ABSTRACT

GURLEVIK, NEVZAT. Stand and soil responses of a loblolly pine plantation to midrotation fertilization and vegetation control. (Under the direction of H. Lee Allen).

This study was conducted in a 14-year-old midrotation loblolly pine (*Pinus taeda* L.) plantation to assess the effects of fertilization and vegetation control (a) on soil net nitrogen mineralization, (b) litter decomposition and (c) foliar nutrient concentrations and use, and vegetation growth. Fertilization (none, 224 kg ha^{-1} N plus 56 kg ha^{-1} P) and vegetation control (none, complete) treatments were applied in a 2x2 factorial design in March 1998. Soil net nitrogen mineralization was assessed by monthly field and laboratory incubations, litter decomposition and nutrient (N, P K, Ca, Mg, S, Mn, Zn, B, Cu) release dynamics were determined by the litterbag method, foliar nutrient use of pines and hardwoods was estimated from litterfall and foliar nutrient concentrations, and growth was determined based on annual measurements of diameter and height. Field net N mineralization rates were 19, 18, 31, and 78 kg ha^{-1} yr^{-1} for control (C, no treatment), fertilization (F), vegetation control (VC), and vegetation control plus fertilization (VC+F) treatments, respectively. Relative treatments responses were similar in the laboratory incubations. Litter mass loss during decomposition was reduced by 9% after 32 months by vegetation control, and fertilization had no effect. The mobility of the nutrients was as follows: Cu≤N≤S<P<Zn≤Ca<K≤Mn<Mg≤B. Pine foliar N and P concentrations, and N and P use were significantly increased by fertilization, while effects of vegetation control on these parameters were usually not significant. Fertilization significantly increased annual volume growth of loblolly pine by up to 7 m^3 ha^{-1} yr^{-1} (32%) over the three years, while vegetation control had no significant effect.

STAND AND SOIL RESPONSES OF A LOBLOLLY PINE PLANTATION TO MIDROTATION FERTILIZATION AND VEGETATION CONTROL

by

NEVZAT GURLEVIK

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APPROVED BY:

Udo Blum	Barry Goldfarb
Daniel L. Kelting	Chair of Advisory Committee H. Lee Allen

BIOGRAPHY

Nevzat Gurlevik was born in a small farming village of Eğerci, in Turkey. He spent most of his childhood years in his family farm helping his parents. During those years, he developed an endless love for nature, which he carried with him through his academic career. After completing primary and secondary school in his Turkish village, he moved to the city of Kayseri for high school. He attended college at the University of Istanbul in 1989. He completed his bachelor's degree in the department of Forestry in 1993. His experience in Istanbul showed him that hard work and dedication could take him anywhere in this world.

After earning a scholarship from the Turkish Ministry of National Education, he moved to the United States in 1995 to continue his education in Forestry. The first task to complete was the mastery of the English language. He attended language school for 6 months at Creighton University, Omaha, NE and then went to Clemson University, Clemson, SC to work with Dr. Ansel E. Miller towards his master's degree. Upon completing his research on loblolly pine growth survival responses to root dipping substances and getting his Master's degree, he moved to Raleigh, NC in 1997 to work towards his Ph.D. at North Carolina State University. There, he met with H. Lee Allen, director of the Forest Nutrition Cooperative, who introduced him the interesting field of intensive forestry and forest nutrition, and guided him through his research during the four years he spent at NCSU.

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I wish to give special thanks to my parents for their support and encouragement. I also want to thank my wife, Dilek, who believed in me and gave me hope during the endless hours of my research.

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CHAPTER 1

Understanding how soil N availability is affected by midrotation vegetation control and fertilization

ABSTRACT

GURLEVIK, NEVZAT. Understanding how soil N availability is affected by midrotation vegetation control and fertilization

Net N mineralization is considered to be an index of soil N availability and we still know little about how it is affected by silvicultural treatments in intensively managed forestlands. In this study, the effects of vegetation control and fertilization on net N mineralization were investigated in a 14-year-old loblolly pine (*Pinus taeda* L.) plantation located in the Piedmont of NC, USA. Treatments including two levels of vegetation control (none and complete) and two levels of fertilization (none and a one-time application of 224 kg ha^{-1} N and 56 kg ha^{-1} P) were applied in March 1998 in a factorial design. Net N mineralization was measured in the top 10 cm of the mineral soil both in the field between July 1998 and July 2000 and in the laboratory between June 1999 and July 2000. Soil temperature was elevated as a result of vegetation control, but soil moisture was not significantly altered by any treatment. Soil N pool (dominated by NH_4^+ with little NO_3^-) was significantly increased by fertilization, especially during the first growing season. Net field mineralization was not significantly affected by either vegetation control or fertilization; however, the combination of these two treatments resulted in a 4-fold increase compared to the control (no treatment). Net nitrification showed a large increase in the combination treatment, accounting for about 83% of the total mineralization. Laboratory estimates were 48 to 105% higher than those from the field, but treatment responses were very similar between the field and the laboratory. The similarity between field and laboratory results suggests that the combination treatment

(vegetation control + fertilization) had a major impact on soil substrate quality, which, in turn, affected mineralization. We hypothesize that the interaction between vegetation control and fertilization may have been caused by a reduction in new C input (through litterfall) after vegetation control and increased N in soil solution after fertilization.

INTRODUCTION

Vegetation control and fertilization have great potential to increase forest productivity by allocating existing resources to crop trees and by increasing the availability of existing resources (Allen et al. 1990, Binkley et al. 1995); however, their effects on soil nutrient availability are not certain. Both of these treatments can have a direct or indirect effect on net nitrogen mineralization as they usually affect the quality and quantity of soil organic matter and the physical soil environment.

Nitrogen becomes limiting as soil supply decreases and stand nutrient demand increases as the stand canopy closes (Wells and Jorgensen 1975, Allen et al. 1990), due to continuing immobilization in the forest floor and in vegetation (Miller et al. 1979, Richter et al. 2000). Mineralization of nitrogen along with internal cycling is thought to be an important factor in supplying plants with nitrogen at these later stages of stand development.

Fertilization typically increases the concentration of N in the forest floor and the mineral soil and has the potential to increase net mineralization (Maimone et al. 1991, Polglase et al. 1992, Carlyle 1995, Hart and Stark 1997). Carlyle (1995) reports that fertilization with 200 kg ha^{-1} N increased N mineralization from 77 kg ha^{-1} N to 155 kg ha^{-1} over two years. Fertilization can also have a long-term effect on site nitrogen mineralization. In *Pinus radiata* stands of Australia, increased N mineralization levels were still evident 4

years after fertilization, although soil mineral-N concentrations were elevated for only about a year (Raison et al. 1992). This continued higher rate of N mineralization was attributed to re-mineralization of immobilized fertilizer N and decomposition of fine roots having higher N content. However, in a similar work by Goncalves and Carlyle (1994), N addition had no lasting effect on N mineralization 5 to 6 years after the treatment. Although ammonium usually dominates soil N pools, net nitrification can increase after fertilization (Raison et al. 1992, Hart and Stark 1997), and this increase seems to be a linear function of the quantity of net mineralization (Goncalves and Carlyle 1994).

Vegetation control may significantly change the soil environment and plant community composition, which, in turn, may alter soil nutrient supply. Decreased canopy cover after vegetation control lets more sunlight reach the forest floor, which may increase temperatures in the forest floor and mineral soil. Effects on soil moisture are less clear; although moisture content may also increase due to decreased precipitation interception and evapotranspiration after the reduction in canopy cover. While temperature controls microbial and enzymatic activities, moisture controls movement of substrate via mass flow or diffusion (Powers 1990, Goncalves and Carlyle 1994, Sierra 1997, Zak et. al 1999), therefore increased temperature and moisture content may result in faster mineralization. Based on laboratory studies, soil net N mineralization seems to be at its maximum when soil moisture content is near field capacity and soil temperature is around 25^{o}C (Goncalves and Carlyle 1994).

Along with these changes in the physical environment, eliminating nutrient-rich hardwoods and herbaceous plants from the stand composition could also affect the chemistry of soil organic matter. Substrate quality, described as soil carbon and nitrogen concentrations, C/N ratio (Powers 1990, Bauhus and Khanna 1999, Piatek and Allen 1999) and lignin:N ratio (Scott and Binkley 1997) plays an important role in organic matter decomposition and mineralization of nitrogen. As long as there is a sufficient amount of organic C in the soil as an energy source for microbes, mineralized N will mostly be used within the microbial population, and net mineralization will occur only when the C/N ratio falls below 20-25 (Morris and Campbell 1991). Wood et al. (1992) reports that loblolly pine stands receiving hardwood and herbaceous control had lower soil substrate quality (i.e. organic N concentration), which resulted in reduced net N mineralization. Polglase et al. (1992) suggested that residues of understory vegetation could be a better supply for available N; however, they also reported an increase in N and P mineralization after sustained weed control and complete fertilization.

This research study was initiated by the NC State Forest Nutrition Cooperative to understand how soil N dynamics are affected by fertilization and vegetation control in a midrotation loblolly pine stand. Specific objectives of this study were (a) to assess the effects of these treatments on soil temperature and moisture, (b) to determine net N mineralization under field and laboratory conditions, (c) to examine the effects of substrate quality by comparing field and laboratory results.

METHODS

Site Description

The study site was located at in the Piedmont physiographic province of Durham County, North Carolina (36°13'N, 78°52'W). Thirty-year (1961-1990) mean annual temperature is 14.5°C, with monthly mean temperatures ranging from 3°C in January to 25°C in July. Mean annual precipitation is 1166 mm, with a fairly uniform seasonal pattern (State Climate Office of North Carolina, North Carolina State Univ, Raleigh, NC). The soils are highly weathered well-drained Georgeville and Cecil soil series of thermic, kaolinitic, Typic Kanhapludults. A-horizon depth was reduced to about 10 cm due to soil erosion during past agricultural practices, and had clay loam to sandy clay loam texture.

The pretreatment stand was a 14-year-old second rotation loblolly pine (*Pinus teada* L.) plantation with a site index (25 year) of 22 m. The site was chopped and burned during the site preparation, and no other silvicultural treatments had been applied. Prior to treatment, the stand had 971 pines ha^{-1} with a basal area of 24 m^2 ha^{-1}. Competing vegetation mainly consisted of Virginia pine (*Pinus virginiana* Mill.) (1.2 m^2 ha^{-1}) and several hardwood species, including sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), southern red oak (*Quercus falcata* Michx.), white oak (*Quercus alba* L.) and black cherry (*Prunus serotina* J.F. Ehrh.), with a combined basal area of about 9 m^2 ha^{-1}.

Experimental Design and Treatments

The experimental design was a 2x2 factorial with 3 replications. A total of twelve 0.16 ha treatment plots were established in winter of 1997-1998. Measurement plots of 0.04 ha, centered within the treatment plots, were used for further sampling. Plots having similar pretreatment stand vegetation characteristics (height, basal area, stand density) were assigned to a single block to minimize within-block variation. Treatments included two levels of vegetation control (none and complete vegetation control) and two levels of fertilization (none and a fertilizer application of 224 kg ha^{-1} N as urea plus 56 kg ha^{-1} P as TSP). Complete vegetation control was performed in March 1998 by chainsaws, eliminating all hardwoods and naturally regenerated Virginia pines. Cut-stumps were then sprayed with a 50% solution of Garlon 3A (triclopyr amine) to prevent sprouting. Slash was left on the ground to decay. Roundup (glyphosate) was applied as needed at recommended rates to eliminate any resprouting or growth of herbaceous plants throughout the study period. Fertilizer application was performed by hand in March 1998, immediately after vegetation control was completed. Hereafter, no-vegetation control + no-fertilization treatment will be called the "control" treatment (C), complete vegetation control + no-fertilization will be "vegetation control" (VC), no-vegetation control + fertilization will be "fertilization" (F), and complete vegetation control + fertilization will be "combination" (VC+F).

Field Mineralization

A sequential *in situ* incubation method described by Raison et al. (1987) was used to determine field net N mineralization. Soil samples were collected monthly at 5 stratified random locations in each plot starting from July 1998 (four months after treatments were applied) until July 2000 for a total of 25 months. The July 1998 incubation lasted for about 2 months, therefore, there was a total of 24 collection dates. Each month, five pre-incubation soil samples (0 to 10 cm depth) were collected from each plot with 3.8 cm (inside diameter) PVC tubes, then were composited by plot. Five more tubes were driven into the soil, then capped to prevent leaching and the soil in the tubes was left intact for field incubation. During this soil sampling process, a temperature probe was inserted to 10 cm depth at five locations in each plot to measure soil temperature. These five readings were averaged to calculate mean soil temperature for each plot at each sampling date. After an incubation period of one month (except for July 1998), incubated samples were collected and also composited by plot. Composite pre-incubation and post-incubation samples were taken to the laboratory and kept cool until extraction. Soil moisture content was measured gravimetrically for each collection date using 10-g subsamples dried at 105^{o}C for 24 hours, and converted to volumetric moisture content by multiplying with a bulk density of 1.2 g cm^{-3}, a value that has been found in nearby sites (Gent et al. 1984).

Laboratory Mineralization

Starting in June 1999 (fifteen months after treatments were applied), an aerobic laboratory incubation was also conducted for a total of 14 months. The same pre-incubation composite soil samples, described above, were used for the laboratory incubation. Duplicate 10-g soil samples were weighed into 50 ml centrifuge tubes, and placed in an incubator set at 28 ^{o}C. Moisture contents of these samples were not statistically different by treatments at the time of incubation for most sampling dates (significantly different only on one date), so they were left at field moisture. Two 500 ml beakers filled with deionized water were also placed in the incubator to prevent soil samples from drying during the incubation. Samples were removed from the incubator for analysis at the same day that field-incubated samples were collected.

Laboratory Analysis

Duplicate 10-g subsamples were extracted in 35 ml of 2M KCl. The soil-KCl suspension was shaken for one hour and then centrifuged for 15 minutes. The supernatant was filtered and kept frozen if not analyzed immediately. Extracts were analyzed colorimetrically for NH_4^+ and NO_3^- using a Lachat autoanalyzer (QuikChem 8000, Zellweger Analytics, Inc., Milwaukee, WI). KCl extractable N was calculated as the sum of ammonium-N (NH_4^+-N) and nitrate-N (NO_3^--N) from pre-incubation samples. Monthly field net N mineralization was calculated by subtracting pre-incubation soil N (NH_4^+-N plus NO_3^--N) from field post-incubation soil N. Similarly, laboratory net mineralization was calculated by subtracting pre-incubation soil N from laboratory post-

incubation soil N. Monthly net mineralization values were then added to calculate total net mineralization for field and laboratory studies. Finally, concentration values were converted to a per hectare basis. Hereafter, NH_4^+-N and NO_3^--N will be called as simply NH_4^+ and NO_3^-.

Soil samples from three different collection dates (11-15 months after treatments) were composited and mixed well to determine total soil C and N for each plot. Mixed soil samples were air-dried for several days and passed through 2 mm screen to separate fine- and coarse-fractions. Fine soil fractions (< 2 mm) were then passed through a 60-mesh screen to further improve the uniformity of the samples. Subsamples of 1 mg were taken from these 60-mesh samples and analyzed for C and N using a CHN elemental analyzer (CE Instruments - NC 2100, CE Elantech Inc., Lakewood, NJ).

Statistical Analysis

All statistical analysis was performed using SAS statistical software (version 8, SAS Institute, Cary, NC). Analyses of variance were conducted using the mixed model procedure to test the effects of treatments, sampling dates and their interactions on monthly estimates of extractable soil N, and field and laboratory mineralization. In addition, annual field and laboratory mineralization, and mean soil temperature, moisture, C and N contents were calculated and analyzed by analyses of variance. Relationships between field and laboratory estimates of net mineralization and nitrification from the same period were examined by linear regression analysis. Slopes of the regression lines

were also compared among treatments to determine if individual treatment responses in the field were similar to those in the laboratory.

Significance was accepted at $p \leq 0.10$ for all analysis, since the soil parameters were expected to be highly variable (Mudano 1986, Adams et al. 1989).

RESULTS

Field Results

Soil Environment

Monthly soil temperatures ranged from 6.6^{o}C in winter to 21.5^{o}C in summer (figure 1a) with an overall mean of about 13.2^{o}C (table 1). Fertilization had no effect, however, the mean soil temperatures was increased by about 1.2^{o}C by vegetation control. VC and VC+F plots warmed up faster in spring, and had 1.8^{o}C higher temperatures during the summer months (June-September). All treatments converged by November and had relatively similar temperatures during the winter months.

Monthly soil moisture contents were within the available water range for clay loam soils, and ranged from 14% in summer to 40% in winter and spring months (figure 1b) with an overall mean of about 28 percent (table 1). Neither F nor VC treatments had significant effects on mean soil moisture content. The lack of treatment differences were partly due

to the fact that two hurricanes hit the study area in September 1999, and resulted in approximately 42 cm of rainfall, which may have overwhelmed any treatment effects.

On average, soils contained about 29.3 Mg ha^{-1} C and 1.5 Mg ha^{-1} N, resulting in a C/N ratio of approximately 20 (table 1). Although fertilized soils had 182 kg ha^{-1} more N and smaller C/N ratios, the differences were not statistically significant.

Extractable N

During the study period of 25 months, extractable N (NH_4^+ plus NO_3^-) pools ranged from 1.2 to 2.2 kg ha^{-1} in the C, 2.6 to 11.0 kg ha^{-1} in the F treatment, 1.3 to 4.4 kg ha^{-1} in the VC treatment, and 4.2 to 18.4 kg ha^{-1} in the VC+F treatment (figure 2a). Extractable soil N pool was significantly affected by both treatments and their interaction (table 2). Fertilization resulted in a large increase in soil N pools, which was 5 to 9 fold greater than that in the C four months after treatments, and declined thereafter. N pools in the F treatment converged with the C and VC treatments over time; however, the VC+F treatment sustained high levels of N throughout the study period.

Similar treatment and date effects were observed when soil the N pool was partitioned into NH_4^+ and NO_3^- pools, except that the increase in the pool sizes due to fertilization was more dramatic for nitrate (27 to 41 fold) than ammonium (3 to 6 fold) (table 2, figures 2b, 2c). NH_4^+ was the larger component of the extractable soil N pool for all treatments. The C and VC treatments had very low levels of NO_3^- throughout the study

period (9 and 6% of total N, respectively). However, the soil NO_3^- pool accounted for 43 and 41% of total extractable N in the F and VC+F treatments, respectively, during the first growing season, and about 5 and 15% of total N during the rest of the study.

Field Mineralization

Monthly net N (NH_4^+ plus NO_3^-) mineralization ranged from –5.0 (net immobilization) to 13.5 kg ha^{-1} across all treatments (figure 3a). Overall, monthly net mineralizations were higher in summer months than winter months for all treatments. Both VC and F, and their interaction significantly affected net mineralization (table 3). During the study period, mean annual mineralization estimates were 19, 18, 31 and 78 kg ha^{-1} N on the C, F, VC and VC+F treatment, respectively (table 4). There was no significant difference between C, VC and F treatment; however, annual net mineralization in VC+F treatment was significantly higher than the other treatments.

When net mineralization was partitioned into NH_4^+ and NO_3^-, treatment effects were more pronounced for NO_3^- than NH_4^+ (table 3). While there were no clear treatment effects on ammonification, nitrification was clearly increased by the VC+F treatments (figure 3b, 3c). Ammonification accounted for 87 to 100% of the net mineralization in C, F and VC treatments, where net nitrification was negligible. However, net nitrification was significantly increased in the VC+F treatment, accounting for about 83% of net mineralization. Net nitrification was especially high where soil C/N ratios were as low as 16, above which net nitrification was small (figure 4).

Laboratory Mineralization

Monthly net mineralization (NH_4^+ plus NO_3^-) ranged from -1 to 28 kg ha^{-1} across all treatments throughout the study period of 14 months (figure 5). Mineralization was very small in soils collected in winter months for the C, F and VC treatments and higher in those collected in the summer, as indicated by date and treatment*date interactions (table 5). The VC+F treatment, too, showed similar seasonal trend; however, monthly mineralization was always higher than 6 kg ha^{-1}. Mean annual net mineralization rates were 35, 41, 54 and 187 kg ha^{-1} in C, VC, F and VC+F treatments, respectively, where VC+F treatment was significantly greater than all the others (table 6).

