NUTRIENT DYNAMICS OF THE SOIL/PLANT/MICROBIAL SYSTEM OF A YOUNG LOBLOLLY PINE PLANTATION: EFFECTS OF FERTILIZER DATE OF APPLICATION AND FORMULATION

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Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the degree of
DOCTOR OF PHILOSOPHY
August, 2003

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SYSTEM OF A YOUNG LOBLOLLY PINE PLANTATION:

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ACKNOWLEDGEMENTS

I would like to express my gratitude to Dr. Thomas Hennessey, my major adviser, for his guidance and support throughout my studies at this university. I also thank Drs. Robert Wittwer, Tom Lynch, William Raun, and Shiping Deng for their advice, assistance, and encouragement. I also appreciate the invaluable input and advice of Drs. Phil Dougherty, Robert Campbell, and Venkatesh Kumar, who have all been highly influential in the creation and completion of this project. Furthermore, the efforts of Bob Heinemann, Dennis Wilson, Randy Holeman, Keith Anderson, and Walt Sanders in conducting the field work in Haworth were very helpful. I also appreciate the assistance of Ed Lorenzi, Paul Lowe, Don Vosburg, Scott Mostoller, and Andy Laviner in carrying out the lab work.

I am very grateful to the Oklahoma State University Department of Forestry for the opportunity to pursue graduate studies at this university and for bestowing me with a research assistantship and financial aid.

Finally, a note of deep thanks goes to my wife Stacy for her late-night help in the lab, patience, and constant support and encouragement throughout my time in graduate school.

TABLE OF CONTENTS

Chapter Page

Chapter Page

MANUSCRIPT III

EFFECTS OF FERTILIZATION AND VEGETATION CONTROL ON SOIL AND FOLIAGE NUTRIENT DYNAMICS OF A YOUNG LOBLOLLY PINE PLANTATION

LIST OF TABLES

Table Page

MANUSCRIPT I

Table Page

MANUSCRIPT III

Table Page

LIST OF FIGURES

Figure Page

MANUSCRIPT I

Figure Page

Figure Page

Figure Page

MANUSCRIPT II

Figure Page

Figure | Page

Figure Page

INTRODUCTION

Fertilization of forests is a silvicultural practice that has dramatically increased in importance over the past 20 years, and its importance will likely continue to escalate in the coming decades. Human population dynamics and attitudes toward natural resource management have driven the use of fertilizer in forest management. The human population is increasing at an exponential rate, which increases the demand for housing materials. The current world population is approximately 6 billion, and the population is anticipated to double within the next 50 to 100 years. This increase is of particular concern to forest managers, for the trees planted at present will reach maturity at a time in which a population of 10 to 12 billion can be reasonably expected. In addition, with increasing literacy rates in the developing world, the demand for fiber will likely be substantially higher in the coming decades than at present. Thus, the trees planted today must provide timber and fiber for an extra 4 to 6 billion people.

While demand for forest products is rising via increasing population and education levels, public attitudes toward usage of forests have shifted in the past 40 years, particularly in the post-industrial countries of North America and Western Europe. Public demands for non-timber forest resources such as wildlife habitat and recreation have brought about a reduction in the land area on which trees are harvested. Therefore, it has become necessary for forest managers to produce more tree biomass per acre on lands chosen for timber production. Intensive forest management appears to be the best means by which timber and fiber demands can be met while reserving large areas of native forests for non-timber forest resources. Fertilization has proven to be an important practice for increasing forest productivity. In response to productivity gains revealed in numerous studies since the late 1960's, use of fertilizer on forestlands has dramatically increased, particularly in the southeast United States. In this region, the practice of fertilization increased ~184% during the 1990's in terms of acreage fertilized. For the past five years, an average of approximately 15 million acres per year have been fertilized in the southeast United States, making the region one of the world's most productive areas for timber and fiber production.

In the southeast United States, forests are most frequently fertilized to alleviate nitrogen and phosphorus limitations of loblolly pine (*Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm.). Nitrogen is typically supplied via urea due to its relatively high N concentration (46%), which minimizes the volume of fertilizer required per acre. Phosphorus is supplied via diammonium phosphate, monoammonium phosphate, or superphosphates. Fertilizer is commonly broadcast-applied by helicopter in late winter in order to minimize losses of applied N to competing vegetation and ammonia volatilization and to capitalize on the high soil moisture typical of this portion of the growing season, which facilitates nutrient transport to pine root systems.

Although current forest fertilization techniques have produced gains in forest productivity, there are reasons to suspect fertilization practices can be improved to increase the effectiveness and environmental soundness of fertilization. Broadcast surface application of fertilizer in late winter is associated with relatively low pine nitrogen uptake efficiencies (NUE's) of approximately 15%. Pine NUE associated with late winter fertilizer applications is likely low since pine roots are not actively growing and evapotranspiration (E_t) rates are low. This low NUE implies that the desired vegetation does not capture the majority of applied nitrogen. Furthermore, some of the applied nutrients not captured by the soil-plant-microbial system may reach water bodies via runoff and leaching, which can lead to algal blooms that deplete water of O_2 and harm aquatic life. Due to its mobility, N is particularly apt to pollute water bodies. Thus, it behooves forest managers to increase pine NUE in order to maximize the benefits of fertilization in regard to tree growth and to minimize negative environmental consequences produced by errant fertilizer-derived elements. Furthermore, ascertaining the influence of forest fertilization on soil chemistry and microbial processes will contribute to understanding the sustainability of this practice.

There are adjustments to current forest fertilization practices that may increase pine NUE. Fertilizing with urea under warmer, wetter conditions has been demonstrated in agricultural studies to increase NUE. Under warmer conditions, nutrient uptake may be greater due to higher root activity and E_t rates. As mentioned above, prevailing rationale has dictated that fertilizing forests with urea under warmer conditions increases the risk of losses of applied nutrients to competing vegetation and ammonia volatilization. However, herbicides can be used to control competing vegetation and volatilization rates may not be as high as conventionally assumed. Soils of coniferous forests tend to be acidic with relatively high organic matter, and ammonia volatilization is suppressed in such soils. It has been demonstrated that pH in the immediate vicinity of urea granules on the soil surface can become quite high (~11) in forest soils; this increase in pH may facilitate the loss of N via volatilization. However, substantial precipitation can flush applied N into the soil, preventing significant volatilization loss. Thus, fertilizing with urea in warmer, wetter conditions could increase pine NUE if competing vegetation is controlled with herbicide. Another means by which pine NUE associated with urea fertilization can be increased may involve improvement of granule formulation. By coating each urea granule with a sealant that prevents urea release until a significant rain event, the risk of ammonia volatilization loss could be reduced. Some slow-release urea fertilizers have been developed, and application of such fertilizers to forests warrants exploration.

This study explores the potential for increasing NUE of juvenile loblolly pine in southeastern Oklahoma by applying fertilizers across a gradient of soil temperature and moisture conditions and by applying different urea formulations. Fertilizers were applied every other month from February 2001 to October 2002 to capture a wide range of edaphic, climatic, and phenological conditions. The performance of a conventional combination of urea and diammonium phosphate (DAP) fertilizers was compared to that of a slow-release coated urea fertilizer (CUF) at each application date. Herbicide treatments were applied to assess the influence of vegetation control on pine growth and NUE. Pine biomass production, foliage nutrient dynamics, and NUE were assessed each month from February 2001 to December 2002. Biomass production, N accumulation, and NUE of herbaceous vegetation were also determined each month to interpret the influence of the presence/absence of competing vegetation on loblolly pine biomass production and nutrient uptake. Furthermore, microbial population dynamics were assessed each month of this study to interpret the influence of the microbial population on loblolly pine nutrient uptake as well as the influence of fertilization and vegetation control on microbial populations. In addition to these biological measurements, monthly measures of soil nutrient dynamics were made throughout the life of this study to explore the abiotic fates of applied nutrients and the influence of a large N influx on soil nutrient dynamics.

This dissertation is comprised of three separate and complete manuscripts. The first, "Nitrogen capture by a juvenile loblolly pine plantation: effects of fertilizer date of application and formulation", was prepared in the format of Forest Ecology and Management journal. The second, "Effects of fertilization and vegetation control on microbial biomass C and dehydrogenase activity in an intensively managed juvenile loblolly pine plantation", was prepared in the format of Soil Science Society of America journal. The third manuscript, "Effects of fertilization and vegetation control on soil and foliage nutrient dynamics of a young loblolly pine plantation", was prepared in the format of Forest Ecology and Management journal. The three manuscripts will be submitted for publication in the respective journals. Since the three manuscripts are interrelated, in this dissertation the first manuscript will be referred to as "Manuscript 1" when cited in other manuscripts, the second manuscript will be referred to as "Manuscript 2", and the third manuscript will be referred to as "Manuscript 3".

Manuscript I

Nitrogen capture by a juvenile loblolly pine plantation: effects of fertilizer date of application and formulation

Abstract

Better timing of fertilization to coincide with environmental and tree physiological conditions that facilitate nutrient uptake may improve the efficiency of forest fertilization operations. This study was conducted to ascertain the climatic, edaphic, and physiological conditions that optimize the N acquisition of juvenile loblolly pine in the northwestern portion of its natural range. The influence of fertilizer formulation on pine N uptake was observed as well; a urea and diammonium phosphate (DAP) mixture was compared to a slow-release coated urea fertilizer (CUF). Effects of herbaceous vegetation on pine N uptake were also assessed. Fertilizer/brush control treatments were applied at 10 dates in 2001 and 2002 that encompassed a gradient of climatic, edaphic, and physiological conditions. Control and herbicide-only treatments were implemented each year as well. Foliar nitrogen uptake efficiency (NUE) was assessed one and two months post-fertilization, and nitrogen use efficiency was measured one year post-fertilization. Bioavailable soil N (NH_4^+-N + NO_3^--N), pine foliage N accumulation, and aboveground herbaceous vegetation N accumulation were determined monthly. Biomass growth was determined at the end of each year and in September 2002. Summer and fall fertilizer applications produced higher foliage NUE and N use efficiencies in both years of this study. Soil N remained elevated in fertilized plots for several months, indicating the immediate N uptake capacity of the pines and the soil-plant buffering capacity had been exceeded. Herbaceous vegetation was a significant competitor for applied N when the stand was 3 years old; loblolly pine N uptake and use efficiencies, N accumulation, and growth responses to fertilization were significantly greater when herbaceous vegetation was suppressed by glyphosate. However,

herbaceous vegetation was a weaker competitor for N at stand age 4; pine N uptake and growth responses were less inhibited by herbaceous vegetation. Use of the slow-release CUF formulation consistently resulted in loblolly pine N uptake and growth responses comparable to that of the urea/DAP mixture. CUF also resulted in higher foliage NUE when there was no precipitation for over a week following fertilization. This study revealed that forest managers might have greater flexibility in when fertilizers are applied, with summer and fall applications potentially producing the highest loblolly pine N uptake and use efficiencies.

1. Introduction

Nutrient addition has emerged as a vital practice in increasing timber production per acre (Fox 2000, Vance 2000). The United States has over 500 million acres of forestland capable of producing timber and fiber. Although physical, elemental, and moisture limitations to tree growth are routinely amended on approximately 13% of U.S. forests, amended forests produce ~40% of domestic forest products. Pine productivity of these intensively managed forests, which are frequently plantations, is up to 200% greater than unamended forests. Fertilization is especially prevalent in the southeastern United States. The practice of fertilization in this region increased 95% during the 1990's; currently approximately 1.5 million acres of southern pine forests are fertilized each year (NCSFNC 2001). Since forest fertilization costs approximately $50 an acre (Johnsen et al. 2001), this represents an annual investment of $75 million.

Nitrogen is the predominant nutrient added to forests (Reich and Schoettle 1988). Considerable research has been conducted on the influence of anthropogenic nitrogen additions to forest ecosystems. A large body of this research has focused on the effects of nitrogen addition on crop tree growth, and positive growth responses and key physiological changes of crop trees in response to nutrient additions are well documented. Tang et al. (1999) demonstrated that area, weight, and length of loblolly pine foliage are increased considerably by N and P additions. Nitrogen additions have been shown to produce higher photosynthetic efficiencies of coniferous species, indicating the vital role of nitrogen in light harvesting and CO_2 fixation (Evans 1983, Murthy et al. 1997). The combination of greater photosynthetic tissue and photosynthetic efficiency per unit of tissue imparts an increased ability to produce biomass. In fact, Adegbidi et al. (2002) have demonstrated that increases in nutrient availability have contributed to a reduction in the difference between the biological potential and actual production of loblolly pine over the past two decades.

Although biomass of crop trees is often increased by nitrogen additions, current nutrient application practices are relatively inefficient in the sense that crop trees acquire only ~15% of applied nitrogen (Johnson and Todd 1988, Li et al. 1991, Aarnio et al. 1996). Nitrogen uptake efficiency of younger forests is particularly low since tree root systems are smaller and understory vegetation is relatively more prevalent. Low nitrogen uptake is, in part, due to losses of applied N via leaching, surface runoff, ammonia volatilization, or denitrification. Lost nitrogen potentially pollutes the atmosphere, groundwater, and surface waters (Binkley et al. 1999). Although some losses of applied N have been quantified, relatively little is known about the underlying physiological and environmental processes that suppress the nutrient uptake efficiency of forests in response to fertilization.

The timing of conventional forest fertilization treatments may partially explain the low nutrient acquisition by southern pines. Fertilizers, particularly N as urea, are typically broadcast surface applied to forests in late winter or early spring to curtail losses of applied nutrients to understory vegetation and microbial populations. It is also perceived that the high soil moisture during this portion of the year facilitates nutrient transfer within the soil. Although loblolly pine is physiologically active during these periods, soil temperatures are likely far below optimum for nutrient uptake given the profound influence of root zone temperature on nutrient uptake (Allen 1987, Bassirirad et al. 1993). In addition, mass transfer of nutrients to roots is also low in cooler periods due to low evapotranspiration. Applying urea at higher temperatures may facilitate transfer of nutrients to roots since evapotranspiration rates will be higher.

Forest fertilization is also conventionally conducted in cooler months to reduce the risk of ammonia volatilization, especially when urea is applied. However, some studies have shown that ammonia volatilization rates are low in forest soils. Mahendrappa (1975) found that ammonia volatilization was not a significant pathway of N loss when urea was applied to forest soil; N volatilization rates were approximately 2%. Other estimates of ammonia volatilization from forest soils have ranged from <5 to ~40%, with estimates being highly dependent on measurement methods (He et al. 1999). Forest soils, especially coniferous forest soils, are characterized by high organic matter and low pH; both these characteristics reduce volatilization potential and perhaps improve N use efficiency (Fenn et al. 1991, Ouyang et al. 1998, He et al. 1999). Since nitrification rates increase with increasing soil temperature, the risk of volatilization may decrease at higher soil temperatures (He et al. 1999). Nason et al. (1988) found that significant precipitation, particularly in early fall, decreased ammonia volatilization. A urea formulation that delays N release until a significant precipitation event (i.e., slow-release formulation) could further decrease the risk of ammonia volatilization (Aarnio et al. 1996). It has also been demonstrated that forest canopies have a significant potential to recapture volatilized ammonia through stomatal uptake, so gaseous ammonia may not be completely lost from forest ecosystems (Nason et al. 1988).

Several forest management components have changed since the empirically-derived dates for applying fertilizer were established. Due to the success of breeding programs, pine genotypes have changed dramatically, such that they grow much more quickly and thus dominate sites more rapidly. Herbicide usage is becoming more prevalent in forestry. Herbicides are commonly used to control competing vegetation prior to planting, and the use of herbicides immediately prior to fertilization later in the rotation is gaining acceptance. Fertilization of younger stands has become more attractive to forest managers. Thornley and Cannel (1992) have proposed that fertilization of young, sapling conifers is the most critical period for applying fertilizers due to the rapid expansion of foliage that occurs at this phase of forest development. Usage of fertilizers that dissolve less rapidly than conventional formulations has increased. With these changes in forest management and fertilizer formulations, it is imperative to explore the environmental and edaphic conditions that optimize loblolly pine's acquisition of applied N. The objectives of this study are: (1) to quantify the N uptake and use efficiencies of juvenile loblolly pine in response to urea applied over a gradient of edaphic and climatic conditions, (2) to quantify the influence of herbaceous vegetation on loblolly pine N acquisition, and (3) to determine the influence of a large influx of N from urea on loblolly pine nutrient capture versus that of a slow, sustained release of N from a slow-release urea formulation.

2. Materials and Methods

2.1. Site description

In 1998, a 15-hectare (37-acre) loblolly pine plantation was established in southeastern Oklahoma. The soil on the site is classified as a Kullit fine sandy loam. This soil type is acidic (pH 4.5), gently sloping (1 to 3% slope), and relatively nutrient poor, with a high available water capacity. Management practices are essential for maintaining or improving soil fertility and structure of this soil type (USDA-SCS 1974). The average annual rainfall of the region is 125 cm (49 in.), and the average annual temperature is 17°C (63°F). Precipitation is usually adequate through May, but droughts two to six weeks in duration are common from June through October. The climate through much of the growing season is hot and humid (Stogsdill 1986). Prior to planting, the site was prepared via a bedding/subsoiling operation, and a mixture of sulfometuron methyl (Oust®) and imazapyr (Arsenal®) herbicides was applied to control competing vegetation for the first year of the rotation. A single coastal North Carolina family of loblolly pine was planted on a 1.8 m × 5.5 m (6.0 ft. × 18.0 ft.) spacing in February 1999.

The plantation was developed into a loblolly pine fertility research area in January 2001. The heights of all trees on the site were measured, and trees of average height for the site were selected as study trees. Each study tree was separated by at least two trees within each row, such that study trees were separated by a buffer space of at least 3.7 m (12 ft.) within each row to prevent contamination of study trees via lateral flow of applied nutrients. Due to the planting spacing, study trees were also separated by at least 5.5 m (18.0 ft.) between rows. Thus, a plot consisted of a study tree and two buffer trees, with one buffer tree on each side of the study tree within a row.

2.2. Treatments

The following treatments (each replicated 10 times) were randomly applied to study trees in 2001 to investigate the nitrogen capture of loblolly pine trees:

1. No brush control, no fertilizer (CONT)
2. Brush control, no fertilizer (BC)
3. Urea/diammonium phosphate mixture, no brush control (UD)
4. Urea/diammonium phosphate mixture, brush control (UDBC)
5. Coated urea fertilizer (CUF), brush control (CUFBC)

Brush control consisted of elimination of herbaceous vegetation. A 10% solution of glyphosate (Accord®) was applied periodically throughout the 2001 growing season to prevent any herbaceous understory vegetation from growing. Herbaceous vegetation was eliminated from a 16-m^2 (168-ft^2) area around study trees chosen for a brush control treatment to isolate the influence of herbaceous vegetation on loblolly pine N uptake. Since the competitive ability of herbaceous vegetation to acquire applied N in a young loblolly pine plantation was of interest in this study, woody vegetation was eliminated from the entire study site with triclopyr (Garlon®) applied in February 2001.

