to 50-ml incubation tubes. There were 36 paired tubes, (18x2 for each soil type, 72 total), one set for time=0 days, and the other set for time=28 days. There were three tubes of

each treatment. Both NH and OP soils were treated with the appropriate mass of treatment extracts (1.06 g for OP soils, and 1.53 g for NH soils) to bring the soil water potential of each tube to 0.01 MPa, as calculated. A DI water treatment was used as the control. The tubes were then centrifuged and shaken by hand to distribute the liquid and soil equally. Forty-ml of 1 M KCl was then immediately added to the time=0 day tubes which were put on a shaker for one hour before storing at 4 ^{0}C, until analysis. Caps of time=28 day tubes were uncovered every three days to keep the experiment aerobic. After twenty eight days 40 ml of 1 M KCl was added to the time=28 day tubes and they were put on a shaker for one hour. After the soil had settled from both sets of tubes (time = 0 day, and time = 28 day) 5-ml aliquots were used to determine the concentrations of NH_4^+ (Koroleff 1976) and NO_3^- in the solution. Net N mineralization rates were measured in the laboratory using colorimetric methods to analyze for NH_4^+, and a Technicon auto-analyzer for the NO_3^- analysis. Mineralization and nitrification rates were calculated as ((NH_4^+-N time = 28 days - NH_4^+-N time = 0 days) / 28 days) and ((NO_3^- -N time = 28 days - NO_3^- -N time = 0 days) / 28), respectively. Ammonium and NO_3^- figures were added to quantify total N mineralization rates for each treatment on each soil type. Results were also analyzed as mg N mineralized/g N soil, to eliminate the effect of different N pool sizes on mineralization within the microcosms.

3.2.6 *Statistical Analyses*

Treatment effects were analyzed using a 2-way ANOVA with SAS (1985). All treatment and interaction effects were considered. Confidence intervals were calculated at a 95 % level.

3.3.0 Results

3.3.1 *Oak Pine Soils*

After the 28-day incubation there was a net loss of inorganic N in all of the OP soil samples. The control and all treatment tubes containing OP soil had less N in the form of NH_4^+ and NO_3^- after 28 days than they had at day 0. Nitrogen in the form of NH_4^+ was lost from the OP soil system at a rate of between -10.10 (2.42) mg $N-NH_4^+$ /kg soil /28 days, for the NH soil extract treatment, and -15.4 (0.56) mg $N-NH_4^+$ /kg soil /28 days for the control de-ionized water treatment (Table 3.2). This is much greater than the amount of N in the form of NO_3^- that was lost from the microcosm, which had the fastest rate of loss of -0.169 (0.279g NO_3^- /kg soil / 28 days, in the OP soils treated with NH herb extracts.

Table 3.2 - Ammonification, nitrification, and total N mineralization rates (mg N /kg soil /28 days) and 95% Confidence Intervals for Oak Pine soils incubated with treatment extracts.

------------------------------Treatment Extracts------------------------

Oak Pine Soil	D.I H_2O	OP Leaf Litter	OP Soil	NH Herbs	NH Leaf Litter	NH Soil
NH4+ (mg N /kg soil /28 days)	-15.40 (0.56)	-12.02 (1.03)	-10.34 (2.39)	-10.43 (1.59)	-10.13 (4.34)	-10.10 (2.42)
NO3- (mg N /kg soil /28 days)	0.085 (0.102)	-0.027 (0.065)	-0.108 (0.095)	-0.169 (0.279)	-0.019 (0.027)	-0.015 (0.110)
Total N-min (mg N /kg soil /28 days)	-15.31 (0.63)	-12.04 (1.09)	-10.44 (2.48)	-10.60 (1.87)	-10.15 (4.35)	-10.11 (2.33)

The N lost from the OP microcosms has not been accounted for. The mineral N in the OP soils must have been either immobilized into microbial biomass, or lost through denitrification. There was no statistically significant difference between extract treatments on N mineralization or nitrification rates in OP soils.

3.3.2 *Northern Hardwood Soils*

The NH soils had positive rates of mineralization and nitrification for all of the extract treatments. Northern hardwood soils had higher mineralization and nitrification rates than OP soils regardless of treatment extracts received. The fastest ammonification rate [21.0 (9.85) mg $N-NH_4^+$ /kg soil / 28 days] and total N mineralization rate [46.93 (12.72) mg N /kg soil/ 28 days] occurred in the NH soils treated with NH soil extract. The fastest nitrification rates occurred in the de-ionized water control tubes, at 28.56 (3.11) mg $N-NO_3^-$ /kg soil / 28 days (Table 3.3).

Results analyzed as milligrams of mineralized N per gram of N in the soil showed the same trend as above (Table 3.4 & 3.5). The most significant effect on the mineralization and nitrification rates was attributed to the soils ($p<0.001$), rather than the treatment extracts. Treatment extracts had a significant effect on the mineralization rates ($p=0.0048$), but the trend was negative for OP soils and positive for NH soils (Table 3.6). There were no significant interaction effects of treatment and soil.

3.4.0 Discussion

The results of this experiment do not support the hypothesis that there is a mineralization promoter in the herb, leaf litter, or soils of the NH stand. There were no

Table 3.3 - Ammonification, nitrification, and total N mineralization rates (mg N /kg soil /28 days) and 95% Confidence Intervals for Northern Hardwood soils incubated with treatment extracts.

-----------------------------Treatment Extracts------------------------

Northern Hardwood Soil	D.I H_2O	OP Leaf Litter	OP Soil	NH Herbs	NH Leaf Litter	NH Soil
NH4+ (mg N /kg soil /28 days)	3.07 (2.30)	12.73 (12.15)	4.46 (5.50)	18.87 (10.0)	18.06 (5.85)	21.0 (9.85)
NO3- (mg N /kg soil /28 days)	28.56 (3.11)	21.84 (6.68)	24.76 (1.30)	21.12 (2.20)	25.2 (1.76)	25.94 (3.17)
Total N-min (mg N /kg soil /28 days)	31.63 (4.68)	34.57 (17.18)	29.62 (3.51)	39.99 (8.16)	43.26 (4.56)	46.93 (12.72)

Table 3.4 - Ammonification, nitrification, and total N mineralization rates and 95% Confidence Intervals for Oak Pine soils incubated with treatment extracts, expressed as mg N/ g soil N/ 28 days. [a]

-----------------------------Treatment Extracts------------------------

Oak Pine Soils	D.I H_2O	OP Leaf Litter	OP Soil	NH Herbs	NH Leaf Litter	NH Soil
NH_4^+ (mg N /g soil N /28 days)	-7.333 (0.267)	-5.724 (0.488)	-4.924 (1.138)	-4.967 (0.757)	-4.824 (2.071)	-4.810 (1.152)
NO_3^- (mg N /g soil N /28 days)	0.041 (0.049)	-0.013 (0.031)	-0.051 (0.045)	-0.081 (0.133)	-0.009 (0.013)	-0.007 (0.052)
Total N-min (mg N/ g soil N /28 days)	-7.292 (0.298)	-5.737 (0.517)	-4.975 (1.180)	-5.048 (0.888)	-4.833 (2.070)	-4.817 (1.109)

[a] values reported as mg N/g soil N eliminate differences caused by different N pool sizes in the microcosms

Table 3.5 - Ammonification, nitrification, and total N mineralization rates and 95% Confidence Intervals for Northern Hardwood soils incubated with treatment extracts, expressed as mg N/ g soil N/ 28 days.[a]

--------------------------------Treatment Extracts------------------------

Northern Hardwood Soil	D.I H_2O	OP Leaf Litter	OP Soil	NH Herbs	NH Leaf Litter	NH Soil
NH_4^+ (mg N /g soil N /28 days)	0.090 (0.067)	0.374 (0.352)	0.131 (0.160)	0.554 (0.290)	0.530 (0.170)	0.616 (0.286)
NO_3^- (mg N /g soil N /28 days)	0.838 (0.090)	0.641 (0.193)	0.727 (0.038)	0.620 (0.064)	0.740 (0.051)	0.761 (0.092)
Total N-min (mg N /g soil N/ 28 days)	0.928 (0.136)	1.015 (0.498)	0.858 (0.102)	1.174 (0.237)	1.270 (0.132)	1.377 (0.369)

[a] values reported as mg N/g soil N eliminate differences caused by different N pool sizes in the microcosms

Table 3.6 - Probability that differences among treatment means occurred by chance alone for nitrification and mineralization rates of Oak Pine and Northern Hardwood soils.

Properties	NO3-	NH4+	N-sum
Treatment Extracts	n.s[a]	0.0048	n.s[a]
Receiving Soils	<0.0001	<0.0001	<0.0001
Treatment Extracts x Receiving Soils	n.s[a]	n.s[a]	n.s[a]

[a] no significant difference (α=0.05)

obvious trends in the OP and NH soils treated with any particular extract. Instead, the OP soil samples had negative ammonification and nitrification rates for each of the five treatment extracts. The DI water control treatment had negative rates as well. In contrast, the NH soil samples had positive rates of ammonification and nitrification, for all treatments, including the DI water control. This suggests that the higher N mineralization and nitrification rates of the NH stand compared to the OP stand are due to inherent differences in the properties of these two soils.

The NH soils had significantly more inorganic N at day 0 than did the OP soils, averaging around 80 mg mineral-N / kg dry NH soil compared to 20 mg mineral-N / kg dry OP soil. This is an expected result since the NH soil has higher mineralization rates than does the OP soil, and more N accumulates in the mineral form in the NH soil. The NH soils also had a net gain of inorganic N after 28 days while the OP soils exhibited a net loss of inorganic N.

The net loss of inorganic N may be attributed to denitrification or to microbial immobilization. Denitrifying bacteria such as those in the genera *Rhizobium, Paracoccus, Pseudomonas, Alcaligenes, Thiobacillus,* and *Rhodopseudomonas* genera may have volatilized the N by converting it into NO, N_2O, or N_2 gas (Paul and Clark 1989). Microorganisms living in the OP soil may be N limited, therefore less willing to re-circulate N back into the soils (Drury et al. 1991). In the NH soils, where there is more available N, microorganisms may be carbon rather than N limited. This may explain the greater flux of N from organic to inorganic form. The microorganisms at the NH site may have more demand for a carbon source, rather than an N source. Therefore, the microorganisms at this site may be more conservative with carbon than with N.

It is also likely that the total N pool in the NH soils is larger than that in the OP soils. This may in turn lead to larger N pools in living and dead biomass as well as stimulate greater N fluxes at this site. If this is the case, there may be more labile N and organic N available at the NH site than at the OP, which would lower the C:N ratio and help to explain the higher mineralization rates of the NH soils.

These results suggest that there is an intrinsic difference in the two soils that may the cause of the differing mineralization rates. However, extracts made from the NH soil did not increase the N mineralization rate when added to OP soil, nor did OP soil extract decrease the N mineralization rate of the NH soils. It seems logical then to ask if the extracts were made strong enough to elicit a treatment response. Although only small amounts of extract were used for the incubations, the concentrations of the extracts, at 3:1 for the litters and herbs, and 1:1 for the soils, should have been well above the concentration of leachate that would occur in nature. Therefore I believe the extracts were of sufficient concentration.

The missing N in the OP soil samples has not been solved. Microbial immobilization is likely the N sink. Carbon to N ratios taken of the OP soil are 33:1. Empirical studies have shown that at ratios greater than 25:1 N is generally taken up from the mineral N pool (Paul and Clark 1989). The NH soils had a C:N ratio of 16:1, which may help explain the net increase in mineral N, if it is a soil characteristic that is responsible for the results.

Alternative hypothesis now need to be tested to explain the higher mineralization rates at the higher elevation site. Compiling an N budget of these two sites may show

different patterns of N use at the two sites. Differences in N pool sizes or fluxes may

help elucidate the enigma.

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CHAPTER 4

CAN NITROGEN BUDGETS EXPLAIN DIFFERENCES IN SOIL NITROGEN

MINERALIZATION RATES BETWEEN OAK PINE AND NORTHERN

HARDWOOD STANDS IN THE SOUTHERN APPALACHIANS, USA?