Treatments effects were somewhat less pronounced for ammonification than nitrification. Ammonification accounted for 76 to 99% of the net mineralization for the C, F, and VC treatments. However, in VC+F treatment, ammonium was immediately oxidized to nitrate, which accounted for more than 100% of the net mineralization.

Field-Laboratory Comparison

Field and laboratory estimates exhibited the same seasonal trend (figure 3 and 5), with summer months having greater mineralization. In addition, only the VC+F treatment resulted in significantly greater mineralization compared to the C under both conditions (4.1 fold increase in the field, 5.3 fold increase in the lab). Finally, under both sets of conditions, net ammonification accounted for almost all of the total net mineralization in

the C, VC and F treatments, whereas net nitrification accounted for most of the net mineralization in the VC+F treatment.

Not surprisingly, the magnitude of mineralization was greater in the laboratory for all treatments (table 7). For the same period between June 1999 and July 2000, laboratory estimates were 48, 76, 56, and 105 % larger than those obtained in the field for C, F, VC and VC+F treatments, respectively. It appeared that the F and especially the VC+F treatments performed better under laboratory conditions; however, we found no significant difference between slopes of the individual treatments when field data was regressed on laboratory data ($p=0.407$, figure 6).

DISCUSSION

Extractable N

As expected, application of N and P fertilizer increased extractable N in the top 10 cm of the soil, especially during the first growing season (figure 2). Throughout the study period of 25 months, the combination treatment (VC+F) resulted in about a 4-fold increase in extractable N levels, while individual effects of fertilization and vegetation control were about 2-fold and 1.4-fold, respectively, compared to the control. Similar increases in soil N pools in response to fertilization are common and increases usually last less than a year (Raison et al. 1992, Carlyle 1995, Hart and Stark 1997, Mewborn

1997). The magnitude and duration of increases also depend on the dose of N application, with both increasing with higher doses (Mudano 1986). In this study, elevated soil N pools lasted for about 9 months in the fertilization-only treatment; however, the effect of fertilization was still evident at the end of the study on plots that had also received vegetation control. This long lasting increase in available soil N is probably a result of reduced uptake by competing vegetation, mainly hardwoods and herbaceous vegetation, which have relatively high use of soil nutrients. Soil extractable N was well correlated with foliar N concentration for the first year after fertilization, and resulted in up to 32% pine volume response over three years (chapter 3).

In undisturbed forest soils, nitrate pools are generally very small; however, they are usually elevated after disturbance (Vitousek and Matson 1985, Raison et al. 1992, Carlyle 1995, Hart and Stark 1997). In this study, the soil nitrate pool was very small in control and vegetation control treatments (<10% of total extractable pool), and it was larger in fertilized soils, especially in the first growing season (about 40% of total, figure 2). Low nitrate pools may be due to low nitrifier populations, low nitrification rates and the mobile nature of nitrate, which may lead to losses through leaching, or immobilization of nitrified N (Mudano 1986, Hart and Stark 1997). The net balance between production and consumption regulates soil N pools, and the pool would be very small where consumption equals or exceeds production. Typically, microbial populations have a preference for NH_4^+, and under high and steady levels of C input, most of the ammonium would be immobilized and little nitrate produced (Davidson et al. 1992, Hart

et al. 1994). In addition, Davidson et al. (1992) reported that nitrate consumption to production ratio was often greater than 1 in a mature coniferous forest; therefore, the reports of small soil nitrate pools are not surprising.

Field Mineralization

In situ incubations revealed that field net N mineralization rates were similar in control and fertilization treatments, resulting in annual estimates of about 19 and 18 kg ha^{-1} net mineralization, respectively (table 4). Similar rates of mineralization were also reported in another 15-year-old loblolly pine stand (Piatek and Allen 1999), where annual rates of mineralization ranged from 19 to 34 kg ha^{-1} for several combinations of chop, burn, disk and herbicide treatments. These estimates of mineralization are far below expected annual uptake. Wells and Jorgenson (1975) reported that a 16-year-old loblolly pine plantation required up to 117 kg ha^{-1} N annually for development of needles, stems and roots. Similarly, Ducey and Allen (2001) estimated uptake rates of 10 to 14 year-old loblolly pine plantations using the NUTREM model, and reported that the plantations required 45 to 101 kg ha^{-1} of N annually. In our study, annual mineralization in the top 10 cm of mineral soil was just about equal to the amount of N transferred to forest floor through litterfall (chapter 3). Therefore, the remaining required N is likely to be supplied from lower soil horizons, release from the forest floor and atmospheric input. However, mineral soil should be the main source of N at midrotation since we found very small, if any, net release of N from decomposing needle litter in the forest floor at this site (chapter 2).

Nitrogen additions through fertilization can increase net N mineralization (Carlyle 1995, Hart and Stark 1997). However, at this site, N and P additions alone did not increase net mineralization. In fact, there was net immobilization of added N at four dates in the control treatment and at seven dates in the fertilization treatments, more commonly in the first year (figure 3). Similar immobilization patterns were also observed by others (Vitousek and Matson 1985, Mudano 1986, Raison et al. 1992). Vitousek and Matson (1985) reported that more than 90% of the applied ^{15}N was quickly immobilized by microbial population in a harvested loblolly pine stand. Similarly, Raison et al. (1992) reported a substantial immobilization of N for the initial 8 months after fertilization (37% of the 400 kg ha^{-1} added N) in *Pinus radiata* stands of Australia. They have also speculated that the large amount of fertilizer added might have dissolved some of the soil C, which may be utilized for microbial immobilization. After the initial immobilization, net mineralization in fertilized soils were 2 to 3 fold greater than non-fertilized soils in that study. However, in this study, mineralizations in fertilized soils were still very similar to those in the control treatment at the end of study.

Immobilization of N in forest soils may be attributed to accumulation forest floor and relatively high C content of top horizons of mineral soil. During the development of a forest stand, soil minerals are depleted due to plant uptake, and increasingly greater amounts of organic matter and mineral nutrients are accumulated in forest floor (Wells and Jorgenson 1975, Richter et al. 2000). This process results in a gradual decrease in soil

N supply and an increasing soil C/N ratio, suggesting a high potential for net N immobilization. The significance of microbial immobilization in C-rich forest soils has been demonstrated by several researchers (Vitousek and Matson 1984, Vitousek and Matson 1985, Raison et al. 1992, Hart et al. 1994, Bauhus and Khanna 1999,). Bauhus and Khanna (1999) reported that about 800 kg ha^{-1} C, 150 kg ha^{-1} N and 45 kg ha^{-1} P can be utilized by microbial populations found in the forest floor and top horizons of the mineral soil in an "average" forest ecosystem. Perhaps this continuous accumulation of organic matter (C) may explain why net N mineralization is lower in established stands (Piatek and Allen 1999)

Additions of P, along with N, may have also played a role in N mineralization in fertilized plots. Piatek and Allen (1999) reported a negative correlation between soil P and field net N mineralization in another midrotation loblolly pine plantation in the Piedmont of NC. In addition, Aggangan et al. (1998) showed that P application either reduced or had no effect on N mineralization potential and cumulative N mineralization in a laboratory incubation study of soils from eucalyptus plantations in Australia. The effect of P additions on net N mineralization is not clear, however, as Qualls (2000) suggested, both dissolved organic matter (i.e. humic and fulvic acids) and soil P ($H_2PO_4^-$) are negatively charged, and compete for the same exchange sites on Fe and Al oxyhydroxides in the soil. Although the dynamics of this relationship are not clear, the amounts of organic acids, which are slowly decomposable, can interact with added P and result in slower rates of net N mineralization.

Vegetation control alone provided some increase in net mineralization (31 kg ha^{-1} yr^{-1}, table 4), but the increase was significant only on one date (data not shown). However, when vegetation control and fertilization were applied together, they resulted in a much greater than additive increase in net mineralization (78 kg ha^{-1} yr^{-1}, 83% nitrate). Apparently, there was a strong interaction between the two treatments and the interaction was likely caused by the vegetation control effect on soil C and the fertilization effect on soil N pools. Vegetation control can substantially reduce above and belowground carbon input into the soil environment via litterfall, fine root turnover and root exudates, and, in turn, reduce the N demand of soil microbial biomass. Although we have not quantified belowground litter input at this site, aboveground input was reduced from about 4800 in control plots to 3300 kg ha^{-1} yr^{-1} (31% reduction) after eliminating competing vegetation from the stand (chapter 3). Assuming a C/N ratio of 8, a C-use efficiency of 50% for microbial biomass (Paul and Clark 1989) and a C concentration of 50% for litterfall, we can roughly estimate that about 47 kg ha^{-1} yr^{-1} less N can be immobilized by microbial biomass after vegetation control. Vitousek and Matson (1985) showed that microbial immobilization of applied ^{15}N was reduced from 90 to 70% when harvest residues were removed and regrowth was suppressed by herbicide in a harvested loblolly pine stand. Application of N fertilizer can further increase soil N pool and reduce the C/N ratio of the soil substrate, resulting in an increased rate of net N mineralization. In fact, two of the VC+F plots which showed the greatest net mineralization and nitrification also had the lowest post-treatment C/N ratios of about 16. While C and N content of the bulk

soil did not differ significantly due to the treatments, changes in these parameters in soil solution and in microsites, where microbial populations are most concentrated and active, may have played a more important role in net mineralization.

Monthly mineralization in the field was generally higher in warm summer months than cool winter months for all treatments (figures 1 and 3), suggesting increased temperatures may have stimulated mineralization in the summer. Strong relationship between temperature and net N mineralization was shown by Goncalves and Carlyle (1994) and Sierra (1997) under laboratory conditions. However, in this study, temperature could account for only 1 to 10% of the variation in monthly mineralization depending on the treatment (data not shown). Furthermore, comparison of the field and laboratory (constant temperature) results (figures 2 and 3) showed not only similar treatment responses (i.e. ranking) but also similar seasonal dynamics in mineralization, suggesting that the relationship between temperature and net N mineralization under field conditions can be confounded by other factors, such as seasonal dynamics of substrate quality.

There can be a major input of dissolved organic carbon (DOC) into mineral soil, and its seasonal dynamics may also affect the rate of mineralization. Almost the entire DOC reaching the mineral soil originates from the fresh litter in the upper forest floor, and it is mainly in the form of humic substances and hydrophobic acids, which are resistant to decomposition (Qualls et al. 1991)). Annual forest floor DOC inputs of 155 kg ha^{-1} were reported by Michalzik and Matzner (1999) for a Norway spruce stand, 317 kg ha^{-1} were

reported by Markawitz et al. (1998) for a loblolly pine stand, and 470 kg ha^{-1} was reported by Qualls et al. (2000) for a hardwood stand. Seasonal dynamics and quality of this input can be greatly influenced by the seasonal litterfall patterns. Qualls et al. (1991) reported that 27% of the C in the freshly fallen hardwood litter is soluble in water, and that this solution is relatively poor in N. In fact, higher DOC/DON (dissolved organic nitrogen) ratios of the forest floor solution were measured 1-3 months after litterfall in the same study. Similarly, Currie et al. (1996) reported that DOC input into mineral soil was highest in the period between July and November both in hardwood and red pine (*Pinus resinosa*) stands, and this is the same period where we found a decline in mineralization rates. Therefore, it can be expected that lower rates of mineralization should occur during and for several months following litterfall.

It is also interesting that labile carbohydrate concentrations in forest vegetation are highest in autumn and winter, and they are lowered by growth in spring and summer (Sampson et al. 2001 and Oleksyn et al. 2000). Some of these labile carbohydrates, along with other metabolites, can be lost through leaching and exudation from above- and belowground plant parts (Tukey 1966, Kozlowski and Pallardy 1997). High stored carbohydrate may mean higher leaching and exudation losses. Therefore, higher C inputs in the fall and winter seasons can result in lower N mineralization. However, there is lack of information on the seasonality of this input, and seasonal dynamics of DOC input may not always be in relation to the amount of labile carbohydrate stored in growing vegetation. Since plants carry a greater amount of leaves during the growing season, there

may actually be a greater chance for leaching of C in summer than in dormant season (Qualls et al. 2000).

Although net nitrification is very low and nitrate rarely accumulates in forest soil, silvicultural treatments, such as harvesting, site preparation and fertilization, have been shown to increase net nitrification (Vitousek and Matson 1995, Hart and Stark 1997). In our study, soil nitrate pools were elevated by fertilization and combination (VC+F) treatments, especially during the first year. However, net nitrification was increased substantially only by the combination treatment, with nitrate accounting for about 83% of the annual net N mineralization. Higher rates of net nitrification may be due to the immobilizing effects of soil C. As suggested by Hart et al. (1994), there may be a critical NH_4^+ pool size for substantial net nitrification to occur, and this pool size is controlled largely by C availability. Under reduced C availability, heterotrophic microbial demand for N would be reduced and more NH_4^+ would become available for autotrophic nitrifiers (Davidson et al. 1992, Hart et al. 1994). Therefore, at this site, reduction of carbon input into soil due to vegetation control and increased available soil N (mainly NH_4^+) due to fertilization may have resulted in greater net nitrification. This assumption about soil C is also supported by Vitousek and Matson (1985) who reported that physical removal of surface organic matter and competition control with herbicide application during site preparation led to reduced immobilization of N and more nitrification in a loblolly pine plantation. In addition, an increase in nitrifier populations or reduced microbial

assimilation of NO_3^- in the presence of high NH_4^+ pools may also result in higher net nitrification (Hart and Stark 1997).

Comparing field and laboratory results

Higher rates of mineralization were expected for all treatments in the laboratory, because temperature during laboratory incubation was about 15^oC higher than mean soil temperature in the field (Goncalves and Carlyle 1994). It was also interesting that treatments ranked similarly both in the field and in the laboratory, and the vegetation control and fertilization interaction was significant for both studies. These similarities resulted in somewhat linear relationship between field and laboratory estimates of net mineralization and nitrification (figure 6). The goodness of the fit was improved to R^2 value of 0.90 and 0.94 for net mineralization and nitrification, respectively, when annual values for each plot were used, instead of monthly values. Carlyle et al. (1998) also reported a strong correlation between field and laboratory net mineralization (R^2=0.89), when they used annual site estimates, and suggested that field mineralization rates can be estimated from laboratory studies once the relationship between the two is established.

In addition to treatment rankings, seasonal dynamics of mineralization were also similar under both conditions, that is greater mineralization rates were observed in soils collected in summer months. Since all soils were exposed to same environmental conditions in the laboratory, the observed differences among treatments and seasons should be due to substrate quality These results also support the hypothesis provided above that changes in

substrate quality (i.e. pool of DOC) due to treatments and due to seasonal variations may be as important as environmental factors such as temperature and moisture in determining net mineralization.

CONCLUSIONS

1. Individually, vegetation control and fertilization resulted in either no change or a slight increase in mineralization compared to the control; however, their combination increased field net N mineralization by a factor of 4.
2. Net nitrification was also significantly elevated by this interaction. We hypothesized that the interaction was mainly caused by combined effects of the reduction in new C input into the soil due to vegetation control and an increase in soil N pool (mainly NH_4^+) due to fertilization.
3. Although the magnitude of the mineralization was much greater in the laboratory than in the field, ranking and seasonal dynamics of the treatments were similar under both conditions.
4. Along with temperature, seasonal changes in DOC input into the mineral soil may have played a significant role in net N mineralization.
5. Linear relationship between laboratory and field net N mineralization (at least for annual plot estimates) suggested that aerobic laboratory incubation may be used to predict field mineralization and relative treatment responses.

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Table 1. Post-treatment mean soil temperature, moisture content, N and C contents by in a midrotation loblolly pine plantation.

Treatment	Temperature (^oC)	Moisture ($cm^3\ cm^{-3}$)	C ($Mg\ ha^{-1}$)	N ($Mg\ ha^{-1}$)
C	12.7	27.7	29.5	1.42
F	12.5	26.7	29.7	1.56
VC	13.9	27.8	29.4	1.39
VC+F	13.7	29.9	28.8	1.61
Root MSE	0.27	2.51	3.65	0.29

Table 2. Result of analysis of variance for monthly KCl-extractable soil N data collected between July 1998 and July 2000.

Effect	Df	p-values		
		$NH_4^+ + NO_3^-$	NH_4^+	NO_3^-
Replication	2	0.769	0.516	0.1200
VC	1	**0.018**	**0.060**	**0.045**
F	1	**0.001**	**0.009**	**0.002**
VC*F	1	**0.098**	0.298	**0.043**
Date	23	**<.001**	**<.001**	**0.001**
VC*Date	23	0.792	0.202	1.000
F*Date	23	**<.001**	**<.001**	**<.001**
VC*F*Date	23	0.921	0.364	1.000

Table 3. Result of analysis of variance for monthly field net N mineralization data collected between July 1998 and July 2000.

Effect	Df	p-values		
		$NH_4^+ + NO_3^-$	NH_4^+	NO_3^-
Replication	2	0.368	0.749	0.374
VC	1	**0.021**	0.427	**0.051**
F	1	**0.097**	0.116	**0.044**
VC*F	1	**0.083**	0.289	**0.056**
Date	23	**<.001**	**<.001**	**0.073**
VC*Date	23	0.403	0.734	0.180
F*Date	23	0.297	**0.061**	**0.071**
VC*F*Date	23	0.731	0.198	0.166

Table 4. Field estimates of net N mineralization, ammonification and nitrification in a midrotation loblolly pine plantation.

Treatment	Net Mineralization (kg ha^{-1} yr^{-1})		
	$NH_4^+ + NO_3^-$	NH_4^+	NO_3^-
C	19.1	19.1	0
F	17.8	15.4	2.4
VC	31.1	30.2	0.9
VC+F	78.3	13.7	64.6
Root MSE	20.2	9.5	22.5

Table 5. Result of analysis of variance for monthly laboratory net N mineralization data collected between June 1999 and July 2000.

Effect	Df	p-values		
		$NH_4^+ + NO_3^-$	NH_4^+	NO_3^-
Replication	2	0.706	**0.042**	0.428
VC	1	**0.028**	0.101	**0.023**
F	1	**0.054**	**0.002**	**0.018**
VC*F	1	**0.070**	**0.003**	**0.026**
Date	13	**<.001**	**<.001**	**0.001**
VC*Date	13	**0.031**	0.445	**0.001**
F*Date	13	**0.013**	**0.003**	**0.001**
VC*F*Date	13	**0.016**	0.476	**0.001**

Table 6. Laboratory estimates of annual net N mineralization, ammonification and nitrification in a midrotation loblolly pine plantation.

Treatment	Net Mineralization (kg ha^{-1} yr^{-1})		
	$NH_4^+ + NO_3^-$	NH_4^+	NO_3^-
C	35.2	34.7	0.6
F	40.6	30.8	9.8
VC	54.3	50.1	4.2
VC+F	186.5	-6.3	192.8
Root MSE	49.7	9.5	53.0

Table 7. Comparing field and laboratory mineralization estimates (kg ha^{-1} yr^{-1}) obtained from the same period.