The UD, UDBC, and CUFBC treatments were applied to separate sets of study trees in February, April, June, August, and October of 2001, i.e., each fertilized plot received one application of fertilizer. For example, 30 study trees were fertilized in February (10 trees per fertilizer/brush control treatment), and 30 different plots were fertilized in April. The application dates were selected to encompass a gradient of soil temperatures, soil moistures, loblolly pine phenological conditions, and competing vegetation activities. The desired conditions associated with each application date were:

1. Late winter (February)
   - Conditions: low soil temperature, high soil moisture, low pine growth rate, low competing vegetation activity
2. Early spring (April)
   - Conditions: moderate soil temperature, high soil moisture, moderate to high pine growth rate, developing competing vegetation
3. Early summer (June)
   - Conditions: high soil temperature, high soil moisture, longest photoperiod, highest pine growth rate, high competing vegetation population and growth rate
4. Late summer (August)
   - Conditions: highest soil temperature, lowest soil moisture, moderate to high pine growth rate, high competing vegetation population (and concomitant low to moderate growth rate)
5. Middle fall (October)
   - Conditions: moderate soil temperature, moderate to high soil moisture, low pine aboveground growth rate, high pine root growth rate, low competing vegetation growth rate

Fertilizers were applied to a 24-m^2 (254-ft^2) area around study trees using hand spreaders. Nitrogen was applied at 202 kg ha^{-1} (180 lb ac^{-1}); phosphorus was applied at 20 kg ha^{-1}

(18 lb ac^{-1}). In addition, CUF (a slow-release fertilizer covered with a P- and B-containing coating that delays release of urea until a significant precipitation event) contributed 0.65 kg ha^{-1} (0.58 lb ac^{-1}) of B to the soil.

In 2002, the CONT, BC, UD, UDBC, and CUFBC treatments were applied to a different set of plots on the same study site in order to ascertain the influence of tree size and age on loblolly pine nutrient uptake when fertilizer is applied over a gradient of climatic, edaphic, and phenological conditions. Again, each treatment was replicated 10 times. The UD, UDBC, and CUFBC treatments were applied in January, April, June, August, and October of 2002. All brush control and fertilization protocol was identical to that followed in 2001.

2.3. Climatic and edaphic measurements

In February 2001, a climate station was established on the study site. A tipping-bucket rain gauge attached to a data logger was established to provide continuous measurement of precipitation amount and velocity. Thermocouples were placed at soil depths of 15 cm and 30 cm to measure soil temperature in plots selected to receive CONT and February 2001 UDBC to elucidate any effects of vegetation control on soil temperature. Daily temperature and relative humidity measurements were obtained from the Oklahoma Climatological Survey Mesonet network (OCS Mesonet 2002).

The neutron scattering technique was used to determine volumetric soil moisture (Gardner and Kirkham 1952); this method is noted for its high precision (Evett and Steiner 1995). In March 2001, cylindrical aluminum tubes 35 cm in length were placed in plots chosen to receive CONT and February 2001 UDBC treatments. These two treatments were selected to represent the differences in soil moisture attributable to competing vegetation control and fertilization. Similarly, tubes were placed in plots receiving CONT and April 2002 UDBC treatments among the set of plots treated and measured in 2002. Thus, aluminum tubes were placed in 40 plots (10 plots per treatment) during this study. A neutron probe (Troxler model 4301, Troxler Electronics Inc.) was used to obtain bi-weekly measurements of volumetric soil moisture at 15 and 30 cm in these plots.

2.4. Bioavailable soil N

Bioavailable soil N (NH_4^+-N and NO_3^--N) was measured using ion exchange resin bags to quantify the amount of soil N not taken up by vegetation or microbes or lost via leaching, ammonia volatilization, or denitrification (Sibbesen 1977, Binkley and Matson 1983). In 2001, resin bags were placed at a depth of 15 cm in the soil within 0.5 m of the base of study trees receiving CONT, BC, and February 2001 UD, UDBC, and CUFBC treatments. Five plots receiving each of these treatments were randomly selected for continuous bioavailable N assessment. Bags were placed in the soil immediately prior to the February 2001 fertilizations and replaced every 30 to 40 days until December 2001. After December 2001, bags were replaced every 60 to 70 days in these plots. Care was taken to minimize soil disturbance during resin bag installation and replacement. Resin bags were also placed in the soil near trees receiving UD, UDBC, and CUFBC treatments in June and August 2001. Each of these bags were placed in 5 plots per treatment immediately prior to fertilization and removed after 30 to 40 days without replacement.

In 2002, similar protocol was used to provide bioavailable N assessments in plots receiving CONT, BC, and April 2002 UD, UDBC, and CUFBC treatments. However, each bag was replaced every 60 to 70 days instead of 30 to 40 days due to laboratory constraints. Resin bags were also placed in the soil near trees receiving UD, UDBC, and CUFBC treatments in January, June, August, and October 2002. Each of these bags were placed in 5 plots per treatment immediately prior to fertilization and extracted after 60 to 70 days without replacement.

After resin bags were removed, they were frozen to prevent N mineralization in any soil particles on the exterior of resin bags prior to processing. NH_4^+-N and NO_3^--N were eluted from the resin and measured using flow injection analysis (Lachat Quick Chem 8000, Lachat Instruments).

2.5. Vegetation N concentration

Foliage N concentration of loblolly pine was monitored throughout this study. Foliage of trees receiving CONT, BC, and February 2001 UD, UDBC, and CUFBC treatments was collected monthly from the second growth flush of 2000 from February through October 2001, and foliage from the first growth flush of 2001 was collected monthly from May through December 2001. Foliage of trees receiving CONT, BC, and April 2002 UD, UDBC, and CUFBC treatments was collected monthly from the first growth flush of 2001 from February through October 2002, and foliage from the first growth flush of 2002 was collected monthly from May through November 2002. All foliage samples were collected from the mid-crown position (Zhang and Allen 1996). Four fascicles were sampled from all study trees per treatment; these foliage samples were then pooled to produce 3 composite samples per treatment. To preserve replication of treatments, each composite sample consisted of fascicles collected from three or four study trees; foliage from the same three or four study trees was composited from month to month. Samples were refrigerated immediately after collection and dried to constant weight at 70°C within 48 h. Dried foliage samples were milled to pass a 20-mesh sieve. Foliage N concentrations were then determined by dry ashing followed by analysis with inductively coupled plasma atomic emission spectroscopy (Beck 2002).

Foliage N concentrations were also monitored on all study trees receiving UD, UDBC, and CUFBC treatments on all other application dates. Foliage collection and processing protocol was similar to that described above, but foliage was collected immediately prior to fertilization and one month post-fertilization.

Nitrogen concentration and dry weight of aboveground herbaceous vegetation biomass was assessed during this study as well. In 2001, herbaceous vegetation was clipped each month from February to December within a 0.09-m^2 (1-ft^2) randomly placed portable PVC quadrat frame (Donegan et al. 2001) in all plots receiving the CONT and February 2001 UD treatments. Herbaceous vegetation was similarly sampled in all plots receiving CONT and February, April, June, and August 2001 UD treatments in September 2001 to measure the N concentration of herbaceous vegetation at its peak biomass. In 2002, herbaceous vegetation was clipped each month from January to December within a randomly placed 1-m^2 portable PVC quadrat frame (Donegan et al. 2001) in plots receiving the CONT and April 2002 UD treatments. In addition, herbaceous vegetation was sampled immediately prior to fertilization and 2 months post-fertilization in plots receiving June and August 2002 UD treatments. Herbaceous vegetation of plots receiving CONT and January, April, June, and August 2002 UD treatments were sampled in September 2002 to measure its peak N content. Herbaceous vegetation was sampled in 5 plots per treatment in 2002. All herbaceous vegetation samples were processed and analyzed using the protocol described above for loblolly pine foliage samples.

2.6. Loblolly pine biomass estimation

To quantify the influence of treatments on loblolly pine biomass, a suite of nonlinear models for predicting each component of tree biomass (foliage, stem, branch, root) were developed. The models were of the following form:

$$Y = b_0 \times (Ht)^{b_1} \times (Dia)^{b_2} \times (crn)^{b_3} \qquad [1]$$

where Y = foliage, branch, stem, or root biomass (g),

Ht = tree height (m),

Dia = diameter of tree at 1.3 m (cm)

crn = crown width of tree (m), and

b_i = coefficients estimated by non-linear regression, where i = 0, 1, 2, 3.

Branch and stem weight predictions yielded by the above model are estimates of the weight of wood and bark. Similar regression models have been successfully used in other studies to model loblolly pine biomass development in response to fertilization (Hynynen et al. 1998, Adegbidi et al. 2002, Xu et al. 2002), irrigation (Albaugh et al. 1998, King et al. 1999), and genotype (Blazier et al. 2002). Adegbidi et al. (2002) stressed the importance of developing site-specific biomass equations to quantify the above- and below-ground biomass responses to fertilizer treatments.

Destructive harvests were conducted in February 2001, August 2001, and August 2002 to develop biomass models. Destructively harvested trees were collected from surplus plots (4 surplus plots per treatment) that were established in January 2001 and January 2002. Surplus plots were treated identically to other plots in each treatment until each destructive harvest was conducted. In each destructive harvest, trees that represented the range of diameters and fertilization treatments of the study site were selected. Diameters of all study trees were measured immediately prior to the destructive harvests, and diameter classes were created. Uniform numbers of trees per diameter class were then selected for destructive harvest. In February 2001, 25 trees were selected for harvest; 5 trees were harvested from each of 5 diameter classes. In August 2001, 36 trees were selected for destructive harvest. Of these 36 trees, 6 were harvested from each of 6 diameter classes. Of the 6 trees per diameter class, 3 were from fertilized plots and 3 from non-fertilized plots. In August 2002, 30 trees were selected for destructive harvest. Five diameter classes were established prior to harvest, and 6 trees (3 fertilized, 3 non-fertilized) were harvested in each diameter class.

Prior to felling of all destructively harvested trees, diameter at 1.3 m, total height, and crown width of each tree were measured. The aboveground portion of each tree was then felled, and all biomass components were separated. The total biomass collected in the February and August 2001 harvests were dried to constant weight at 70°C to yield the dry weight of each biomass component of destructively harvested trees.

Due to the larger size of trees in August 2002, it was necessary to modify protocol for obtaining the dry weight of biomass components. After measurement and felling, a subsample of 9 branches (branchwood + foliage) per tree (3 branches per crown third) was collected. The branch and foliage of each subsample were separated, and their fresh weights were determined. Biomass components of each tree were then separated, and the total fresh weight of all branches and foliage was measured. Stems of each tree were cut into 1-m bolts, and the fresh weight of each bolt was measured. Disks ~3 cm thick were then cut from the base and top of each bolt, and their fresh weights were measured. The branch, foliage, and stem subsamples were then dried to constant weight at 70°C to obtain their dry weights. The fresh:dry weight ratios of the branch, foliage, and stem subsamples were then multiplied by the fresh weights of each destructively harvested tree's biomass components to estimate the dry weight of each biomass component (Blazier 1999).

Root biomass was extracted with a backhoe during the August 2001 and August 2002 destructive harvests. Due to logistical constraints, it was not possible to extract root systems of all destructively harvested trees. In August 2001, the root systems of 12 destructively harvested trees (6 fertilized, 6 non-fertilized) were extracted, and in August 2002 root systems of 10 trees (5 fertilized, 5 non-fertilized) were extracted. A 1-m^3 pit was dug around each root system. Root systems were extracted from the loosened soil; soil was then washed from the roots. Any coarse and medium roots extending from the pit were extracted as well. Although some fine roots were lost in extraction, our procedures successfully removed the majority of pine root systems. Roots were dried to constant weight at 70°C.

Dry weights of each biomass component were used in conjunction with tree dimensions to derive regression models for prediction of the biomass component weights of study trees (Adegbidi et al. 2002, Xu et al. 2002). Model-fitting procedures will be discussed in a following section. Total tree height, diameter at 1.3 m, and crown width of study trees were regularly measured to provide model inputs. Measurement of these dimensions commenced in February 2001 for all trees receiving CONT, BC, and February 2001 UD, UDBC, and CUFBC treatments; measurements were then taken each month through December 2001. All study trees receiving UD, UDBC, and CUFBC treatments in other months were measured immediately prior to fertilization and monthly thereafter. All trees treated in 2001 were also measured one year post-fertilization and in August 2002. Trees receiving CONT, BC, and April UD, UDBC, and CUFBC treatments in 2002 were measured monthly from January to November 2002, and trees receiving UD, UDBC, and CUFBC treatments in other months were measured immediately prior to fertilization and monthly thereafter. Each estimate of biomass components for months in which destructive harvests were not carried out were based on a weighted average of estimates yielded by two models, with Julian date used as the weighting factor. For example, estimates of biomass for May 2001 consisted of weighted averages of biomass components yielded by models created using February and August 2001 destructive harvest data.

2.7. Vegetation N acquisition

Foliage N concentration data was coupled to foliage weight estimates to yield measurements of the N captured by loblolly pine trees. N accumulation was quantified using the following formula:

$$Naccum = \left(Conc_{postfert} \times Folwt_{postfert}\right) - \left(Conc_{prefert} \times Folwt_{prefert}\right) \qquad [2]$$

where *Naccum* = Foliage biomass N accumulation (g),

$Conc_{postfert}$ = Post-fertilization foliage N concentration (%),

$Folwt_{postfert}$ = Post-fertilization foliage weight (g),

$Conc_{prefert}$ = Pre-fertilization foliage N concentration (%), and

$Folwt_{prefert}$ = Pre-fertilization foliage weight (g).

Since the dimensions used as model inputs and foliage N contents of CONT, BC, February 2001 and April 2002 UD, UDBC, and CUFBC treatments were measured monthly, it was possible to determine the monthly N accumulation rates of previous- and current-year foliage for trees receiving these treatments. Since the aboveground N concentration and biomass of herbaceous vegetation was measured monthly in response to CONT and February 2001 and April 2002 UD treatments, it was possible to determine the N accumulation of herbaceous vegetation with Equation 2 as well.

Foliage NUE was calculated in response to all fertilizer treatments one month post-fertilization using the following formula:

$$NUE = \frac{(Naccum)}{FertN} \qquad [3]$$

where NUE = Foliage nitrogen uptake efficiency (%),

$Naccum$ = Foliage N accumulation (g), and

$FertN$ = N applied per tree (g).

The foliage N accumulation data used in each determination of NUE was from mature flushes of foliage present at the pre- and post-fertilization sampling dates. For example, NUE calculated in response to October fertilization dates included foliage N accumulation data from only the foliage of the current year since the previous season's foliage had fallen by the post-fertilization sampling in November. Likewise, NUE determined in response to June and August was comprised of the foliage N accumulation of both previous and current season's foliage.

The N use efficiency of loblolly pines fertilized in 2001 were calculated one year post-fertilization to provide an indication of the amount of stem biomass produced per unit of fertilizer applied (Li et al. 1991). The following equation was used to determine N use efficiency:

$$Nuse = \frac{\left(Stemwt_{postfert} - Stemwt_{prefert}\right)}{FertN} \qquad [4]$$

where $Nuse$ = nitrogen use efficiency (%)

$Stemwt_{postfert}$ = Post-fertilization stem dry weight (g)

$Stemwt_{prefert}$ = Pre-fertilization stem dry weight (g)

$FertN$ = N applied per tree (g)

2.8. Statistical Analysis

During biomass model development, the influence of fertilization on the relationship between each biomass component and tree dimensions (height, diameter, crown width) was investigated using procedures described by Blazier et al. (2002). Dummy variables that accounted for fertilizer influence were incorporated into a linear version of Equation 1. When significant dummy variables were found, separate models for prediction of a biomass component were estimated for fertilized and non-fertilized study trees. When no significant dummy variables were found, data were pooled and a single biomass model for prediction of a biomass component was estimated for fertilized and non-fertilized study trees.

After the need for separate or single models was assessed with analyses of dummy variables, a stepwise procedure was performed on each linear model using a significance level of $P = 0.15$ due to the exploratory nature of the procedure. The stepwise procedures were conducted to ensure that only variables that significantly affected branch, foliage, stem, and root weight were included in the regression equations. Residual analyses were then performed on each model to investigate any significant departures from linearity. Cook's distance and DFFITS tests were conducted to search for any outliers that substantially influenced each model (Neter et al. 1996). After stepwise procedures, residual analyses, and outlier tests were completed, each model was converted to its antilog (multiplicative) form, and the NLIN procedure of the SAS System (SAS Institute Inc., Cary, NC) was used to estimate regression coefficients for each nonlinear biomass model. Models created by these procedures are provided in the Appendix.

Analyses of all treatment effects were conducted by analyses of variance (ANOVA's) using the MIXED procedure of the SAS System. Various models were used in the analyses depending on the variable assessed, and they will be discussed below. When the null model likelihood ratio test revealed heterogeneous variances in a dataset, the GROUP option of MIXED was utilized to perform ANOVA's using different variances for all treatment combinations. When an ANOVA indicated significant treatment effects, treatment means were calculated and separated by the DIFF and SLICE options of the LSMEANS procedure. The DIFF option provided multiple comparisons of treatment means by invoking t-tests to determine significant differences between all possible treatment combinations. The SLICE option provides t-tests of treatment means in which the effect of one treatment is evaluated at each level of another treatment. The SLICE option was used to investigate treatment main effects when significant 2-way interactions were found.

Measurements of volumetric soil moisture taken in 2001 and 2002 were analyzed as a one-way treatment structure with 2 levels (CONT, UDBC). ANOVA procedures were performed on a repeated measures model with an autoregressive correlation structure with: (1) sampling date, and (2) treatment, and (3) the interaction between sampling date and treatment as fixed effects.

The models associated with NUE and N use efficiency measurements taken in 2001 and 2002 consisted of a 3 × 5 treatment factorial arranged in a completely randomized design. ANOVA procedures were performed using a model with the following fixed effects: (1) fertilizer/brush control treatment (UD, UDBC, CUFBC), (2) application date [January (2002 only), February (2001 only), April, June, August, October], and (3) the interaction between fertilizer/brush control treatment and application date.

The correlation between NUE, soil moisture, and soil temperature, and the number of days from fertilizer application to a precipitation event was explored using the PROC CORR procedure of the SAS System. This procedure generates Pearson correlation coefficients and the probabilities associated with these statistics. The procedure was also used to determine the correlation between NUE and N use efficiency measurements.