4.0.0 Abstract

Nitrogen (N) mineralization rates in forest systems typically decrease with decreasing temperature. Temperature decreases with increasing elevation. Thus, N mineralization rates are expected to decrease with increasing elevation. However, soil N mineralization rates at the Coweeta Hydrologic Lab (CHL), N.C. are higher at the highest elevation. Causes of higher mineralization rates at the higher elevation have yet to be explained. Alternative hypotheses to explain higher mineralization rates at the higher elevation, Northern Hardwoods site (NH) compared to the Oak-Pine site (OP) include: 1) a mineralization promoter in decomposing herbs, leaf litter, or soil of the high elevation, 2) low pH in OP soils which inhibit mineralization, 3) differences in total N pools, 4) low moisture availability in OP soils, 5) differences in soil texture, and 6) differences in biological communities. Previous studies did not support our N mineralization promoter hypothesis, nor does soil pH explain mineralization rates. In this study we constructed N budgets for the NH and OP sites to determine if differences in N pools and fluxes are sufficient to explain differences in N mineralization rates. Evaluating N in the upper 0-10 cm of mineral soil, forest floor, overstory biomass, annual canopy litterfall, understory

herb turnover, rainfall, canopy throughfall, and in soil solution, we found that NH has more stored N and greater N fluxes than OP. The NH site has many characteristics of a stand in an early stage of N-saturation, while the OP stand characterizes an N-limited forest. Causes of greater N storages and fluxes at the NH site are not obvious.

4.1.0 Introduction

Nitrogen (N) is generally considered the single element most likely to be limiting to forest production, and is therefore important in regulating ecosystem processes (Vitousek et al. 1997; Mitter et al. 1984). Although there are typically large quantities of N in soil ecosystems, most is bound in organic forms unavailable to plants. Only small quantities of N are in accessible mineral forms, such as ammonium (NH_4^+) and nitrate (NO_3^-). The availability of NH_4^+ and NO_3^- is believed to limit forest production because many forests show a growth response to these mineral N fertilizers (Pastor et al.1984). Consequently, natural rates of N mineralization, the conversion of organic N to mineral forms, are of interest to forest and soil scientists.

A wide variety of organisms including decomposer microorganisms such as bacteria and fungi mineralize N. Nitrogen in excess of microbial requirements is released as NH_4^+ (Drury et al. 1991). Nitrification, the conversion of NH_4^+ to NO_3^-, is typically associated with certain chemoautotrophic bacteria in the genera *Nitrosomonas*, *Nitrosospira*, *Nitrosococcus*, and *Nitrosovibrio*, which are able to oxidize ammonia (NH_3) to nitrite (NO_2-) (Paul and Clark 1989). Nitrite is then oxidized to NO_3- by species in the genera *Nitrobacter*, *Nitrosospira*, and *Nitrococcus* (Paul and Clark 1989). Typical

N mineralization rates among temperate forests range from 2 to12 g $N/m^2/yr$ (Zak et al.1993).

Nitrogen cycling processes occur in solid, liquid, and gaseous phases. Common inputs of N to forest systems include dry and wet deposition, and microbial N-fixation. For instance, Boring and Swank (1984) report that 3.0 to 7.5 g $N/m^2/yr$ was fixed by symbiotic bacteria on *Robinia pseudoacacia* roots in a forested Southern Appalachian watershed. Leaflitter and its decomposition and mineralization rates are also important in regulating forest nutrient circulation patterns (Monk and Day 1985; Gosz et al. 1976). Forest ecosystems may lose N as volatile gaseous forms such as NO_x, NO, and N_2O, or dissolved N-forms such as nitrate and organic compounds, which are known to leach out of forest ecosystems in aqueous phase (Qualls and Haines 1991; Boring et al. 1988).

Nitrogen cycling is generally considered to be more rapid on sites with high availability of N (N-rich sites), although this trend usually is associated with differences in tree species composition. However, Prescott et al. (2000) found faster rates of N cycling and decomposition on N-rich sites, in the absence of changes in tree species composition. They noted that, even without changes in tree species composition, sites with greater soil N capital returned more N in annual litterfall and had faster turnover of N in the forest floor. This supported Gosz's (1981) hypothesis that vegetation on N-rich sites produces litter with high N concentrations, leading to faster rates of decomposition and N mineralization. In N-poor ecosystems, plants grow slower, use N more efficiently, and produce lower quality litter (i.e. higher lignin content and greater C:N ratio) (Hobbie 2000, 1992). On N-poor sites, not only is decomposition slower, but a smaller proportion of the litter N is mineralized and removed from the forest floor (Prescott et al. 2000).

Soil N mineralization rates often differ with forest type, elevation, and topographic position, and are attributed to site variations in soil organic matter content, temperature, soil water availability, and litter quality (Knoepp and Swank 1998). Low C:N ratios are known to favor N mineralization (Paul and Clark 1989). The critical C:N ratio below which net N mineralization occurs is commonly considered as being in the range of 25-30:1 (Prescott et al. 2000). At low C:N ratios decomposers are not N limited, and a net release of inorganic N to the soil solution occurs. Litter fall with high C:N favors N retention by decomposers and reduces N availability in the soil. Low soil N availability leads to high nitrogen use efficiency (NUE) and production of litter with a higher C:N ratio (Vitousek 1982).

Reich et al. (1997) reported that soil properties had significant impacts on N mineralization rates and annual net primary production (ANPP) in hardwood and conifer stands across Wisconsin and Minnesota, USA. Their results support the paradigm that productivity of temperate forest ecosystems is linked to their N status. Prescott et al. (2000) found that soil N capital was positively correlated with soil C capital. However, net N mineralization was most affected by the N concentration in the forest floor and less tightly linked to soil N capital and associated site factors (Prescott et al. 2000). This may be due to the fact that the majority of soil N occurs in fractions resistant to microbial degradation (Zak et al.1993).

Environmental conditions such as low temperature or low soil water potential reduce microbial activity and therefore reduce N mineralization rates (Drury et al. 1991). As elevation increases temperatures decrease, and N mineralization rates are predicted to decrease with increasing altitude. Contrary to this prediction, N mineralization rates

measured at Coweeta Hydrologic Lab, N.C. are highest at the colder higher elevations, and lowest at the warmer lower elevations (Knoepp and Swank 1998). Other studies have found similar trends in soil and forest floor N mineralization (Fernandez et al. 2000; Morecroft et al. 1992). Causes of higher N mineralization rates at the northern hardwood (NH) higher elevation stand, compared to a lower elevation oak-pine (OP) stand have not been explained.

Nutrient budgets have been used as accounting methods to elucidate complex nutrient cycles (Monk and Day 1985; Gosz et al. 1976; Duvigneaud and Denaeyer-De Smet 1970). I am testing the hypothesis that low N mineralization rates occur on sites circulating small amounts of N annually, while higher N mineralization rates occur on sites circulating larger amounts of N (Vitousek 1982). To test this hypothesis N budgets for a low elevation oak-pine (OP) site and high elevation northern hardwood (NH) stand were constructed to estimate and compare N pool sizes and fluxes, and to determine which N pools or fluxes may account for the high N mineralization rates at the NH site. It is predicted that high N mineralization rates at the NH site are a result of larger N pools at this site than at the OP site, and these larger N pools are responsible for larger annual N fluxes at the NH site. These larger annual N fluxes may stimulate N mineralization rates.

4.2.0 Methods

4.2.1 *Site Location*

This study location was at the Coweeta Hydrologic Lab (CHL), a USDA Forest Service facility and a Long Term Ecological Research site (LTER), located within the

Blue Ridge physiographic province in the southern Appalachians of North Carolina, latitude 35°03'N, longitude 83°25'W (Swift et al. 1988). The highest mean monthly temperatures occur in late summer (20° C) and the lowest in early winter (5° C) (Knoepp and Swank 1998).

This study compares two of five gradient plots that have been set up as part of an LTER study. Each plot is 80 x 80 m in area. Many studies comparing vegetation and ecosystem processes have been conducted on these gradient plots. Data including soil carbon and nitrogen mineralization rates, decomposition rates, throughfall chemistry, soil solution chemistry, forest floor mass and chemistry, above ground productivity, and root productivity have been collected on these sites for over a decade (Knoepp and Swank 1998). In this study I am constructing and comparing N budgets of the gradient plot (WS1-18) lowest in elevation (702 m) to that gradient plot (WS5-27) highest in elevation (1347 m).

4.2.2 *Site Description*

The low elevation site, a south facing xeric Oak Pine (OP) stand, has the lowest N mineralization rate (1.9 mg N/ kg soil/ 28 days) of the gradient plots (Knoepp and Swank 1998). The Oak Pine site has mean annual air temperature of 12.7 ^{o} C, a mean average soil temperature of 13.34 ^{o} C, and it receives an average of 204 cm of precipitation annually (L. Swift unpublished) (Table 4.1). The OP stand is dominated by tree species including *Pinus rigida*, *Quercus prinus*, *Quercus rubra*, and a woody understory species *Kalmia latifolia* (Knoepp et al. 2000). There is no annual herb layer at this site. The soil

at the OP stand is a well-drained Evard-Cowee gravelly loam with 12.1 % organic matter. The OP soil has a pH of 3.9 and a bulk density of 0.75 g/cm^3 (Knoepp et al. 2000).

The northern hardwood (NH) stand has a north facing aspect and the highest N mineralization rate (33.1 mg N/ kg soil/ 28 days) of the 5 gradient plots (Knoepp and Swank 1998). This site receives 260.7 cm of precipitation annually, and has a mean annual air temperature of 9.4 ^{o}C, and soil temperature of 8.79 °C. (L. Swift unpublished) (Table 4.1). Hardwood tree species including *Betula alleghaniensis*, *Liriodendron tulipifera*, and *Quercus rubra*, dominate this site and a woody perennial understory of *Rhododendron maximum* and annual herbs including non-woody composites and ferns occur. The soil at the NH stand is of the Cullasaja-Tuckasegee complex, a fine sandy loam that is moderately well drained with a pH of 4.0 and a bulk density of 0.54 g/cm^3 (Knoepp et al. 2000). The slope at the NH site (33 degrees) is comparable to that of the OP site (34 degrees).

Table 4.1 - Site Data For an Oak Pine (WS 1-18) and Northern Hardwood Forest (WS 5-27) at Coweeta Hydrologic Laboratory, N.C.[a]

Property	*Oak Pine*	*Northern Hardwoods*
Elevation (m)	782	1347
Mean Annual Air Temperature (°C)	12.66	9.42
Degree Days (°C)	4621	3438
Mean Annual Soil Temperature (°C)	13.34	8.79
Mean Annual Precipitation (cm/yr)	204.0	260.7
Throughfall Inputs 1997 (mg N/L/yr)	2.222	2.982
Leaching Outputs (mg N / L)	-1.53	-0.54
Mean Annual Soil Moisture (%)	15.69	21.45

[a] Data compiled from Coweeta LTER program records.

4.2.3 *Nitrogen Budget Development*

Nitrogen pools and fluxes were determined for both gradient plots in order to construct budgets for each site. Nitrogen pools accounted for in the budget were soil (top 0 to10 cm), root biomass (top 0 to 10 cm), forest floor biomass, coarse woody debris (CWD), understory plant biomass, and overstory plant biomass. Annual N fluxes accounted for were fine root turnover, litterfall, insect defoliation/frass inputs, rainfall and canopy throughfall inputs, annual herb turnover, forest floor N mineralization, CWD N mineralization, soil N mineralized, and soil leaching. N fluxes were determined on an annual basis.