Treatment	$NH_4^+ + NO_3^-$		NH_4^+		NO_3^-	
	Field	Lab	Field	Lab	Field	Lab
C	23.9	35.2	23.9	34.7	0	0.6
F	23.1	40.6	20.3	30.8	2.8	9.8
VC	34.8	54.3	34.1	50.1	0.6	4.2
VC+F	90.8	186.5	16.0	-6.3	74.8	192.8

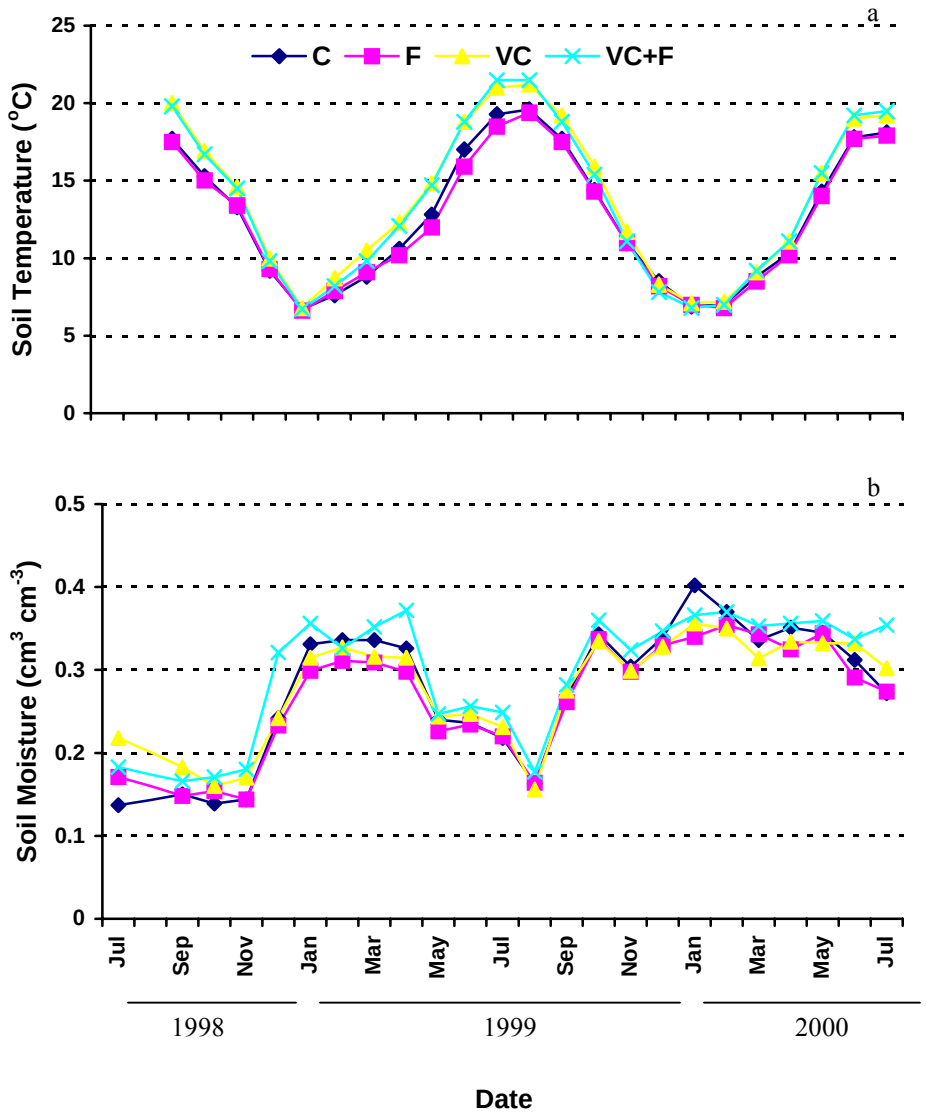

Figure 1. Monthly soil temperatures (a) and moisture contents (b) in a midrotation loblolly pine plantation (measurements were taken at 0-10 cm depth).

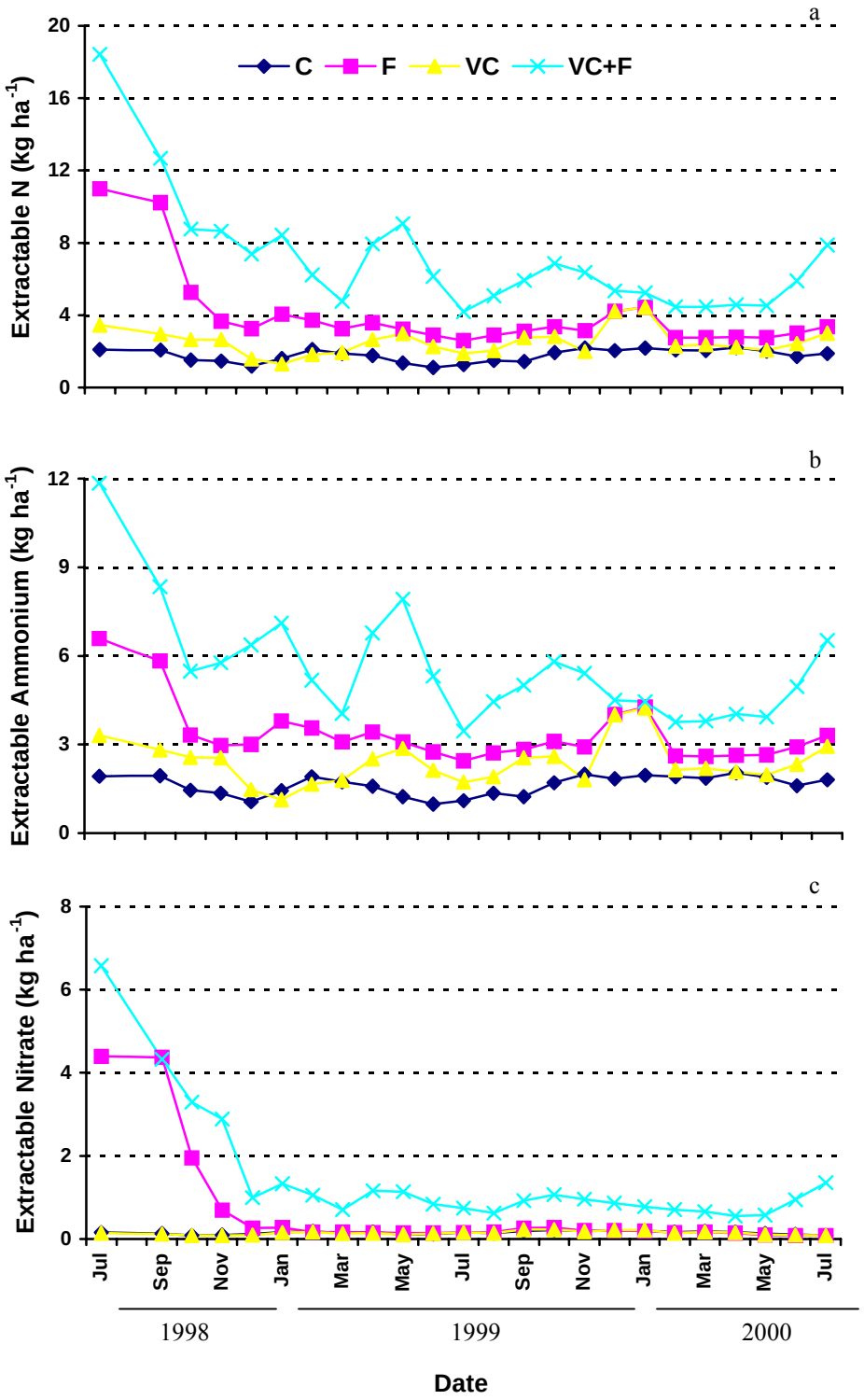

Figure 2. Monthly extractable soil N (NH_4^+ plus NO_3^-), ammonium-N and nitrate-N pools (treatments were applied in March 1998).

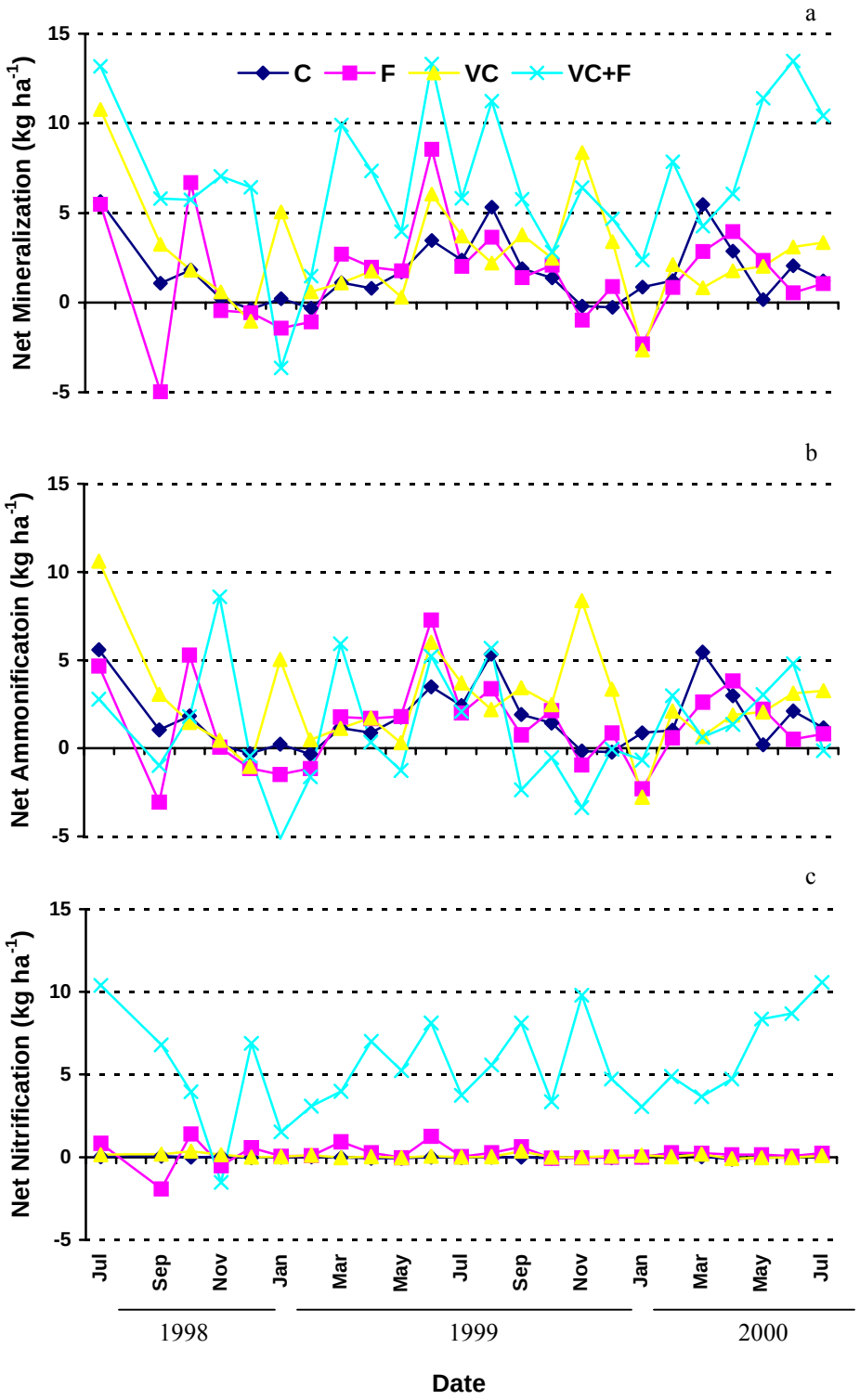

Figure 3. Monthly field estimates of net N mineralization ($NH_4^+ + NO_3^-$), ammonification and nitrification for in a midrotation loblolly pine plantation (treatments were applied in March 1998).

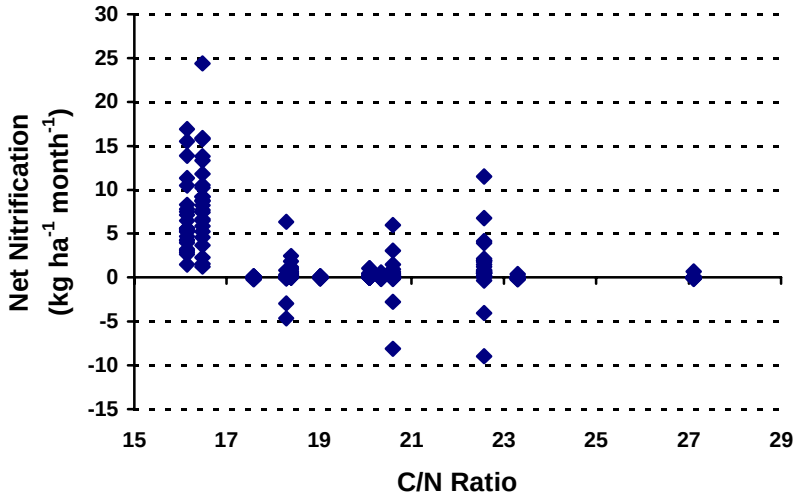

Figure 4. Relationship between net nitrification and soil substrate C/N ratio in a midrotation loblolly pine plantation.

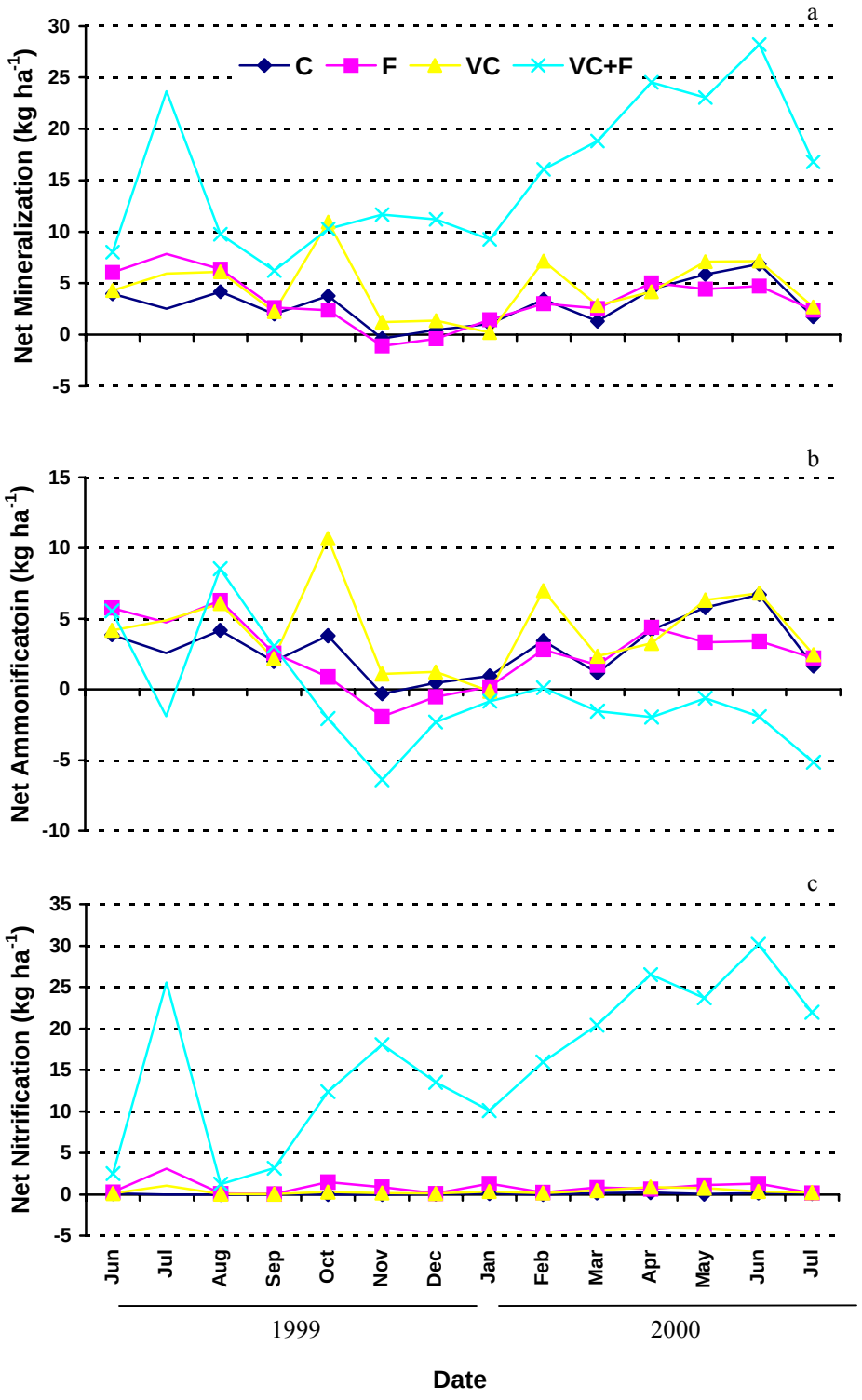

Figure 5. Monthly laboratory estimates of net N mineralization ($NH_4^+ + NO_3^-$), ammonification and nitrification in a midrotation loblolly pine plantation (treatments were applied in March 1998).

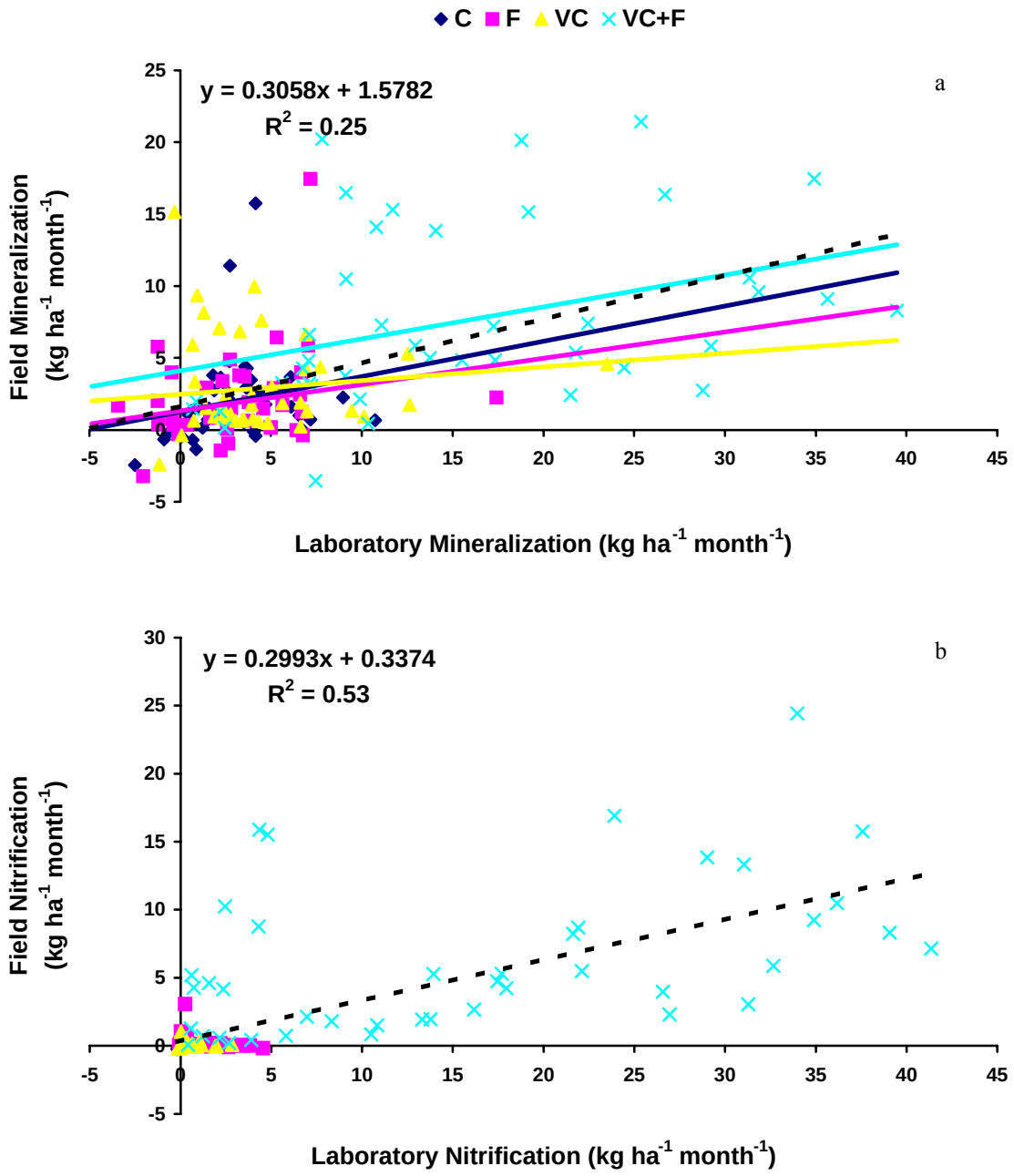

Figure 6. Relationship between field and laboratory net N mineralization (a) and nitrification (b) in a midrotation loblolly pine plantation (each point represents a monthly estimate, solid trendlines represent individual treatments, dotted trendlines and equations represent data from all treatments).