Monthly measurements of foliage N accumulation in response to the February 2001 and April 2002 fertilizer applications were analyzed as a one-way treatment (fertilizer/brush control) with 3 levels (UD, UDBC, CUFBC) plus 2 controls (CONT, BC). Due to this treatment structure, it was necessary to conduct the analyses in two steps. First, the fertilizer/brush control treatments were analyzed with a repeated measures model with an autoregressive correlation structure with: (1) fertilizer/brush control treatment, (2) month, and (3) the interaction between fertilizer/brush control and month as fixed effects. Next, the controls were compared to fertilizer/brush control treatments using CONTRAST statements. The fertilizer/brush control and control treatments were pooled and analyzed using ANOVA procedures performed on a model with treatment (CONT, BC, UD, UDBC, CUFBC) as a fixed effect. Contrast statements that compared N accumulation associated with CONT and BC treatments to that of the fertilizer/brush control treatments were used in conjunction with ANOVA procedures to identify significant differences between control and active treatments. This comparison of controls to active treatments was conducted for each month of the study to identify when foliage N accumulation of trees receiving CONT and BC treatments were significantly different from that of trees receiving fertilizer/brush control treatments.

Monthly assessments of bioavailable soil N in response to the CONT, BC, February 2001 and April 2002 fertilizer/brush control treatments were analyzed with procedures identical to that described above for foliage N accumulation analysis. However, it was necessary to perform log transformations of bioavailable soil N values to rectify large, 200-fold differences in standard errors in the data. One- and two-month post-fertilization bioavailable soil N was analyzed using ANOVA procedures performed on a model with fertilizer/brush control treatment (UD, UDBC, CUFBC treatments applied in January/February, April, June, October, December) as a fixed effect.

In December 2001 and September 2002, growth of all biomass components (stem, foliage, branch, root) in response to the 2001 treatments was determined. Biomass growth responses to 2002 treatments were likewise observed in November 2002. These measurements were analyzed as a 3×5 factorial plus 2 controls. Analysis was performed in two stages, as described above for the analysis of foliage N accumulation. However, the model differed in that (1) fertilizer/brush control treatment, (2) application date, and (3) the interaction between fertilizer/brush control treatment and application were the fixed effects, and it was not a repeated measures model.

Monthly measurements of herbaceous vegetation N accumulation in response to February 2001 and April 2002 UD treatments were assessed with a repeated measures model. ANOVA procedures were performed on a repeated measures model with an autoregressive correlation structure with (1) fertilizer/brush control treatment (CONT, UD), (2) month, and (3) the interaction between fertilizer/brush control treatment and month as fixed effects. The assessments of herbaceous vegetation N in September 2001 and 2002 and were analyzed as a one-way treatment structure with 5 levels of fertilizer/brush control treatment (CONT, UD applied in months prior to September 2001 or 2002). ANOVA procedures were performed with a model with fertilizer/brush control treatment as a fixed effect. The two-month post-fertilization herbaceous vegetation N were analyzed as a one-way treatment structure with 3 levels of UD treatments (April, June, and August UD treatments). ANOVA procedures were performed with a model with UD treatment as a fixed effect.

3.0. Results

3.1. Climatic and edaphic conditions

The yearly precipitation for 2001 (Figure 1) was average for the region; however, the monthly precipitation amounts varied from higher to lower than average in months in which fertilizer was applied (OCS Mesonet 2001). Precipitation in February and August approximately doubled the monthly averages. June and October rainfall was average for the region, and April rainfall was lower than the monthly average. The yearly precipitation for 2002 (Figure 1) was likewise average for the region, with monthly averages fluctuating from higher to lower than average in months in which fertilizer was applied. Precipitation amounts each month in which fertilizer treatments were applied in 2002 differed from those in the same months in 2001. Rainfall in January, June, and August was lower than the regional average, April rainfall was comparable to the monthly average, and October precipitation nearly doubled the regional average.

In both 2001 and 2002, soil temperature rapidly rose from early spring through early summer, plateaued through August, then declined for the remainder of the year (Figure 2). The decline in soil temperature from August through November was somewhat more pronounced in 2001 than in 2002. Soil temperatures were similar in CONT and UDBC plots throughout much of the year. The greatest differentiation in temperatures occurred in the summer, with soil temperatures being higher in UDBC plots and the lowest temperatures in the CONT plots at the 30 cm depth.

In both 2001 and 2002, volumetric soil moisture (Figure 3) remained stable until early spring, gradually declined from early spring through early summer, declined rapidly through the summer, and increased in the fall. Moisture was consistently higher at the 30 cm depth, and the CONT and UDBC plots did not significantly differ at either depth.

3.2. Bioavailable soil N

In 2001, the bioavailable soil N of plots receiving CONT and BC treatments were similar throughout the year (Table 1). In August, there were no differences in soil N among the treatments, presumably due to low soil moisture that reduced mass flow of N to the ion exchange resin bags. From March to May, available soil N was comparable among plots given UD, UDBC, and CUFBC treatments in February, and soil N in fertilized plots significantly exceeded that of CONT and BC plots. By June, soil N of UD plots was significantly less than that of UDBC and CUFBC plots but still significantly greater than N of CONT and BC plots. After June, soil N of UD plots was comparable to CONT and BC plots. Available soil N in UD, CONT, and BC plots was similar for the remainder of the year. The UDBC and CUFBC treatments produced the highest soil N values for most of 2001, and the soil N in plots receiving these two treatments was statistically similar at all sampling dates. However, mean soil N for the UDBC treatment was consistently higher than the CUFBC treatment. Available soil N beyond February 2002 (not shown) was similar for all treatments.

In response to the April 2002 fertilizer treatments, available soil N in plots receiving UDBC and CUFBC treatments from May/June through November/December was consistently higher than plots receiving CONT and BC treatments (Table 2). Soil N in plots fertilized in 2002 was generally lower than that observed in fertilized plots in 2001. Soil N in plots that were given the UD treatment was statistically similar to the UDBC and CUFBC treatments until September/October and was also statistically similar to CONT and BC treatments throughout the year. As in 2001, soil N in CONT and BC plots was similar throughout the year. By January 2003, bioavailable soil N of all treatments was comparable.

In 2001, application date significantly (P=0.04) affected the amount of bioavailable N in the soil for the month immediately following application among the application dates tested (February, June, August). The August application produced significantly (P=0.02) greater soil N in the month after fertilization than did the February and June applications. In 2002, application date did not significantly influence the bioavailable N in the soil for the two-month period after fertilization.

3.3. Vegetation N accumulation

In 2001, the February UD, UDBC, and CUFBC treatments significantly (P<0.0001) affected N accumulation of previous-season foliage (Figure 4). Foliage N accumulation associated with the UD treatment was lower than that of the UDBC (P=0.0002) and CUFBC (P<0.0001) treatments, while the N accumulations produced by the UDBC and CUFBC treatments were similar. The N accumulation of previous-season foliage was comparable in CONT and BC treatments until October, in which BC foliage N accumulation exceeded (P=0.04) that of the CONT treatment. Foliage N accumulation in response to the CONT treatment was consistently lower (P=0.01±0.01) than the UDBC and CUFBC treatments. After April, N accumulation of previous-season foliage in response to the February UD treatment was comparable to that of the CONT and BC treatments. N accumulation in response to the BC treatment was lower (P<0.0001) than all fertilizer treatments in April, but was comparable to that of UD and UDBC treatments in all other months. The foliage N accumulation of the BC treatment was lower

(P=0.03±0.01) than that of the CUFBC treatment until October. In general, foliage N accumulation rose in all treatments until May, fell sharply by June, then remained stable until needlefall in October.

February 2001 UD, UDBC, and CUFBC treatments also significantly affected (P<0.0001) N accumulation of current-season foliage (Figure 5). Foliage N accumulation in response to the UD treatment was lower than that produced by the UDBC (P<0.0001) and CUFBC treatments (P<0.0001). N accumulation of current-season foliage was similar in response to the UDBC and CUFBC treatments. The CONT treatment was associated with lower foliage N accumulation than the BC (P=0.004±0.001) and UDBC (P=0.01±0.01) treatments from July through December. N accumulation of current-season foliage in response to the CONT treatment was significantly lower (P=0.01±0.001) than that of the CUFBC treatment from September through December. Current-season foliage N accumulation in response to the February 2001 UD treatment did not exceed that of the CONT treatment, and it was significantly lower (P=0.004±0.004) than that of the BC treatment each month. N accumulation of current-season foliage associated with the BC treatment was comparable to those of UDBC and CUFBC treatments each month. Current-season foliage N accumulation increased from June through October, with a more rapid increase occurring in response to BC, UDBC, and CUFBC treatments. After October, N accumulation remained stable.

The April 2002 UD, UDBC, and CUFBC significantly (P=0.0003) affected N accumulation of previous-year foliage (Figure 6). The UD treatment was associated with N accumulation significantly lower than those of the UDBC (P=0.0001) and CUFBC (P=0.002) treatments. Foliage N accumulation in response to the CONT treatment was lower (P=0.04±0.01) than the BC treatment most months from July through September, with the exception of August. N accumulation in response to the CONT treatment was also lower (P<0.0001) than the UDBC and CUFBC treatments from May through October; the CONT treatment also produced lower (P=0.002±0.004) N accumulation than the UD treatment in all months except August. The BC treatment produced foliage N accumulation that was lower (P<0.0001) than the UD, UDBC, and CUFBC treatments in May and June. After June, foliage N accumulation of trees receiving the BC treatment remained lower than the UDBC (P=0.01±0.01) and CUFBC (P=0.02±0.01) treatments through October. During the same period, N accumulation of BC trees was comparable to that of trees receiving the April 2002 UD treatment. Foliage N accumulation continually rose from February through October, with a more marked increase occurring in response to the UD, UDBC, and CUFBC treatments.

The April 2002 UD, UDBC, and CUFBC treatments also significantly (P=0.01) affected N accumulation of current-season foliage (Figure 7). Foliage N accumulation was similar in response to the UD and UDBC treatments. N accumulation of trees receiving the April 2002 CUFBC treatment was significantly greater than that associated with the UD (P=0.002) and UDBC (P=0.03) treatments. The foliage N accumulation associated with the CONT and BC treatments were comparable each month. N accumulation of the CONT treatment was significantly lower (P=0.01±0.01) than the April 2002 UDBC and CUFBC treatments each month except June and September. The foliage N accumulation of the BC treatment was significantly lower (P=0.01±0.01) than that of the CUFBC treatment each month after June. The BC treatment also yielded lower N accumulation than the UD treatment (P=0.03±0.01) in June and November and the UDBC treatment (P=0.02±0.01) in August, September, and November.

In 2001, analysis of herbaceous vegetation N accumulation revealed a significant interaction (P=0.03) between fertilizer and month of observation. In May, July, and September 2001 N accumulation of the February 2001 UD treatment exceeded (P=0.02±0.02) that of the CONT treatment (Figure 8). Analysis of herbaceous vegetation N accumulation of CONT and all 2001 UD treatments as of September 2001 indicated no significant effects of application date on herbaceous vegetation N accumulation.

The April 2002 UD treatment did not significantly increase N accumulation of herbaceous vegetation in 2002 (Figure 9). Herbaceous N accumulation of 2002 was lower than that of 2001 (Figures 8 and 9), which is indicative of the lower prevalence of herbaceous vegetation observed in 2002. In September 2002, no significant differences in herbaceous N contents were observed between the 2002 CONT and UD treatments; thus, application date did not affect herbaceous N accumulation by September. However, application date significantly (P=0.03) affected the N accumulation of herbaceous vegetation 2 months post-fertilization. The April UD treatment yielded higher (P=0.02±0.002) herbaceous N accumulation 2 months after fertilization than did the June and August UD treatments.

3.4. Nitrogen uptake and use efficiency

A significant (P=0.0002) fertilizer × application date effect was found when one-month post-fertilization foliage NUE in response to the 2001 UD, UDBC, and CUFBC treatments (Figure 10) were analyzed. Significant (P<0.0001) application date effects were found for every level of the fertilizer/brush control treatments (Table 3). For all fertilizer/brush control treatments, the February and April applications were associated with the lowest foliage NUE's whereas the June and August applications yielded the highest foliage NUE's. For each fertilizer/brush control treatment, the mean foliage NUE's produced by the June and August applications were more than three times that of the February application. Within the April and August applications, the UDBC and CUFBC treatments produced higher NUE's than the UD treatment (Figure 10). Within the October application, the UD and CUFBC treatments generated higher foliage NUE's than the UDBC treatment. A strong positive correlation (r=0.68, P<0.0001) was found between foliage NUE of 2001 and soil temperature, and a strong negative correlation (r=-0.72, P<0.0001) between NUE and soil moisture. NUE was also negatively correlated (r=-0.59, P<0.0001) with the number of days until precipitation.

Application date significantly (P<0.0001) affected one-month post-fertilization foliage NUE in 2002 (Figure 11). The January applications produced the lowest foliage NUE's, and the June, August, and October applications produced the highest foliage NUE's. The UD, UDBC, and CUFBC treatments produced comparable NUE's at each application date, i.e., fertilizer/brush control treatment effects were non-significant in 2002. As in 2001, one-month post-fertilization foliage NUE was positively correlated with soil temperature (r=0.55, P<0.0001) at the time of application and negatively correlated with soil moisture (r=-0.49, P<0.0001). The foliage NUE's in response to the January and April 2002 treatments were similar to those of February and April 2001, while the foliage NUE's of the June, August, and October applications were nearly double that found in response to the same application dates in 2001.

A significant (P=0.004) fertilizer × application date effect was found in the analysis of two-month post-fertilization foliage NUE in response to 2002 UD, UDBC, and CUFBC treatments (Figure 12). Significant (P<0.0001) application date effects were detected for each level of the fertilizer/brush control treatments (Table 4). For fertilizer/brush control treatments, the January and April application dates produced the lowest foliage NUE's, and the June and August applications produced the highest foliage NUE's. Within the June and August application dates, significant (P=0.01±0.003) fertilizer effects were detected (Figure 12). In June, the UDBC treatment produced the highest 2-month foliage NUE, and in August the UD treatment yielded the highest foliage NUE. Two-month post-fertilization was positively correlated (r=0.66, P<0.0001) with soil temperature at the time of application and negatively correlated (r=-0.41, P<0.0001) with soil moisture at the time of application.

Fertilizer/brush control treatment and application date both significantly (P=0.0003±0.0002) affected one-year post-fertilization N use efficiency. For all application dates, the UD treatment produced lower (P=0.02±0.03) N use efficiencies than the UDBC and CUFBC treatments, and the UDBC treatment generated higher (P=0.04) N use efficiencies than the CUFBC treatments (Figure 13). The August and October 2001 fertilizer/brush control treatments were associated with the highest N use efficiencies, and the February 2001 applications yielded the lowest (Table 5). One-year post-fertilization N use efficiency was positively correlated with one-month post-fertilization foliage NUE (r=0.44, P<0.0001).

3.5. Biomass responses to treatments

Fertilizer/brush control treatments applied in 2001 significantly (P=0.001±0.002) affected the growth of biomass components in December 2001 (Figure 14). No significant effects of application date on growth were found. However, response times for the various UD, UDBC, and CUFBC treatments were different. A lack of application date differences indicated later application dates produced growth comparable to earlier applications in less time. For each biomass component (stem, foliage, branch, root), the UD treatment yielded lower growth than those of the UDBC and CUFBC treatments, and the UDBC and CUFBC treatments produced similar growth. Growth of all biomass components of trees receiving the CONT treatment was lower (P=0.002±0.004) than that of the BC treatment. Stem growth of CONT trees was lower (P=0.02±0.01) than those of trees receiving UDBC and CUFBC treatments. Stem growth of trees receiving the BC treatment was comparable to all UDBC and CUFBC treatments. Branch, foliage, and root growth of CONT trees were significantly lower (P=0.01±0.0001) than that of all fertilized trees except those receiving the October UD treatment. The branch, foliage, and root growth of BC trees were equivalent to that of trees receiving all UDBC and CUFBC treatments, equivalent to the February, April, June, and August UD treatments, and greater than the October UD treatment.

Significant fertilizer effects (P<0.0001) were observed for growth of each biomass component as of September 2002 (Figure 15); no significant application date effects were observed. Again, response times were different for the various UD, UDBC, and CUFBC treatments. As in December 2001, the UD treatment was associated with biomass component growth lower (P<0.0001) than that of the UDBC and CUFBC treatments, and the UDBC and CUFBC treatments similarly affected growth. The growth of each component of trees receiving the CONT treatment was less than (P=0.01±0.01) that of those receiving the BC treatment. Stem growth of the CONT treatment was lower (P=0.002±0.002) than that of all 2001 fertilizer/brush control treatments except the February UD treatment. Stem growth of BC trees was equivalent to all 2001 UD, UDBC, and CUFBC treatments. Foliage growth of CONT trees was lower (P=0.002±0.003) than that of all fertilizer/brush control treatments except the October UD treatment. Foliage growth associated with the BC treatment was significantly lower (P=0.01±0.01) than all 2001 UDBC and CUFBC treatments and equivalent to all UD treatments. Branch and root growth of CONT trees were lower (P=0.003±0.011) than those produced by all 2001 UD, UDBC, and CUFBC treatments. Branch and root growth associated with the BC treatment were similar to those of the UD treatments and lower (P=0.02±0.01) than the February, April, June, and August UDBC and CUFBC treatments.

Significant (P=0.01±0.003) differences among 2002 UD, UDBC, and CUFBC treatments in stem and root growth were observed in November 2002 (Figure 16). No significant application date effects were observed; response times differed for the various UD, UDBC and CUFBC treatments. The 2002 UDBC and CUFBC treatments promoted greater (P=0.02±0.02) stem and root growth than the UD treatment; the growth of the UDBC and CUFBC treatments were similar. Growth of foliage, stem, and branches were equivalent in response to the CONT and BC treatments. The BC treatment produced greater (P=0.047) root growth than the CONT treatment. All 2002 UD, UDBC, and CUFBC treatments significantly (P=0.01±0.001) increased foliage and branch biomass growth above that of the CONT treatment. The BC treatment was associated with lower branch biomass growth than all UDBC treatments, April and June CUFBC treatments, and June, August, and October UD treatments. Trees receiving the BC treatment also had significantly lower (P=0.01±0.01) foliage growth than those receiving UD, UDBC, and CUFBC treatments in all months, with the exception of the August CUFBC treatment. Stem growth of all UDBC, January and June UD, and February, April, and June CUFBC treatments exceeded (P=0.02±0.03) those of the CONT treatment. The BC treatment produced lower (P=0.02±0.01) stem growth than the January and June CUFBC and the April and June UDBC treatments. All UDBC and the January and April CUFBC treatments increased (P=0.004±0.01) root growth above that of the CONT treatment. Root growth was increased (P=0.02±0.01) above that of the BC treatment by the April and June UDBC and CUFBC treatments. In general, biomass growth of 2002 was nearly double that observed over the same time in 2001.