Data previously collected and stored in the Coweeta LTER archives were synthesized along with new data to construct N budgets for both gradient plots. Data used to construct these budgets include: *in-situ* N mineralization rates (short-term incubations) between 1991 and 1996 (Knoepp and Swank 1998); root biomass and turnover data (Table 4.2) (Davis 1993); annual litterfall data collected and quantified for 1995 to 1997 (Table 4.3) (D.A. Crossley unpublished data);   forest floor and coarse woody debris biomass (Knoepp et al. 2000), hourly climate records, including precipitation, soil moisture, soil and air temperature (Table 4.1) (L. Swift unpublished data); baseline canopy herbivore frass inputs (M. Hunter unpublished data); throughfall and lysimeter data collected over the last decade (W.T. Swank unpublished data); vegetation biomass data (Table 4.4) (Day and Monk 1977a; J. Clark unpublished data); and, vegetation and root N contents and N uptake and reabsorbtion rates (Table 4.5) (Knoepp et al. 2000; Martin et. al. 1998; Griffith 1993; Monk and Day 1985; Day and Monk 1977b).

Table 4.2 - Root Biomass, Turnover, and % N Data For an Oak Pine (WS 1-18) and Northern Hardwood Forest (WS 5-27) at Coweeta, N.C.

Property	Oak Pine	Northern Hardwoods
Root biomass 0 to 2-cm[a]	506.6	428.9
Root Biomass 2 to 5-cm[a]	337.6	153.5
Root Biomass 5 to 10-cm[a]	220.0	60.3
Root Biomass >10-cm[a]	218.8	127.5
Total Average Dry Root Mass	1283	770.2
Root Nitrogen % N[b]	0.70 %N	0.72 %N
Root Turnover[a]	953(SE 507) - 878 (SE 308)	745 (SE 369)-1015 (SE 628)

[a] From Davis 1993. Biomass expressed as g/m^2/0 to 10-cm. Root turnover values expressed as (appearance – disappearance) yr^{-1}. Samples collected between August and September 1993 and 1994.
[b] From Martin et al. 1998.

Table 4.3 - Litter, Herb, Forest Floor, and Coarse Woody Debris (CWD) Mass (g/m^2) and Nitrogen Concentration Data For an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) Forest at Coweeta, N.C.

Property	Oak Pine	Northern Hardwoods
Leaf Litter % N	0.61	1.19
Leaffall (g/m^2) [b]	404.1 (28.6)	304.4 (14.9)
Annual Herbs % N	0	2.71
Annual Herbs C:N	0	16.72
Forest Floor (Oi & Oa) (g/m^2)[a]	2102.7	615.3
Forest Floor % N	0.87	1.84
Forest Floor C:N	59.9	26.3
Forest Floor N Min. Rate ($g-N/m^2$/yr)	242	302
Coarse Woody Debris (g/m^2)[a]	3975.3	5632.1
CWD N-Min Rate (ug/g/day)	0.16	0.16

[a] From Knoepp et al. 2000.
[b] From D.A.Crossley Jr.unpublished. Leaffall mass (g/m^2/yr) is an average between 1992 and 1994.

Table 4.4 - Overstory and Understory Biomass (g/m^2) For an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) Forest at Coweeta, N.C.[a]

Property	Oak Pine (OP)	Northern Hardwoods (NH)
Overstory Branch	1472.63	3792.10
Overstory Bark	1082.25	1728.44
Wood	6049.69	11,545.89
Total Tree Biomass	**8604.60**	**17,066.44**
Understory leaves	26.9	153.2
Understory stems	303.8	750.4
Total Understory Biomass	**330.7**	**903.6**

[a] allometric equations used to calculate overstory biomass from Martin et al 1998.

Table 4.5 - Overstory and Understory Growth (g/m^2/yr), % N reabsorption and N Uptake Rates (g N/m^2/yr) for an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) Forest at Coweeta, N.C.

Property	Oak Pine	Northern Hardwoods
Overstory NPP[a]	400	400
Overstory %N reabsorption[b]	1.19	1.01
Total N reabsorbtion	0.029	0.037
Overstory N uptake rate	**4.23**	**6.76**
Understory leaves NPP[c]	12.94	26.34
Understory stems NPP[c]	15.77	41.31
Understory N Uptake Rate [c]	**0.16**	**0.35**

[a] From Knoepp et al. 2000.
[b] From Griffith 1993.
[c] From Monk and Day 1985.

4.2.4 *Sampling and Calculations*

On July 2, 2000, ten random 1/4 m^2 quadrats were used to sample annual herbs, forest floor, and soils. Samples of 2-mm sieved soil collected at a 10-cm depth from both sites, forest floor, and herb material was analyzed for % C and % N using a Carlo Erba analyzer (Milan, Italy). From this, herb biomass and N flux could be quantified. Soil % N, along with previously reported values of soil density and N mineralization rates, were

used to calculate the annual flux of N in the soil, and the total soil N pool size, both at a 0 to 10-cm depth. Forest floor % N was multiplied by the forest floor mass to determine this N pool, N mineralization rates from literature were used to estimate forest floor N flux (Knoepp et al. 2000; Fernandez et al. 2000). Soil texture was determined using the hydrometer method (Carter 1993). Average annual leaf litter biomass values, estimated by averaging annual values obtained using litterfall traps, and % N concentrations of this litter were used to quantify the amount of N circulating annually through the leaf litter component of each system (Griffith 1993; D.A. Crossley unpublished data). The total N stored in roots was calculated by combining the biomass of all root sizes, to a 0 to 10-cm depth, and multiplying this value by the average % N of roots (Davis 1993; Day and Monk 1977b). Fine root appearance minus disappearance was used to estimate root turnover, and concentration of root N was used to quantify this N flux (Davis 1993). Estimates of overstory bark, branch, and wood biomass were calculated with allometric equations using diameter at breast height (DBH) values for each tree in the quadrat (Martin et al. 1998; J. Clark unpublished data). Nitrogen concentration of these components was used to estimate the total pool size of N stored within the overstory biomass, as well as the CWD (Martin et al 1998; Santee and Monk 1981). CWD N mineralization rates were estimated from the literature (Hart 1999). Understory woody biomass (leaf and stem) and N concentration values from previous Coweeta studies were used in this budget (Monk and Day 1985; Day and Monk 1977b). Frass inputs were calculated by multiplying baseline frass quantities for each site by frass % N (M. Hunter unpublished data). Throughfall inputs were calculated by multiplying quantity of precipitation by concentration of N in samples of these components (W.T. Swank

unpublished data). System losses of N through soil leaching was estimated using lysimeter data, and assuming the quantity of throughfall was equal to the quantity of deep drainage (W.T. Swank unpublished). Nitrogen concentrations of lysimeter samples were multiplied by total amount of throughfall (L. Swift unpublished). Nitrogen uptake rates were estimated by combining the annual plant N flux with the net plant N accretion (Knoepp et al. 2000). All calculations were determined as g N per meter squared per 0 to 10-cm depth per year (g m^{-2} 0 to 10-cm^{-1} yr^{-1}). Conservative estimates have been made in these calculations.

4.3.0 Results

4.3.1 *Soil and Plant Litter Analysis*

As shown in table 4.6, the C:N ratio of NH soil (16.8) was 50 % that of the OP soil (33.9). Similarly, the C:N ratio of leaflitter at the NH site (26.3) was 44 % that of the OP site (59.7). The C:N ratios of the herb layer at the NH site was 16.7. There was no annual herb layer at the OP site.

The NH soil is much finer in texture than the OP soil (43.7 % sand, 48.9 % silt, 7.4 % clay), and there is twice as much organic matter in the NH soil than in the OP soil. The % N was four-fold greater in the NH soil (0.85 %) than in the OP soil (0.21 %). There is also a greater soil microbial N pool at the NH stand. Many characteristics of NH soils and litter favor N mineralization.

Table 4.6 – Soil Data for an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27)

Forest at Coweeta, N.C.

Property	*Oak Pine*	*Northern Hardwoods*
Soil Texture [c]	43.7, 48.9, 7.4	13.5, 76.2, 10.3
Soil N mineralization rates (mg N/kg soil/ yr)[a]	11	209
Soil Nitrification (mg N/kg soil/ yr)[a]	0.91	83
Soil Denitrification (g N/m^2/yr)	<0.1	<0.1
Soil pH[a]	3.9	4.0
Soil %N	0.21	0.85
Soil C:N	33.9	16.8
% Soil Organic Matter	12.1	24.3
Soil Bulk Density (g /cm^3)[a]	0.75	0.54
Microbial Biomass N (g N/m^2/0 to 5-cm)[b]	3.77	5.64

[a] From Knoepp et al. 2000.
[b] From Hu et al. 1997 (estimates microbial C:N as 8:1).
[c] soil texture (% sand, % silt, % clay).

4.3.2 *Nitrogen Pools*

Although the OP soil had a greater bulk density than the NH soil, the total soil N pool at the OP site was only 34 % of that for the NH site, due to the higher soil % N at the NH site (Table 4.6). The OP site had 62 % more N stored in the florest floor than did the NH site. The OP site also had a root N pool 62 % greater than did the NH site. However, the OP site had only 34 % of the overstory biomass and 67 % of the CWD as did the NH site. The OP site only had 12 % as much N in the understory as did the NH site, though this pool was the smallest and cycles slowly. The total N pool was almost twice as large at the NH site. Most of the N at both sites was in the soil component of the system.

Table 4.7 - Forest Nitrogen Pools (g N/m^2) for an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) Forest at Coweeta, N.C.

Property	Oak Pine	Northern Hardwoods
Soil N[a]	157.5	459.5
Bark N	9.74	15.55
Branch N	5.89	15.17
Wood N	18.15	34.64
Total Overstory N	33.78	65.36
Understory leaves N[b]	0.16	1.45
Understory stems N[b]	0.01	0.02
Total Understory N	0.17	1.47
Forest Floor N	18.29	11.32
CWD N	15.9	22.53
Root N[a]	8.98	5.55
TOTAL N POOL	234.62	565.73

[a] Soil and root measurements are to a depth of 0 to 10-cm.
[b] From Monk and Day 1985.

4.3.3 *Nitrogen Fluxes*

Annually, 13.6 times more N is mineralized in the NH soils than in the OP soils (Table 4.8). Annual inputs of leaflitter contributed the most N to both the NH and the OP sites. More N (47 %) circulated through the leaflitter at the NH site than at the OP site, despite greater annual leaflitter biomass at the OP site (404.1 g/m^2/yr) compared to the NH site (304.4 g/m^2/yr). This was due to the higher N content of NH leaflitter. Forest floor N mineralization released 23 % less mineral N at the NH site than at the OP site, despite faster N mineralization rates for the NH stand. Although there was an annual atmospheric input of 0.89 and 0.81 g N/m2/yr for the NH and OP site, respectively, N concentrations in throughfall were less than N-concentrations in atmospheric deposition, signifying leaf or microbial uptake. The NH site received 73 % more throughfall N-inputs than did the OP site. The NH site had a net loss of 270 g/m^2/0 to 10-cm/yr of fine roots, releasing 1.94 g N/m^2/0 to 10-cm/yr to the system, while the OP site had a net gain of 75

g/m^2/0 to 10-cm/yr fine roots, absorbing 0.53 g of mineral N/m^2/0 to 10-cm/yr. Baseline

levels of canopy herbivory and CWD fluxes for both sites are relatively small (Reynolds

2000; Hunter unpublished data). The NH site has an annual herb layer which turns over

0.49 g N/m^2/yr. Over twice as much N is lost through soil leaching at the OP site than at

the NH site.

Table 4.8 - Forest Nitrogen Fluxes (g N/m^2/yr) For an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) Forest at Coweeta, N.C. Root and soil measurements are to a depth of 10 cm.

Property	*Oak Pine*	*Northern Hardwood*
Litterfall[a]	2.47	3.62
Root Litter[b]	-0.53	1.94
Herb Litter	0	0.4853
Rainfall Inputs[c]	0.81	0.89
Throughfall Inputs 1997[c]	0.412	0.706
Canopy frass (baseline)[d]	0.0575	0.045
Total N Returns	**2.41**	**6.80**
Soil Mineralized[e]	0.825	11.29
Forest Floor Mineralization	1.62	1.25
Course Woody Debris N-Min[e]	0.16	0.16
Total N mineralization	**2.61**	**12.7**
Total Leaching Losses	**-0.31**	**-0.14**

[a] From D.A. Crossley Jr. unpublished.
[b] From Davis 1993.
[c] From Coweeta LTER program records.
[d] From M. Hunter unpublished.
[e] From Knoepp et al. 2000.