CHAPTER 2

Needle decomposition and nutrient release dynamics in a loblolly pine plantation as affected by vegetation control and fertilization

ABSTRACT

GURLEVIK, NEVZAT. Needle decomposition and nutrient release dynamics in a loblolly pine plantation as affected by vegetation control and fertilization.

This study examined the effects of vegetation control and N+P fertilization on decomposition and nutrient release dynamics of needle litter in midrotation loblolly pine (*Pinus taeda* L.) stands. A standard needle litter placed in litterbags was left to decompose on the forest floor, and changes in mass loss, nutrient (N, P, K, Ca, Mg, S, Mn, Zn, B, Cu) concentrations and contents were observed at 2 to 6 month intervals for 32 months. Vegetation control resulted in warmer, but drier, forest floor, which led to reduced mass loss and decay rate constant (k=0.28 yr^{-1} for the vegetation controlled plot, k=0.39 yr^{-1} for plots with no vegetation control). Fertilization had no effect on mass loss and decay rate. Concentrations of N, P, Ca, S, Zn and Cu were increased 2 to 3 fold over the 32 months, while concentrations of K, Mg, Mn, and B declined, increased or did not change depending on time and treatment. Based on the release dynamics, the nutrient mobility series was as follows: Cu≤N≤S<P<Zn≤Ca<K≤Mn<Mg≤B. All ten nutrients showed at least some net release after 32 months, but only those other than Cu and N showed net release for all treatment combinations. Fertilization had no effect on release dynamics; however, vegetation control reduced release of N, P, S, and Zn, and increased release of boron.

INTRODUCTION

Most forest ecosystems have a unique characteristic of having a forest floor develop over the mineral soil as a result of litterfall accumulation. Litterfall inputs into the forest floor increase with age, reach a peak, and then decline at older ages in southern pine plantations (Switzer and Nelson 1972, Wells and Jorgensen 1975, Gholz et al. 1985). Nutrient storage in the forest floor also increases over time and can amount for as much as 350-400 kg ha^{-1} of N at age 30 (Wells and Jorgensen 1975) or 740 kg ha^{-1} of N at age 40 (Richter et al. 2000). In contrast to this accumulation, soil nutrient supply is usually reduced as stands age due to plant uptake and immobilization (Wells and Jorgensen 1975, Miller et al. 1979, Allen et al. 1990, Richter et al. 2000), resulting in nutrient limitations to forest productivity. It has been hypothesized that the forest floor becomes a more important factor in the nutrient supply of midrotation plantations. However, the importance of the forest floor as a source of nutrients is uncertain. Switzer and Nelson (1972) and Jorgensen et al. (1980) calculated that forest floor releases substantial amounts of macronutrients, but, more recently, others (Piatek and Allen 2001, Sanchez 2001) suggested that the forest floor is largely a sink for N and P while releasing other macronutrients. In addition, decomposition studies have mainly focused on macronutrient release, and there is a lack of information about micronutrient release dynamics for stands of most forest species.

Midrotation fertilization and vegetation control have become common silvicultural practices in intensively managed forest plantations to alleviate nutrient limitations that occur at midrotation through increasing the availability of existing resources and allocation the existing resources to crop trees (Allen et al. 1990). In additions to these direct effects on nutrient supply and allocation, these practices can also affect the cycling of organically bound nutrients stored in the forest floor by altering biological, chemical and physical factors of the decomposition environment.

Fertilization can directly affect forest floor nutrient pools, thus, influencing the decay rate and nutrient release dynamics (Sanchez 2001). Fertilized stands usually have higher needle nutrient concentration (Adams et al. 1987, Valentine and Allen 1990, Finer 1996), which may result in more rapid decomposition. Polglase et al. (1992) reported that fertilization doubled the concentration of total P in fresh needle litter in southern pine plantations, and suggested that recycling of this P through organic residues of fertilized plots has the potential to enhance long-term productivity beyond the immediate benefits derived from fertilizer uptake. Decomposition has also been found to be more rapid at sites with larger soil N capital (Prescott et al. 2000a), probably because better sites produce higher quality litter with lower amounts of phenolics (Gosz 1981). However, studies have shown no clear effect of fertilization on litter decomposition. Although Prescott et al. (2000b) suggested that the C/N ratio of the forest floor can be a closely related to N mineralization from the forest floor, Chappell et al. (1999) showed that N fertilization did not affect N turnover in the forest floor of Douglas fir (*Pseudotsuga*

menziessii (Mirb.) Franco) stands, even though C/N ratios of both litterfall and the forest floor were lower in fertilized stands. Similarly, Prescott et al. (1999) reported that higher litter nutrient concentrations did not result in faster decomposition in fertilized plots of trembling aspen (*Populus tremuloides* Michx). Coarse root decomposition was also shown to be unaffected by fertilization (King et al. 1997). Nitrogen has also been found to limit decomposition at high concentrations, which may explain why research results are not consistent. Nitrogen can react with lignin at late stages of the decomposition, creating more recalcitrant compounds, and it can suppress activities of lignin degrading white-rot fungi (Berg 2000).

Vegetation control can significantly alter plant community composition, which, in turn, may affect the quality of forest floor. In general, hardwood litter decomposes and releases nutrients faster than coniferous litter, due to higher nutrient concentrations and lower lignin and phenolics concentrations (White et al. 1988, Harmon et al. 1990, Bockheim et al. 1991, Prescott et al. 2000c, Piatek and Allen 2001). Vegetation control may also alter forest floor temperatures and moisture contents, which, in turn, influence the rates of decomposition since they have effects on microbial activity and diffusion of substrate. The effects of these environmental factors are usually important only during the initial stages of the decomposition, and litter quality becomes more important in later stages (Johansson 1994, Edmonds and Thomas 1995).

In this study, mass loss and nutrient release dynamics of needle litter was quantified Specifically, the objectives of this study were to determine the effects of vegetation control and fertilization on (i) needle decomposition rates, and (ii) macro- and micronutrient release dynamics in a midrotation loblolly pine plantation.

METHODS

Site Description

The study site was located at in the Piedmont physiographic province of Durham County, North Carolina (36^{o}13'N, 78^{o}52'W). Thirty-year (1961-1990) mean annual temperature is 14.5^{o}C, with monthly mean temperatures ranging from 3^{o}C in January to 25^{o}C in July. Mean annual precipitation is 1166 mm, with a fairly uniform seasonal pattern (State Climate Office of North Carolina, North Carolina State Univ, Raleigh, NC). The soils are highly weathered well-drained Georgeville and Cecil soil series of thermic, kaolinitic, Typic Kanhapludults. A-horizon depth was reduced to about 10 cm due to soil erosion during past agricultural practices, and had clay loam to sandy clay loam texture.

The pretreatment stand was a 14-year-old second rotation loblolly pine (*Pinus teada* L.) plantation with a site index (25 year) of 22 m. The site was chopped and burned during the site preparation, and no other silvicultural treatments had been applied. Prior to treatment, the stand had 971 pines ha^{-1} with a basal area of 24 m^{2} ha^{-1}. Competing vegetation mainly consisted of Virginia pine (*Pinus virginiana* Mill.) (1.2 m^{2} ha^{-1}) and

several hardwood species, including sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), southern red oak (*Quercus falcata* Michx.), white oak (*Quercus alba* L.) and black cherry (*Prunus serotina* J.F. Ehrh.), with a combined basal area of about 9 m^2 ha^{-1}.

Experimental Design and Treatments

The experimental design was a 2x2 factorial with 3 replications. A total of twelve 0.16 ha treatment plots were established in winter of 1997-1998. Measurement plots of 0.04 ha, centered within the treatment plots, were used for further sampling. Plots having similar pretreatment stand vegetation characteristics (height, basal area, stand density) were assigned to a single block to minimize within-block variation. Treatments included two levels of vegetation control (none and complete vegetation control) and two levels of fertilization (none and a fertilizer application of 224 kg ha^{-1} N as urea plus 56 kg ha^{-1} P as TSP). Complete vegetation control was performed in March 1998 by chainsaws, eliminating all hardwoods and naturally regenerated Virginia pines. Cut-stumps were then sprayed with a 50% solution of Garlon 3A (triclopyr amine) to prevent sprouting. Slash was left on the ground to decay. Roundup (glyphosate) was applied as needed at recommended rates to eliminate any resprouting or growth of herbaceous plants throughout the study period. Fertilizer application was performed by hand in March 1998, immediately after vegetation control was completed. Hereafter, no-vegetation control + no-fertilization treatment will be called the "control" treatment (C), complete vegetation control + no-fertilization will be "vegetation control" (VC), no-vegetation control +

fertilization will be “fertilization” (F), and complete vegetation control + fertilization will be “combination” (VC+F).

Litterbag Preparation and Collection

Fresh litter which had fallen in the 1997-1998 fall-winter season was collected from the uppermost layers of the forest floor in the first week of April 1998. Since the treatments had already been applied one month prior to collection, litter was collected from an adjacent stand. Collected litter was air-dried for four weeks prior to litterbag preparation. Loblolly pine needles were separated from other litter types (Virginia pine needles, hardwood leaves, branches, barks, etc) by hand. Loblolly pine needles were mixed well and kept for litterbags, while other litter types were discarded.

Subsamples of approximately 20 g were picked randomly from the litter pool and placed in mesh bags with 1 mm openings. All bags were tagged, numbered, and their litter weights were recorded. A total of 288 bags were prepared and randomly assigned to each of 12 plots. In May 1998, 24 bags were placed on the forest floor at the center of each plot and lightly covered with fresh litter. In addition to those bags placed in the field, 6 subsamples of 20 g were drawn from the same litter pool to determine initial litter nutrient concentrations and contents.

Starting in July 1998, two bags were collected from each plot at 2 to 6 month intervals (2, 4, 6, 8, 12, 16, 20, 26, 32 months after deployment). Litterbags were placed in plastic

bags immediately after lifting from the forest floor to prevent moisture loss, and transferred to the laboratory in a cooler. Forest floor temperatures were also measured with a temperature probe inserted underneath the litterbags every month.

The forest floor was also sampled in April 1998 by a circular sampler (diameter=30.5cm) at five stratified random locations within each plot (four near the corners and one at the center). The forest floor was cut vertically with the sampler, and all the organic material within the sampler was picked up and placed in paper bags. During this process, forest floor was divided into two layers, including litter layer (O_i), characterized as undecomposed, recognizable organic matter, and fermentation plus humus layers (O_e + O_a), characterized as partially and completely decomposed matter. Each layer was analyzed separately for weight and nutrient concentrations.

Laboratory Analysis

All litter samples were analyzed for oven-dry weight, moisture content, ash content, and nutrient concentrations (N, P, K, Ca, Mg, S, Mn, Zn, B, Cu). First, field-lifted samples were cleaned by hand of exogenous materials, such as mineral soil and plant roots, that had adhered to the outside of the litterbags. The litter samples were then removed from the litterbags, weighed immediately to determine fresh weight, and transferred to paper bags. Subsequently, they were dried at 70 ^{o}C for at least 24 hours, weighed again to determine oven-dry weight and moisture content. Dried samples were ground to pass through 1-mm screen for determination of nutrient concentrations and ash content.

Litter N concentrations were determined by either Lachat autoanalyzer (QuikChem 8000, Zellweger Analytics, Inc., Milwaukee, WI) after Kjeldahl digestion or by CHN elemental analyzer (CE Instruments - NC 2100, CE Elantech Inc., Lakewood, NJ). For the initial (time=0) samples and first four collection dates (between July 1998 and January 1999), N concentrations were determined using Lachat after subsamples of 0.2 g were digested in sulfuric acid/hydrogen peroxide (Parkinson and Allen 1975). For collection dates following January 1999, subsamples of 8.5 mg were analyzed by CHN elemental analyzer using a dry combustion technique. The pine standard from the National Institute of Standards and Technology (standard reference material no. 1575) was used in each set of analyses for quality control and showed that nutrient concentrations determined by the two methods were not different.

In addition to N, concentrations of P, K, Ca, Mg, S, Mn, Zn, B and Cu were determined by an inductively coupled plasma atomic emission spectrometer (ICP-AES, Varian ICP, Liberty series 2, Varian Analytical Instruments, Walnut Creek, CA). For the first four collection dates, sulfuric acid/hydrogen peroxide digested samples were analyzed for P, K, Ca, and Mg. For the rest of the dates, 0.8 g subsamples were digested in nitric acid (Zarcinas et al. 1987), which allowed determination of S, Mn, Zn, B and Cu. Again, the pine standard was used with both digestion methods for quality control and showed that the results of the two methods were the same.

Ash contents of the samples were determined by the loss-on-ignition technique. One-gram subsamples of each were ignited at 500 ^{o}C for 8-10 hours in a muffle furnace and weight loss was recorded. The ash content was used to adjust all litter weights and nutrient concentrations to an ash-free basis. Mass remaining at each collection time was divided by initial mass before decomposition to calculate proportion mass remaining, and nutrient concentrations were multiplied by mass remaining to calculate nutrient contents at each collection.

Forest floor samples were also dried at 70 ^{o}C for 24 hours, ground to pass a 1-mm screen, and analyzed for N (Lachat autoanalyzer), P, K, Ca and Mg (ICP-AES) after sulfuric acid/hydrogen peroxide digestion. Ash-free weights and nutrient concentrations were also determined as described above.

Statistical Analysis

Mass loss dynamics of the decomposing litter were analyzed by fitting an exponential decay model (Olson 1963) in the form of;

$$X = X_0 * e^{-kt}$$

where;

t = time (in years),

X = the sample mass at a given time (time = t),

X_0 = the initial sample mass (time = 0), and

k = decay rate constant.

Nonlinear regression (SAS Institute Inc., Cary, NC) was used in to calculate the decay rate constants for each plot, which represented dynamics of mass loss throughout the study period of 32 months. Based on the decay rates, half lives (HL) of the decomposing litter were also calculated by solving the above model for time (t). These were simply calculated as $0.693/k$ (Olson 1963). Finally, analyses of variance were performed to test for treatment effects on mass and nutrient proportions remaining at the last sampling date, decay rate constants, and mean temperature and moisture contents during the study period.

RESULTS

Litter and Forest Floor Characteristics

Initial litter and forest floor characteristics are summarized in tables 1 and 2. Nutrient concentrations in fresh needle litter used in the litterbags were lower than fresh litter collected from the forest floor. Similarly, the concentrations were lower in overlaying layers of the forest floor (litter layer, O_i) than in bottom layers (fermentation layer, O_e and humus layer, O_a). The humus layer was either very small or entirely lacking, and, when combined with the fermentation layer, made up 56% of the total forest floor mass and contained 65, 67, 86, 59, and 66% of the total forest floor N, P, K, Ca and Mg contents, respectively.

Vegetation control had no effect on forest floor (all layers) nutrient concentrations one month after treatments. However, fertilization increased P concentration by 82% ($p=0.003$), but had no effect on N and other macronutrient concentration.

Environmental Factors

Vegetation control significantly increased forest floor temperatures (tables 3 and 4) and the increase in temperature was about 2.5^{o}C when averaged across time. Vegetation control plots (VC and VC+F) warmed up faster in spring, and had up to 11^{o}C higher temperatures during the summer months (figure 1). All treatments converged by fall and had relatively similar temperatures during the winter months. Fertilization had no effect on temperature.

Vegetation control reduced forest floor moisture content by an average of 42% (figure 1, table 3). Moisture content in vegetation control plots was especially lower during the summer and reached as low as 12%. Fertilization resulted in a significant increase in moisture content, and a much greater effect was observed on plots without vegetation control (significant F and VC*F effects, table 4).

Mass Loss

Throughout the study, litter in VC and VC+F lost significantly less mass than litter with no vegetation control (figure 2, table 4). The difference in mass loss due to vegetation

control diverged up to 12th month reaching a maximum difference of 12%, and then remained constant thereafter. After 32 months, the VC and VC+F treatments had 43% mass remaining, while the C and F treatments had 34% mass remaining (table 3). Fertilization did not have a significant effect on mass loss (table 4). Annual decay rate constants ranged from 0.27 to 0.40 for the four treatments (table 3). Similar to mass loss dynamics, only the VC and VC+F treatments significantly reduced decay rates, while fertilization had no effect (table 4). Half-lives calculated from the decay rates were 0.7 years greater with vegetation control (table 5).

Nutrient Release Dynamics

The mobility series of the ten 10 nutrients measured was as follows across all treatments (from least released to most released): $Cu \leq N \leq S < P < Zn \leq Ca < K \leq Mn < Mg \leq B$ (figure 3). Roughly, three groups of nutrients were identified based on their nutrient immobilization or release dynamics during the decomposition period of 32 months. The first group of nutrients (Cu, N and S) was the least mobile, showing either very little or no release at all, and had 2.4 to 2.9x greater concentrations in the 32nd month than they did originally. The second group of nutrients (P, Zn and Ca) had 18 to 48 % release after 32 months, although they had 1.9 to 2.2x greater concentrations at the last collection. The increases in concentrations were mostly linear and common across treatments for these first two groups. The third group of nutrients (K, Mn, Mg and B) was the most mobile, and their release rates ranged from 48 to 66% in proportion to their initial contents. Concentrations of these nutrients increased, declined, or showed no change over time,

and changes in time differed among treatments. In general, vegetation control reduced the concentrations of all nutrients, except for Zn and Cu. Vegetation control also reduced the release of N, P, S and Zn, and increased the release of B (Table 6). Fertilization had no significant effect on release dynamics of any of the 10 nutrients.

DISCUSSION

Mass Loss Dynamics

The concentrations of nutrients in fresh needle litter were lower than those in litter layer (Oi) of the forest floor, indicating rapid immobilization of nutrients in the forest floor (tables 1 and 2). Atmospheric deposition and translocation of nutrients from lower nutrient-rich layers (i.e., Oe) of forest floor through microbial transfer (i.e., via hyphal connections) may play important role in this enrichment. It this study, forest floor (all layers) accumulated about 156 kg ha^{-1} N and 15 kg ha^{-1} P over 14 years. These estimates were somewhat lower than the 193 to 270 kg ha^{-1} N and somewhat higher than the 5.2 to 7.0 kg ha^{-1} P obtained by Piatek and Allen (2001) in another 14-year-old loblolly pine stand in NC. Greater P content in this study was partially due to a strong fertilizer effect on forest floor P concentrations, which was raised from 0.6 to 1.2 g kg^{-1} after the treatment. The estimates from both of these studies were also lower than the 350-400 kg ha^{-1} of N and the 30-40 kg ha^{-1} of P estimated in 32 to 39 year-old loblolly pine stands

(Wells and Jorgensen 1975), indicating that accumulation of organic matter and nutrients in forest floor of our site may continue for another 10-15 years.

Decomposing needle litter lost about 31% of its initial mass after 12 months, and 66% after 32 months in control plots, resulting in an annual decay rate of 0.39 (figure 2, table 3). This estimate is comparable to first year mass loss of 30% (k=0.42 yr^{-1}) found in a loblolly pine stand of the same age in NC (Piatek and Allen 2001), and somewhat lower than 44% found in a 19-year-old loblolly pine stand in TN (Thomas 1968).

Mass loss dynamics of the decomposing litter were not affected by fertilization throughout the 32-month period. Similarly, we did not find a change in net N mineralization in mineral soil due to fertilization either (chapter 1). The lack of mass loss response to fertilization may be due to the fact that the litterbags were placed on the forest floor about 2 months after the fertilizer application, so only a small amount of added N may have contributed to the chemistry of our confined litter. In addition, the one time application of 224 kg ha^{-1} N and 56 kg ha^{-1} P may not have caused enough of a shift in forest floor nutrient pools and dynamics to affect decomposition. In fact, there was no significant increase in forest floor N concentration about a month after the fertilizer application (data not shown).

While some research has shown that N additions and litter N content can have a positive effect on decomposition under field (Sanchez 2001) and laboratory (Vestgarden 2001)

conditions, others showed no such effect (Chappell et al. 1999, Prescott et al. 1999). Chadwick et al. (1998) suggested that litters exposed to N- and Ca-rich environments may have faster decomposition. Furthermore, Chappell et al. (1999) reported that while inherent soil N capital significantly increased N turnover (litterfall/forest floor mass ratio) in forest floors of nine coastal Douglas fir stands, fertilization did not have an influence 8 to 12 years after repeated applications, indicating fertilization alone may not always achieve expected improvement in N turnover. Similarly, Prescott et al. (1999) reported that higher nutrient concentrations did not result in faster decomposition in trembling aspen foliar litter 4 years after single fertilization.