4.0. Discussion

The short-term foliage NUE's (Figures 10-12) reflected the environmental and physiological conditions at the time of fertilizer application that affected pine N uptake. The low foliage NUE's consistently observed in response to winter and spring applications could be attributable to low pine sink strength and unfavorable soil temperature conditions. Late winter and early spring urea applications are ineffective in promoting tree N uptake since root functioning is decreased at lower soil temperatures via higher water viscosity and decreased root permeability and metabolic activity. This decreased root functioning in turn decreases nutrient uptake and use (Bhat 1983, Dong et al. 2001).

The higher foliage NUE's and N use efficiencies (Figures 10-13) observed in response to June, August, and October applications could be indicative of better timing of fertilizer applications to match loblolly pine demand and uptake capacity for N. Foliage biomass increased as the growing season progressed, which can increase loblolly pine sink strength and transpiring area (Powers and Reynolds 1999). Developing leaf tissues are strong sinks for N (Zhang and Allen 1996, Dong et al. 2001), and greater evapotranspiration increases N uptake (Powers and Reynolds 1999, Ottman and Pope 2000). In 2002, trees had much higher foliage weights than in 2001, which promoted foliage NUE's in June, August, and October of 2002 that were nearly double that observed in the same months in 2001 (Figures 10 and 11). Photosynthetic rates increase through the growing season as the photoperiod lengthens and the number of sunny days increases. These higher rates increase foliage demand for N (Shoji et al. 1991), and higher tree N content allows for better utilization of carbohydrates for growth (Rogers et al. 1996). Timing of fertilization to coincide with pine foliage expansion is analogous to the agricultural practice of timing N fertilization to leaf emergence, which has been shown to increase N use efficiency (Stecker et al. 1993). Loblolly pine root expansion also proceeds through middle to late summer, and root length is one of the most important factors controlling N uptake (Li et al. 1991). In addition, root metabolic activity increases with increasing root temperature, which in turn increases N uptake (Bhat 1983, Dong et al. 2001). The relatively higher foliage NUE's observed in this study in June and August are consistent with the maximum seasonal N uptake rates observed by Bhat (1983) from May to August for apple trees.

Ludovici et al. (2002) recently proposed that winter forest fertilization applications are beneficial since they coincide with peak foliage starch contents. However, initial growth in late winter and early spring is largely dependent on remobilization of stored N (Dong et al. 2001). Penultimate increases in foliage starch concentrations occur during the summer in conjunction with secondary foliage growth flushes (Adams et al. 1986) at a time in which trees depend more heavily upon current N uptake to satisfy N demands (Dong et al. 2001). Thus, summer applications likely correspond to a period of the growing season in which N can be more readily utilized for growth.

The fall applications may have produced high N use efficiencies by coinciding with high root demand for N. Although October applications typically had lower foliage NUE than summer applications (Figures 10 and 12), the one-year post-fertilization N use efficiencies of October applications were comparable to August fertilizer treatments (Figure 13). As aboveground growth and photosynthetic rates decline later in the growing season, roots become stronger sinks for N (Adams et al. 1986, Sung et al. 1997). As such, fall fertilization can be advantageous since it increases root N reserves that can be used for growth immediately after fertilization and in the following spring (Dong et al. 2001). Increasing fall nutrient availability also extends root growth and plasmalemma-ATPase activity (Iivonen and Vapaavuori 2002), which can impart further growth advantages in the following season.

In the absence of direct NH_3 volatilization measurements, inferences about volatilization must be made on the basis of environmental measurements. Volatilization risks are decreased if 10 to 25 mm of precipitation is received within 6 days of urea application (Stecker et al. 1993). Both years of this study were characterized by average precipitation patterns for the region, and several applications received between 10 to 25 mm of precipitation within 7 days of fertilization (Figure 17). October 2001 had the longest post-fertilization dry period, with 20 days post-fertilization without rainfall (Figure 18). October 2001 was the only application date in which the NUE of the UD treatment exceeded that of the UDBC treatment (Figure 10); Kissel (2002) observed that bare forest soil is associated with higher NH_3 volatilization rates than soil with an intact organic layer. In 2001, the August fertilizer/brush control treatments yielded higher foliage NUE than the June and October applications (Figure 10). The August treatment received much more precipitation within one week of application than did the June and October applications (Figure 17). Volatilization may have contributed to these results.

In both years of this study, the highest foliage NUE's were associated with summer applications. The summer applications were consistently associated with lower soil moistures and precipitation events soon after application (Figure 18). Kissel (2002) found that volatilization rates of a loblolly pine forest floor amended with urea were ~10% lower when urea was applied to dry soil. The same study demonstrated that urea dissolved by rain moved freely into soil, whereas urea dissolved by dews reprecipitated and was protected against downward movement in soil. Consequently, as the time between urea application and precipitation increased, NH_3 volatilization losses increased. The higher NUE's of summer applications observed in this study could in part have been due to a combination of dry soil and timely precipitation that reduced volatilization risk. The April and October 2001 applications were followed by more than 15 days without rain (Figure 18); consequently, the CUFBC treatment produced higher NUE's than the UDBC treatments for these 2 application dates (Figure 10). The delayed release of urea from CUF until precipitation likely suppressed volatilization rates relative to the standard urea formulation. Given that southeastern Oklahoma is among the most xeric portions of the natural range of loblolly pine, adequate summer precipitation patterns cannot be expected each year. However, regions within loblolly pine's range characterized by moderate to frequent summer precipitation may typically receive adequate moisture to minimize volatilization risks.

Herbaceous vegetation negatively impacted loblolly pine N acquisition and growth responses. Several UD treatments yielded lower foliage NUE's than the UDBC and CUFBC treatments, and all UD treatments were associated with significantly lower N use efficiencies than UDBC and CUFBC treatments (Figures 10-13). In addition, foliage N accumulation of the February 2001 and April 2002 UD treatments was lower than the UDBC and CUFBC treatments (Figures 4-7). Negative impacts of herbaceous vegetation on crop tree responses to fertilizer applications are well documented (Baker et al. 1974, Colbert et al. 1990, Morris et al. 1993, Jokela et al. 2000). Morris et al. (1993) found that panicum grass (*Panicum dichotomiflorum* L.) and broomsedge (*Andropogon* spp.) were highly competitive for applied N in a young loblolly pine plantation. Both species were prevalent at our site as well. Blackberry (*Rubus argutus* L.) and ragweed (*Ambrosia artemsiifolia* L.) were also abundant on our site; ragweed predominance particularly increased after fertilization. Few studies provide quantification of the competitive influence of understory vegetation on pine nutrition (Powers and Reynolds 1999). The significant increases in herbaceous vegetation N accumulation (Figure 8) and decreases in bioavailable soil N (Table 1) observed in UD plots in 2001 provide evidence of the affinity of understory vegetation for applied N early in the rotation.

In 2002, the lack of differences in NUE between UD, UDBC, and CUFBC treatments (Figure 11) as well as the absence of increases in herbaceous vegetation N accumulation (Figure 9) may be indicative of a fading competitive ability of herbaceous vegetation from stand ages 3 to 4. During the first five years of loblolly pine rotations, pines increasingly dominate the site (Morris et al. 1993, Cain 1999). However, Baker et al. (1974) found greater herbaceous vegetation competition for N at age 4 of a loblolly pine plantation than at age 3, which was attributed to a high preponderance of sunflowers at age 4. No sunflowers were observed in this study.

Xu et al. (2002) suggested that maintenance of herbaceous vegetation on site in conjunction with fertilization improves overall capture of applied nutrients. The nutrients accumulated by understory vegetation may benefit the following rotation. The greater vegetation N acquisition could also be beneficial in preventing nitrate migration into groundwater. Furthermore, understory vegetation may help capture NH_3 emitted through volatilization (Nason et al. 1988). In this study, overall vegetation N acquisition was greater in response to UD treatments in 2001. However, in 2002 loblolly pine was the dominant vegetation N sink (Figure 19). As such, total vegetation N content was comparable for UD, UDBC, and CUFBC treatments as of the peak biomass N assessment of September 2002. The faster decline in soil N in UD than in UDBC and CUFBC plots is also indicative of the increased vegetation N uptake when herbaceous vegetation is maintained (Tables 1 and 2). However, biomass growth of trees receiving the UD treatments was significantly less than those receiving UDBC and CUFBC treatments (Figures 14-16). If maximization of crop tree biomass is the management objective, a regular regimen of fertilization in conjunction with understory control may be preferable, with vegetation control being more essential to maximizing fertilizer responses of younger stands.

The BC treatment increased pine resource use efficiency and growth. The soil N levels of the BC treatment were consistently comparable to those of the CONT treatment throughout this study (Tables 1 and 2). Herbicide treatments have been demonstrated to increase soil N availability via reduction in N competition and increases in N mineralization (Zutter et al. 1999, NCSFNC 2001). Some evidence for increased N mineralization was found in a separate study on the same site (Manuscript II). The lack of an increase in soil N levels in the BC treatment and foliage N accumulation rates in excess of the CONT treatment are likely indicative of adequate pine buffering of N released by herbicide treatments.

In 2001 the N accumulation of previous-season foliage (Figure 4) associated with the BC treatment was comparable to the UD and UDBC treatments throughout the season, and the N accumulation of current-season foliage (Figure 5) was comparable for the BC, UDBC, and CUFBC treatments. These similarities in foliage N accumulation between BC and fertilized treatments could indicate that the herbicide treatments released N levels near the N capacity of foliage biomass in 2001. In 2002, the BC treatment produced foliage N accumulation significantly lower than the UDBC and CUFBC treatments in 2001 foliage (Figure 6) and lower than UD, UDBC, and CUFBC treatments in 2002 foliage (Figure 7). The greater amount of foliage present on trees in 2002 represented a larger sink and consequent demand for N than in 2001.

The comparable biomass growth of BC, UDBC, and CUFBC treatments by December 2001 (Figure 14) may also signify comparable satisfaction of pine N needs in 2001 by these 3 treatments. The September 2002 assessment of biomass growth of trees treated in 2001 (Figure 15) revealed that foliage, branch, and root growth rates of UDBC and CUFBC treatments were significantly greater than the BC treatment. Fertilization likely increased internal N reserves in all biomass components more than the BC treatment; the extra N in these trees could have been remobilized for growth as the tree increased in size (Zutter et al. 1999). Thus, although 2001 fertilizer treatments seemed to exceed pine N demands for growth at age 3, the stored N was utilized for growth at age 4. The sustained growth increase from fertilization and shorter-term growth increases from herbicide treatments were consistent with those observed for young *Pinus radiata* in New Zealand (Mason and Milne 1999). By November 2002 (Figure 16), several UDBC and CUFBC treatments produced branch, foliage, and stem growth greater than the BC treatment, which further indicates the higher N capacity of trees in 2002. The biomass growth and foliage N accumulation in response to the BC treatment were frequently comparable to or greater than those of the UD treatment. Colbert et al. (1990) similarly found that growth responses to herbicide-only and fertilizer-only treatments were comparable for juvenile loblolly pine in the Lower Coastal Plain.

The UDBC and CUFBC treatments yielded the highest levels of bioavailable soil N in both years of this study (Tables 1 and 2). Raun and Johnson (1995) found that N rates in excess of that required for maximum crop yield did not raise soil inorganic N until the soil-plant buffer for soil inorganic N was surpassed, at which point soil inorganic N would increase. The high levels of soil N observed in response to the UDBC and CUFBC treatments, and to a lesser extent the UD treatment, suggest that the N rate used in this study exceeded the buffer capacity of the soil-plant system for much of the first growing season after application. The UDBC treatment, with its more soluble formulation, yielded higher mean soil N than the CUFBC treatment. The 202 kg N ha^{-1}

fertilization rate was consistent with the biologically optimum N rate determined for juvenile loblolly pine in North Carolina and north Florida (Ballard 1981, Jokela and Stearns-Smith 1993), but may have exceeded the N demand for juvenile loblolly pine in the more xeric southeastern Oklahoma region. Nevertheless, the dissipation of soil N levels in fertilized plots in this study was consistent with the observation that inorganic N levels return to background levels within 2 years of fertilization of loblolly pine plantations (Johnson and Todd 1988). Thus, although the buffer capacity of the soil-plant system was initially exceeded since loblolly pine N demand was surpassed, within a year the soil-plant system buffered against a long-term increase in soil N levels. Aarnio et al. (1996) proposed that most tree recovery of urea N occurs in the first year. Since no significant increases in microbial populations were observed in fertilized plots (Manuscript II), loblolly pines were the dominant pool for N immobilization in UDBC and CUFBC plots. However, some N may have leached below the top 15 cm of soil in which bioavailable N was assessed in this study, and some volatilization losses likely occurred.

The UDBC and CUFBC treatments were associated with the highest foliage N accumulation in each year of this study (Figures 4-7), and N accumulation was consistently similar for the two treatments. Precipitation frequently occurred soon enough after fertilization to prompt some dissolution of both formulations (Figure 18). The soil N values observed after the February 2001 (Table 1) and April 2002 (Table 2) applications demonstrate that CUF releases N comparable to the urea/DAP mixture when there is sufficient rainfall. The application followed by the longest dry period, October

2001, revealed an advantage to the CUFBC treatment's delayed release of N since it produced higher NUE than the UDBC treatment (Figure 10).

The UDBC and CUFBC treatments promoted similar biomass growth responses, and both treatments produced the highest increases in biomass growth (Figures 14-16). Substantial biomass growth increases in response to fertilizer/brush control treatments are well documented (Colbert et al. 1990, Haywood and Tiarks 1990, Jokela et al. 2000, Borders and Bailey 2001). In September 2002, biomass allocation patterns of the 2001 UDBC and CUFBC treatments (Figure 15) differed from the CONT and BC treatments. These findings contrast with the results of Retzlaff et al. (2001), which demonstrated that biomass allocation patterns of fertilized juvenile loblolly pine trees were unchanged by fertilization. Stem growth as a proportion of total biomass in response to UDBC and CUFBC treatments were 4% lower than in response to the CONT and BC treatments. Stem growth of loblolly pine is less promoted by fertilization than foliage expansion (Adams et al. 1986). The UDBC and CUFBC treatments had 4.5% higher foliage growth as a proportion of total biomass and 4% higher branch growth than the CONT and BC treatments. Colbert et al. (1990) demonstrated that loblolly pine increases branching and foliage production in response to fertilization in order to maximize the leaf area exposed to sunlight. The increased nutrient availability led to decreased root:shoot ratios of fertilized trees. The average root:shoot ratio observed in September 2002 was 0.47 and 0.49 for the UDBC and CUFBC treatments, respectively. The root:shoot ratios for CONT and BC treatments were 0.56 and 0.51. Similar results were observed in November 2002 in response to the 2002 UDBC and CUFBC treatments. UDBC and CUFBC treatments had 7% lower stem growth, 3% greater foliage growth, and 5%

greater branch growth as a proportion of total biomass than CONT and BC treatments. However, root:shoot rates were similar for fertilized and non-fertilized treatments. It is noteworthy that in both 2001 and 2002 the latter-season UDBC and CUFBC applications promoted growth gains comparable to the earlier applications within a shorter response time, which could be indicative of having better coincided pine growth demand for N.

Over time, differences in the performance of trees receiving CUFBC and UDBC treatments may emerge. Throughout the study, the foliage N concentrations were consistently highest in response to the CUFBC treatment (Manuscript III). The N accumulation of the most recent foliage flush observed in this study was greatest in response to the CUFBC treatment. As the trees grow, N demand and uptake capacity will increase, and the CUFBC treatment may prove superior to the UDBC treatment in providing N. CUF proved to be an effective vector for boron (Manuscript III), and boron facilitates nutrient uptake by increasing integrity of plasmalemma H^+ pumping ATPase (Marschner 1995). The higher foliage N contents of trees treated with CUFBC could be indicative of an increased ability to sequester N. The trees on our site will continue to be monitored to observe longer-term growth responses to the fertilizer/brush control treatments.

5.0. Conclusions

This study demonstrated that forest managers likely have greater flexibility in applying fertilizers than conventional guidelines suggest. The application dates in this study, which encompassed a broad range of climatic and edaphic conditions typical for the northwestern edge of the natural range of loblolly pine, were equally effective in promoting loblolly pine growth within the two years of this study. Loblolly pine NUE increased as the growing season progressed, with the highest NUE and N use efficiencies occurring in response to summer applications. Summer applications coincide with physiological and environmental conditions that facilitate N uptake and use, such as secondary foliage growth flushes and maximum soil temperatures and evapotranspiration rates. In regions characterized by moderate to high summer precipitation, summer applications of urea may be a feasible management strategy for maximizing fertilization efficiency. A more conservative strategy for increasing fertilization efficiency may be application of fertilizer in early fall, which coincides with peak pine root N demand, higher precipitation for reducing volatilization risks, and warm soil temperatures. The N reserves yielded by fall applications can be utilized for aboveground biomass growth the following spring. Application of N fertilizers less prone to volatilization than urea could further increase efficiency of fertilizer applications. Properly timing forest fertilization to match pine nutrient demand increases the amount and speed of pine uptake of applied nutrients. These benefits could in turn increase the cost-effectiveness and minimize the environmental impacts of forest fertilization operations.

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TABLE 1. Average bioavailable N (NO_3-N + NH_4-N) (mg g^{-1}) adsorbed to ion exchange resin per day in response to fertilizer treatments administered to a juvenile loblolly pine plantation in southeastern Oklahoma in February 2001 and glyphosate brush control treatments.

Treat[1]	Mar 01	Apr 01	May 01	Jun 01	Jul 01	Aug 01	Sept 01	Oct 01	Nov 01	Dec 01	Jan/Feb02
CONT	0.06 *a*	0.09 *a*	0.04 *a*	0.04 *a*	0.16 *a*	0.09 *a*	0.04 *a*	0.07 *a*	0.05 *a*	0.05 *a*	0.01 *a*
BC	0.01 *a*	0.13 *a*	0.08 *a*	0.07 *a*	0.37 *a*	0.13 *a*	0.20 *ab*	0.38 *a*	0.04 *a*	0.06 *ab*	0.03 *ab*
UD	1.67 *b*	2.65 *b*	0.85 *b*	0.26 *b*	0.27 *a*	0.11 *a*	0.10 *b*	0.09 *a*	0.04 *a*	0.19 *abc*	0.05 *ab*
UDBC	2.37 *b*	4.91 *b*	5.93 *b*	3.82 *c*	3.92 *b*	0.24 *a*	0.89 *c*	4.15 *b*	0.43 *b*	0.21 *bc*	0.24 *b*
CUFBC	0.97 *b*	1.48 *b*	3.27 *b*	1.65 *c*	1.44 *b*	0.19 *a*	1.36 *c*	0.76 *b*	0.25 *b*	0.61 *c*	0.05 *ab*

NOTE: Means within a column followed by different letters differ significantly at $P < 0.05$.