Total annual N inputs and internal fluxes, excluding soil N mineralization, are 2.8

times greater for the NH site than for the OP site. Although the annual flux of N at the OP

site may account for the amount of N mineralized in the OP soil, the annual flux of N at

the NH site is not large enough to account for the amount of N mineralized in the NH soil.

As shown in table 4.9, there is more N mineralized at the NH site than is taken up by vegetation at this site, annually. In contrast, the OP stand has an annual N uptake rate that is greater than the annual N mineralization rate. Nitrogen appears to be much more limiting in the OP stand.

Table 4.9 - Nitrogen Budget For an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) Forest at Coweeta, N.C. All units in g N/m^2/yr. Root and soil data are to a depth of 10 cm.

Property	*Oak Pine N*	*Northern Hardwood N*
Total N Uptake Rate	**4.39**	**7.11**
Overstory N uptake rate	4.23	6.76
Understory N uptake rate [a]	0.16	0.35
Total N Returns	**2.41**	**6.80**
Leaflitter [b]	2.47	3.62
Root Litter [c]	-0.53	1.94
Herb Litter	0	0.4853
Throughfall Inputs 1997[d]	0.412	0.706
Canopy frass (baseline)[e]	0.0575	0.045
Total N mineralization	**2.61**	**12.7**
Soil Mineralized[f]	0.825	11.29
Forest Floor N Mineralization	1.62	1.25
Course Woody Debris N-Min	0.16	0.16
Total Leaching Losses	**-0.31**	**-0.14**
Unaccounted For N	**0.32**	**12.25**

[a] From Monk and Day 1985.
[b] From D.A. Crossley Jr. unpublished.
[c] From Davis 1993.
[d] From Coweeta LTER program records.
[e] From M. Hunter unpublished.
[f] From Knoepp and Swank 1998.

4.4.0 Discussion

The initial hypothesis that low N mineralization rates occur in sites circulating low amounts of N and greater N mineralization rates occur in sites circulating greater amounts of N was supported by the results. The NH site, which had the greater N mineralization rate, also had a larger total N pool. The estimates show the NH site has approximately twice as much N in its system than does the OP site, most of which is in organic soil fractions. The NH also has greater annual N flux than the OP site in both biotic and abiotic (soil) components. The NH site circulates over three times more N each year in litterfall, root turnover, and annual herbs than does the OP site (Table 4.8). The N uptake rate is greater at the NH site than at the OP site, a trend often found between deciduous and coniferous temperate forests (Cole 1981).

The NH site seems to characterize an N-rich site and the OP an N-poor site. As an N-rich site, the leaf litter and soil at the NH site have low C:N ratios and higher % N, relative to the OP site, indicating a greater nitrogen supply at the NH site. Interestingly, the N uptake rate calculated in this study and others (Monk and Day 1988) for the NH site is lower than the amount of N mineralized, perhaps an early sign of N-saturation (Aber et al. 1989). The excess N does not appear to be leaching, and may be assimilated by microorganisms, or become attached to humic compounds in the forest floor and organic soil horizons (Currie and Nadelhoffer 1999; Drury et al. 1991).

Nitrogen seems to be much more limiting at the OP site, and therefore is used and cycled more efficiently. However, the apparently N limited OP site had more N loss through soil leachate than did the NH site, possibly due to the sandy soil texture and low soil organic matter. In contrast to the NH stand, more N is mineralized in the forest floor

than in the soil of the OP stand, and a greater % N is reabsorbed by trees at the OP site, signifying a tighter internal N-cycle (Table 4.5). Soil cores at the OP site showed thick mycorrhizal root mats, an important mechanism for N supply to host trees, especially in N-limited forests (Abuzinadah and Read 1986). Litter at the OP site had lower N-concentrations, and there was more root biomass and a larger root N pool for this stand than at the NH site, despite greater overstory biomass at the NH site. Large root infrastructures often are noted for N-poor forests, which have to invest more into their nutrient acquisition system at the expense of aboveground biomass (Gundersen et al. 1998). It is possible that the OP forest is meeting N requirements through organic N assimilation by the ectomycorrhiza associated with their root infrastructure (Chalot and Brun 1998).

Although the NH site has a greater internal N flux than does the OP site, the total input and flux of N annually in the NH system is not sufficient to account for the amount of N mineralized in the soil. Most N input is from the overstory leaf litter, which is higher in % N at the NH than the OP site, probably due to the higher % N of its soils and their faster N mineralization rate. Much of the more accessible N in the litter layer is probably turned over quickly by microorganisms, while more recalcitrant N and directly assimilated N ends up as humified matter in the soil from which mineral N is released more slowly (Currie and Nadelhoffer 1999).

Both C:N ratios and % N have been used as predictors of N mineralization rates, with lower C:N ratios and higher % N favoring faster rates (Fernadez et al. 2000). The soil, leaflitter, and forest floor of the NH site each contained at least twice the % N (by weight) than did the OP site, and C:N ratios 50 % those of the OP site. In particular, the

soil C:N ratio at the NH site (16.8) is in the range often cited to allow net N release due to N- mineralization by microorganisms (Vitousek 1982). Other parameters such as litter quality, in particular lignin:N ratio and lignin concentration, have also been shown to be important in influencing net N mineralization independent of climate (Hobbie 2000; Scott and Binkley 1997). Important feedbacks exist between soil nutrient availability and plant litter characteristics (Pastor et al. 1984). Dominant overstory *Pinus rigida* and understory species *Kalmia latifolia* at the OP site are known to have high lignin concentrations (White et al. 1988).

It seems most likely that the high N mineralization rates of the NH soils are partly a result of a much larger soil N pool at this site than the OP site, a more favorable soil texture, and a larger soil water content. The colder temperatures at the NH site may result in the accumulation of organic matter over time, serving as a reservoir of nutrients that are gradually released over time. Soil and forest floor organic matter prevents nutrients from leaching, conserves soil moisture, and is composed of N fractions of varying quality. Some fractions may be recalcitrant and slowly turned over, while others, such as microbial biomass contents, may be turned over more rapidly (Diazravina et al. 1993). Both contribute to the N that is mineralized.

In response to concerns regarding the impacts of increased atmospheric deposition on forest ecosystems (Aber et al. 1989; Nihlgård 1985), a series of long-term N addition experiments are being carried out in European and U.S. forests under the NITREX and EXMAN programs (Magill et al. 2000; Gundersen et al. 1998). Results after 9 years of chronic N addition at the Harvard Forest, U.S. report that between 68-84 % of the N added was retained in the soil organic matter (Magill et al. 2000). Hardwood and conifer

stands treated with NH_4NO_3 addition showed an increase in foliage N concentration and increases in extractable NH_4^+ and NO_3^- from soils. Hardwood stands showed a significant increase in net N mineralization rates, but conifer stands did not. European and US forests subjected to long-term N additions resulted in increases in forest N status and litter N concentrations, and decreases in root biomass and forest floor mass (possibly due to the decrease of roots) (Magill et al. 2000; Gundersen et al. 1998). These studies report an initial increase in net N mineralization rates with N fertilization, followed by a decrease over time. Changes in forest floor and vegetation N-status occurred before changes in the mineral soil N-status.

The NH site at CHL, in contrast to the OP site, compares to those forests that have been manipulated with N-additions. There is a lower root biomass and forest floor biomass at the NH site. Concentrations of N in important forest components (ie. soil, forest floor, leaf litter) are higher than at the NH site, and C:N ratios lower. There is a greater N-status at the NH site, and N mineralization rates are high (which may possibly decline within the next decade). The NH forest shares many characteristics of a forest in an early phase of N-saturation (Aber et al. 1989, 1998).

Still, how the quantity of N at the NH site was initially fixed into the system remains unknown. The region of the Appalachian mountains that Coweeta is situated has been reported to have relatively low levels of atmospheric N deposition (Swank and Vose 1997). The high N-status of the NH stand could be a legacy effect of previous forest disturbance and succession cycles (Goodale and Aber 2001). Early successional N-fixing species, such as black locust (*Robinia pseudoacacia*), may have occupied this site after the creation of light gaps due to the Chestnut (*Castanea dentata*) decline in these stands

in the 1930s, forest fires, or after blow-down events which periodically occur (Day et al. 1988; Swank and Crossley 1988; Boring and Swank 1984). Symbiotic N-fixation can be a significant N-source, especially in early successional stages, and may contribute between 3-7.5 g-N/m^2/yr in forests at CHL (Boring et al. 1988).

Many assumptions occur within this budget, the biggest of which arise from the complexities implicit in scaling. For example, in this budget small soil and root samples were used and scaled up to a square meter and conversely, allometric equations were used to estimate overstory biomass data and scaled down to a square meter. Both have inherent errors associated with them. Scaling across distance and across temporal scales continues to be a challenge in ecological research.

Certain components such as symbiotic and non-symbiotic rates of N-fixation, microbial N and turnover rates, mycorrhizal associations, and organic N assimilation rates were left out of this budget despite their significance, either due to lack of data or incomplete data (Chalot and Brun 1998; Drury et al. 1991; Boring et al. 1988; Abuzinadah and Read 1986). Methods of analysis and interpretation of these components still proves difficult. Dissolved organic nitrogen (DON) leaching, N$_2$O and other N volatilization and losses of N from the system have been left out of this budget as well, though some data exists for these relatively small but important fluxes (Michael and Matzner 1999; Qualls and Haines 1991; Davidson and Swank 1990).

Other difficulties and errors may occur from the use of data collected by different researchers over different time frames, using different methods. However, working in an LTER site has the advantage that raw data and collection methods are archived and available for such synthesis studies. A forest is a mosaic of biotic and abiotic factors and

patterns which change temporally and spatially. Having access to long-term data sets provides an important step in understanding these dynamic systems. Although there are necessary assumptions, and results may need to be interpreted with care, general patterns may emerge that would otherwise be neglected.

4.5.0 Conclusion

In conclusion, the results show that the NH site has many characteristics favorable to N mineralization and faster N-turnover rates through the forest system. The NH forest has an N pool over twice as large as the OP site, an N flux more than twice as rapid (excluding soil N mineralization), and a soil N mineralization flux 13 times greater. All the components of the NH forest (leaflitter, forest floor, soil, herbs, roots) had higher N-concentrations, than did the OP forest. In addition, soil properties at the NH site such as low C:N ratios, high organic matter, low % sand, and moderate % N all promote N mineralization. There is also more rainfall and a higher soil moisture at the NH than at the OP site, which may provide more favorable environmental conditions to soil microbes, despite the colder temperatures. Still, it is hard to distinguish cause and effect, and high soil N mineralization rates cannot be attributed to any particular variable. It is most likely an emergent property arising from many of these variables. Historical disturbance at these two sites may also be important in understanding the current pattern of nutrient cycling, and may account for the large N pools at the NH stand. While the OP stand characterizes an N-limited forest, the NH site has many characteristics of a stand in an early phase of N-saturation.

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CHAPTER 5

MODELING THE NITROGEN BUDGETS OF AN OAK PINE AND NORTHERN

HARDWOOD STAND IN THE SOUTHERN APPALACHIANS, USA

5.0 Abstract:

Nitrogen (N) mineralization rates typically decrease with decreasing temperatures. Temperatures decrease with increasing elevation, therefore N mineralization rates are predicted to decrease with increasing elevation. However, previous studies at Coweeta Hydrologic Laboratory in NC, have shown that nitrogen (N) mineralization rates are over an order of magnitude higher at a colder high elevation forest stand compared to a warmer stand lower in elevation. Elevated N deposition has been suggested to explanation this phenomena. Previous work synthesizing N budgets for these two sites has shown that the total N pool at the high elevation site is twice as large as that of the lower elevation site. Nitrogen fluxes at the high elevation site are twice as large as well. In this study N cycles for both sites was modeled using STELLA 6.0 to determine which factors are most important in controlling N mineralization rates for these two sites. Simulations were run for 200 year iterations and patterns of N cycling, with and without variation of sensitive parameters, were described. Model results show N deposition cannot account for the larger N pool size or faster N mineralization rate at the high elevation site. N mineralization was most sensitive to soil temperature, moisture, and soil N pool size. Inherent differences of N mineralization

constants between both sites was also found to be important in explaining present day N cycling. The high elevation site has a faster N mineralization rate constant than the lower elevation site, perhaps due to higher quality substrate, differences in microbial communities, or land disturbance history.