Unlike fertilization, vegetation control significantly reduced the rate of mass loss (figure 2, tables 3 and 4). These results are consistent with reduced decay rate constants due to herbaceous and woody vegetation control reported by Lockaby et al. (1995). About 25% of the total basal area was removed in our study, creating two distinct communities, one with a very thick canopy cover and the other with patchy openings. The reduced canopy cover led to more direct sunlight and elevated forest floor temperatures (up to 11^{o}C, figure 1). On the other hand, higher temperatures resulted in reduced forest floor moisture contents, which were as low as 12% during hot summer months. Considering that air-dry litter samples had about 11% moisture content before being deployed in the field, these very low summer moisture contents probably have had detrimental effects on the decomposition process. The effects of climatic factors can also be seen in the mass loss dynamics (figure 2), where the slope of the curve was greater between the 16th and 20th

months, which corresponds to a warm and moist fall season. Similar changes in seasonal decomposition rates were observed by Gholz et al. (1985) and Piatek and Allen (2001).

In addition to these microclimatic factors, changes in vegetation composition, which in turn influence litter quality, may have also played some role in the reduced decomposition rate of needle litter after vegetation control. Hardwoods and herbaceous vegetation produce litter with greater nutrient concentrations and lower recalcitrant compounds. Decomposition and nutrient release rates are usually faster for broadleaf litter than conifer litter, especially during the initial stages of the decomposition (Bockheim et al. 1991, Elliot et al. 1993, Prescott et al. 2000c). Therefore, when placed with nutrient-rich broadleaf litter, conifer litter may be expected to decompose faster. Piatek and Allen (2001) reported that decomposition rates of loblolly pine needle litter were increased in a 5:1 needle:leaf mixture but not in 1:5 mixture. Others (Thomas 1968, Prescott et al. 2000c) reported no such increases in decomposition rates of coniferous litter after mixing with broadleaf litter.

One interesting result was that the differences in mass loss due to vegetation control increased up to the 12^{th} month, reaching a maximum of 12%, and then declined to about 9% at 32^{nd} month (figure 2). Our estimates of decay rates also increased from 0.23 yr^{-1} between months 0 and 12 to 0.28 yr^{-1} between months 12 and 32 in vegetation control plots, but it did not change in plots receiving no vegetation control. If this trend continues, all treatments may converge in time. It is usually thought that climatic factors

and abundance of readily decomposable fractions (soluble compounds and carbohydrates, i.e., cellulose and hemicelluloses) control initial stages of decomposition; but that, and as decomposition progresses, litter quality, particularly the lignin/N ratio, becomes more important in determining decay rates (Edmonds and Thomas 1995, Scott and Binkley 1997, Johansson 1994, McClaugherty et al.1985, Jamaludheen and Kumar 1999, Harmon et al. 1990, White et al. 1988). Therefore, this trend was not so surprising, since we used a standard litter for all treatments. In addition, the large temperature and moisture content differences observed after vegetation control would diminish over time as litterbags are subsequently buried in the forest floor by new additions of litter and as the gaps in the forest canopy close.

Nutrient Release Dynamics

After 32 months, nutrient mobilities across all treatments were (from least to most): Cu≤N≤S<P<Zn≤Ca<K≤Mn<Mg≤B. High mobility of K, Mg (Laskowski et al.1995, Bockheim et al. 1991, Vogt et al. 1983), B and Mn (Bockheim et al. 1991) have been noted previously. Perhaps, the immobilization and very slow release, if any, of N and P (Piatek and Allen 2001, Laskowski et al.1995, Vogt et al. 1983) in decomposing litter is more important from the standpoint of forest productivity, since they are the most commonly limiting nutrients (Allen et al. 1990). Jorgensen et al. (1980) reported that N was the most slowly released macronutrient with only about 27% of it released over 8 years. In our study, only about 13% of N and 29% of P was released in control plots after 32 months. In another study by Piatek and Allen (2001), N release was similar to our

result. They also reported sustained P immobilization throughout 26 months, which may be due to lower initial P concentration (0.2 vs. 0.4 g kg^{-1} in our study).

During the decomposition period of 32 months, N, P, Ca, S, Zn and Cu concentrations increased 2 to 3 fold, while concentrations of more mobile nutrients such as K, Mg, Mn and B slightly increased, decreased or did not change, depending on the time and treatment. Similar concentration dynamics were observed for these 10 nutrients by Bockheim et al. (1991) in decomposing foliar litters of jack pine (*Pinus banksiana* Lamb.) and several hardwoods. These increases in nutrient concentrations of recent litter can be caused by atmospheric deposition (rainfall, throughfall and canopy leaching), new input of nutrient rich-litter (pollen, green foliage, etc.), transfer of nutrients from other nutrient-rich substrate to nutrient poor brown foliage through fungal connections and diffusion via water films, and downward movement of litter into nutrient–rich lower layers of forest floor (Oe and Oa). The importance of the fluxes also may differ for each element. These enrichments were partially confirmed by our data, showing a concentration gradient of: Oa and Oe > Oi > fresh-brown litter (from highest to lowest). Jorgensen et al. (1980) reported that throughfall and fine material (pollen, insect, dust, etc.) inputs accounted for up to 37, 16, 59, 18 and 27% of N, P, K, Ca and Mg, respectively, of annual total input (needles, leaves, branches, fine material, throughfall, etc.) to the forest floor in an 11-year-old loblolly pine plantation. These concentration gains can also be the result of mass loss, since faster utilization and release of C relative

to other nutrients leads to lower C/nutrient ratios over time (Jorgensen et al. 1980, Sanchez 2001).

Release rates of N, P, S and Zn were significantly reduced and B release was increased by vegetation control. The reduction and increase in nutrient release was due to the combined effects of reduced mass loss and concentrations after vegetation control. Release was observed where mass loss was relatively greater than reduction in concentration, and vice versa. Fertilization had no effect on nutrient release dynamics. However, total per-hectare flux of nutrients can still be elevated after fertilization since leaf area and litter production would be increased after nutrient additions (Prescott et al 1999). Input of N through needle litter was increased up to 33% after fertilization in a Scots pine stand (Finer 1996) and such an increase is usually correlated with increased turnover of N in the forest floor (Vitousek et al. 1982). In this site, foliar N and P returned to the forest floor via needlefall were up to 31 and 73% greater in the fertilization treatment, and 58 and 114% greater in the VC+F combination treatment, respectively, (chapter 3). Therefore, per-hectare nutrient turnover should be higher in fertilized plots even with similar (per unit of mass) release rates.

Whether the forest floor is a source or a sink for nutrients, especially for N and P, has many implications in forest productivity and management and, unfortunately, research on this subject has produced conflicting results. Jorgensen et al. (1980) has reported that forest floor released about 18 kg ha^{-1} N and 5 kg ha^{-1} P annually in an 11-year-old

loblolly pine stand, and Switzer and Nelson (1972) reported that the release from forest floor can account for about 40 and 23% of the N and P requirement, respectively, in a 20-year-old stand, indicating the forest floor is an important source of these, and other, nutrients in midrotation pine plantations. However, Piatek and Allen (2001) have found that "fresh" litter was a sink for N and P, and there was no net mineralization of N from partially decomposed "old" litter. These contradictory results may be partly an artifact of the methods used. Use of the litterbag technique by Piatek and Allen (2001) and in this study may have resulted in reduced rates of decomposition due to exclusion of macrofauna.

Another reason for the contradiction is, perhaps, the definition of "forest floor." Most litterfall estimates and litterbag studies use foliar litter to determine the contributions of the forest floor to the nutrient cycle, simply because the foliar fraction makes up most of the litter input into the forest floor by weight and it is easy to measure. However, other types of inputs such as reproductive litter, atmospheric deposition and throughfall can be substantial and they can significantly alter forest floor nutrient dynamics. For example, Greenfield (1996) reported that pollen production ranged from 0.19 to 14.4 kg $tree^{-1}$ (with a mean of about 4 kg $tree^{-1}$) among nine coniferous species (ages ranging from 8 to 40 years). Pollen contains large amounts of water-soluble carbohydrates, amino acids and proteins, with an average N concentration of 2.4% for gymnosperms, and provides a readily availably source of nutrients (Greenfield 1999). Assuming a stocking of 400 trees ha^{-1}, we can estimate a pollen production of 1.6 t ha^{-1}, containing about 38 kg ha^{-1} N.

Similarly, Pregitzer and Burton (1991) reported that reproductive litter production (flower and seeds, not including pollen) ranged from 0.3 to 1.6 Mg ha^{-1} yr^{-1} in five sugar maple (*Acer saccharum* Marsh.) stands, containing up to 41 kg ha^{-1} N, which accounted for 36% of the total N in aboveground litter. When these inputs are taken into consideration, our estimates of nutrient release dynamics of the forest floor can be expected to change. Jorgensen et al. (1980) reported that annual input of fine material (pollen, dust, etc.) plus throughfall accounted for 35, 16 and 49% of total N, P, and K input, respectively, into the forest floor of an 11-year-old loblolly pine plantation. When fine litter and throughfall were included in the analysis, there was no immobilization of N in the early stages of decomposition, and a linear annual release rate of about 4 to 5% was found. Therefore, exclusion of these other nutrient inputs may result in underestimation of nutrient dynamics of forest floor.

Leaching from the forest floor can transfer significant amount of nutrients into the mineral soil. However, these nutrients are almost entirely in organic forms, resistant to decomposition (Qualls et al 1991), and their value as a source of nutrients is unclear. Currie et al. (1996) reported that annual flux of dissolved N into mineral soil was about 9 g m^2 yr^{-1} (67% organic) in a hardwood stand, and about 17 g m^2 yr^{-1} (56% organic) in a red pine (*Pinus resinosa*) stand, indicating that the forest floor is a strong sink for inorganic N arriving in throughfall, especially in hardwood stands (Qualls et al. 1991). However, inorganic N may account for the majority of total dissolved N after fertilization (Currie et al. 1996), or where the site is N-saturated (Michalzik and Matzner 1999).

CONCLUSIONS

The forest floor at this site had accumulated about 156 kg ha^{-1} N and 15 kg ha^{-1} P by the age of 14. Considering that needle litter lost only a fraction of its initial N and P content after 32 months, it is likely that these estimates will increase as stand ages. Overall, the mobility series of the nutrients was as follows: Cu≤N≤S<P<Zn≤Ca<K≤Mn<Mg≤B. Fertilization had no effect on needle mass loss and nutrient release dynamics of pretreatment cohort; however, fertilized stands would have larger fluxes of nutrients over time as they produce greater quantities of litter with higher nutrient concentrations. If that happens, these stands should also benefit from long-term recycling of the added N and P. On the other hand, vegetation control slowed down the decomposition, and negatively influenced the release rates of N and P. Considering that vegetation control would also reduce litterfall input of these nutrients, per-hectare cycling of these elements would also be reduced in these stands.

Based on the slow release rates of N and P from needle litter, it can be assumed that mineral soil should be the main source of these elements for the stand. However, estimates solely based on needle litter most likely underestimate actual contribution of forest floor in site nutrient cycles. Although, small in weight, other inputs such as seeds, pollens, buds etc, may contribute substantially to total nutrient inputs into the forest floor since they are richer in nutrients and easily decomposed.

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Table 1. Initial ash-free weight and nutrient concentrations of loblolly pine litter used in decomposition bags.

Ash-free weight (g)	17.26
C (g kg^{-1})	480
N (g kg^{-1})	4.95
P (g kg^{-1})	0.41
K (g kg^{-1})	0.71
Ca (g kg^{-1})	3.52
Mg (g kg^{-1})	0.75
S (g kg^{-1})	0.61
Mn (mg kg^{-1})	549.4
Zn (mg kg^{-1})	39.2
B (mg kg^{-1})	9.9
Cu (mg kg^{-1})	2.4

Table 2. Average forest floor mass, macronutrient concentrations and contents of a 14-year-old loblolly pine plantation.

	Forest Floor Layers		
	O_i	$O_e + O_a$	All Layers
Ash-free weight (kg ha^{-1})	7127	9160	16287
Nutrient Concentrations			
N (g kg^{-1})	7.64	11.08	9.58
P (g kg^{-1})	0.70	1.08	0.92
K (g kg^{-1})	0.87	4.16	2.72
Ca (g kg^{-1})	7.29	8.29	7.85
Mg (g kg^{-1})	0.93	1.41	1.20
Nutrient Contents			
N (kg ha^{-1})	54.5	101.5	156.0
P (kg ha^{-1})	5.0	9.9	14.9
K (kg ha^{-1})	6.2	38.1	44.3
Ca (kg ha^{-1})	52.0	75.9	127.9
Mg (kg ha^{-1})	6.6	12.9	19.6

Table 3. Percent mass remaining at the last collection, decay rate, and mean forest floor temperature and moisture contents for 32 months.

Treatment	Mass Remaining (%)	Decay Rate (yr^{-1})	Temperature (^oC)	Moisture (%)
C	34.4	0.39	14.9	83.5
F	34.2	0.40	14.9	104.8
VC	42.1	0.27	17.4	53.0
VC+F	43.6	0.29	17.4	56.3
Root MSE	4.28	0.01	0.31	6.19

Table 4. ANOVA results for percent mass remaining at the last collection, decay rate, and mean forest floor temperature and moisture contents.

Source	Mass Remaining	Decay Rate	Temperature	Moisture
Replication	0.675	**0.010**	0.862	0.816
F	0.815	0.111	0.771	**0.014**
VC	**0.013**	**<.001**	**<.001**	**<.001**
VC*F	0.730	0.967	0.906	**0.046**

Table 5. Half-lives for decomposing loblolly pine needle litter in a midrotation plantation.

Treatment	HL	HL_{mean}
	-------- years --------	
C	1.79	1.76
F	1.73	
VC	2.55	2.49
VC+F	2.44	
Root MSE	0.10	

HL: Half life = 0.693 / *k* (Olsen 1963).

Table 6. ANOVA results for N, P, K, Ca, Mg, S, Mn, Zn, B and Cu proportions remaining at 32nd month.

Source	N	P	K	Ca	Mg	S	Mn	Zn	B	Cu
Replication	0.461	0.345	0.610	0.477	0.654	0.975	0.464	0.696	0.275	0.343
F	0.330	0.662	0.748	0.402	0.062	0.719	0.439	0.809	0.287	0.720
VC	**0.001**	**0.006**	0.542	0.604	0.949	**0.038**	0.468	**0.013**	**0.026**	0.125
VC*F	0.451	0.762	0.237	0.412	0.260	0.783	0.934	0.325	0.436	0.121

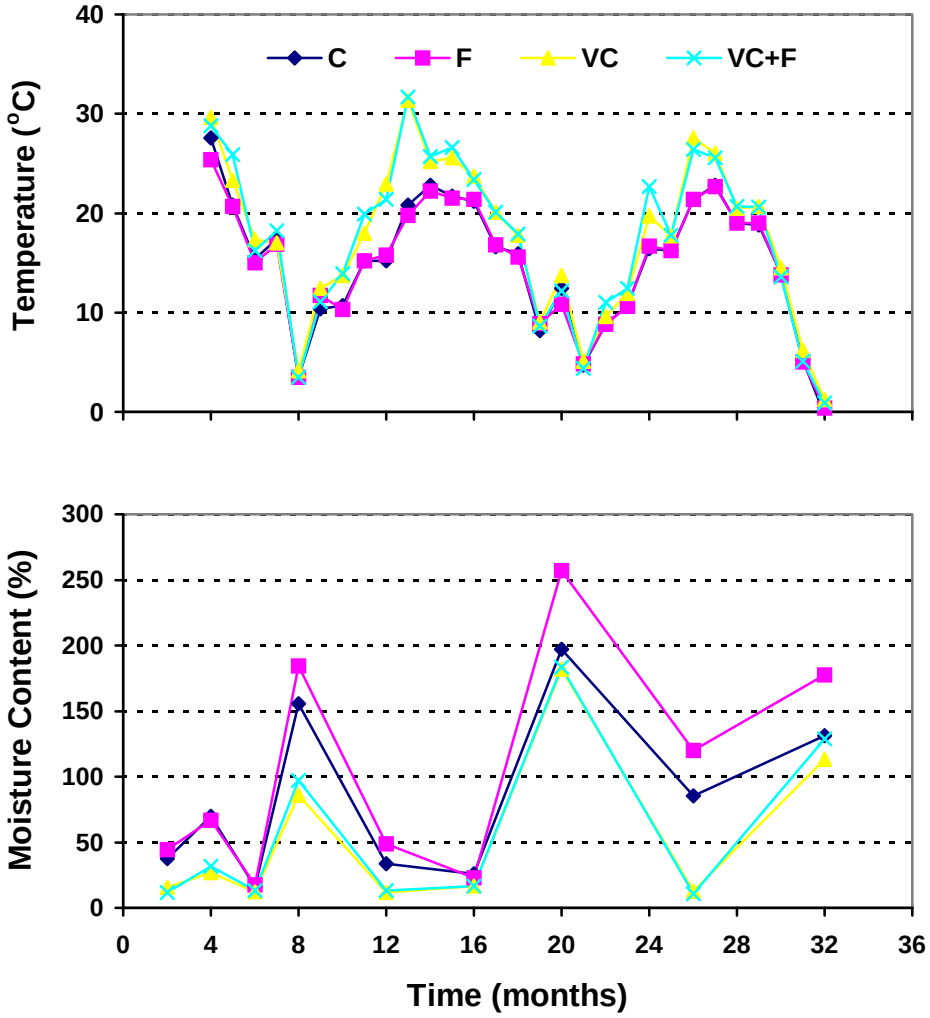

Figure 1. Forest floor temperatures and moisture contents (by weight) in a midrotation lobllolly pine plantation (time=0 is May 1998).

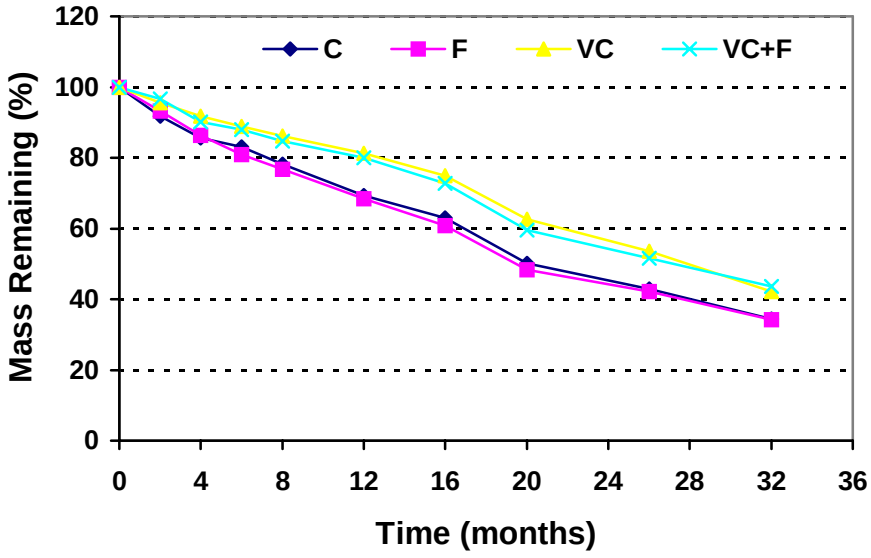

Figure 2. Mass loss dynamics of decomposing pine litter in a midrotation loblolly pine plantation (time=0 is May 1998).