[1]CONT = no fertilizer/no brush control treatment
BC = no fertilizer/brush control treatment
UD = urea and diammonium phosphate/no brush control treatment
UDBC = urea and diammonium phosphate/brush control treatment
CUFBC= coated urea fertilizer/brush control treatment

TABLE 2. Average bioavailable N (NO_3-N + NH_4-N) (mg g^{-1}) adsorbed to ion exchange resin per day in response to fertilizer treatments administered to a juvenile loblolly pine plantation in southeastern Oklahoma in April 2002 and glyphosate brush control treatments.

[1]Treatment	May/June 02	July/Aug 02	Sept/Oct 02	Nov/Dec 02	Jan 03
CONT	0.33 *a*	0.01 *a*	0.02 *a*	0.01 *a*	0.05 *a*
BC	0.02 *a*	0.02 *a*	0.02 *a*	0.02 *a*	0.60 *a*
UD	0.51 *ab*	0.61 *b*	0.07 *ab*	0.10 *a*	0.07 *a*
UDBC	0.97 *b*	1.03 *b*	0.22 *b*	0.40 *b*	0.30 *a*
CUFBC	2.04 *b*	0.69 *b*	0.18 *b*	0.17 *b*	0.20 *a*

NOTE: Means within a column followed by different letters differ significantly at $P < 0.05$.
[1]CONT = no fertilizer/no brush control treatment
BC = no fertilizer/brush control treatment
UD = urea and diammonium phosphate/no brush control treatment
UDBC = urea and diammonium phosphate/brush control treatment
CUFBC= coated urea fertilizer/brush control treatment

TABLE 3. Effects of application date on one-month post-fertilization foliage nitrogen uptake efficiency (%). Fertilizer and glyphosate brush control treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in 2001.

	Application date				
Treatment[1]	February	April	June	August	October
UD	0.32 *a*	0.57 *a*	1.91 *b*	2.33 *b*	1.58 *b*
UDBC	0.68 *a*	0.94 *a*	2.36 *b*	3.68 *c*	0.69 *a*
CUFBC	0.56 *a*	1.14 *b*	1.91 *c*	3.16 *d*	1.10 *ab*

NOTE: Means within a row followed by different letters differ significantly at $P < 0.05$.
[1]UD = urea and diammonium phosphate/no brush control treatment
UDBC = urea and diammonium phosphate/brush control treatment
CUFBC= coated urea fertilizer/brush control treatment

TABLE 4. Effects of application date on two-month post-fertilization foliage nitrogen uptake efficiency (%). Fertilizer and glyphosate brush control treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in 2002.

	Application date				
Treatment[1]	January	April	June	August	October
UD	0.41 *a*	2.03 *b*	7.36 *c*	15.09 *d*	6.83 *c*
UDBC	0.47 *a*	2.45 *b*	13.20 *d*	14.05 *cd*	8.24 *c*
CUFBC	0.54 *a*	2.08 *b*	8.04 *c*	9.19 *c*	7.24 *c*

NOTE: Means within a row followed by different letters differ significantly at $P < 0.05$.
[1]UD = urea and diammonium phosphate/no brush control treatment
UDBC = urea and diammonium phosphate/brush control treatment
CUFBC= coated urea fertilizer/brush control treatment

TABLE 5. Effects of application date on one-year post-fertilization nitrogen use efficiency (%). Fertilizer and glyphosate brush control treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in 2001.

	Application date				
Treatment[1]	February	April	June	August	October
UD	6.26 *a*	7.17 *b*	9.14 *c*	14.82 *d*	14.84 *d*
UDBC	7.64 *a*	11.03 *b*	12.92 *c*	16.97 *d*	16.50 *d*
CUFBC	7.01 *a*	9.42 *b*	11.64 *c*	14.99 *d*	15.94 *d*

NOTE: Means within a row followed by different letters differ significantly at $P < 0.05$.
[1]UD = urea and diammonium phosphate/no brush control treatment
UDBC = urea and diammonium phosphate/brush control treatment
CUFBC= coated urea fertilizer/brush control treatment

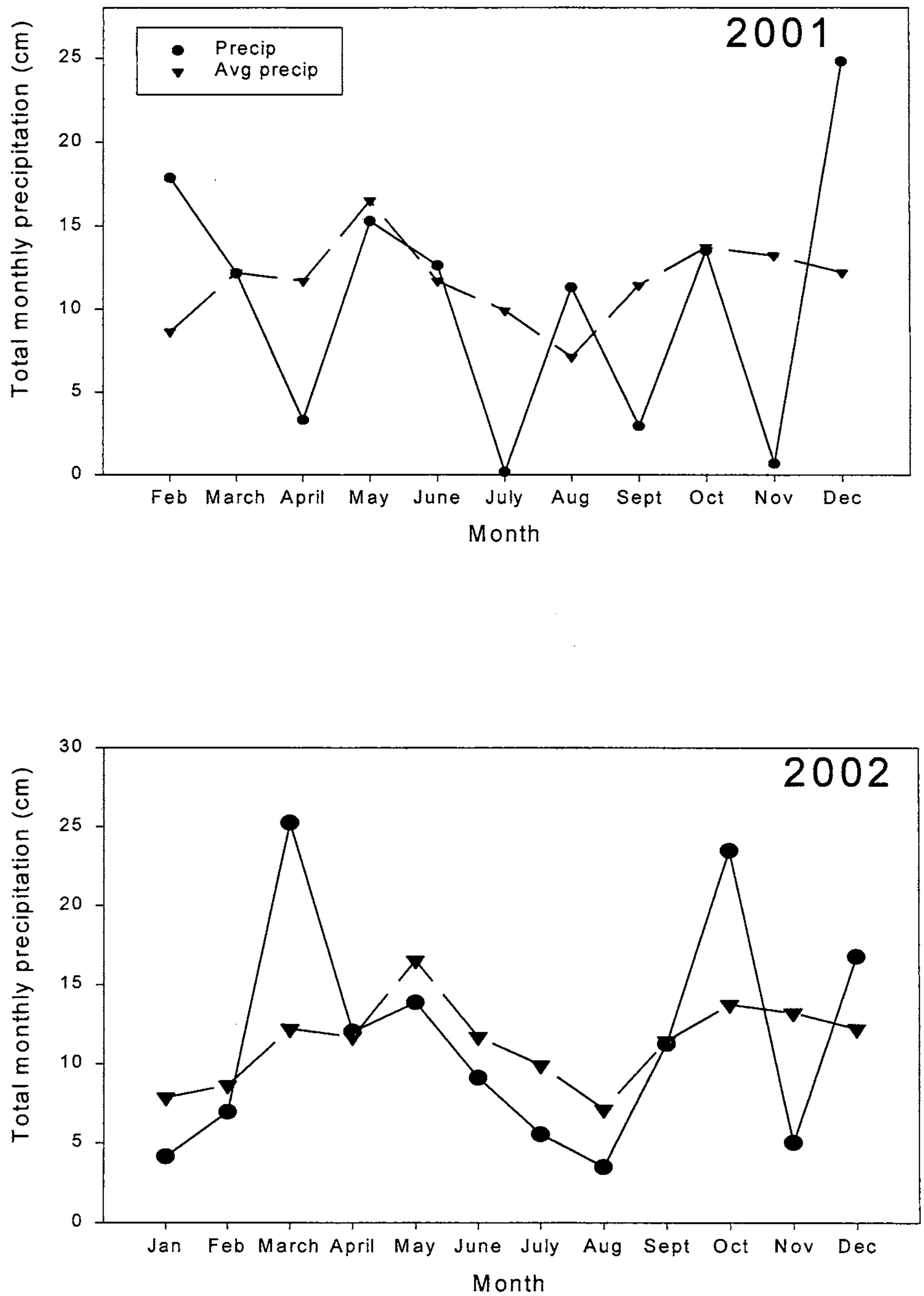
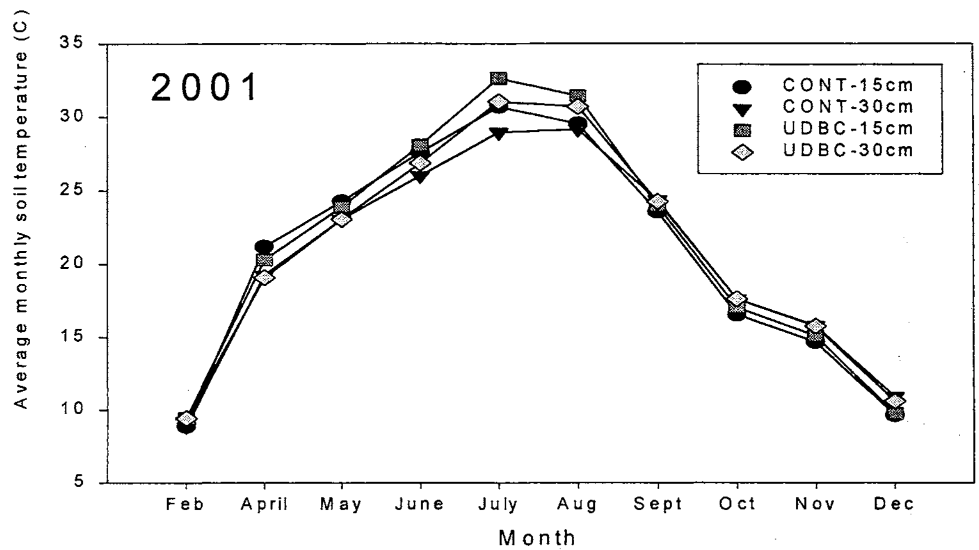


Figure 1. Monthly precipitation patterns observed in 2001 and 2002 in a loblolly pine plantation in southeastern Oklahoma and the average monthly precipitation patterns for the region.



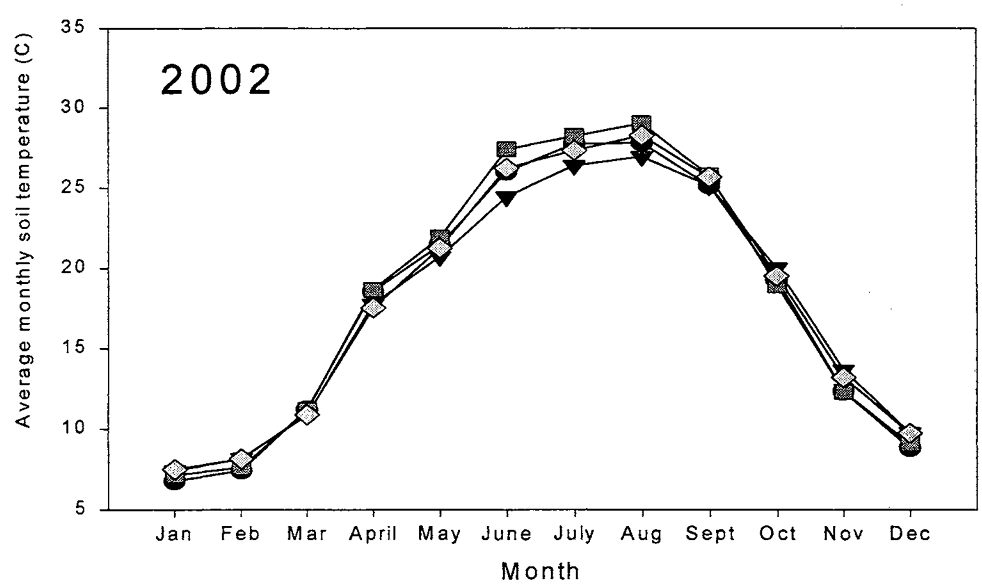
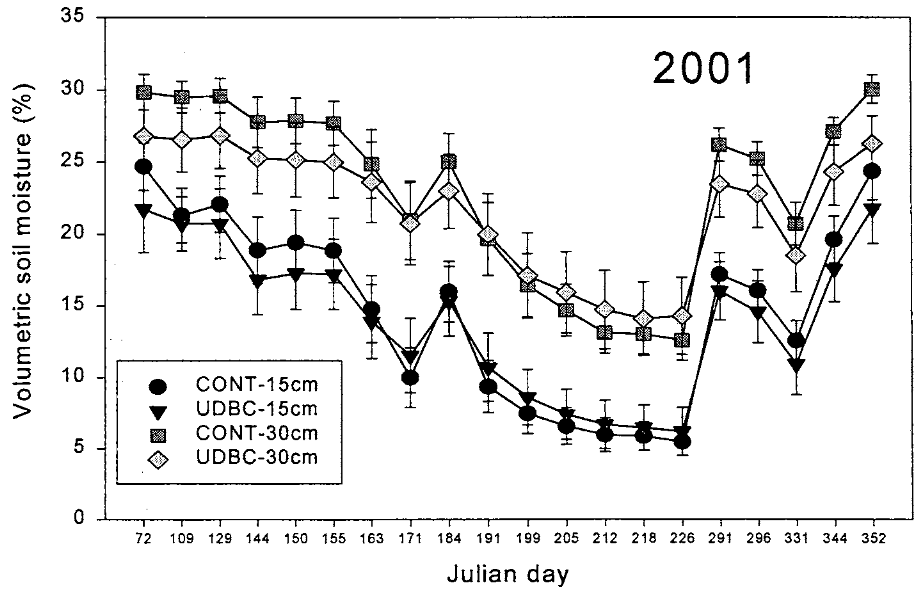


Figure 2. Monthly soil temperature trends at 15 and 30 cm in the presence and absence of herbaceous vegetation in a juvenile loblolly pine plantation in southeastern Oklahoma, 2001 and 2002.



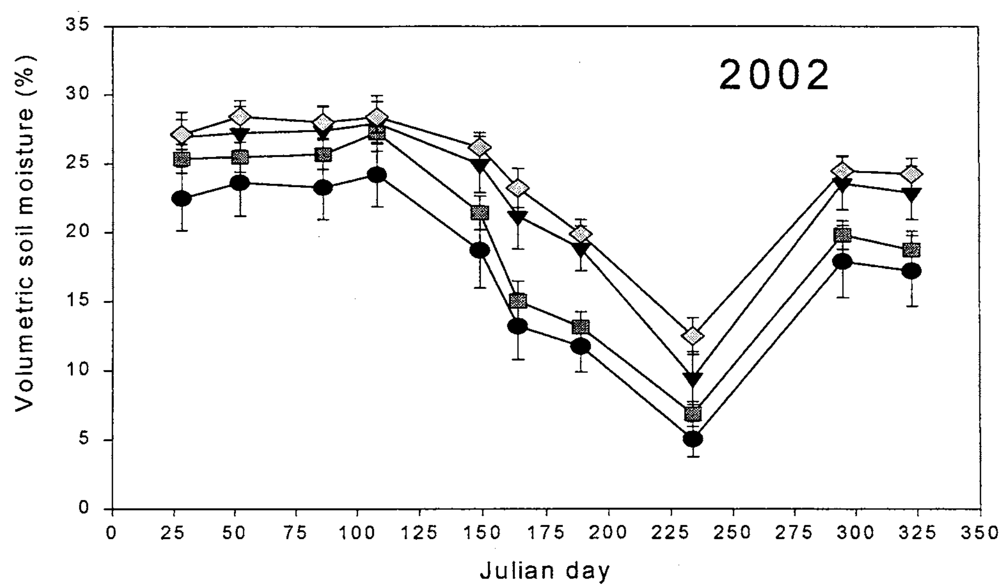


Figure 3. Monthly volumetric soil moisture trends at 15 and 30 cm in the presence and absence of herbaceous vegetation in a juvenile loblolly pine plantation in southeastern Oklahoma, 2001 and 2002. Error bars show 1 SE.

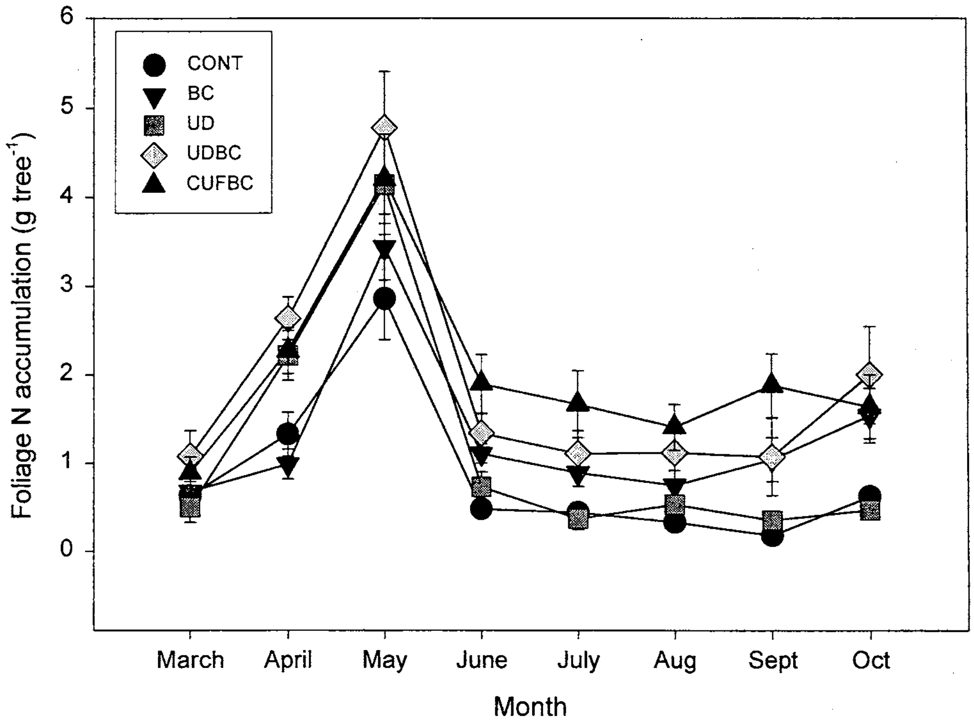


Figure 4. Accumulation of nitrogen in previous-season foliage in response to N and P fertilizers applied in February 2001 and glyphosate treatments. Fertilizer/brush control treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars show 1 SE.