Keywords: Nitrogen mineralization; Nitrogen cycling; STELLA models; Forest soils

5.1.0 Introduction

Production of temperate forests is often limit by nitrogen (N) availability (Vitousek 1982). However, human industrial processes have increased the amount of N deposition falling on temperate regions traditionally considered to be N limited (Aber et al. 1998, 1989; Vitousek et al. 1997). The effects of elevated N deposition on forest N and other biogeochemical cycles, especially at the landscape scale, are still unresolved (Magill et al. 2000; Gunderson et al. 1998).

Previous work synthesizing long-term data sets have resulted in N budgets for a high elevation northern hardwood (NH) and a low elevation Oak Pine (OP) site at the Coweeta Hydrologic Laboratory (CHL), located in the southern Appalachian mountains in NC. Field soil incubations at these sites have shown that soil N mineralization rates are more than an order of magnitude greater at the colder NH (WS 5-27) than the OP (WS 1-18) site (Knoepp and Swank 1998). The cause of the faster N mineralization rates at the colder high elevation site is still unknown, although elevated N deposition has been a proposed culprit. However, N deposition levels at < 0.9 g $N/m^2/yr$ are not exceptionally high (Swank and Vose 1997).

Results from N budgets of these two sites show that the total N pool is twice as large at the NH than the OP site (Table 5.2), and annual N returns from canopy herbivory, leaf, root, and herb litter is over twice as large at the NH site (Table 5.3). Analytical data also show that the % N in the soil, forest floor, and litter is more than twice as great at the NH site, and forest floor and soil C:N ratios at this site are half as large as at the OP site (Table 5.1).

In this study the N cycles for both the OP and NH site were modeled using modeling software package STELLA 6.0. These process-oriented models were parameterized using N budgets constructed from field data for each site. Objectives of this study were to determine which factors are most important in controlling N mineralization rates at these two sites, and to describe patterns of N-cycling occurring in these two systems over time with and without variation of sensitive parameters.

5.2.0 Methods

5.2.1 *Site Location*

The two sites being compared in this study are within the Coweeta Hydrologic Laboratory (CHL), a USDA Forest Service facility and a Long Term Ecological Research site (LTER). Coweeta is situated within the Blue Ridge physiographic province in the southern Appalachians of North Carolina, latitude 35°03'N, longitude 83°25'W (Swift et al. 1988). The two sites being compared are both 80 x 80 m^2 in area.

5.2.2 *Site Description*

The OP stand is at an elevation of 782 m, on a xeric south facing slope (Table 5.1). The mean soil temperature at the OP is 13.34^o C, and an average of 204 cm of precipitation falls annually at this site (L. Swift unpublished). The OP stand is dominated by tree species including *Pinus rigida*, *Quercus prinus*, *Quercus rubra*, a woody understory species *Kalmia latifolia*, and there is no annual herb layer (Knoepp et al. 2000). The soil at the OP stand is a well-drained Evard-Cowee gravelly loam (43.7 % sand, 48.9 % silt, and 7.4 % clay) with 12.1 % organic matter. The OP soil has a pH of 3.9 and a bulk density of 0.75 g/cm^3 and has an N mineralization rate 0.825 $g/m^2/0$-10cm/yr (Knoepp and Swank 1998).

In contrast, the high elevation (1347m) north facing NH stand has a soil N mineralization rate of 11.29 $g/m^2/0$-10cm/yr (Knoepp and Swank 1998). This site receives 260.7 cm of precipitation annually, and has a mean annual soil temperature of 8.79 °C (L. Swift unpublished) (Table 5.1). Hardwood tree species including *Betula alleghaniensis*, *Liriodendron tulipifera*, and *Quercus rubra*, dominate this site and a woody perennial understory of *Rhododendron maximum* and annual herbs including non-woody composites and ferns are present. The soil at the NH stand is of the Cullasaja-Tuckasegee complex, a fine sandy loam that is moderately well drained with a pH of 4.0 and a bulk density of 0.54 g/cm^3 (Knoepp et al. 2000). The NH soil has a finer texture (13.5 % sand, 76.2 % silt, and 10.3 % clay) and more organic matter (24.3 %) than does the OP soil. The slope at the NH site (33 degrees) is comparable to that of the OP site (34 degrees).

5.2.3 *Constructing N Budgets for the OP and NH Site*

Data from previous studies were compiled along with new data to construct N budgets for the OP and NH sites. These N budgets represent a synthesis of archived data from the Coweeta LTER project. Nitrogen pools (Table 5.2) and fluxes (Table 5.3) were determined for both forest stands. Nitrogen pools accounted for in the budget were soil (top 0-10 cm), root biomass (top 0-10 cm), forest floor biomass, coarse woody debris biomass, understory plant biomass, and overstory plant biomass. Annual N fluxes accounted for were fine root turnover, litterfall, insect defoliation/frass inputs, canopy throughfall inputs, annual herb turnover, forest floor N mineralization, soil N mineralized, and soil leaching. N Fluxes were determined on an annual basis.

Table 5.1 - Site Characteristics for the Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) Forest Stands at Coweeta Hydrologic Laboratory, NC.

Property	*Oak Pine (OP)*	*Northern Hardwoods (NH)*
Elevation (m)[a]	782	1347
Degree Days (°C)[a]	4621	3438
Mean Annual Soil Temperature (°C)[a]	13.34	8.79
Mean Annual Soil Moisture (%)[a]	15.69	21.45
Soil Bulk Density (g/cm^3)[b]	0.75	0.54
Soil % Organic Matter[b]	12.1	24.3
Soil Texture (% sand, silt, clay)	43.7, 48.9, 7.4	13.5, 76.2, 10.3
Microbial Biomass N (g N/m^2/10cm)[c]	5.49	11.28
Soil %N	0.21	0.85
Soil C:N	33.9	16.8
Forest Floor % N	0.87	1.84
Forest Floor C:N	59.9	26.3
Leaf Litter % N	0.61	1.19
Annual Herbs % N	0	2.71
Annual Herbs C:N	0	16.72
Soil N mineralization Rate (mg N/kg soil/yr)[b]	11	209

[a] Data from Coweeta LTER program records.
[b] From Knoepp et al. 2000.
[c] From Hu et al. 1997.

Table 5.2 - Forest Nitrogen Pools (g-N/m^2) for an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) sites at the Coweeta Hydrologic Laboratory, NC.

Property	Oak Pine (OP)	Northern Hardwoods (NH)
Soil Nitrogen[a]	157.5	459.5
Total Overstory Nitrogen[b]	33.78	65.36
Total Understory Nitrogen[b]	0.17	1.47
Forest Floor Nitrogen[b]	18.29	11.32
Coarse Woody Debris Nitrogen[b]	15.9	22.53
Root Nitrogen[a]	8.98	5.55
TOTAL N POOL[b]	**234.62**	**565.73**

[a] Soil and root data are for a 0-10 cm depth. Values expressed as (g N/m^2/0-10 cm).
[b] From Bonito et al. unpublished.

Table 5.3 - Annual Forest Nitrogen Fluxes (g N/m^2/yr) for an Oak Pine (WS 1-18) and Northern Hardwood (WS 5-27) sites at the Coweeta Hydrologic Laboratory, NC.

Property	Oak Pine	Northern Hardwood
Litterfall[b]	2.47	3.62
Root Litter[a]	-0.53	1.94
Herb Litter[b]	0	0.4853
Throughfall Inputs 1997[b]	0.412	0.706
Canopy frass (baseline)[b]	0.0575	0.045
Total N Returns[b]	**2.41**	**6.80**
Soil Mineralized[a]	0.825	11.29
Forest Floor Mineralization[b]	1.62	1.25
Course Woody Debris N-Min[b]	0.16	0.16
Total N Mineralization[b]	**2.61**	**12.7**
Total Leaching Losses[b]	**-0.31**	**-0.14**

[a] Root and soil are for a 0-10 cm depth. Values are expressed as (g N/m^2/0-10 cm/yr).
[b] From Bonito et al. unpublished.

5.2.4 *Structure of STELLA N Models*

Nitrogen flow models based on a conceptual model of forest N cycling were constructed using STELLA 6.0. The goals of this project were to determine N

economy patterns of the OP and NH sites over time, and to determine which variables best explain N mineralization rates. The models used an annual time step with the fourth Runge-Kutta integration method. Flow rates were based on first order kinetics and simulations conducted for 200 years. Data from N budgets and literature parameters were used to initialize the models.

State variables in these models included soil, inorganic, overstory, understory, root, and forest floor N pools (Figure 5.1). Soil N, forest floor N, and canopy throughfall N both flow into the inorganic N pool. Some inorganic N is lost through soil leaching, and the rest is partitioned between the root, overstory, and understory pools. Overstory and understory N pools flow into the forest floor N pool. Root and forest floor N both flow into the soil N pool. In summary, the flows which were modeled included soil and forest floor mineralization; overstory, understory and root litter N; forest floor humification; canopy throughfall; soil leaching; and overstory, understory and root N uptake (Figure 5.1).

Soil temperature (^{o} C) and moisture (water potential) are considered to be driving forces in this model. The temperature factors (TF) were calculated for each site using the average soil temperature (TEMP), and the equation:

TF = (TEMP-5)/TEMP.

The moisture factors (MF) used for each site were based on the average % soil moisture (MOIST), the drain upper limit soil water potential (DUL), and the air dried soil water

potential (AD). Literature values based on soil texture were used for estimating DUL and

AD (Ratliff et al. 1983). The equation used to calculate the MF was:

MF=(MOIST-AD)/(DUL-AD).

The soil TF and MF interacted with the soil N pool to affect the amount of soil N
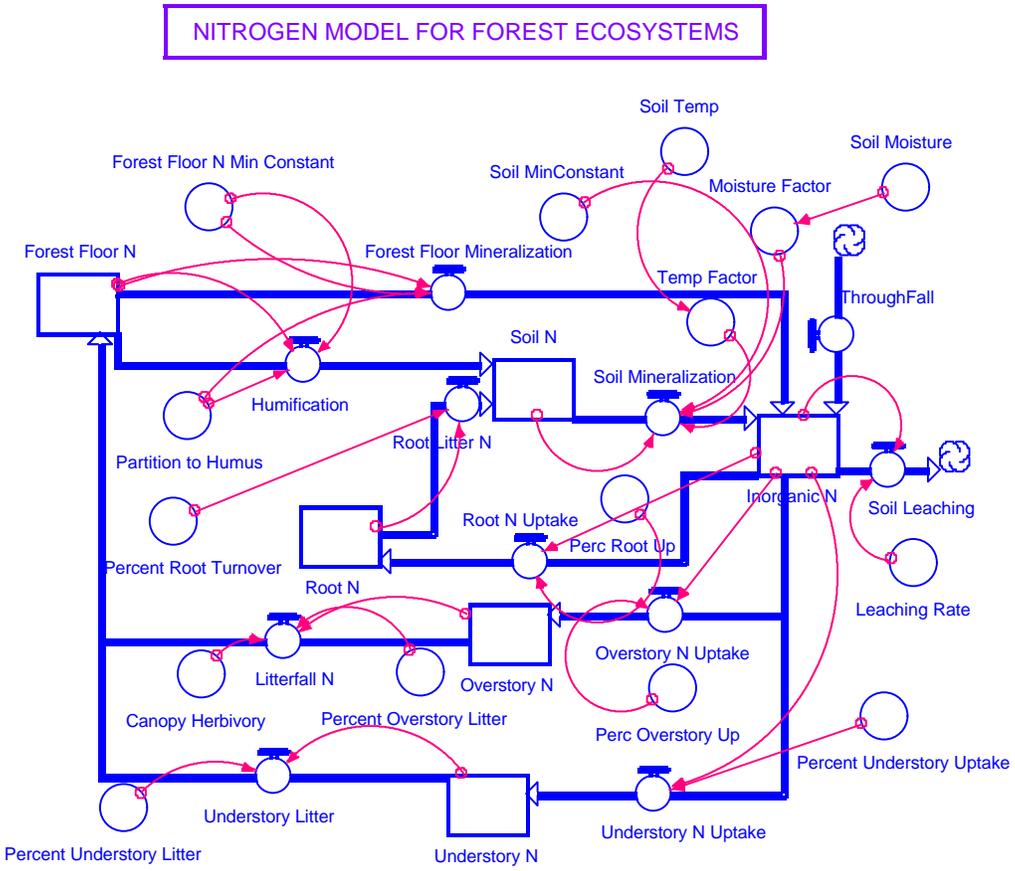
mineralized annually.