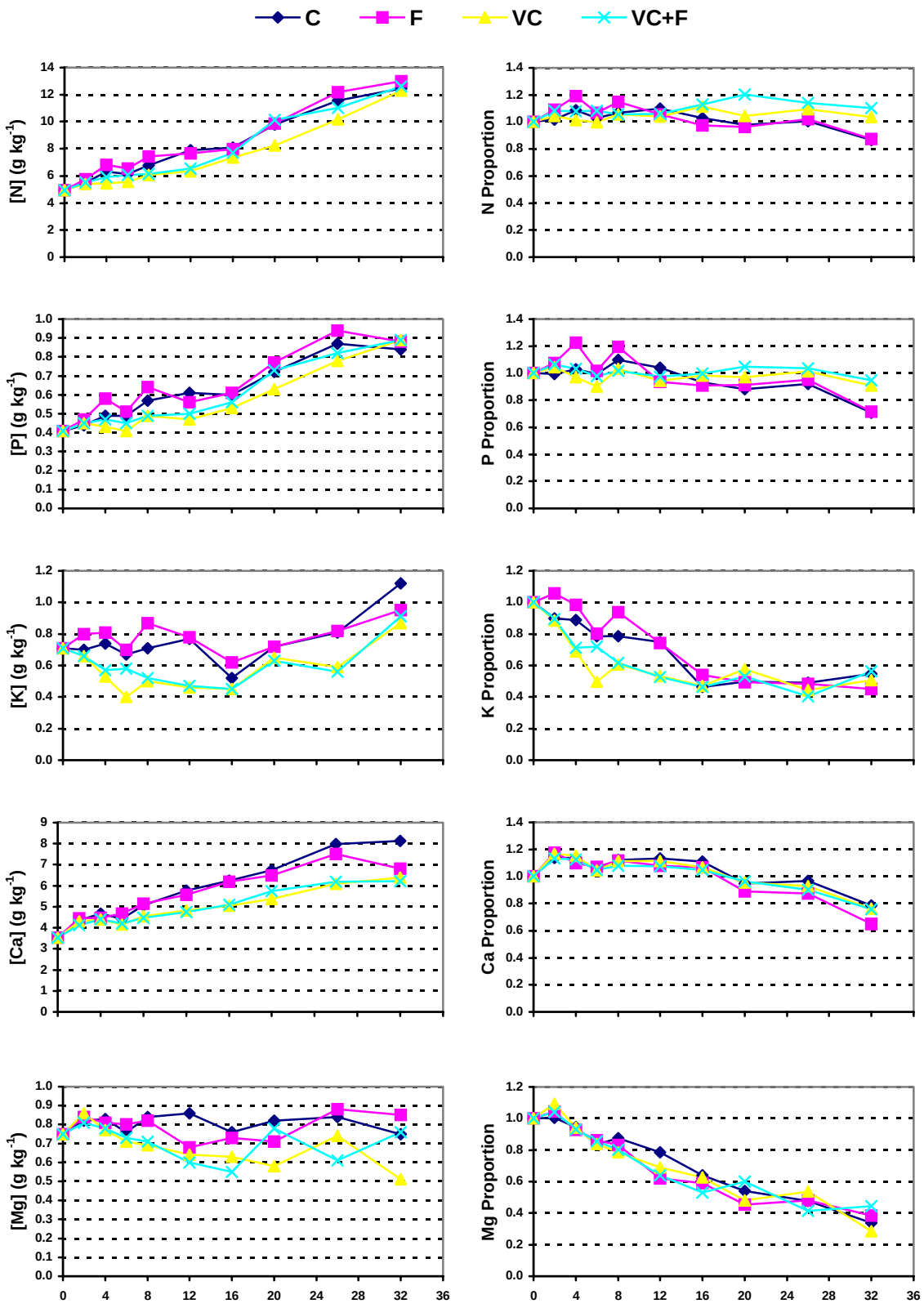

Figure 3. Dynamics of nutrient concentrations and proportions in decomposing loblolly pine litter.

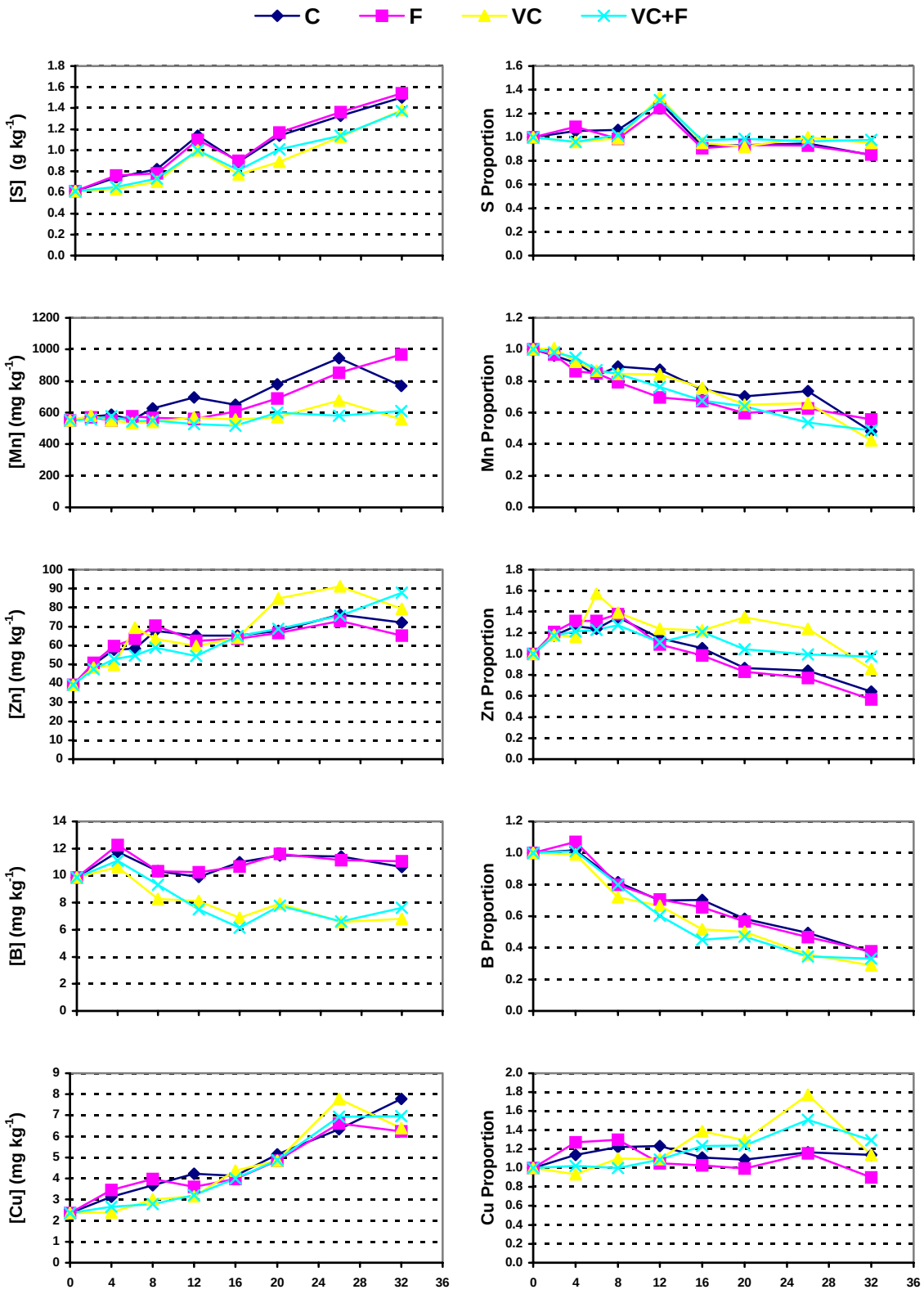

Figure 3 (continued). Dynamics of nutrient concentrations and proportions in decomposing loblolly pine litter.

CHAPTER 3

Growth, foliar, and litter responses of a midrotation loblolly pine plantation to vegetation control and fertilization

ABSTRACT

GURLEVIK, NEVZAT. Growth, Foliar, and Litter Responses of Midrotation Loblolly Pine Plantation to Vegetation Control and Fertilization

Loblolly pine growth response to vegetation control and fertilization has been well documented for early rotation stands; however, it is uncertain if these treatments can result in the same response when applied after crown closure. In this study, growth, foliar and litter responses to these treatments were determined in a 14-year-old loblolly pine plantation over a three-year period. Treatments were applied in a factorial design with two levels of vegetation control (none, complete) and two levels of fertilization (none, 224 kg ha^{-1} N plus 56 kg ha^{-1} P). Pine foliar N and P concentrations, use and litter concentrations and contents were significantly increased by fertilization, especially where competing vegetation was controlled. Effects of vegetation control alone on these parameters were usually not significant. Retranslocation of N and P was reduced by both treatments in the first year. Afterwards, only fertilization had negative impact on P retranslocation. Pine peak leaf area index and needlefall were not affected by either treatment over the three years. Fertilization significantly increased annual diameter (54%), height (14%), basal area (41%), and volume growth (27%) of loblolly pine over the three years, while vegetation control had no significant effect. Annual needlefall and foliar N use both accounted for 64% of the variation in pine volume growth. Similar growth, foliar and litter responses to treatments were observed for hardwoods; however, the effects were rarely significant.

INTRODUCTION

Actual forest production is usually far below potential because physiological processes are often limited by environmental factors (Kramer 1986, Powers and Reynolds 1999), such as water and nutrient availability (Linder 1987, Allen et al. 1990). These limitations may be especially critical at midrotation when demand for these resources is high, while soil supply is low (Wells and Jorgensen 1975, Allen et al. 1990). This lack of resource availability can be manipulated by intensive silvicultural treatments, including vegetation control, which allocates existing resources to crop trees, and fertilization, which actually increases availability of limiting nutrients (Farnum et al. 1983, Allen et al. 1990).

Biomass production is correlated with the capacity to intercept light and light interception is largely a function of leaf area (Jarvis and Leverenz 1983, Cannell 1989). Leaf area index (LAI) of forest stands has also been considered an indicator for its water availability and productivity (Linder 1987, Gholz et al. 1990). For loblolly pine, the strong positive relationship between LAI and growth is well documented (Teskey et al. 1987, Vose and Allen 1988, Albaugh et al. 1998). LAI of loblolly pine stands commonly ranges from 1.5 to 3 m^2 m^{-2}, levels that are below optimal for maximum production (Allen et al. 1990).

Fertilization has become a common tool in improving soil nutrient supply and site productivity where intensive forest management is practiced. Fertilization has been

shown to increase leaf area and stemwood production (Linder 1987, Vose and Allen 1988, Albaugh et al. 1998). Vose and Allen (1991) showed an increase in needlefall biomass by as much as 75 % after nitrogen fertilization. Fertilizer application may also affect foliar nutrient concentrations (Adams et al. 1987, Valentine and Allen 1990, Zhang and Allen 1996), shoot and foliage growth phenology (Zhang et al. 1997), stem volume growth efficiency (volume growth per unit LAI) and allocation of biomass production (Cannell 1989, Albaugh et al. 1998). Proportional and absolute amount of biomass allocation to aboveground parts is greater on more fertile sites (Cannell 1989, Gower et al. 1994), usually at the expense of fine root production (Albaugh et al. 1998).

Vegetation control may also have a dramatic effect on productivity by decreasing stand basal area, which, in turn, can decrease interception of precipitation, evapotranspiration, and increase water and nutrient availability to crop trees (Richardson 1993, Gholz et al. 1990, Allen et al. 1990, Farnum et al. 1983). Ludovici and Morris 1997 showed that pine seedling survival, height, and diameter growth were reduced in the presence of crabgrass. Many studies have consistently shown that vegetation control increases foliar biomass and nutrient contents (Zutter et al. 1999) and greater volume growth (Cain 1996, Schabenberger and Zedaker 1999, Quicke et al. 1999, Fredericksen et al. 1991, Shelton and Murphy 1997) in early-rotation stands. However, other studies have reported positive (Fortson et al. 1996) or no (Williams and Farrish 2000) response to vegetation control after crown closure in established stands.

While many studies focused on pine responses to only fertilization or only vegetation control, there is only limited information about simultaneous responses to both treatments. Pines usually respond positively to early-rotation application of both treatments, while response to vegetation control can be greater, especially on dry sites (Mason and Milne 1999, Powers and Reynolds 1999) and the most intensive treatment results in the greatest response (Borders and Bailey 2001). However, in established stands, fertilization appears to be more important for pine growth. Williams and Farrish (2000) reported that volume response to fertilization was 3-4 m^3 ha^{-1} yr^{-1}**,** while response to vegetation control was not significant in ten 20- to 30-year-old loblolly pine stands. Also, most of these studies focused only on growth responses, and underlying causes of such growth are poorly understood.

Objectives of this study were; 1) to quantify the magnitude of growth responses of planted loblolly pine and canopy hardwoods to complete vegetation control and N+P fertilization, 2) to determine foliar responses of both loblolly pine and hardwoods, including foliage production, leaf area, foliar and litter nutrient concentrations, foliar nutrient use and retranslocation, and 3) to examine the relationships between pine volume growth and foliar characteristics.

METHODS

Site Description

The study site was located at in the Piedmont physiographic province of Durham County, North Carolina (36°13'N, 78°52'W). Thirty-year (1961-1990) mean annual temperature is 14.5°C, with monthly mean temperatures ranging from 3°C in January to 25°C in July. Mean annual precipitation is 1166 mm, with a fairly uniform seasonal pattern (State Climate Office of North Carolina, North Carolina State Univ, Raleigh, NC). The soils are highly weathered well-drained Georgeville and Cecil soil series of thermic, kaolinitic, Typic Kanhapludults. A-horizon depth was reduced to about 10 cm due to soil erosion during past agricultural practices, and had clay loam to sandy clay loam texture.

The pretreatment stand was a 14-year-old second rotation loblolly pine (*Pinus teada* L.) plantation with a site index (25 year) of 22 m. The site was chopped and burned during the site preparation, and no other silvicultural treatments had been applied. Prior to treatment, the stand had 971 pines ha^{-1} with a basal area of 24 m^2 ha^{-1}. Competing vegetation mainly consisted of Virginia pine (*Pinus virginiana* Mill.) (1.2 m^2 ha^{-1}) and several hardwood species, including sweetgum (*Liquidambar styraciflua* L.), yellow poplar (*Liriodendron tulipifera* L.), red maple (*Acer rubrum* L.), southern red oak (*Quercus falcata* Michx.), white oak (*Quercus alba* L.) and black cherry (*Prunus serotina* J.F. Ehrh.), with a combined basal area of about 9 m^2 ha^{-1}.

Experimental Design and Treatments

The experimental design was a 2x2 factorial with 3 replications. A total of twelve 0.16 ha treatment plots were established in winter of 1997-1998. Measurement plots of 0.04 ha, centered within the treatment plots, were used for further sampling. Plots having similar pretreatment stand vegetation characteristics (height, basal area, stand density) were assigned to a single block to minimize within-block variation. Treatments included two levels of vegetation control (none and complete vegetation control) and two levels of fertilization (none and a fertilizer application of 224 kg ha^{-1} N as urea plus 56 kg ha^{-1} P as TSP). Complete vegetation control was performed in March 1998 by chainsaws, eliminating all hardwoods and naturally regenerated Virginia pines. Cut-stumps were then sprayed with a 50% solution of Garlon 3A (triclopyr amine) to prevent sprouting. Slash was left on the ground to decay. Roundup (glyphosate) was applied as needed at recommended rates to eliminate any resprouting or growth of herbaceous plants throughout the study period. Fertilizer application was performed by hand in March 1998, immediately after vegetation control was completed. Hereafter, no-vegetation control + no-fertilization treatment will be called the "control" treatment (C), complete vegetation control + no-fertilization will be "vegetation control" (VC), no-vegetation control + fertilization will be "fertilization" (F), and complete vegetation control + fertilization will be "combination" (VC+F).

Growth, Leaf Area, Foliage, and Litterfall Measurements

Growth measurements, including diameter at breast height (D, 1.4m) and height (H), were taken annually from 1998 to 2001 during the dormant season between January and February. All loblolly and Virginia pines within the measurement plots were measured, while hardwood measurements were limited only to canopy hardwoods. Plot means were calculated for each year for D, H, basal area and volume. The following equations were used to calculate individual tree stem volumes (wood + bark);

Loblolly pine: $\text{Volume} = 0.02364 + 0.00274616 * D^2 * H$ (Smalley and Bower 1968)

Virginia pine: $\text{Volume} = 0.00589 * (D^2 * H)^{0.91582}$ (Saucier 1982)

Hardwoods: $\text{Volume} = 0.00382 * (D^2 * H)^{0.94065}$ (Clark et al. 1986)

where volume was in ft^3, D in inches, H in feet. Individual tree volumes were summed per plot and then converted to m^3 per hectare. Three-year mean annual D, H, basal area and volume growth was calculated as the difference between year 2001 and 1998, divided by three.

Stand leaf area index was measured monthly from April 1998 to February 2001 using a Li-Cor LAI2000 plant canopy analyzer (Li-Cor 1991). Each month, 10 below-canopy measurements were taken along a transect in each plot using a 90^o view cap. At the same time, a second Li-Cor unit was placed in an adjacent opening to take above canopy measurements. For each plot, LAI was calculated based on the difference between above and below canopy measurements using software provided with the instrument. Leaf area

index measurements included both hardwoods and pine leaf area in C and F plots. To partition this "total" LAI into pine and hardwood LAI's, a linear model in the form of

$$Y = a + bX$$

was used, where Y is needle litter weight, X is pine peak LAI, and a and b are constants. This model was developed based on the data from VC and VC+F plots where no hardwoods were present. It was then solved for C and F plots for pine LAI, assuming that the relationship between litter weight and leaf area would be same for all treatments. Finally, estimated pine LAI was subtracted from "total" LAI to calculate peak LAI for hardwoods. Growth efficiency was also calculated as stem volume growth per unit of leaf area.

Pine foliage samples were collected annually from 1998 to 2000 between January and February from 5 dominant or codominant loblolly pine trees in each measurement plot. Measurement trees were marked to ensure that the same trees were measured each year. At each sampling, 100 fascicles (20 from each tree) were collected from the upper 1/3 of the live crown. Only entire, healthy fascicles from the first flush produced during the most recently completed growing season were included in the samples.

Hardwood foliage samples were collected annually in 1999 and 2000 between August and September from 2 to 5 sweetgum trees, the only canopy hardwood species common

to most plots. At each collection, 50 fully grown leaves were sampled from the fully exposed upper 1/3 of the crown. Both pine and hardwood foliage samples were placed in paper bags, transferred to laboratory and kept cool ($4^{o}C$) until drying. No foliage samples were taken from Virginia pines.

Litter was collected using 0.75 m^2 fiberglass traps at monthly intervals from July 1998 to February 2001. Five traps were systematically placed in each measurement plot, four toward the corners and one at the center. At each collection, litter that had fallen into the traps was emptied in paper bags and composited by plot. During the collection, litter was separated into 3 fractions; pine needles, hardwood leaves and other (wood, bark, flowers, seeds etc.). Needle litter consisted of both loblolly and Virginia pine needles.

Both foliage and litter samples were dried at $70^{o}C$ for two days and weighed. Monthly litter weights (from March to February of the next year) were summed to calculate annual litter production for each plot. For example, litter collected between March 1998 and February 1999 represented 1998 litterfall (1997 foliar production), and so on. However, there was no litter collection before July 1998 and 1998 litterfall was annualized based on 1999 and 200 data that showed that the July-February season accounted for 94% of annual needle production, 98% of the annual leaf production, and 72% of the other litter fractions.

Litter nutrient N and P contents were calculated by multiplying N and P concentrations with litter weight for each collection, and individual collection contents were summed to estimate annual contents. Then, the annual contents were divided by annual litter weight to calculate mean concentrations.

Foliar N and P uses for both pine and hardwoods were calculated by multiplying annual foliar production and N and P concentrations in fresh foliage. Retranslocation of N and P was calculated by the difference between fresh foliar content and litter content, and expressed as a percentage. This calculation is actually a difference between concentrations in the green and brown foliage, assuming weight of the foliage does not change during translocation.