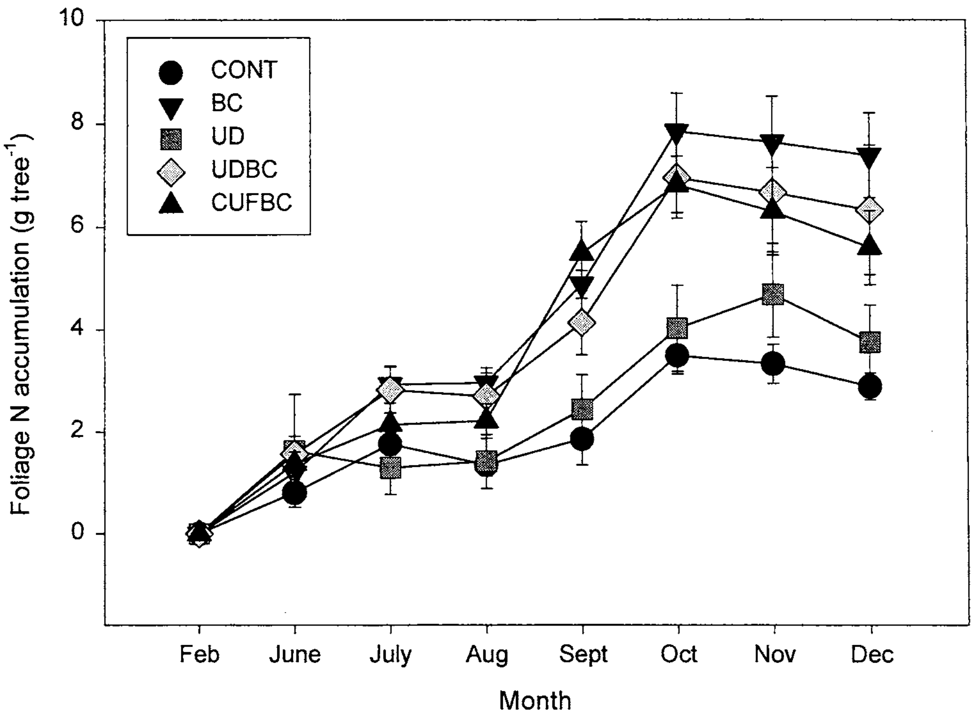


Figure 5. Accumulation of nitrogen in current-season foliage in response to N and P fertilizers applied in February 2001 and glyphosate treatments. Fertilizer/brush control treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars show 1 SE.

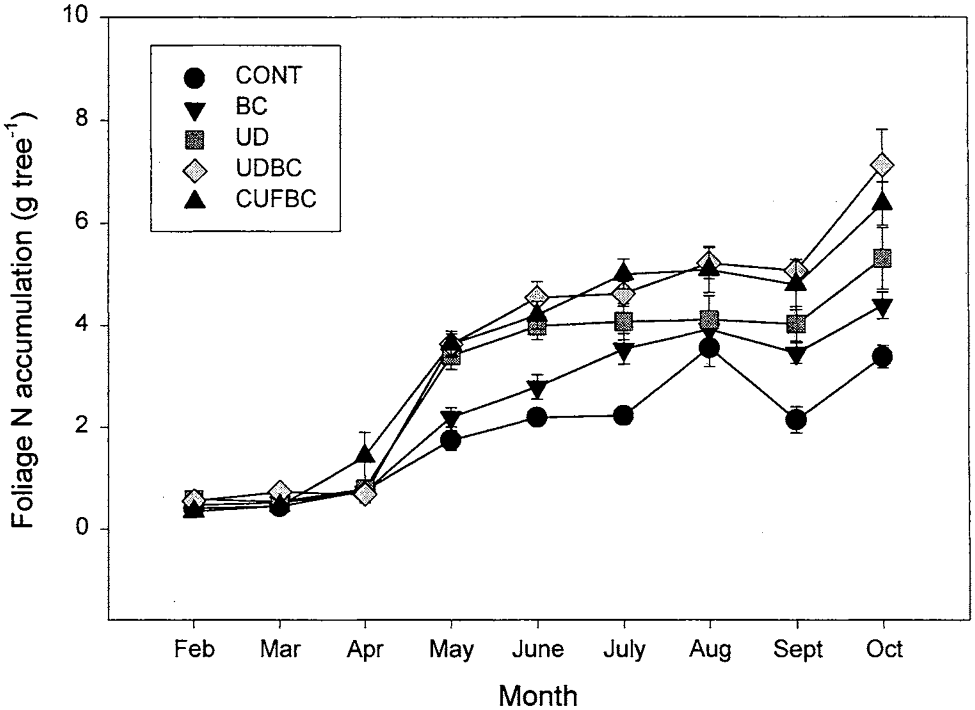


Figure 6. Accumulation of nitrogen in previous-season foliage in response to N and P fertilizers applied in April 2002 and glyphosate treatments. Fertilizer/brush control treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars show 1 SE.

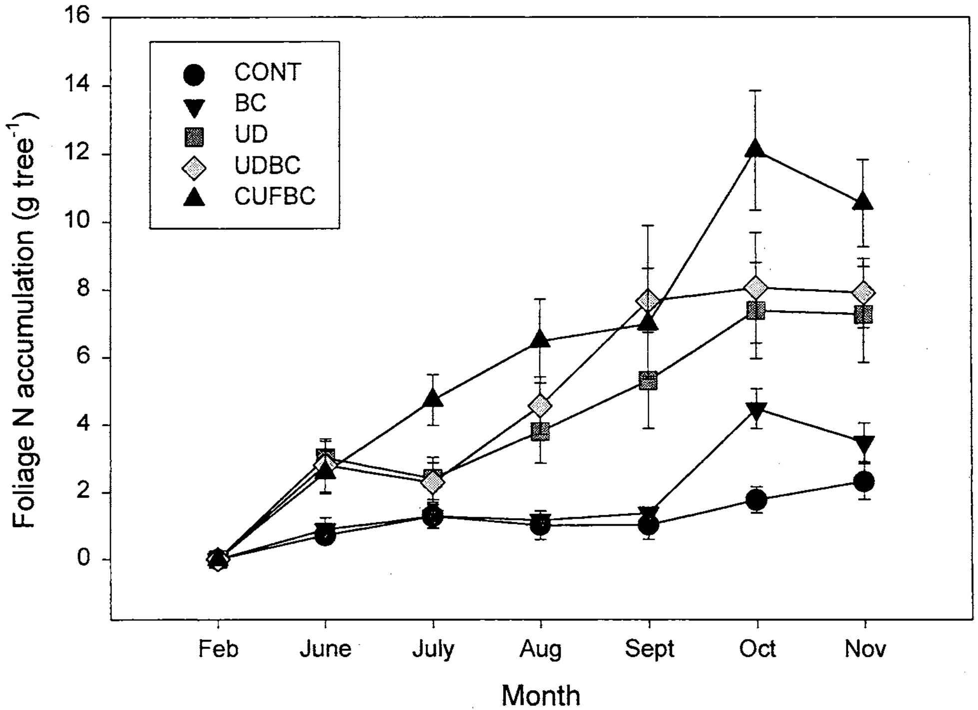


Figure 7. Accumulation of nitrogen in current-season foliage in response to N and P fertilizers applied in April 2002 and glyphosate treatments. Fertilizer/brush control treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars show 1 SE.

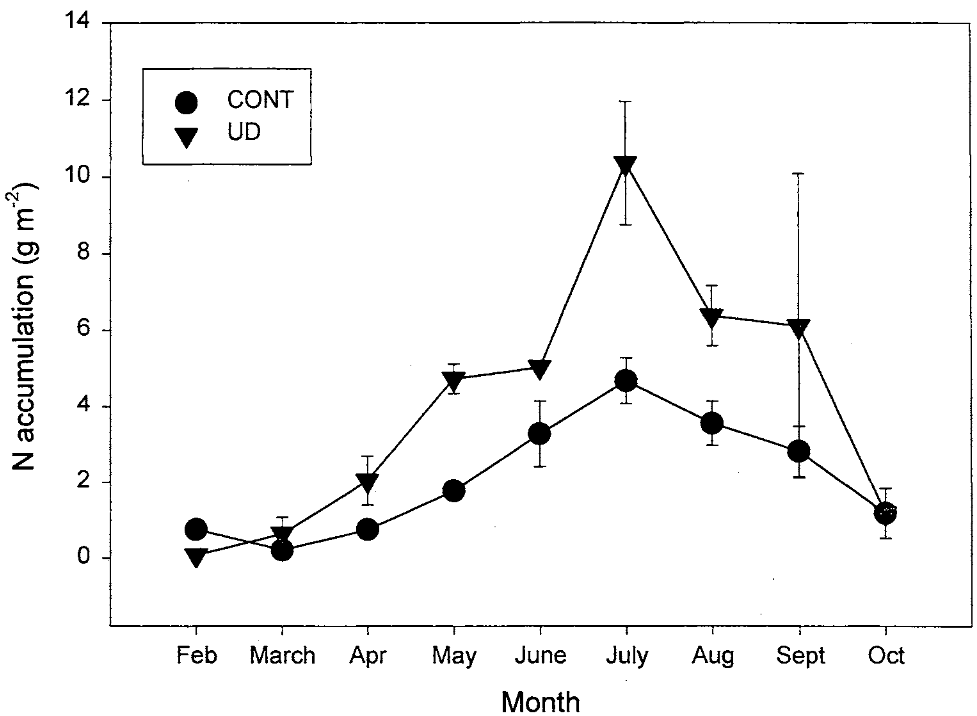


Figure 8. Accumulation of nitrogen in herbaceous vegetation growing in a juvenile loblolly pine plantation in southeastern Oklahoma. A control treatment is compared to a urea/diammonium phosphate mixture applied in February 2001. Error bars show 1 SE.

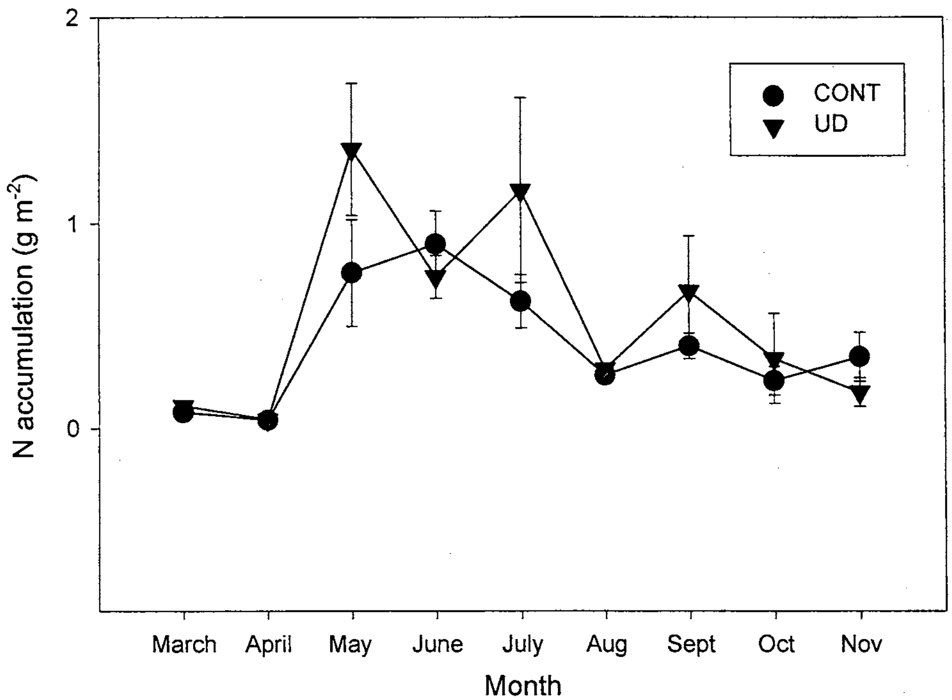


Figure 9. Accumulation of nitrogen in herbaceous vegetation growing in a juvenile loblolly pine plantation in southeastern Oklahoma. A control treatment is compared to a urea/diammonium phosphate mixture applied in April 2002. Error bars show 1 SE.

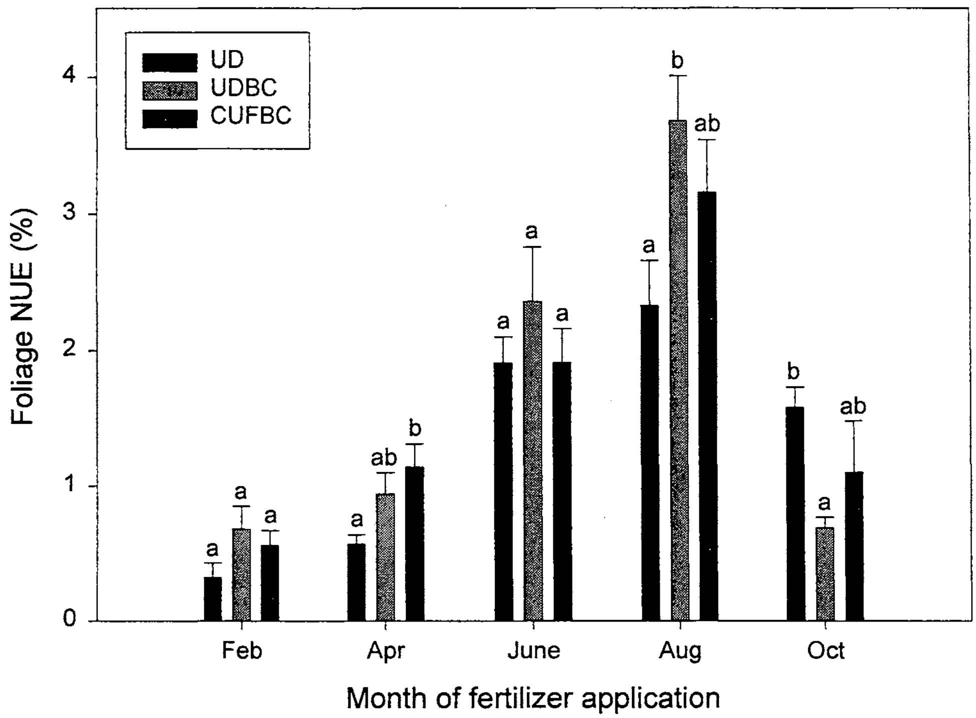


Figure 10. Foliage nitrogen uptake efficiency one month after fertilization in response to N and P fertilization at various dates of application. Fertilizers were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in 2001. Within each month of application, columns headed by different letters differ significantly at $P < 0.05$. Error bars show 1 SE.

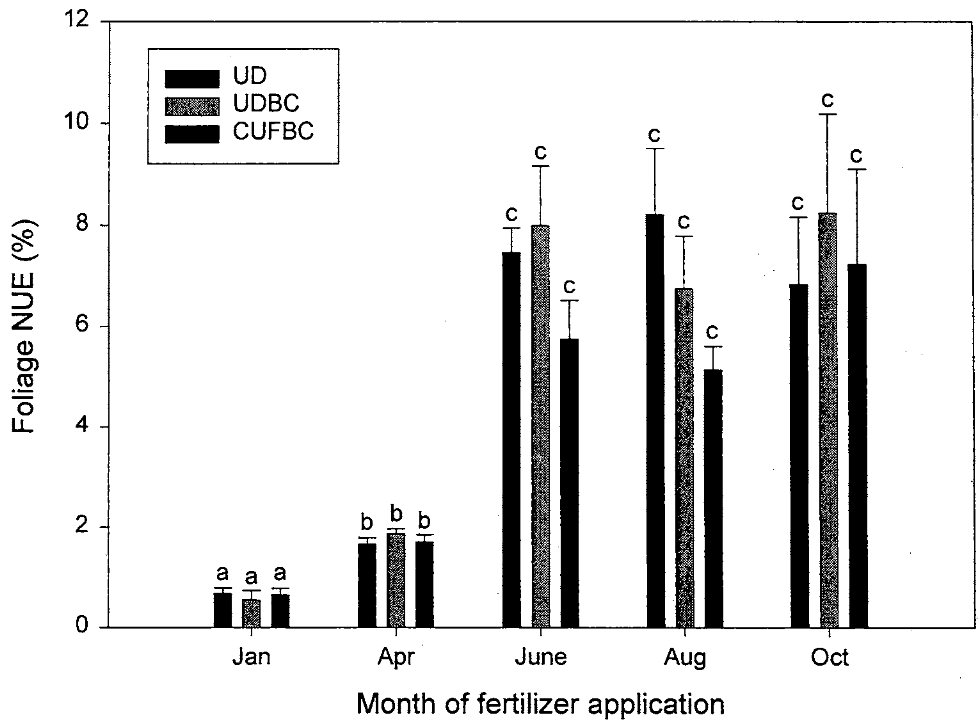


Figure 11. Effect of application date on foliage nitrogen uptake efficiency one month after fertilization in response to N and P fertilization at various dates of application. Fertilizers were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in 2002. Columns headed by different letters differ significantly at $P < 0.05$. Error bars show 1 SE.

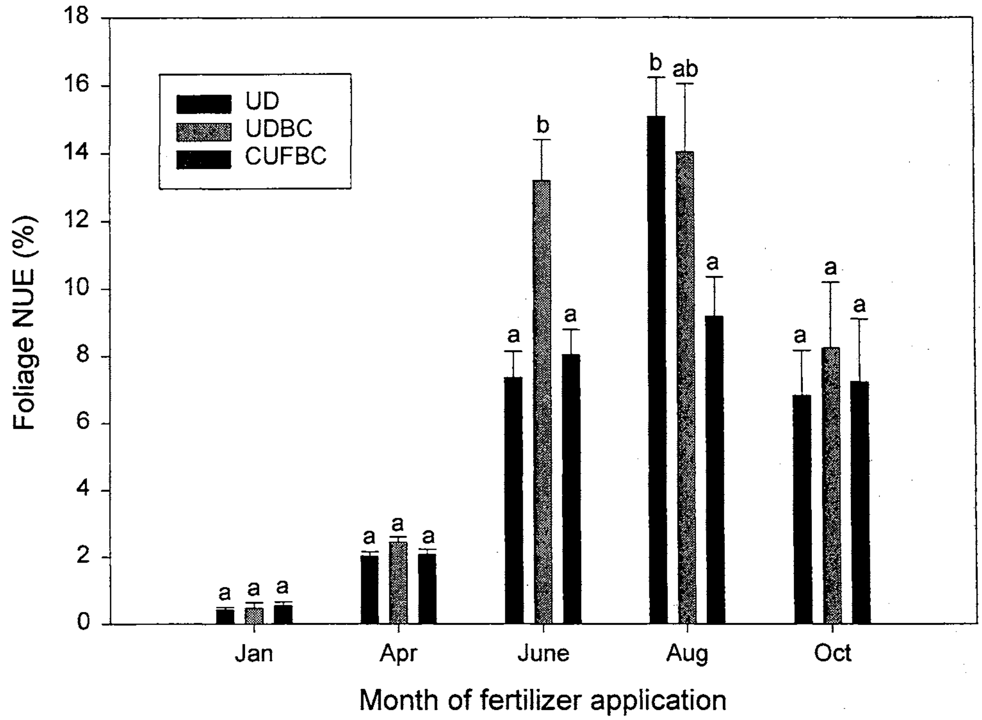


Figure 12. Foliage nitrogen uptake efficiency two months after fertilization in response to N and P fertilization at various dates of application. Fertilizers were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in 2002. Within each month of application, columns headed by different letters differ significantly at $P < 0.05$. Error bars show 1 SE.