Figure 5.1 – STELLA model for N Cycling through Forest Ecosystems.

5.2.5 *Analysis of Stella Models*

The models were first run using actual field N mineralization constants to determine how the pools and fluxes responded over time. A second simulation used small, medium, or large soil N mineralization constants in the two models to examine how the pattern of N cycling at each site responds to changes in soil N mineralization constants, and how the sites behaved under the same N mineralization rate constant. The small constant was that of the OP site, the large that of the NH, and the medium constant was the average of these two. A third simulation incorporated soil temperature and moisture factors into the soil N mineralization flux to determine if these abiotic factors can explain the greater N mineralization constant at the NH site. Simulations using an increase in throughfall N were also run to calculate how long it would take to the NH site to accumulate the currant amount of soil N. Sensitivity analyses were performed to assess which factors had the most influence over soil N mineralization. These were done by increasing and decreasing each parameter by 10, 20 and 30 % and running the model to assess how soil N mineralization was affected.

5.3.0 Results

5.3.1 *Simulations of Ecosystem N Flows*

Patterns of N flow through the ecosystem differed between these two forests but remained fairly consistent through time, especially after the first 20 years, which had the most fluctuation in N pools and fluxes. The OP site was characterized by decreasing N pools (Figure 5.2) and fluxes throughout the 200 year simulation, with the only exceptions being the understory and soil N pools, and the soil N mineralization flux. The

amount of annual N mineralizaton increased 48 % during the 200 year simulation, directly proportional to the increase in the soil N pool. According to the model there was not enough mineral N to support the overstory or root demands, shown by a decrease in overstory (-61 %) and root N (-74 %) pools, and resulting in a decrease in overstory litter and root N. The decrease in the overstory litter N flux led to a decrease in the forest floor. However, the OP model seemed to perform fairly stable and without drastic fluctuations, aside from a large increase (1035 %) of the understory N pool, which still remained a relatively small pool. There was a net increase of N at the OP site after 200 years, which accumulated in the soil N pool.
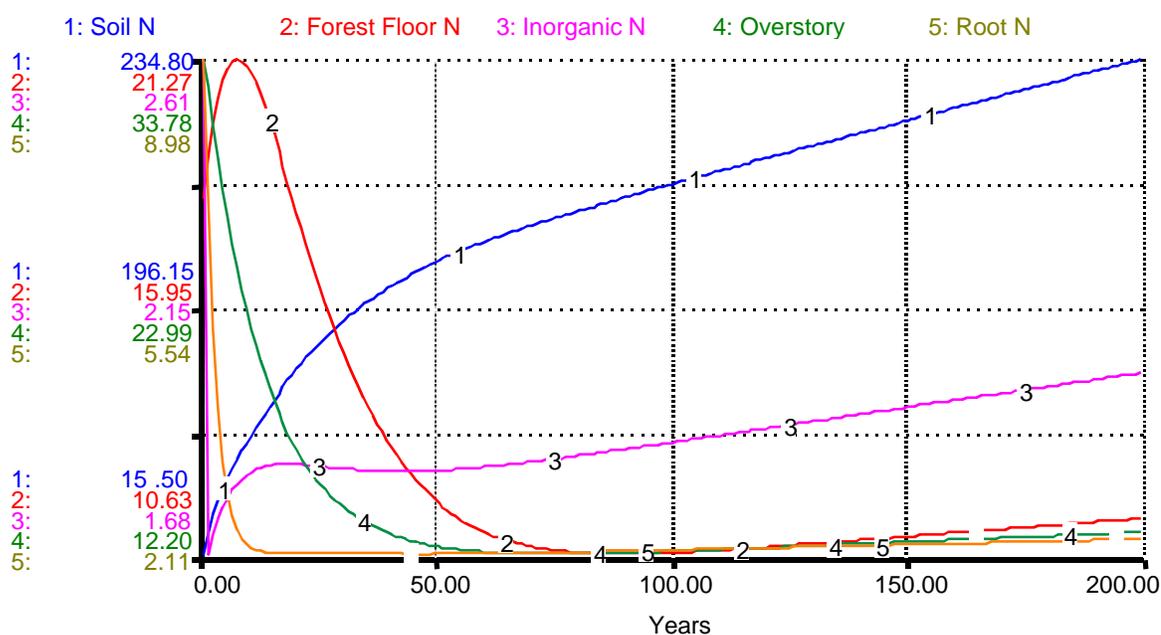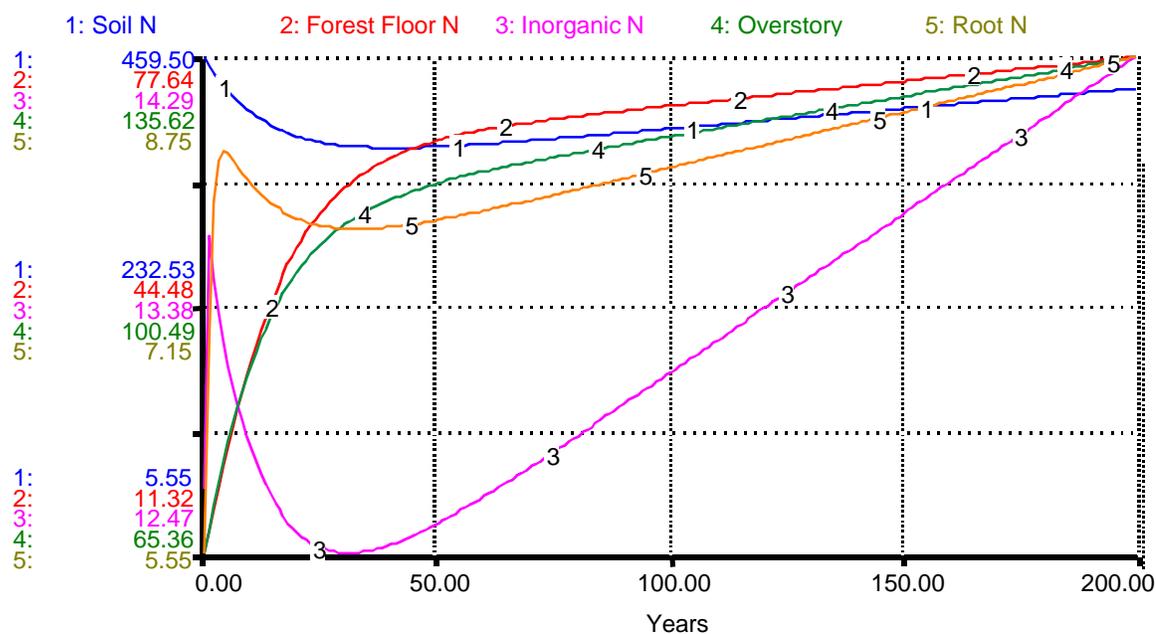

Figure 5.2 – Simulation of Major N Pools (g N/m^2/yr) for an Oak Pine Site (WS 1-18). Note: scales are not the same for different N pools.

In contrast to the OP site, all N pools (Table 5.3) and fluxes increased over time at the NH site, except for the soil N pool and soil N mineralization flux. Due to the high mineralization rate at the NH site, slightly more N was mineralized from the soil than flowed into the soil as root litter or forest floor humus. Both the soil N pool and annual soil N mineralized decreased by 6 % during the 200 year simulation. The NH site also accrued N during the 200 years, which ended up mostly in the overstory and forest floor N pools. The results from the NH model were also fairly stable, aside from the large increase in overstory biomass, and the associated feedbacks involved with increasing this pool.

Figure 5.3 - Simulation of Major N Pools (g N/m^2/yr) for a Northern Hardwood site (WS 5-27). Note: scales are not the same for different N pools.

5.3.2 *Ecosystem Response to N Simulations Using the Same N Mineralization Rate Constants*

Simulations of the OP site using the N mineralization constant of the NH site (0.0278) had a dramatic effect on the systems pattern of N cycling. Rather than increasing the amount of soil N mineralized, a faster N mineralization constant at the OP site led to a 31 % reduction in the size of the soil N pool and soil N mineralized annually. The forest floor and the soil inorganic N pool increased. Consequently, soil N leaching increased and the system lost an average of 0.5 % annually over the 200 year simulation.

Using the OP soil N mineralization constant (0.006) in NH site simulations also resulted in dramatic changes in patterns of system N cycling. Under a lower rate of soil N mineralization pools of inorganic, overstory, understory, and root N decreased at the NH site, while the soil and forest floor N pools increased. Soil N mineralization increased in proportion to the increase in soil N pool, and soil leaching decreased in proportion to the decrease in the inorganic N pool. The system gained N at an average rate of 0.4 % annually over the 200 year simulation.

A trend appears when comparing the two sites under the same soil N mineralization constants. Under the small soil N mineralization constant, root, inorganic, overstory N pools decreased and soil N pools increased at both sites. The total amount of N mineralized increased as well, in proportion to the increase in the soil N pool. Under the large soil N mineralization constant the soil N pool and amount of annual soil N mineralized decreased for both sites. Also, soil N leaching increased in both sites, as did the forest floor, inorganic, and understory N pools. With a medium rate constant, the amounts of yearly N mineralized were larger than observed for the OP site and smaller

than observed at the NH site (Figure 5.4). This suggests the two systems have different N
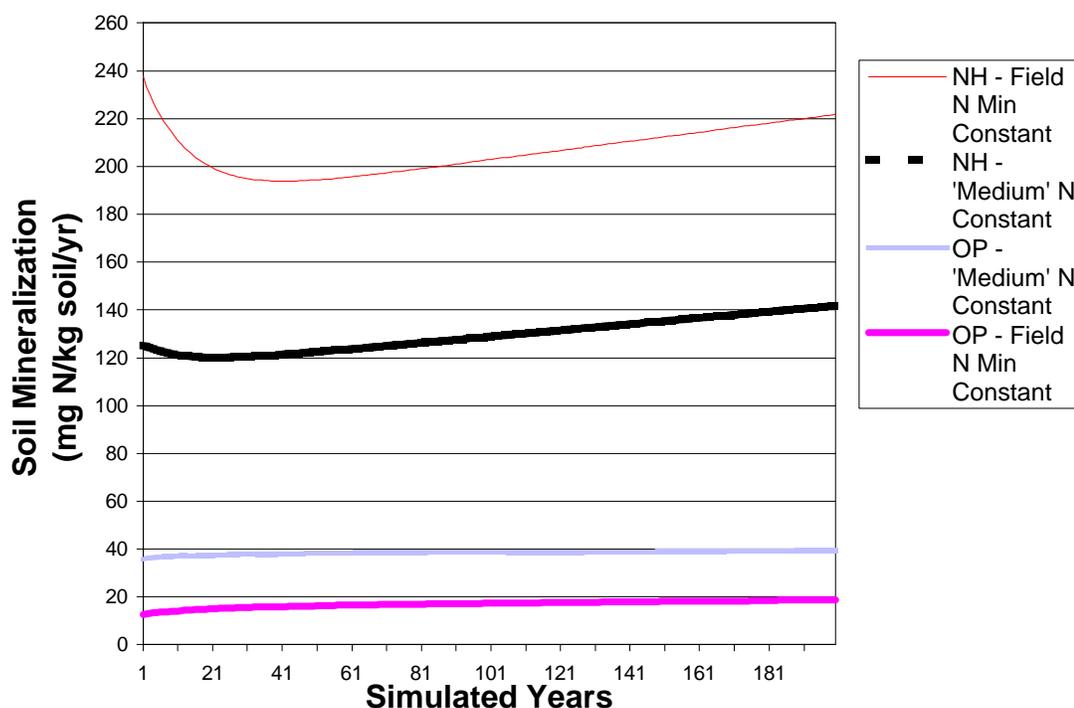
mineralization rate constants.