Laboratory Analysis

Dried foliage and litter samples (at 70^{o}C for two days) were ground to pass through a 1-mm screen. Ground samples were then analyzed for N and P concentrations. Samples collected before November 1998 were digested in sulfuric acid/hydrogen peroxide mixture (Parkinson and Allen 1975). Concentration N was determined colorimetrically by a Lachat autoanalyzer (QuikChem 8000, Zellweger Analytics, Inc., Milwaukee, WI), and concentration of P was determined by an inductively coupled plasma atomic emission spectrometer (ICP-AES, Varian ICP, Liberty series 2, Varian Analytical Instruments, Walnut Creek, CA). However, samples collected after November 1998 were analyzed differently. Nitrogen concentration was determined by a CHN elemental

analyzer (CE Instruments - NC 2100, CE Elantech Inc., Lakewood, NJ), which uses a dry combustion technique, while concentration of P was determined by ICP-AES after nitric acid digestion (Zarcinas et al. 1987). For all analyses, ten percent sample duplication and the pine standard from the National Institute of Standards and Technology (standard reference material no. 1575) were used for quality control.

Statistical Analysis

Analyses of variance were used to test treatment effects on diameter, height, basal area and volume growth, foliar N and P concentrations, litter weights, litter N and P concentrations and contents, foliar N and P use and retranslocation, separately for each year and for both pine and competing vegetation. Significance was accepted at $p \leq 0.05$ for all analysis, and ANOVA results are presented in the appendix. Relationship between pine litterfall, N use and volume growth were also examined with regression analysis.

RESULTS

Foliage Nutrient Concentrations

Pretreatment (1998) foliar nutrient concentrations were 11.7 g kg^{-1} for N and 1.11 g kg^{-1} for P for loblolly pine with no significant difference among treatments (table 1). For the next two years; however, both N and P concentrations were increased by fertilizer

application. The increase was especially large one year after the application, reaching up to 32% for N and 18% for P for the combination treatment. Effects of vegetation control on foliar N and P concentrations were significant only in 1999. There was no pretreatment foliar data available for hardwoods, and for the following years, fertilizer effect on hardwood foliar N and P concentrations was not significant.

Leaf Area Index

Leaf area index (LAI) values ranged from 1.7 to 2.4 m^2 m^{-2} at the first measurement in April 1998 (figure 1). LAI increased due to new foliage production during the spring, reaching a peak in July and August. The increase was especially dramatic where hardwoods were present (C and F treatments), reaching up to 7 m^2 m^{-2}. There was a strong reduction in total LAI due to vegetation control ($p<0.001$), while fertilization had no significant effect.

Peak pine LAI values ranged from 2.3 to 3.2 over the three years and did not differ among treatments (table 2). There was a general trend for increasing leaf area over the three years for all treatments, and, individually, C, F, VC, and CV+F treatments had 15, 15, 31 and 41% greater LAI's, respectively, in 2000 than in 1998. Hardwood leaf area ranged from 2.8 to 4.2 over the three years, with no significant fertilizer effect at any year. In addition, hardwoods appeared to produce equal or more leaf area as loblolly pine, even though they made up a rather small amount of total stand basal area.

Litter Production

Annual production of needle biomass ranged from 3129 to 5084 kg ha^{-1} across all treatments and years, with no significant treatments effects (table 3). Over the years; however, greater amounts of litter were produced by all treatments, and the increases from 1998 to 2000 were 16, 22, 34, and 64% for C, F, VC and VC+F treatments, respectively. Annual production of hardwood leaf litter ranged from 841 to 1415 for all three years, with no significant response to fertilization.

When all litter types were included, vegetation control significantly reduced total litter production by 31% for the first year. The reduction was significant for all three years, but the magnitude was decreased over time. Over the three years, needle litter accounted for the majority of the total litterfall, 67% where competing vegetation was left intact, and 91% where vegetation control was performed.

Litter Nutrient Concentrations and Contents

Needle litter N and P concentrations ranged from 4.4 to 7.4 and 0.3 to 0.6 g kg^{-1}, respectively, for the first year and were increased by both vegetation control and fertilization treatments (table 4). The combination treatment increased N and P concentration by 68 and 100%, respectively. Similar treatment effects were observed for the following two years, however the magnitude of the increase was reduced for nitrogen.

Needle N and P contents ranged from 16.0 to 23.0 and 1.1 to 1.9 kg ha^{-1}, respectively, for the first year and were increased by both treatments. For the following two years, similar treatment effects were observed and the combination treatment resulted in the greatest increase compared to the control, increasing up to 58% for N and 114% for P in 2000.

Hardwood leaf N and P concentrations were 7.6 and 0.5 g kg^{-1} for the control during the first year and were significantly increased by up to 32 and 40%, respectively, after fertilization. For the following two years, similar increases were observed; however, the increases were not always significant. Hardwood litter contained 7.5 and 0.5 kg ha^{-1} N and P, respectively, in control plots in 1998. Similar to concentration responses, fertilization increased N and P contents up to 89% for N in 1998 and 120% for P in 2000 compared to the control.

Foliar Nutrient Use and Retranslocation

Foliar N use and P use ranged from 36.0 to 42.8 and 3.5 to 4.1 kg ha^{-1} yr^{-1}, respectively, for loblolly pine in year 1997 (pretreatment) with no significant difference among treatments (table 5). Fertilization had a positive significant effect on both variables in the following years. The greatest effect was observed in the combination treatment, resulting in an interaction between VC and F and increasing both N use and P use up to 49 and 40%, respectively, in 2000 compared to the control treatment.

There were no pretreatment measurements of fresh hardwood leaf nutrient concentrations; therefore, we couldn't estimate hardwood N and P uses for 1997. In the following years, annual nutrient use ranged from 10.3 to 20.9 kg ha^{-1} for N and 0.9 to 2.4 kg ha^{-1} for P, with no significant treatment effects.

During the first year after treatment (1998), retranslocation of N and P ranged from 40 to 63% and 48 to 72%, respectively, for loblolly pine (table 6). Both vegetation control and fertilization resulted in reduced retranslocation of N and P in this year and the treatment effects were additive. During the following two years, N retranslocation ranged from 63 to 68%, with no significant difference among treatments. However, P retranslocation ranged from 56 to 72% and the negative effects of fertilization were still evident. Retranslocation of N and P in hardwoods was not significantly affected by fertilization. In addition, hardwoods appeared to retranslocate somewhat less N than loblolly pine for all years.

Vegetation Growth

Pretreatment stand characteristics, annual growth over 3 years and treatment responses compared to control are shown in table 7. Pretreatment diameter, height, basal area and volume were similar for all treatments for loblolly pine. Fertilization had positive significant effects on all four growth parameters, while vegetation control had no significant effect. Response to fertilization was greatest for diameter growth (up to a 57% increase) and smallest for height growth (up to 16%). Three-year mean annual volume

growth was 20 m^3 ha^{-1} yr^{-1} in untreated control plots, and it was increased by up 7 m^3 ha^{-1} yr^{-1} (32%) after fertilization. Three-year growth efficiencies were also increased from 7.5 and 7.3 in C and VC to 9.9 and 8.8 m^3 ha^{-1} yr^{-1} in F and VC+F treatments, respectively (table 2). Pretreatment characteristics of the competing vegetation were also similar in the different treatments and the treatments did not result in a significant increase in growth over the next three years.

Volume, Litterfall and Foliar Nutrient Use Relationships

There was a significant ($p<0.001$, $R^2 = 0.64$) positive relationship between stem volume production and annual needlefall for pines (figure 2a). Similarly, the relationship between volume growth and annual needle N use ($p<0.001$, $R^2 = 0.64$, figure 2b) and P use ($p<0.001$, $R^2 = 0.69$) were also highly significant.

DISCUSSION

Foliage Nutrient Concentrations

Pretreatment loblolly pine foliar N and P concentrations were 11.7 and 1.11 g kg^{-1}, respectively (table 1). These concentrations were slightly above the critical values (11.0 and 1.10 g kg^{-1} for N and P, respectively) proposed for loblolly pine (Allen 1987), indicating marginal deficiencies for these nutrients. Following N and P additions, foliar

concentrations of these nutrients increased significantly, especially where competing vegetation was controlled. Similar increases after fertilization were also shown by others in 9- to 14-year-old loblolly pine plantations (Adams et al. 1987, Valentine and Allen 1990). Also, a positive pine response to vegetation control alone was observed in the second year of this study, but disappeared in the following year. This lack of consistency in pine response to vegetation control may be due to the fact that mid- to late-rotation stands already have a 'tight' nutrient budget (Miller et al. 1979) and eliminating competition may not increase inherent site resource availability enough to meet the already high nutrient demand by crop pines. A similar response to vegetation control was also shown by Zutter et al. (1999), who reported that loblolly pine foliar N concentration and content were increased after herbaceous and woody control at age 2, but later diminished by age six. This diminishing response is perhaps due to the fact that soil N availability (measured as net N mineralization) is high at stand establishment and declines rapidly as stands reach canopy closure. Piatek and Allen (1999) reported that net N mineralization in the surface 15 cm of mineral soil was almost 3 times greater a year after site preparation than at 14 years of age (77 vs. 28 kg ha^{-1} between May and November) in a Piedmont site. In this study, vegetation control alone did not have an effect on net N mineralization at midrotation (chapter 1). In addition, extractable soil N contents averaged at 1.8, 4.0, 2.5 and 7.1 kg ha^{-1} for C, F, VC and VC+F treatments, respectively, over 25 months (chapter 1) and, in general, corresponded well with the observed changes in foliar N concentrations. In fact, average extractable soil N contents

for 1998 accounted for 75% of the variation (p=0.003) in N concentrations of foliage produced in that year (data not shown).

Leaf Area Index and Litter Production

Peak LAI of loblolly pine ranged from 2.3 to 3.2 m^2 m^{-2} (with an additional 2.8 to 4.2 m^2 m^{-2} for hardwoods) over three years although there were no significant difference among treatments (table 2). These observed LAI values are lower than the optimal levels for maximum production (Vose and Allen 1988). Similar to LAI estimates, annual needle litter production did not differ greatly due to treatments and ranged from 3129 to 5084 kg ha^{-1}, levels that are comparable to values reported by Wells and Jorgensen (1975), Lockaby et al. (1995) and Piatek and Allen (2000) for loblolly pine stands of similar basal areas.

The lack of leaf area response to the treatments, particularly to fertilization, was also indicative of 'marginal' nutrient deficiency. Albaugh et al. (1998) reported substantial increases in LAI after 'complete' fertilization (up to 101%) on a poor sandy site in NC, and Vose and Allen (1991) reported that needlefall response to N fertilization was as large as 75% on N-deficient sites, while productive sites did not respond at all, indicating that the inherent site productivity is an important factor in determining responsiveness to treatments. In addition, leaf area development in response to the treatments is not immediate and may require several year. In fact, percent increase over three years revealed that LAI was increased 11, 15, 31 and 41% in C, F, VC and VC+F treatments,

respectively, from year 1998 to 2000. Corresponding values for annual needlefall were 16, 22, 34 and 64 percent (table 3). In both cases, percent increases were significantly affected by vegetation control ($p=0.011$ for peak LAI, $p=0.022$ for litterfall). In addition, height-to-live crown (distance to lowest live branch from the ground) for trees in vegetation control plots was increasing more slowly than those in no-vegetation control plots (data not shown), indicating that trees retained their lower branches in response to vegetation control. Assuming this trend continues for another couple of years, VC and especially VC+F treatments would produce significantly greater foliar biomass in the near future.

Litter Nutrient Concentrations and Contents

Annual N and P transfer to the forest floor through litterfall ranged from 14.7 to 28.5 kg ha^{-1} for N and 1.1 to 3.0 kg ha^{-1} for P over three years (table 4), similar to values reported by Piatek and Allen (2000). Wells and Jorgensen (1975) also reported litter N and P transfer of as large as 53 and 8 kg ha^{-1} N and P, respectively, but those values corresponded to higher basal area (up to 49 m^2 ha^{-1}) stands. Hardwoods added another 6.0 to 14.2 kg ha^{-1} of N and 0.4 to 1.1 kg ha^{-1} of P to transfer in this site. For both needle and hardwood leaf litterfall, increased transfer rates were observed after fertilizer application, indicating larger cycling of nutrients in fertilized plots. Perhaps, the greater recycling of these added nutrients between vegetation and soil could be expected to have an impact on long-term response to fertilization (Finer 1996) and can explain, to some extent, why growth response to fertilization can last up to 10 years (Allen 1987, Binkley et al. 1995).

At this site, one time fertilizer application did not affect nutrient release dynamics of N and P from decomposing needles of pretreatment cohort (chapter 2), but per-acre N and P turnover may be increased due to greater transfer to the forest floor after fertilization. Fine material that passed through the litter traps (which was not estimated here) can also account for a significant part of total nutrient transfer to the forest floor. Wells and Jorgensen (1975) reported that this fine material accounted for about 5% of the total litter weight, but contained 20% of the N and 12% of the phosphorus.

Foliar Nutrient Use and Retranslocation

Retranslocation serves as an important source of nutrients for newly developing foliage and shoots (Zhang and Allen 1996), and it may be especially important for trees growing on poor sites (Miller et al. 1979). In control plots of this study, annual needle N and P uses (3-year average) were about 47.1 and 4.3 kg ha^{-1} (table 5) and. retranslocation was 66 and 72% for N and P (table 6), respectively, accounting for 31.1 kg ha^{-1} yr^{-1} N and 3.1 kg ha^{-1} yr^{-1} P. Similar rates of uses and retranslocations were also reported by others (Zhang and Allen 1996, Piatek and Allen 2000). The significance of internal cycling was also reported by Switzer and Nelson (1972), who estimated that a 20-year-old loblolly pine stand required 69.2 and 5.5 kg ha^{-1} N and P, respectively, and retranslocation contributed to 39 and 60% of the requirement for aboveground biomass. In this study, foliar N and P uses were increased up to 49 and 40%, respectively, after fertilization, especially where competition was controlled. Retranslocation percentages of both nutrients were reduced significantly within the first year by both treatments and,

afterwards, only P retranslocation was reduced by fertilization. However, since foliar contents were higher after fertilization, absolute (kg ha^{-1}) retranslocation was either equal or sometimes even higher in fertilized plots. The reduction in percent retranslocation may be partially due to premature needlefall in fertilized and/or vegetation controlled plots (Vose and Allen 1991). In fact, in July 1998, litter N content was three times larger in vegetation control and the combination treatments. This kind of effect was not observed during the rest of the study.

Foliar nutrient requirement supplied from the soil can be estimated as the difference between "use" in the current year and "retranslocation" form the previous year. This estimate roughly equals "transfer to litter" under steady state conditions. That means, what is lost through litterfall during previous year must be supplied from the soil in the following year. If this assumption holds, soil supply is needed at approximately 16, 20, 18 and 25 kg ha^{-1} yr^{-1} N (what is transferred to litter annually over three years) for C, F, VC, VC+F treatments, respectively. For the same treatments, annual net N mineralization rates were 19, 18, 31 and 78 kg ha^{-1}, respectively, in the top 10 cm of the mineral soil (chapter 1). The similarity in ranking between these values may indicate that cycling of N between vegetation and soil appears to be limited by N cycle within the soil. Therefore, it is not surprising that some studies (Vitousek et al. 1982) reported positive relationships between soil N availability and litterfall N transfer to soil.

Vegetation Growth, Litterfall and Foliar N Use Relationships

Only fertilization had a positive effect on loblolly pine growth parameters, while there were no vegetation control or VC*F interaction effects (table 7). Three-year mean annual stem volume growth was 20 m^3 ha^{-1} yr^{-1} in control plots, while fertilization resulted in an additional 5 to 7 m^3 ha^{-1} yr^{-1} increase (22-32%). This response is typical for N or N+P fertilization, which commonly ranges from 2 to 8 m^3 ha^{-1} yr^{-1} and lasts up to 10 years or more (Allen 1987, Binkley et al. 1995, Williams and Farrish 2000). These growth rates are still much lower than the maximum reported values for loblolly pine (up to 37 m^3 ha^{-1} yr^{-1}) grown at various locations throughout the world (Borders and Bailey 2001), indicating the actual production at this site may be below potential productivity.

Positive response to fertilizers is perhaps due to several factors, including soil and physiological factors. In this study, soil extractable N pools were increased dramatically by fertilization, and effects lasted at least a year (chapter 1). Increased soil N pools were also reflected in the foliar N concentrations. Up to 75% of the foliar N is in enzyme proteins and located in chloroplasts (Marschner 1986). Therefore, increased foliar N concentrations can have a direct positive effect on photosynthetic efficiency. Murthy et al. (1996) reported that fertilization resulted in 24% increase in light-saturated net photosynthesis (A_{max}) of foliage of field grown loblolly pine trees. In addition, N fertilization was shown to increase foliar water potential (Tang et al. 1999, Woods et al. 1992, Sheriff 1996), which can also influence photosynthesis, cell expansion and leaf area development.

Since peak LAI did not change due to the treatments in all three years, perhaps photosynthetic efficiency may have played an important role in observed growth differences among treatments. In fact, stem volume growth per unit of leaf area (growth efficiencies, GE) were 7.7, 7.3, 10.1, and 8.8 m^3 ha^{-1} yr^{-1} in C, VC, F and VC+F treatments, respectively, and significantly increased by about 32% due to fertilization ($p=0.002$). Similarly, Albaugh et al. (1998) reported that stem volume GE was increased from 7.1 in untreated control plots to 9.2 where repeated "complete" fertilization applied. However, in addition to photosynthetic efficiency, GE is also a function of allocation; greater allocation to stemwood versus roots results in greater stem volume GE, even when photosynthetic efficiency is the same. Many studies (Albaugh et al. 1998, Cannell 1989) have reported higher allocation to stemwood in fertile sites than in poor sites in the expense of allocation to fine roots. While there were no significant treatment effects on LAI, there still was a strong positive relationship between needlefall and annual pine volume growth based on individual plot values ($r^2=0.64$, $p=<0.001$). Similar relationship was also observed between stem volume growth and foliar N use, which incorporated both foliar biomass (i.e. needlefall) and foliar N concentration.

Although, negative relationship between pine yield and competing vegetation amounts was shown by several researchers (Fredericksen et al. 1991, Fortson et al. 1996, Shelton and Murphy 1997, Schabenberger and Zedaker 1999), our results indicated no pine response to vegetation control. This was perhaps due to several factors. Most of these

reports come from early rotation stands where pines are more susceptible to stresses induced by competing vegetation. Young pines can be overtopped by fast growing hardwood sprouts and herbaceous vegetation; however, this shouldn't be a problem at our site since pines were in dominant position. In addition, competition induced water stress is well documented (Zutter et al. 1986, Woods et al 1992, Ludovici and Morris 1997), and pines are responsive to vegetation control where water is limited (Powers and Reynolds 1999); however, at our site we found no increase in soil moisture content due to vegetation control (chapter 1). Seasonal distribution of precipitation is fairly uniform (8.4 to 11.2 cm per month), and clay loam soils have good water holding capacity; therefore, water stress should not be a big concern in this site. Water manipulation through vegetation control and thinning may be more beneficial on soils with lower water holding capacity and seasonal precipitation deficits. Nutritional stress must be the major concern for this site, and vegetation control failed to ameliorate this problem. Foliar N and P concentration were only slightly increased by vegetation control (only in 1999) while leaf area, foliar N and P use were not affected at all. Also, vegetation control had either slight or no significant effects on either extractable N or annual rates of net N mineralization in the top 10 cm of the mineral soil (chapter 1). In addition, vegetation control can only make the potential availability of site recourses (per tree) larger, but trees still need to spend time and energy to reach and exploit that resource. Lastly, adverse effects of applied herbicides can diminish any possible response to vegetation control (Williams and Farrish 1994, Quicke et al. 1996). In fact, several trees died within a few months after

herbicide application, and others showed some signs of stress (i.e., yellowing of needles) for the first growing season in this study.

CONCLUSIONS

Midrotation fertilization in established stands should be an attractive silvicultural option where wood production is the main management objective and nutritional stress is of concern. Our three-years results showed a strong positive growth response to N+P fertilization (5 to 7 m^3 ha^{-1} yr^{-1}) at age 14, and the response was attributed mainly to greater growth efficiency, which was perhaps increased by higher foliar N and P concentrations and use after fertilization. The growth response to midrotation fertilization usually persists for up to 10 years, perhaps due to greater recycling of added nutrients within plants and between plant and soil.