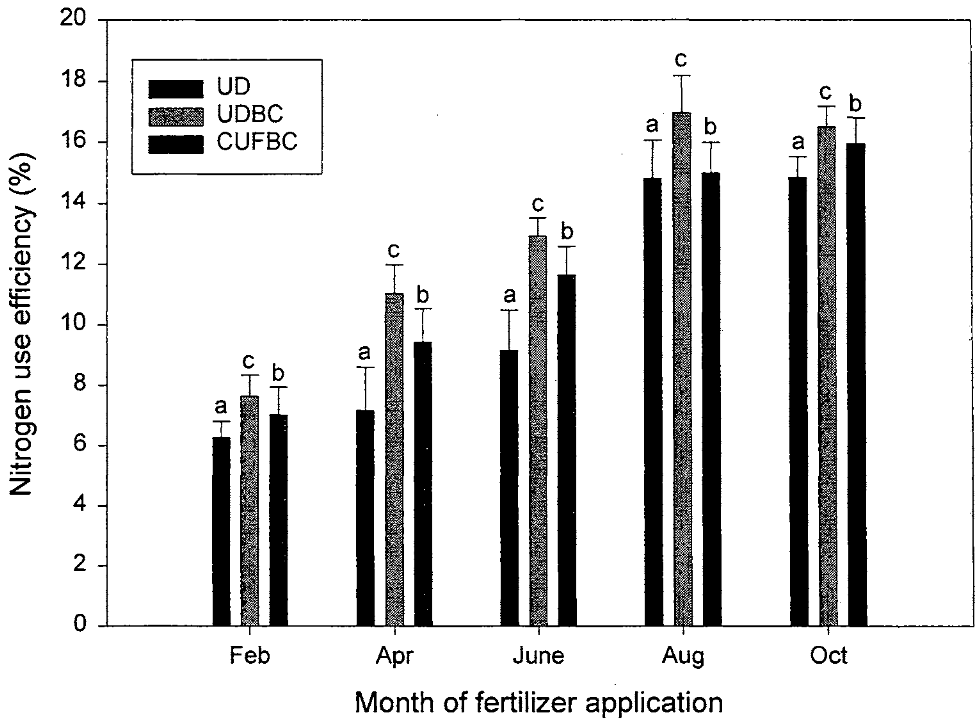


Figure 13. Nitrogen use efficiency one year after fertilization in response to N and P fertilization at various dates of application. Fertilizers were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in 2001. Within each month of application, columns headed by different letters differ significantly at $P < 0.05$. Error bars show 1 SE.

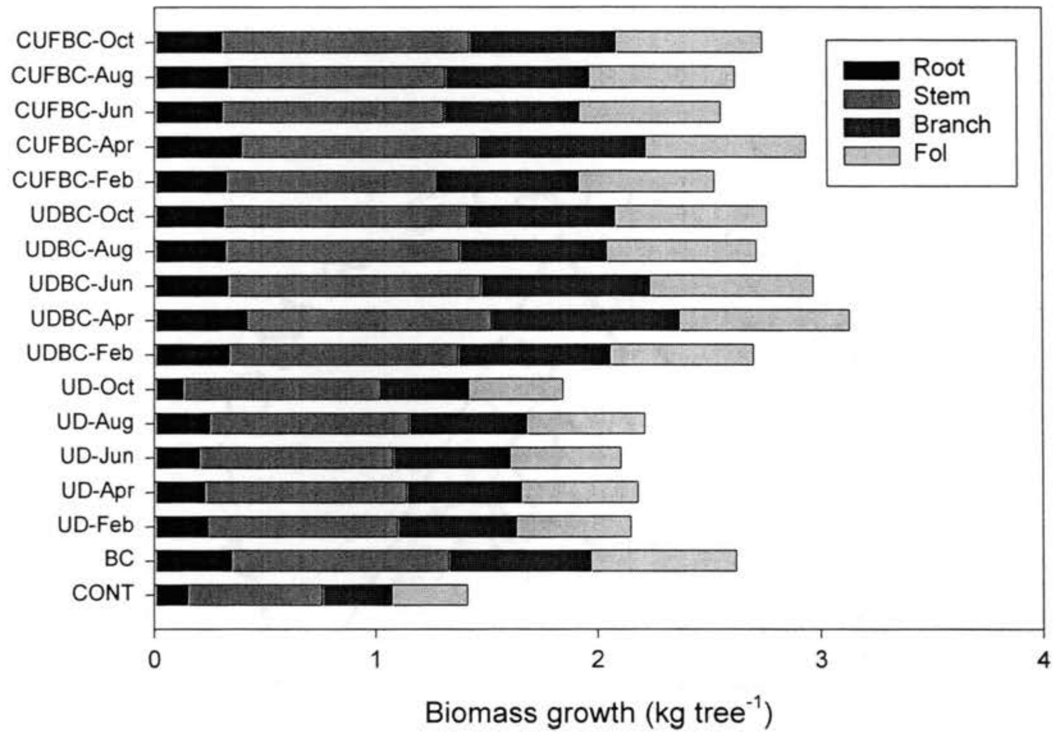


Figure 14. Growth of biomass components of juvenile loblolly pine in southeastern Oklahoma from February to December 2001 in response to fertilizer applied at various dates in 2001 and glyphosate.

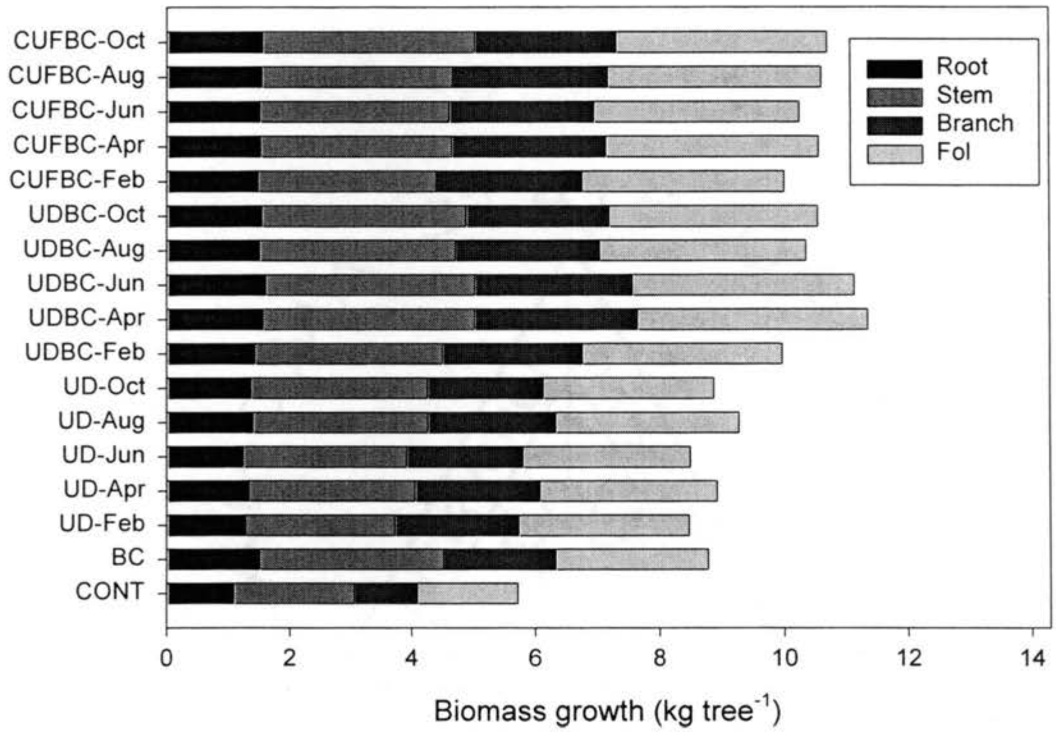


Figure 15. Growth of biomass components of juvenile loblolly pine in southeastern Oklahoma from February 2001 to September 2002 in response to fertilizer applied at various dates in 2001 and glyphosate.

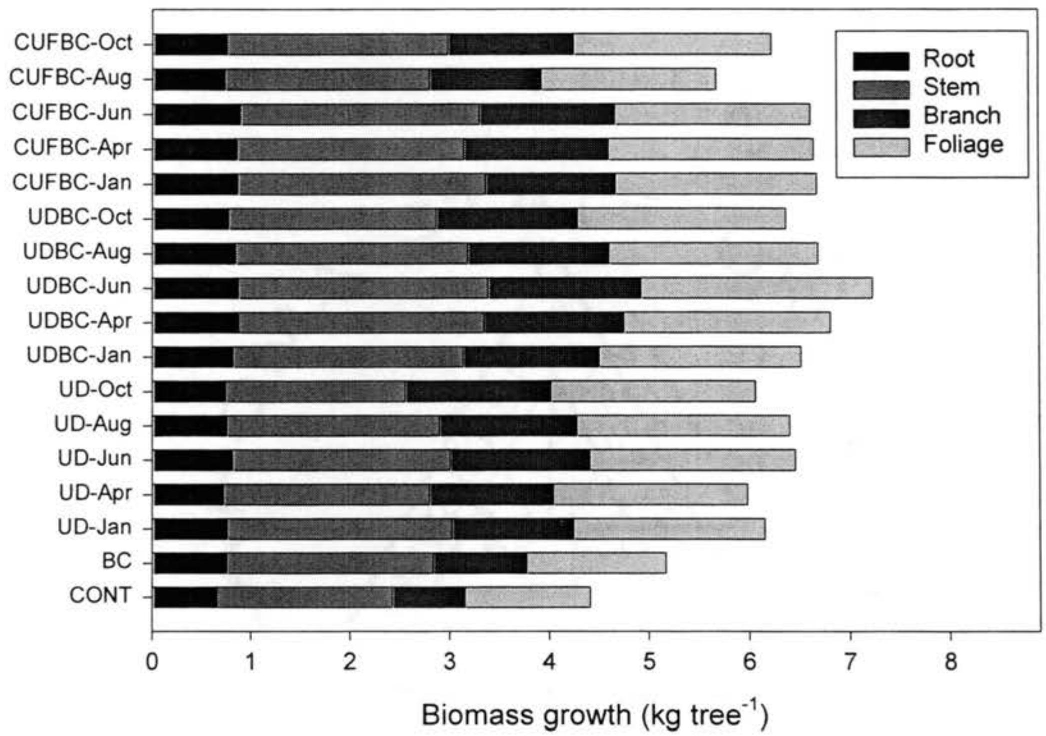


Figure 16. Growth of biomass components of juvenile loblolly pine in southeastern Oklahoma from February to November 2002 in response to fertilizer applied at various dates in 2002 and glyphosate.

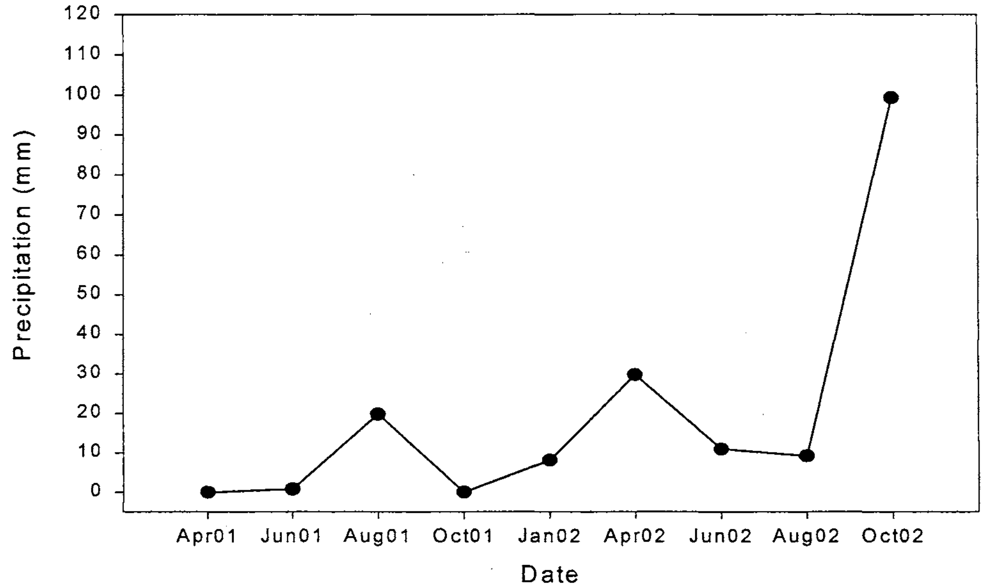


Figure 17. Precipitation within 1 week of N and P fertilization of a juvenile loblolly pine plantation in southeastern Oklahoma carried out at various dates in 2001 and 2002.

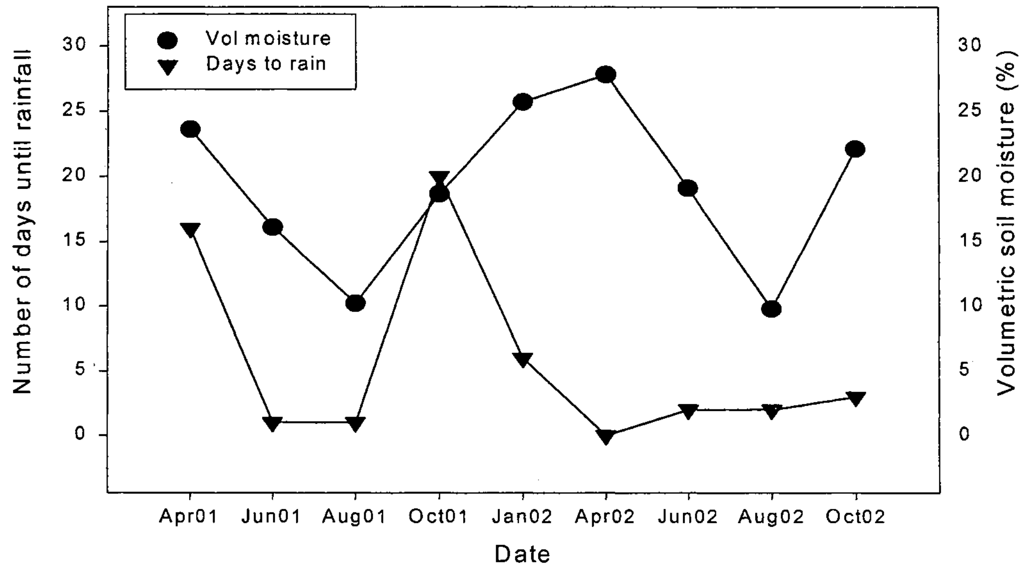
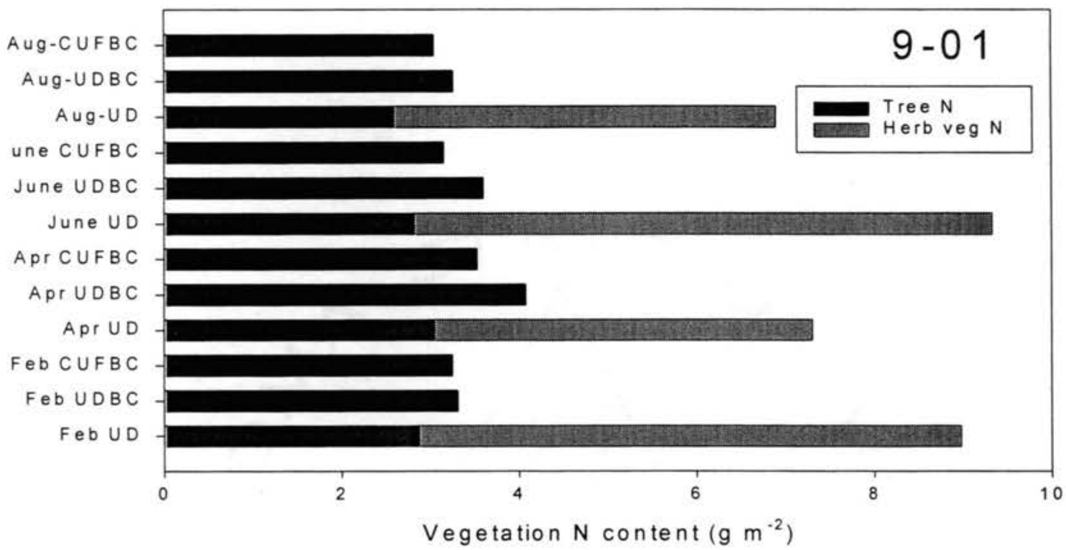


Figure 18. Volumetric soil moisture at the time of fertilization and the number of days until a precipitation event. N and P fertilizers were applied to a juvenile loblolly pine plantation in southeastern Oklahoma at various dates in 2001 and 2002.



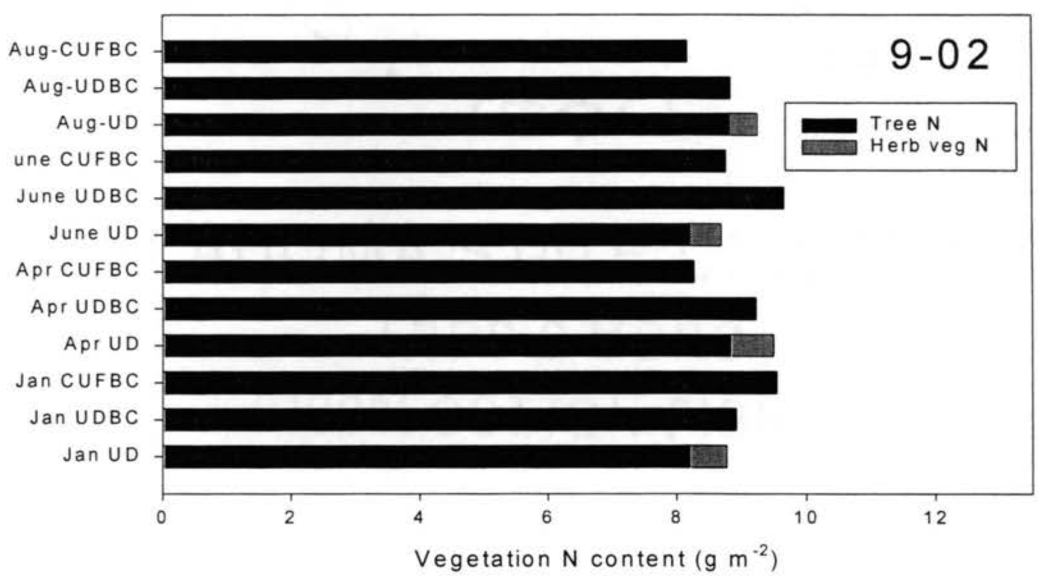


Figure 19. Total N accumulation of loblolly pine and herbaceous vegetation in response to N and P fertilization and glyphosate treatments as of September 2001 and September 2002. Fertilizers were applied at various dates in 2001 and 2002 to a juvenile loblolly pine plantation in southeastern Oklahoma.

APPENDIX

Site-specific regression equations used in prediction of biomass components of juvenile loblolly pine in southeastern Oklahoma

Regression coefficients for equations used in prediction of foliage, branch, stem, and root biomass of juvenile loblolly pine in southeastern Oklahoma, 2001-2002.