Figure 5.4 – Soil N Mineralization simulations under field and 'Medium' N Mineralization rate constants.

5.3.3 *The Importance of Temperature and Moisture Factors*

Soil N mineralization is limited by soil temperature more at the NH site than at

the OP site, while soil moisture limits soil N mineralization more at the OP site than at

the NH site.   In simulations, soil moisture and temperature factors dampened the changes

in N pools and fluxes but did not change the overall pattern of N cycling at these sites.

Sensitivity analyses show, at the OP site, the four factors soil N mineralization is most sensitive to are (in decreasing order): changes in the soil N pool, soil moisture, soil temperature, and the soil N mineralization constant (Figure 5.5). For the NH site, soil N mineralization is most sensitive to (in decreasing order): changes in soil temperature, soil moisture, soil N mineralization constant, and the soil N pool (Figure 5.6). The model is not sensitive to other parameters relative to these.
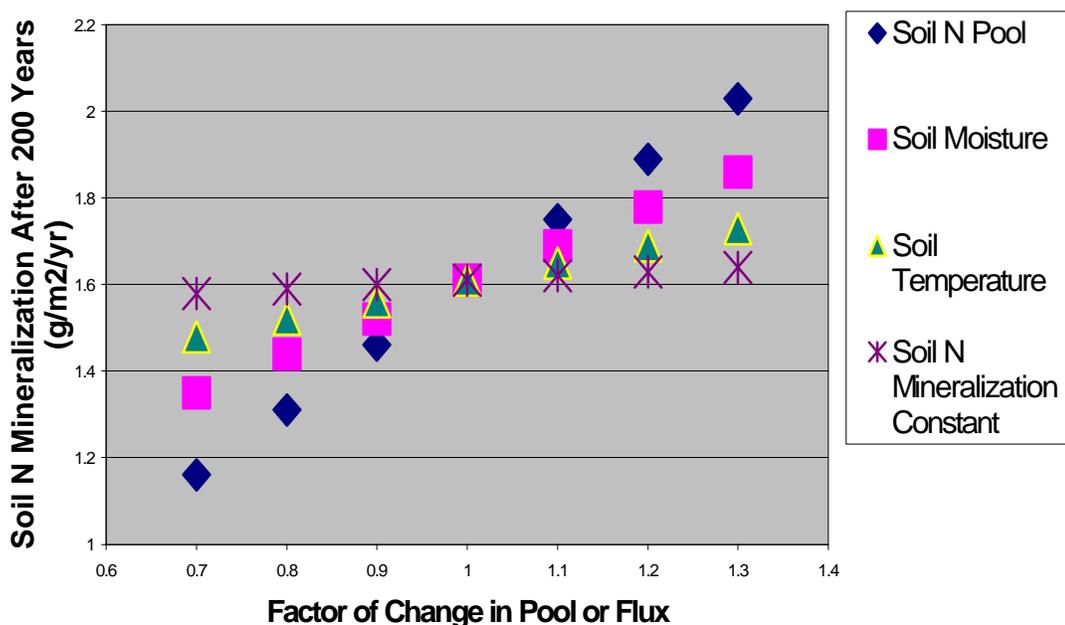

Figure 5.5 – Sensitivity Analysis of a STELLA model for Soil N Mineralization of an Oak Pine forest.
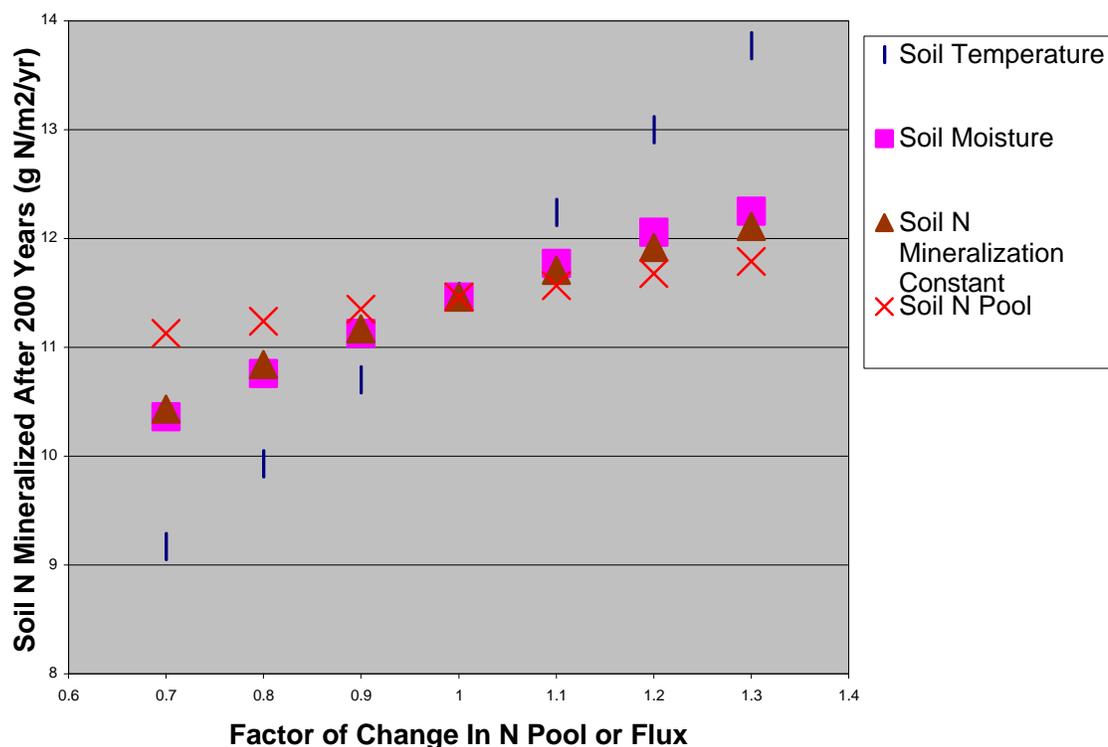
Figure 5.6 – Sensitivity Analysis of a STELLA model for Soil N Mineralization of an Oak Pine forest.

5.3.4 *The Impact of N Deposition on Soil N Mineralization*

Although N deposition, represented by throughfall N, was not as sensitive as other parameters at the NH site it is one way a forest can accrue N over time. Based on the model and using current thoughfall concentration and amount, it would take 1000 years to reach the present day soil N pool size and soil N mineralization rates. At double the throughfall inputs it would only take 480 years to reach the same scenario. However, since human caused N deposition became significant only after the industrial revolution,

it is unlikely to be as significant a contributor to forest N inputs as symbiotic and free-living N-fixing bacteria (Boring et al. 1988).

5.4.0 Discussion

Environmental conditions, particularly soil moisture and soil temperature which are known to constrain the activity soil organisms and ecosystem processes (Gundersen et al. 1998; Heneghan et al. 1997), appear to be the main drivers affecting the rate of soil N mineralization for these modeled sites. The size of the soil N pool is also important because soil N mineralization is proportional to the size of this pool. Hence, even under equal soil N mineraliation constants, the site with a larger soil N pool will have a higher rate of soil N mineralization. However, studies show that although soil and humus provide long term N sinks, direct assimilation of N by microbes and microbial turnover are important internal N cycling mechanisms that were not directly accounted for by this model (Currie and Nadelhoffer 1999; Drury et al. 1991)

Faster rates of soil N mineralization may have positive or negative feedback effects on the amount of N mineralized annually over time. These simulations showed that under faster rates of soil N mineralization the amount of soil N mineralized decreases due to decreases in the soil N pool size. Simulations using the small soil N mineralization constant show the soil N pool and the amount of soil N mineralized annually increase at the same proportion. Lower temperatures and soil moisture increased the rate of soil N accumulation, while higher temperature and soil moisture decreased the rate of soil N accumulation.

At the OP site soil moisture was more limiting to soil N mineralized than was soil temperature. At the NH site, soil temperature was more limiting to soil N mineralization than was soil moisture. However, differences in soil moisture and temperature are not sufficient to account for differences in the rate of soil N mineralized between sites. The size of the soil N pool and the soil N mineralization constant for each site are also important. Throughfall (N-deposition) may be partially responsible for current N pool size and N mineralization rates at the NH site, but unlikely to be the main cause. Higher levels of N deposition are likely to occur in the future and other studies and models have predicted forests to respond initially with higher N mineralization rates, followed by a decline in rates (Gundersen et al. 1998; Magill et al. 2000). This model predicts an increase in both N mineralization and N pool size but, perhaps due to lack of a modeled feedback effects, no decline.

Not only was the soil N pool at the NH site 2 to 3 times larger than at the OP site throughout the 200 year simulations, but the soil N mineralization constant was also over 5 times greater at the NH site suggesting that the N at this site is more mineralizable (higher quality) or the microbial community at the NH site is larger, turns over quicker, and is more efficient at mineralizing N than at the OP site. Previous studies along this same elevational gradient have in fact shown an increase in soil and litter oribatid mite diversity with increasing elevation, changes in canopy arthropod guild structure along this same gradient, and greater microbial biomass at the highest elevation site (Lamoncha and Crossley 1998; Reynolds and Crossley 1997; Hu et al. 1997). Other microbes and arthropod guild structures probably vary as well along the elevation gradient.

Intrinsic patterns of N cycling differ between these two sites. Given the same N mineralization constant and soil N pool size, the two systems diverge over time. Under a high soil N mineralization constant, the OP site depletes the soil N pool more quickly than does the NH site. Under low rates of soil N mineralization the OP site accumulates soil N much slower than does the NH site. In all simulations the NH site had more soil N mineralized than the OP site.

Many difficulties in modeling soil, root, nutrient and forest systems have been noted (Fu et al. 2000; Goodale et al. 2000; Grote and Erhard 1999; Santantonio and Grace 1987). Lack of organism feedback in process-oriented models, and difficulties in estimating and validating internal parameters in organism-oriented models are the main challenges to more realistic modeling (Fu et al. 2000). Uncoupling temperature, moisture, and other environmental factors also continues to be problematic (Gundersen et al. 1998). Land-use history and N deposition history affect present N pools and cycles and were not adequately accounted for in this model (Currie and Nadelhoffer 1999). Models are limited by design. Difficulties estimating some parameters, assumptions made during model construction and lack of data to calibrate the model are potential sources of error in this study.

In conclusion, because N mineralization is proportional to the size of the soil N pool, the size of this pool can explain much but not all of the variation in soil N mineralization between these two sites. Temperature and moisture appear to be major driving factors at both sites; temperature more limiting at the NH site, and lack of moisture more limiting at the OP site. Perhaps the colder temperatures at the NH allow the N to accumulate in the soil over time. However, even after equilibrating the soil N

pool size, temperature and moisture, the NH site had a faster N mineralization constant than the OP site. This may be due to higher quality substrate or a different microbial community structure at the NH site. Feedbacks occurring do to forest disturbance, land-use history, and vegetation are also affecting present day N cycling.