Early-rotation vegetation control has proven to be an important tool to improve growth of pines, however, response to midrotation vegetation control is still not clear. Our result indicated no positive growth response to vegetation control over three years, and it was attributed mainly to lack of increase in soil water content and foliar nutrient use and also to adverse effect of herbicide applications on crop pines. Effects of fertilization on pine growth were similar with or without vegetation control, which indicated that fertilizer application is beneficial even when hardwood component makes up about 30% of the

total stand basal area. Therefore, fertilization should receive a more direct attention than vegetation control to ameliorate limiting site resources, except on most droughty sites.

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Table 1. Foliar N and P concentrations for loblolly pine and hardwoods in a 14-year-old loblolly pine plantation.

Treatment	1998 (pretreatment)		1999		2000	
	N	P	N	P	N	P
	---------- g kg^{-1} ----------					
Loblolly						
C	11.8	1.11	12.9	1.08	12.5	1.18
F	11.8	1.09	14.8	1.17	14.2	1.31
VC	11.2	1.09	13.7	1.15	12.1	1.15
VC+F	12.2	1.15	17.0	1.33	15.4	1.38
Root MSE	0.54	0.05	0.91	0.03	1.12	0.07
Hardwood						
C			13.4	1.05	13.1	1.18
F	not available		14.7	1.33	16.1	1.86
Root MSE			2.76	0.09	0.67	0.12

Table 2. Peak leaf area index for pine[1] and hardwoods[2,] and three-year growth efficiencies in a 14-year-old loblolly pine plantation.

Treatment	1998	1999	2000	GE[3]
	----------	m^2 m^{-2}	----------	m^3 ha^{-1} yr^{-1}
Pine				
C	2.59	2.55	2.88	7.5
F	2.48	2.69	2.85	10.1
VC	2.42	2.56	3.16	7.3
VC+F	2.28	2.71	3.22	8.8
Root MSE	0.37	0.35	0.23	0.7
Hardwood				
C	3.18	2.79	3.12	
F	4.08	3.33	4.19	
Root MSE	0.42	0.28	0.49	

[1] LAI for C and F was estimated from a regression developed for VC and VC+F.
(Litter weight $_{(kg/ha)}$ = 1432 * LAI $_{(pine)}$ – 70, r^2=0.73)
[2] LAI for hardwoods was calculated by subtracting estimated pine LAI from "total" LAI from Li-Cor.
[3] GE is stem volume growth per unit of leaf area.

Table 3. Annual production of needle and leaf litter, and total litter production including all types of litter in a 14-year-old loblolly pine plantation.

Treatment	1998	1999	2000
	---------- kg ha^{-1} yr^{-1} ----------		
Pine			
C	3649	3556	4216
F	3415	3831	4150
VC	3202	3424	4282
VC+F	3129	3869	5084
Root MSE	499	429	392
Hardwood			
C	1000	876	841
F	1415	1261	1295
Root MSE	231	292	282
All litter types[1]			
C	4771	5889	5842
F	5189	6219	6165
VC	3339	4081	4644
VC+F	3283	4501	5494
Root MSE	579	525	429

[1] Include pieces of wood, bark, flowers, seeds, etc., as well as needle and leaf litter.

Table 4. Litter N and P concentrations and contents for pine and hardwoods in a 14-year-old loblolly pine plantation.

Treatment	1998				1999				2000			
	N		P		N		P		N		P	
	g kg^{-1}	kg ha^{-1}	g kg^{-1}	kg ha^{-1}	g kg^{-1}	kg ha^{-1}	g kg^{-1}	kg ha^{-1}	g kg^{-1}	kg ha^{-1}	g kg^{-1}	kg ha^{-1}
Pine												
C	4.4	16.0	0.3	1.1	4.1	14.7	0.3	1.1	4.3	18.0	0.3	1.4
F	5.5	18.9	0.4	1.4	5.1	19.3	0.5	1.9	4.9	20.4	0.6	2.3
VC	5.9	18.7	0.5	1.5	4.7	15.9	0.4	1.4	4.5	19.1	0.4	1.6
VC+F	7.4	23.0	0.6	1.9	5.9	22.8	0.6	2.1	5.6	28.5	0.6	3.0
Root MSE	0.5	1.8	0.05	0.2	0.4	1.2	0.03	0.2	0.1	1.8	0.03	0.3
Hardwood												
C	7.6	7.5	0.5	0.5	6.9	6.0	0.5	0.4	7.4	6.3	0.6	0.5
F	10.0	14.2	0.7	0.9	8.3	10.4	0.7	0.9	8.4	10.7	0.9	1.1
Root MSE	0.7	1.1	0.04	0.1	0.7	1.5	0.12	0.1	0.7	1.8	0.02	0.2

Table 5. Foliar nutrient use[1] for pine and hardwoods in a 14-year-old loblolly pine plantation.

Treatment	1997 (pretreatment)		1998		1999	
	N	P	N	P	N	P
	kg ha^{-1} yr^{-1}					
Pine						
C	42.8	4.1	45.8	3.8	52.6	5.0
F	40.1	3.7	56.4	4.5	58.5	5.4
VC	36.0	3.5	46.7	3.9	51.5	4.9
VC+F	38.4	3.6	66.1	5.2	78.4	7.0
Root MSE	6.7	0.6	5.6	0.5	5.4	0.5
Hardwood						
C			11.2	0.9	10.3	0.9
F	not available		18.5	1.7	20.9	2.4
Root MSE			7.9	0.4	1.5	0.4

[1] Use $_{year\ (i)}$ = Foliar Concentration $_{year\ (i)}$ x Litter production $_{year\ (i+1)}$.

Table 6. Foliar N and P retranslocation[1] for pine and hardwoods in a 14-year-old loblolly pine plantation.

Treatment	1998		1999		2000	
	N	P	N	P	N	P
	%					
Pine						
C	63	72	68	71	66	72
F	53	62	66	58	65	56
VC	47	57	66	65	63	69
VC+F	40	48	65	58	63	57
Root MSE	6.0	2.6	2.6	2.8	2.8	3.7
Hardwood						
C			48	55	45	56
F	not available		41	47	48	52
Root MSE			17.1	4.4	4.4	2.4

[1] Retranslocation = (foliar content – litter content) / foliar content.

Table 7. Pretreatment diameter, height, basal area and volume, annual growth over 3 years, and percent increase compared to control for loblolly pine and competing vegetation (includes both Virginia pine and overstory hardwoods) in a 14-year-old loblolly pine plantation.

Treatment	Diameter			Height			Basal Area			Volume		
	1998[1]	Growth[2]	Response[3]	1998	Growth	Response	1998	Growth	Response	1998	Growth	Response
	(cm)	(cm yr^{-1})	%	(m)	(m yr^{-1})	%	(m^2 ha^{-1})	(m^2 ha^{-1} yr^{-1})	%	(m^3 ha^{-1})	(m^3 ha^{-1} yr^{-1})	%
Loblolly												
C	17.7	0.46	-	13.4	0.69	-	25.6	1.40	-	178	20.3	-
F	17.6	0.69	51	13.7	0.80	16	24.4	2.02	45	173	26.8	32
VC	17.1	0.49	7	13.6	0.68	-2	23.7	1.44	3	169	20.0	-2
VC+F	18.0	0.72	57	14.0	0.78	12	22.4	1.92	37	161	24.7	22
Root MSE	0.50	0.03		0.47	0.04		2.37	0.12		22.2	2.25	
Competing Vegetation												
C	9.4a	0.15a	-	10.2a	0.45a	-	3.0a	0.10a	-	17.2	1.4	-
F	9.0a	0.26a	67	10.3a	0.43a	-6	3.4a	0.20a	95	19.4	2.0	47
Root MSE	2.17	0.04		0.62	0.01		1.91	0.08		12.7	1.06	

[1] Represents pretreatments conditions.
[2] Growth means 3-year mean annual increment.
[3] Response = $(growth_{treatment(i)} - growth_{control}) / growth_{control} * 100$.

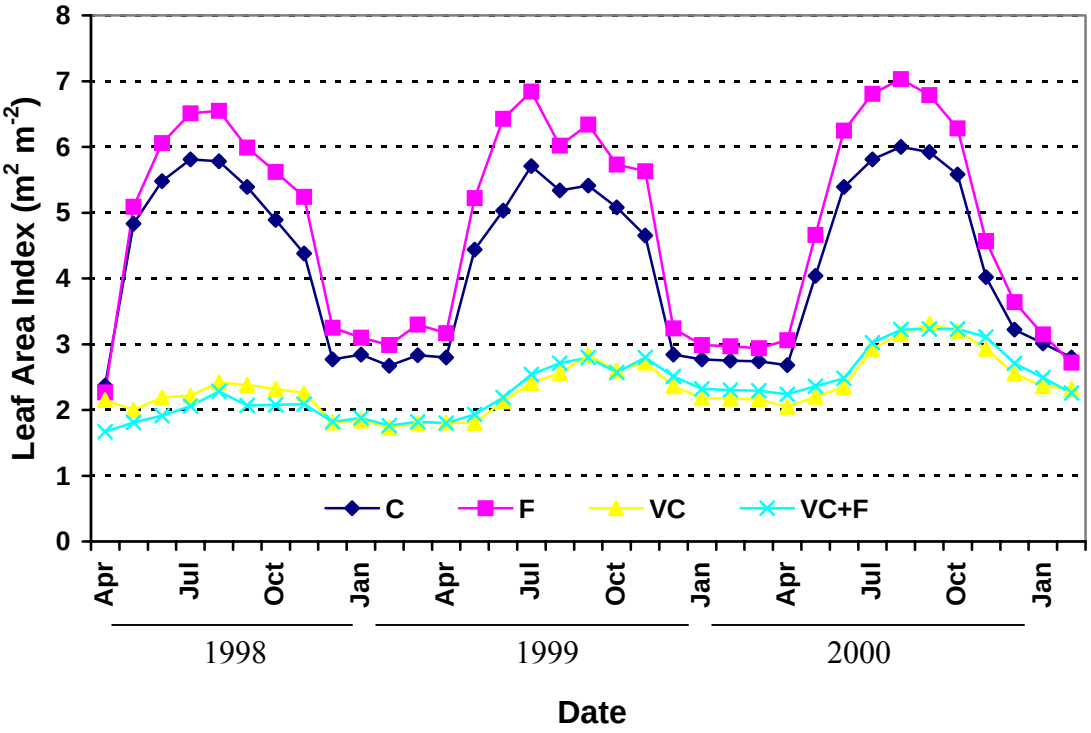

Figure 1. Seasonal leaf area index dynamics for a midrotation loblolly pine stand (LAI for C and F includes both pine and competing vegetation, VC and VC+F includes only pine).

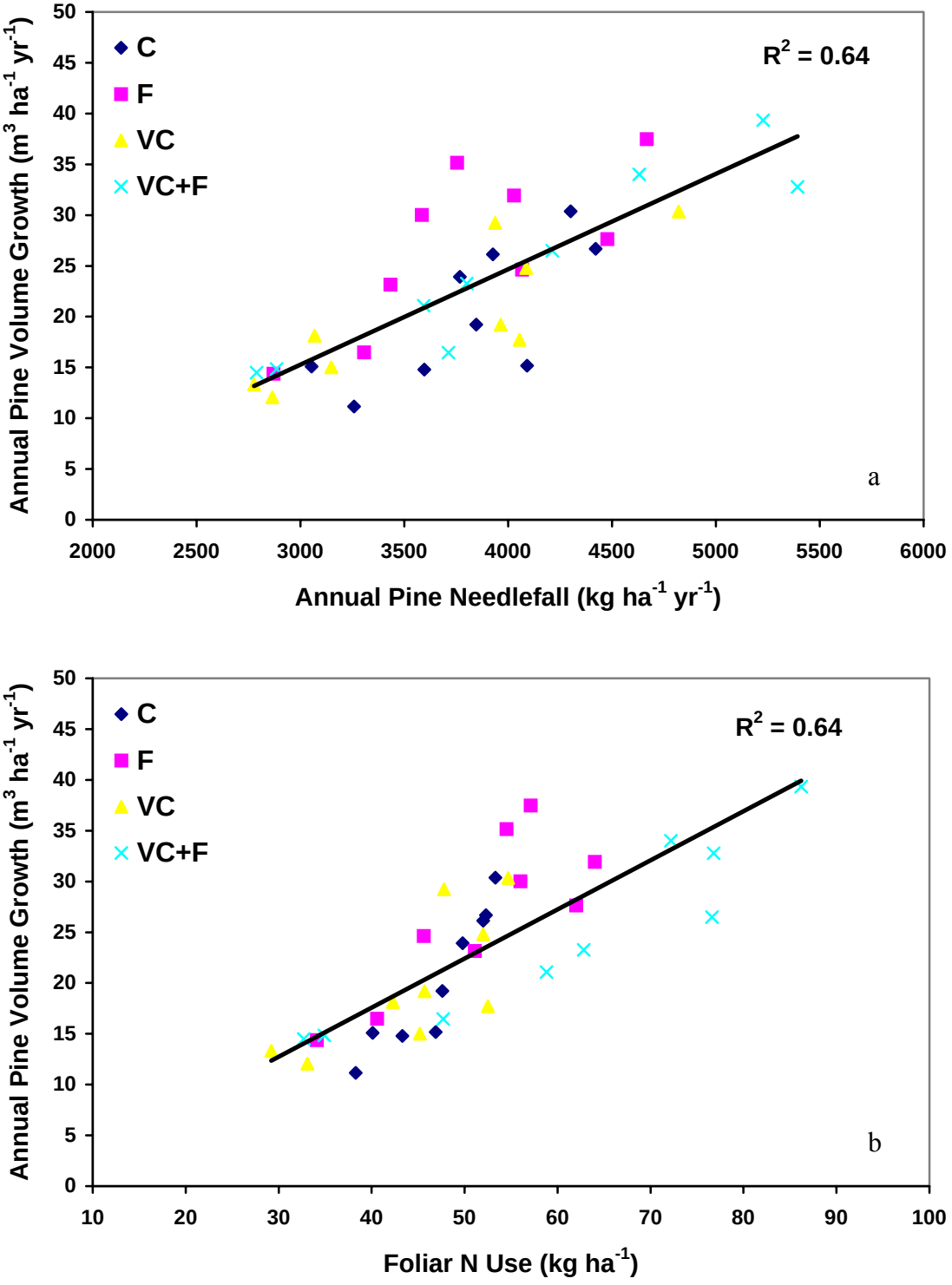

Figure 2. Relationship between annual volume growth and needlefall (a), and volume growth and foliar N use (b) in a 14 year-old loblolly pine plantation.

APPENDIX

This appendix includes analysis of variance tables for foliar and liter nutrient concentrations and contents, foliar nutrient use and retranslocation, leaf area and litterfall, and 3-year growth variables.

Table 1. P values for foliar N and P concentrations for loblolly pine and hardwoods in a 14-year-old loblolly pine plantation.

Source	1998		1999		2000	
	N	P	N	P	N	P
Loblolly						
Replication	0.590	0.288	0.972	0.355	0.289	0.094
VC	0.848	0.568	**0.028**	**<0.001**	0.560	0.617
F	0.136	0.502	**0.003**	**<0.001**	**0.008**	**0.005**
VC*F	0.156	0.253	0.224	**0.034**	0.249	0.256
Hardwood						
Replication	-	-	0.531	0.722	0.384	0.869
F	-	-	0.992	0.198	0.127	0.111

Table 2. P values for peak leaf area index for pine and hardwoods and three-year growth efficiencies in a 14-year-old loblolly pine plantation.

Source	1998	1999	2000	GE
Pine				
Replication	0.503	0.959	0.617	0.185
VC	0.422	0.939	0.060	0.055
F	0.569	0.559	0.911	**0.002**
VC*F	0.959	0.994	0.738	0.295
Hardwood				
Replication	0.642	0.285	0.966	
F	0.150	0.089	0.194	
All Leaf Area				
Replication	0.314	0.675	0.691	
VC	**<0.001**	**<0.001**	**<0.001**	
F	0.306	0.129	0.066	
VC*F	0.155	0.296	0.096	

Table 3. P values for annual production of needle and leaf litter, and total litter production including all types of litter in a 14-year-old loblolly pine plantation.

Source	1998	1999	2000
Pine			
Replication	0.219	0.223	0.324
VC	0.250	0.856	0.069
F	0.614	0.196	0.155
VC*F	0.789	0.744	0.103
Hardwood			
Replication	0.779	0.875	0.849
F	0.158	0.248	0.188
All Litter			
Replication	0.167	0.153	0.459
VC	**0.003**	**0.001**	**0.009**
F	0.609	0.263	0.056
VC*F	0.505	0.886	0.329

Table 4a. P values for litter N and P concentrations for pine and hardwoods in a 14-year-old loblolly pine plantation.

Source	1998		1999		2000	
	N	P	N	P	N	P
Pine						
Replication	0.745	0.222	0.729	0.435	0.260	0.259
VC	**<0.001**	**<0.001**	**0.026**	**0.005**	**<0.001**	0.143
F	**0.003**	**0.004**	**0.005**	**<0.001**	**<0.001**	**<0.001**
VC*F	0.598	0.711	0.609	0.393	**0.009**	0.943
Hardwood						
Replication	0.727	0.113	0.892	0.455	0.334	**0.016**
F	**0.044**	**0.032**	0.126	0.144	0.232	**0.004**

Table 4b. P values for litter N and P contents for pine and hardwoods in a 14-year-old loblolly pine plantation.

Source	1998		1999		2000	
	N	P	N	P	N	P
Pine						
Replication	**0.033**	0.064	**0.033**	0.639	0.455	0.409
VC	**0.018**	**0.023**	**0.014**	0.080	**0.004**	0.060
F	**0.013**	**0.050**	**<0.001**	**0.001**	**0.001**	**<0.001**
VC*F	0.545	0.826	0.147	0.915	**0.012**	0.190
Hardwood						
Replication	0.368	0.327	0.813	0.690	0.650	0.819
F	**0.016**	**0.036**	0.068	**0.031**	0.095	**0.048**

Table 5. P values for foliar nutrient use for pine and hardwoods in a 14-year-old loblolly pine plantation.

Source	1997 (pretreatment)		1998		1999	
	N	P	N	P	N	P
Pine						
Replication	0.344	0.204	0.161	0.249	0.956	0.589
VC	0.312	0.361	0.151	0.185	**0.023**	**0.044**
F	0.971	0.764	**0.003**	**0.012**	**0.002**	**0.007**
VC*F	0.524	0.595	0.218	0.315	**0.015**	**0.036**
Hardwood						
Replication	-	-	0.899	0.762	0.206	0.567
F	-	-	0.505	0.272	0.071	0.142

Table 6. Foliar N and P retranslocation for pine and hardwoods in a 14-year-old loblolly pine plantation.

Source	1998		1999		2000	
	N	P	N	P	N	P
Pine						
Replication	0.745	0.146	0.683	0.569	0.462	0.375
VC	**0.006**	**<0.001**	0.389	0.103	0.225	0.503
F	**0.046**	**<0.001**	0.441	**<0.001**	0.969	**<0.001**
VC*F	0.745	0.610	0.587	0.074	0.750	0.424
Hardwood						
Replication	-	-	0.692	0.250	0.492	0.258
F	-	-	0.644	0.867	0.406	0.855

Table 7. P values for pretreatment diameter, height, basal area, volume, and 3-year growth variables for loblolly pine and competing vegetation (includes both Virginia pine and overstory hardwoods) in a 14-year-old loblolly pine plantation.

Source	Diameter		Height		Basal Area		Volume	
	1998	Growth	1998	Growth	1998	Growth	1998	Growth
Loblolly								
Replication	**0.002**	0.129	0.061	0.250	0.055	0.160	0.064	0.133
VC	0.769	0.158	0.416	0.419	0.197	0.622	0.450	0.405
F	0.237	**<0.001**	0.296	**0.005**	0.383	**<0.001**	0.662	**0.005**
VC*F	0.128	0.927	0.978	0.798	0.961	0.344	0.911	0.536
Competing Vegetation								
Replication	0.952	0.441	0.384	0.079	0.723	0.757	0.792	0.831
F	0.848	0.101	0.851	0.171	0.840	0.275	0.853	0.535