5.5.0 Appendices

5.5.1 *Appendix A – STELLA Equations for the Oak Pine Site*

Forest_Floor_N(t) = Forest_Floor_N(t - dt) + (Litterfall_N + Understory_Litter - Humification - Forest_Floor_Mineralization) * dt

INIT Forest_Floor_N = 18.29

INFLOWS:

Litterfall_N = (Overstory_N*Perc_LitterFall)+(Overstory_N*Canopy_Herbivory)

Understory_Litter = Understory_N*Percent_Understory_Litter

OUTFLOWS:

Humification = Forest_Floor_N*Forest_Floor_N_Min_Constant*Partition_to_Humus

Forest_Floor_Mineralization = Forest_Floor_N*Forest_Floor_N_Min_Constant*(1-Partition_to_Humus)

Inorganic_N(t) = Inorganic_N(t - dt) + (Soil_Mineralization + ThroughFall + Forest_Floor_Mineralization - Overstory_N_Uptake - Understory_N_Uptake - Soil_Leaching - Root_N_Uptake) * dt

INIT Inorganic_N = 2.61

INFLOWS:

Soil_Mineralization = Soil_N*Moisture_Factor*Soil_MinConstant*Temp_Factor

ThroughFall = .412

Forest_Floor_Mineralization = Forest_Floor_N*Forest_Floor_N_Min_Constant*(1-

Partition_to_Humus)

OUTFLOWS:

Overstory_N_Uptake = Inorganic_N*Perc_Overstory_Up

Understory_N_Uptake = Inorganic_N*Perc_Understory_Up

Soil_Leaching = Inorganic_N*Leaching_Rate

Root_N_Uptake = Inorganic_N*Perc_Root_Up

Overstory_N(t) = Overstory_N(t - dt) + (Overstory_N_Uptake - Litterfall_N) * dt

INIT Overstory_N = 33.78

INFLOWS:

Overstory_N_Uptake = Inorganic_N*Perc_Overstory_Up

OUTFLOWS:

Litterfall_N = (Overstory_N*Perc_LitterFall)+(Overstory_N*Canopy_Herbivory)

Root_N(t) = Root_N(t - dt) + (Root_N_Uptake - Root_Litter_N) * dt

INIT Root_N = 8.98

INFLOWS:

Root_N_Uptake = Inorganic_N*Perc_Root_Up

OUTFLOWS:

Root_Litter_N = Root_N*Perc_Root_TO

Soil_N(t) = Soil_N(t - dt) + (Humification + Root_Litter_N - Soil_Mineralization) * dt

INIT Soil_N = 158

INFLOWS:

Humification = Forest_Floor_N*Forest_Floor_N_Min_Constant*Partition_to_Humus

Root_Litter_N = Root_N*Perc_Root_TO

OUTFLOWS:

Soil_Mineralization = Soil_N*Moisture_Factor*Soil_MinConstant*Temp_Factor

Understory_N(t) = Understory_N(t - dt) + (Understory_N_Uptake - Understory_Litter) *

dt

INIT Understory_N = 0.17

INFLOWS:

Understory_N_Uptake = Inorganic_N*Perc_Understory_Up

OUTFLOWS:

Understory_Litter = Understory_N*Percent_Understory_Litter

Canopy_Herbivory = 0.0017

Forest_Floor_N_Min_Constant = 0.089

Leaching_Rate = 0.1187

Moisture_Factor = (Soil_Moisture-5.7)/(25-5.7)

Partition_to_Humus = 0.8

Percent_Understory_Litter = 0.02

Perc_LitterFall = 0.073

Perc_Overstory_Up = .49

Perc_Root_TO = 0.34

Perc_Root_Up = .39

Perc_Understory_Up = 0.02

Soil_MinConstant = 0.0186

Soil_Moisture = 15.7

Soil_Temp = 13.3

Temp_Factor = (Soil_Temp-5)/Soil_Temp

5.5.2 *Appendix B– STELLA Equations for the Northern Hardwood Site*

Forest_Floor_N(t) = Forest_Floor_N(t - dt) + (Litterfall_N + Understory_Litter_N -

Humification - Forest_Floor_Mineralization) * dt

INIT Forest_Floor_N = 11.32

INFLOWS:

Litterfall_N =

(Overstory_N*Percent_Oversory_Litter)+(Overstory_N*Canopy_Herbivory)

Understory_Litter_N = Understory_N*Percent_Understory_Litter

OUTFLOWS:

Humification = Forest_Floor_N*Floor_N_Mineralizaton_Rate*Partition_to_Humus

Forest_Floor_Mineralization = Forest_Floor_N*Floor_N_Mineralizaton_Rate*(1-

Partition_to_Humus)

Inorganic_N(t) = Inorganic_N(t - dt) + (Soil_Mineralization + ThroughFall +

Forest_Floor_Mineralization - Overstory_N_Uptake - Understory_N_Uptake -

Soil_Leaching - Root_N_Uptake) * dt

INIT Inorganic_N = 12.7

INFLOWS:

Soil_Mineralization = Soil_N*Moisture_Factor*Soil_Min_Constant*Temp_Factor

ThroughFall = 0.706

Forest_Floor_Mineralization = Forest_Floor_N*Floor_N_Mineralizaton_Rate*(1-

Partition_to_Humus)

OUTFLOWS:

Overstory_N_Uptake = Inorganic_N*Overstory_N_uptake_rate

Understory_N_Uptake = Inorganic_N*Understory_N_up_Rate

Soil_Leaching = Inorganic_N*Leaching_N_rate

Root_N_Uptake = Inorganic_N*Rate_of_Root_N_Uptake

Overstory_N(t) = Overstory_N(t - dt) + (Overstory_N_Uptake - Litterfall_N) * dt

INIT Overstory_N = 65.36

INFLOWS:

Overstory_N_Uptake = Inorganic_N*Overstory_N_uptake_rate

OUTFLOWS:

Litterfall_N =

(Overstory_N*Percent_Oversory_Litter)+(Overstory_N*Canopy_Herbivory)

Root_N(t) = Root_N(t - dt) + (Root_N_Uptake - Root_Litter_N) * dt

INIT Root_N = 5.55

INFLOWS:

Root_N_Uptake = Inorganic_N*Rate_of_Root_N_Uptake

OUTFLOWS:

Root_Litter_N = Root_N*Perc_Root_Turnover

Soil_N(t) = Soil_N(t - dt) + (Humification + Root_Litter_N - Soil_Mineralization) * dt

INIT Soil_N = 0

INFLOWS:

Humification = Forest_Floor_N*Floor_N_Mineralizaton_Rate*Partition_to_Humus

Root_Litter_N = Root_N*Perc_Root_Turnover

OUTFLOWS:

Soil_Mineralization = Soil_N*Moisture_Factor*Soil_Min_Constant*Temp_Factor

Understory_N(t) = Understory_N(t - dt) + (Understory_N_Uptake -

Understory_Litter_N) * dt

INIT Understory_N = 1.9553

INFLOWS:

Understory_N_Uptake = Inorganic_N*Understory_N_up_Rate

OUTFLOWS:

Understory_Litter_N = Understory_N*Percent_Understory_Litter

Canopy_Herbivory = 0.00069

Floor_N_Mineralizaton_Rate = 0.11

Leaching_N_rate = 0.011

Moisture_Factor = (Soil_Moisture-7.35)/(29-7.35)

Overstory_N_uptake_rate = .54

Partition_to_Humus = 0.8

Percent_Oversory_Litter = 0.0554

Percent_Understory_Litter = 0.2482

Perc_Root_Turnover = 0.62

Rate_of_Root_N_Uptake = .38

Soil_Min_Constant = 0.0995

Soil_Moisture = 21.45

Soil_Temp = 8.79

Temp_Factor = (Soil_Temp-5)/Soil_Temp

Understory_N_up_Rate = 0.0

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CHAPTER 6

CONCLUSIONS

6.0 Conclusions

The objective of these series of studies was to elucidate possible mechanisms or variables which could explain why N mineralization rates are faster at a colder, high elevation, northern hardwood (NH) site than at a low elevation Oak Pine (OP) site (Knoepp and Swank 1998). A series of alternative hypotheses which may explain the phenomena included: 1) there is an N mineralization promoter in the soil, leaf litter, or herbs of the NH site, 2) the NH site has more N in its system than the OP site, 3) differences in microbial community structure, 4) the OP site is limited by low moisture, 5) the OP site is limited by low pH, and 6) land-use and disturbance history.

This first study took an experimental approach to search for a putative N mineralization promoter, based on findings that root exudates, including simple sugars and amino acids, stimulate N mineralization (Jaeger et al.1999). Cold water extracts were made from soil, leaf litter, and herb layers from both sites and incubated with soils at a favorable water tension (Quemada and Cabrera 1997). Results of the first study did not support the N mineralization promoter hypothesis. The NH soils mineralized significantly more N than did the OP soils, regardless of what treatment was added to the soils. The results from the first experiment suggest that the fast mineralization rates of

the NH forest are due to intrinsic soil properties, such as soil texture, N pool size or quality, or microbial structure, rather than a chemical mineralization promoter.

The second study addressed the hypothesis that sites with a greater N status circulate more N through their systems (Vitousek 1982). Taking advantage of the large data base maintained by the Coweeta Long-term Ecological Research (LTER) program, previously collected data was integrated with current data to construct total N budgets for each site. Nutrient budgets can be very useful tools for understanding and diagnosing changes in system functioning (Monk and Day 1985; Duvigneaud and Denaeyer-De Smet 1970). By comparing the N budgets many characteristics favorable to N mineralization and faster N-turnover rates are present. For instance, the NH forest has an N pool over twice as large as the OP site, an N flux more than twice as rapid (excluding soil N mineralization). This may be a least partly responsible for a soil N mineralization flux 13 times greater at the NH site than at the OP site.

Properties of the soil at the NH site may also help explain faster N mineralization rates at this site. These soils had low C:N ratios, high organic matter, low % sand, and moderate % N are all known to be favorable for N mineralization (Prescott et al. 2000; Schlesinger 1991). Other components of the NH forest (leaflitter, forest floor, soil, herbs, roots) also had higher N-concentrations than did the OP forest. In addition, more rainfall and a higher soil moisture at the NH than at the OP site, may provide more favorable environmental conditions to soil microbes, despite the colder temperatures. From the N budgets it became clear how different the two sites were. While the OP stand characterizes an N-limited forest with its large root biomass and high C:N ratios, the NH site has many characteristics of a stand in an early phase of N-saturation such as large N

pools, fast rates of N mineralization, a smaller root biomass, and low C:N ratios (Aber et al. 1998, 1989; Swank and Vose 1997).

The third study used process-oriented models constructed using STELLA 6.0 to tease apart environmental and site variables responsible for N mineralization rates. Data from the N budgets were used to initiate the model based on first order reactions. Although model behavior is an artifact of design, some interesting findings occurred with these simulations. First, due to the larger N pool at the NH site and soil N mineralization being proportional to the soil N pool size, N mineralization was always greater at this site. Second, N mineralization at both sites was sensitive to moisture and temperature changes. The OP was more sensitive to moisture than to temperature and the NH was more sensitive to temperature than to moisture. Third, the levels of N deposition were not adequate to explain the high levels of N mineralization at the NH site. Lastly, equilibrating the two sites in terms of temperature, moisture, N pool size, and N deposition, the NH site still had a faster N mineralization rate. This suggests that the two sites have different inherent soil N mineralization rate constants. This maybe due to differences in the microbial community structure or to a higher quality, more mineralizable substrate at the NH site.

From the culmination of these three studies the N cycling within these two forest systems can better be understood. Still, it is hard to distinguish cause and effect, and high soil N mineralization rates cannot be attributed to any particular variable. Part of the difficulty arises from the many differences between the sites. For instance, the sites differ from each other in terms of soil texture and quality, overstory and understory vegetation species, moisture and temperature regimes, aspect, nutrient cycling, and

microbial and microarthropod communities (Knoepp et al. 2000; Lamoncha and Crossley 1998; Hu et al. 1997). This inherent differences complicate comparisons, but are a good example of how patchy landscapes may be, and how elevational gradients have characteristics similar to those latitudinal gradients.

Through these three studies the high mineralization rates observed at the NH site can be better put into perspective. This site has a large soil N pool, good quality litter, favorable soil texture, and a high N mineralization rate constant, perhaps due to the microbial community. The site disturbance history may provide a clue into how so much N was initially fixed into the NH system (Boring et al. 1998). Nitrogen deposition is unlikely the cause. Undoubtedly the high rates of N mineralization at the NH site are an emergent property arising from many interacting variables.

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