Dependent Variable[1]	Parameter estimates				Standard errors of parameter estimates				Statistics[2]	
	b_0	b_1	b_2	b_3	b_0	b_1	b_2	b_3	FI	SE
00FOL201[A]	41.338	0.778	1.097	------	16.874	0.163	0.317	------	0.908	5123.5
BR201[A]	19.070	0.604	1.581	------	8.724	0.185	0.359	------	0.899	666.7
STM201[B]	6.548	1.429	------	------	1.867	0.097	------	------	0.953	18624.9
00FOL801[C]	34.815	1.554	1.510	------	12.938	0.455	0.538	------	0.673	14335.3
01FOL801[A]	65.146	0.524	1.394	------	31.320	0.178	0.413	------	0.722	35707.3
BR801[A]	60.832	0.336	2.256	------	38.455	0.239	0.587	------	0.634	42334.2
STM801[B]	6.893	1.430	------	------	2.653	0.107	------	------	0.866	27118.4
RT801[D]	136.800	2.479	------	------	19.040	0.248	------	------	0.931	1843.4
01FOL802[A]	3.460	1.146	------	------	6.510	0.483	0.423	------	0.437	48672.3
02FFOL802[E]	51.116	1.025	0.314	1.251	129.600	0.884	0.689	0.555	0.451	348117
02UFOL802[A]	172.000	0.389	0.819	------	313.300	0.513	0.496	------	0.530	80109.5
FBR802[C]	148.100	0.844	1.758	------	110.200	0.525	0.360	------	0.711	131558
UBR802[A]	108.200	0.308	1.768	------	276.100	0.705	0.625	------	0.653	125251
STM802[B]	3.731	1.624	------	------	4.657	0.304	------	------	0.539	349093
RT802[A]	65.683	0.674	0.506	------	169.100	0.684	0.633	------	0.935	131559

[1]Variable nomenclature explained on following page.

[2]FI = Fit Index

SE = Standard error of the estimate

[A, B, C, D, E]Model forms listed on following page.

Variables used in Appendix table:

00FOL201 = Dry weight of foliage produced in 2000 based on February 2001 destructive harvest data

BR201 = Dry weight of branches (wood + bark) based on February 2001 destructive harvest data

STM201 = Dry weight of stem (wood + bark) based on February 2001 destructive harvest data

00FOL801 = Dry weight of foliage produced in 2000 based on August 2001 destructive harvest data

01FOL801 = Dry weight of foliage produced in 2001 based on August 2001 destructive harvest data

BR801 = Dry weight of branches (wood + bark) based on August 2001 destructive harvest data

STM801 = Dry weight of stem (wood + bark) based on August 2001 destructive harvest data

RT801 = Dry weight of coarse and medium roots based on August 2001 destructive harvest data

01FOL802 = Dry weight of foliage produced in 2001 based on August 2002 destructive harvest data

02FFOL802 = Dry weight of foliage produced by fertilized trees in 2002 based on August 2002 destructive harvest data

02UFOL802 = Dry weight of foliage produced by non-fertilized trees in 2002 based on August 2002 destructive harvest data

FBR802 = Dry weight of branches (wood + bark) of fertilized trees based on August 2002 destructive harvest data

UBR802 = Dry weight of branches (wood + bark) of non-fertilized trees based on August 2002 destructive harvest data

STM802 = Dry weight of stem (wood + bark) based on August 2002 destructive harvest data

RT802 = Dry weight of coarse and medium roots based on August 2002 destructive harvest data

Model forms associated with coefficients listed in Appendix table:

A: $Y = b_0 \times dbh^{b_1} \times crn^{b_2}$

B: $Y = b_0 \times dbh^{b_1}$

C: $Y = b_0 \times ht^{b_1} \times crn^{b_2}$

D: $Y = b_0 \times crn^{b_1}$

E: $Y = b_0 \times ht^{b_1} \times dbh^{b_2} \times crn^{b_3}$

where: *Y* = Foliage, branch, stem, or root dry weight (g)
dbh = diameter of tree at 1.3 m (mm)
crn = average crown width (m)
ht = total height of tree (m)

Manuscript II

Effects of fertilization and vegetation control on microbial biomass C and dehydrogenase activity in an intensively managed juvenile loblolly pine plantation

ABSTRACT

Management of loblolly pine (*Pinus taeda* L.) plantations increasingly includes elimination of competing vegetation and fertilization, beginning early in rotations, in an effort to meet global demand for forest products. Soil microorganisms, which mediate nutrient availability to plants through the mineralization-immobilization process, can be affected by vegetation control and fertilization. However, there is a lack of information on the effects of these practices on soil microorganism biomass and activity in young loblolly pine plantations. The objective of this study was to characterize the influence of understory vegetation suppression and fertilization on microbial biomass and activity. Microbial biomass C (C_{mic}), dehydrogenase activity, and the ratio of microbial biomass C to soil organic C (C_{org}) were measured monthly in response to (1) an untreated control, (2) continuous brush control, (3) tree removal, (4) tree removal in conjunction with continuous brush control, (5) a combination of continuous brush control and application of a urea and diammonium phosphate (DAP) mixture, and (6) a combination of continuous brush control and application of a slow-release coated urea fertilizer. Dehydrogenase activity and C_{mic} declined in response to vegetation removal. Declines in C_{mic} to C_{org} ratios in response to herbaceous vegetation suppression suggested that understory vegetation provides soil microorganisms with C substrates that are more readily utilizable than that provided by loblolly pine root systems. The application of urea/DAP in conjunction with continuous brush control decreased C_{mic}, dehydrogenase activity, and C_{mic} to C_{org} ratios to a greater extent than brush control alone. Short-term increases in C_{mic}, dehydrogenase activity, and C_{mic} to C_{org} ratios after fertilization suggest C utilization efficiency is temporarily increased by urea/DAP fertilization, and the

decreases in these parameters throughout the remainder of the year imply that microbial biomass and activity decline after the short-term enhancement of C utilization exhausts readily available C sources. The slow-release urea fertilizer did not decrease C_{mic} and dehydrogenase activity as greatly as did the urea/DAP mixture, which suggests buildup of osmotic potential partially contributed to decreases in microbial biomass and activity in response to fertilization. Results of this study suggest that intensive forest management practices such as vegetation control and fertilization decrease microbial biomass and activity, and soil microbial populations in young, intensively managed pine plantations do not appear to serve as significant competitors for applied N.

INTRODUCTION

Forest managers face an increasingly complex array of conditions and demands influencing the choice of management strategies applicable to forests under their care. The demand for forest products is escalating annually due to population expansion, increased literacy rates, and improved standards of living. However, the land area available for tree harvest is declining in industrialized countries due to urban sprawl and increasing demands for non-commodity uses and values, such as recreational activities. Forest area is substantially declining in developing countries (200 million ha lost since 1980) due to exploitation of unmanaged forests leading to deforestation and forest degradation. Furthermore, forestry has been traditionally relegated to relatively infertile soils unsuitable for agricultural uses. Thus, forest managers are adopting practices, such as fertilization and vegetation control, that improve and redistribute site resources to maintain the supply of forest products required by the world's rising population while preserving large areas of native forests for conservation and preservation purposes (Fox, 2000).

The United States has over 500 million acres of forestland capable of producing timber and fiber. Although physical, elemental, and moisture limitations to tree growth are routinely amended on approximately 13% of U.S. forests, amended forests produce ~40% of domestic forest products. Pine productivity of these intensively managed forests, which are frequently plantations, is up to 200% greater than unamended forests (Fox, 2000; Vance, 2000). The practice of fertilization in the southern United States increased 95% during the 1990's; currently approximately 1.5 million acres of southern pine forests are fertilized each year, which has helped make the forests of the region among the world's most productive (NCSFNC, 2001). Nitrogen, often added as urea, is most commonly added to forests (Reich and Schoettle, 1988). Considerable research has been conducted on the influence of anthropogenic nitrogen additions to forest ecosystems. A large body of this research has focused on the effects of nitrogen addition on crop tree growth, and convincing evidence of improved nutrient concentrations, survival, biomass growth (leaf weight, leaf area, stemwood, branchwood, roots), and photosynthetic capacity has been produced (Vose and Allen, 1988; Colbert et al., 1990; Haywood et al., 1997; Murthy et al., 1997). Research on the influence of vegetation control in forests has likewise focused primarily on tree growth; substantial evidence of improved tree nutrition, survival, growth, and yield has been found (Haywood and Tiarks, 1990; Allen and Wentworth, 1993; Cain, 1996; Mason and Milne, 1999; Zutter et al., 1999).

Soil microorganism populations are of paramount importance in forest soil fertility. Soil microbes carry out biochemical transformations of organic matter, which meets most of the nutrient requirements of trees and understory vegetation. These organisms act as both sources and sinks of nutrients in soils through the mineralization-immobilization process, which largely mediates nutrient availability to plants (Diaz-Raviña et al. 1993, Gallardo and Schlesinger 1994). Zak et al. (1990) assessed the competition between microbes and plants for N in an unfertilized northern hardwood forest and determined that the microbial population represented a much larger sink for N than vegetation. Stark and Hart (1997) found that microbial populations have a high capacity to prevent N losses in undisturbed coniferous forests. N losses were found to be inconsequential in unfertilized mixed pine-hardwood forests, which had retention efficiencies approaching 100% (Richter et al., 2000).

Chronic N influx has been found to negatively affect microbial biomass and activity in mature temperate riparian and lodgepole pine (*Pinus contorta* Dougl. ex Loud) forests, which implies the N-removal potential of microorganisms may be threatened by substantial nutrient additions. Such inhibition of microorganisms may lead to N losses from forest ecosystems under N inputs (Ettema et al., 1999; Thirukkumaran and Parkinson, 2000). The microbe inhibitory effects of inorganic N have been attributed to rising of osmotic potential to toxic levels, lowering of soil pH, inhibition of fungal ligninolytic enzyme production, and decreased production of enzymes that degrade N-containing organic matter (Söderström et al., 1983; Smolander et al., 1994; Ettema et al., 1999; Vance and Chapin, 2001). Other studies have revealed negative, positive, and neutral influences of fertilization on forest soil microbial populations; inconsistencies of these studies have been attributed to differences in fertilizer rate and formulation, productivity of the forest studied, and time scale of each study (Thirukkumaran and Parkinson, 2000). However, studies of the microbial responses to N and P fertilization of the economically significant loblolly pine forests (*Pinus taeda* L.) of the southeastern United States are lacking.

Coniferous forest soils are often characterized by low organic matter quality (e.g. high C:N, high lignin, high lignin:N, low pH) that reduces the supply of labile C substrates to microbes. In such systems, microbial population growth and activity may be inhibited more by a lack of labile C than N supply (Vance and Chapin, 2001). Several studies have highlighted the importance of labile C sources such as root exudates in sustaining soil microorganism populations (Gallardo and Schlesinger, 1994; Kozdrój and van Elsas, 2000; Donegan et al. 2001; Högberg et al., 2001). Consequently, the presence of abundant, vigorously growing vegetation promotes microbial growth (Gallardo and Schlesinger, 1994; Donegan et al. 2001). Reduction of understory vegetation in response to herbicide applications may in turn reduce microbial biomass and activity due to a concomitant reduction in root exudates. Busse et al. (1996) found a significant decline in microbial biomass in a ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) forest in response to long-term vegetation control. However, another study on long-term vegetation control in a ponderosa pine forest revealed no significant influences of vegetation control on microbial communities (Busse et al., 2001).

Given the prevalence of intensive management of loblolly pine in the southeastern United States, it is vital to assess its impact on key biological components of these ecosystems. There have been few studies on soil microorganism responses to fertilization and vegetation control in loblolly pine (*Pinus taeda* L.) forests. Furthermore, most prior research has been done in older forests, but forest managers are increasingly fertilizing and suppressing understory vegetation of younger loblolly pine plantations. In this study of a juvenile loblolly pine plantation in southeastern Oklahoma, the objective was to characterize the influence of understory vegetation suppression and fertilization on microbial biomass and activity.

MATERIALS AND METHODS

Study site

A complete description of the study site is given in Manuscript 1; key characteristics of the site will be described here. The site is a 15-hectare (37-acre) loblolly pine plantation in southeastern Oklahoma planted in February 1999 on a 1.8 m × 5.5 m (6.0 ft. × 18.0 ft.) spacing with a single coastal North Carolina family. Prior to planting, the site was prepared via a bedding/subsoiling operation, and a mixture of sulfometuron methyl (Oust®) and imazapyr (Arsenal®) herbicides was applied to control competing vegetation. The soil is a nutrient-poor, acidic, sandy loam (USDA-SCS, 1974). Average annual rainfall of the region is 125 cm (49 in.), and average annual temperature is 17°C (63°F) (Stogsdill, 1986).

The plantation was developed into a loblolly pine fertility research area in January 2001. Trees of average height in January 2001 were chosen as study trees. The experimental units for this study were 24-m^2 (254-ft^2) plots each containing a single study tree, and each plot was separated by a buffer space of 3.7 m (12 ft.) within each row and at least 5.5 m (18.0 ft.) between rows to prevent contamination of study trees via lateral flow of applied nutrients.

Treatments

In 2001, the following treatments were randomly applied to study trees in 2001 to investigate the influence of vegetation control and fertilization on soil microbial biomass C and dehydrogenase activity:

1. No brush control, no fertilizer (CONT)
2. Brush control, no fertilizer (BC)
3. Brush control, urea and diammonium phosphate mixture (UDBC)

The CONT treatment served as a control, the BC treatment isolated the influence of brush control on microbial biomass and activity, and the UDBC treatment provided an indication of the influence of N and P fertilizers and brush control on microbial biomass and activity. There were five replicates of each treatment.

Brush control consisted of elimination of herbaceous vegetation. A 10% solution of glyphosate (Accord®) was applied periodically throughout the 2001 growing season to prevent any herbaceous understory vegetation from growing. Herbaceous vegetation was eliminated from a 16-m^2 (168-ft^2) area around study trees in plots receiving BC and UDBC treatments. Woody vegetation was controlled with triclopyr (Garlon®) applied in February 2001. Since the influence of the presence of herbaceous vegetation (the predominant vegetation present in early rotations of loblolly pine forests) on microbial biomass and activity was of interest in this study, woody vegetation was eliminated from the entire study site. Fertilizers were applied in February 2001 to the 24-m^2 (254-ft^2) area around study trees using hand spreaders. Nitrogen was applied at 202 kg ha^{-1} (180 lb ac^{-1}); phosphorus was applied at 20 kg ha^{-1} (18 lb ac^{-1}).

In 2002, more treatments were randomly applied to a different set of plots established on the same study site to ascertain the effects of climatic variations, tree size, and tree age on the response of microbial populations to fertilizer and brush control. Although tree age differed by only one year, the trees had nearly doubled in volume in that time; therefore, it was possible that tree size differences could exert an influence on microbial populations. Two treatments in which trees were removed from plots were added to the study in 2002 to further explore the influence of labile C sources on microbial populations. Furthermore, a treatment in which a slow-release urea formulation was applied in conjunction with brush control treatments was added to the study to determine the effects of the rate of fertilizer dissolution on microbial populations. The treatments applied in 2002 were:

1. No brush control, no fertilizer (CONT)
2. Brush control, no fertilizer (BC)
3. Pine removed, no brush control, no fertilizer (NP)
4. Pine removed, brush control, no fertilizer (NPBC)
5. Brush control, urea and diammonium phosphate mixture (UDBC)
6. Brush control, coated urea fertilizer (CUFBC)

CONT, BC, and UDBC treatments served the same purposes as in 2001. The NP treatment isolated the influence of the presence of herbaceous vegetation on microbial biomass, and the NPBC treatment was applied to explore the effects of the absence of vegetation on microorganisms. Coated urea fertilizer (CUF) is a slow-release urea formulation that delays the release of urea until a significant precipitation event. CUF provided N and P at the same rates as the urea/DAP mixture and 0.65 kg ha^{-1} (0.58 lb ac^{-}

^{1}) of B. All treatments were replicated ten times. Trees in plots receiving the NP and NPBC treatments were cut and removed in January 2002. Brush control protocol was identical to that followed in 2001. The UDBC and CUFBC treatments were applied in April 2002 using the same procedures followed in 2001. The fertilization was carried out in April 2002 to explore whether the date of application affected microbial responses to fertilization.

Environmental and edaphic measures

A description of the methods used to determine several environmental parameters have been described in a preceding paper (Manuscript I); key aspects of the methods will be discussed here. Thermocouples were placed at depths of 15 cm and 30 cm to measure soil temperature in plots receiving CONT and UDBC treatments to elucidate influences of vegetation control and fertilization on soil temperature. A tipping-bucket rain gauge attached to a data logger was established to provide continuous measurement of precipitation amount and velocity. Volumetric moisture at 15 and 30 cm was measured in plots receiving CONT and UDBC treatments in 2001 and 2002 using the neutron scattering technique (Gardner and Kirkham, 1952, Evett and Steiner, 1995).

Soil nitrogen was measured monthly in conjunction with soil microbial parameters as part of concurrent studies on the same study site. Bioavailable soil N (NH_4^+-N and NO_3^--N) was measured monthly throughout the study using ion exchange resin bags placed at 15 cm (Manuscript I). Soil NO_3 was also quantified monthly using a nitrate meter (Manuscript III).

Soil samples used in determination of pH and organic matter were collected concurrently with soil samples used in determination of C_{mic} and dehydrogenase activity.

Samples were collected from the top 15 cm of soil using a soil auger. In each plot, a single sample was collected approximately 1 m from the base of the study tree. These samples were then composited to create three composite samples per treatment.

Soil pH was measured using a pH meter (ROSS® Sure-Flow™ pH Electrode, Orion Research) (Thomas, 1996). Soil organic matter content was determined via loss on ignition (Nelson and Sommers, 1996). Organic matter content values produced by this method are reported as correlated with Walkley and Black (1934) organic matter values. Soil organic carbon (C_{org}) was estimated by dividing organic matter content values by 1.724 (Nelson and Sommers, 1996).

Soil sampling and microbial measurement

In 2001, soil samples were collected monthly from all plots per treatment from February to December. Samples were collected from the top 15 cm of soil using a soil auger. In each plot, two samples (one from the tree base, one from the edge of the dripline) were collected and pooled. This sampling procedure was used to account for microsite variations in edaphic conditions, which can create heterogeneous distribution of soil microorganism populations (Ettema et al. 1999). Thus, five composite samples (each consisting of 2 soil samples) were collected per treatment. Soil samples were refrigerated at approximately 4°C during transport and storage.

In 2002, soil samples were taken monthly from the top 15 cm of soil from all plots per treatment from January to December. Two samples per plot were collected and pooled as described above. The composite samples from each plot were further pooled to create 3 composite samples per treatment, with each composite sample consisting of soil samples from 3 or 4 plots. Each month, soil from the same plots was pooled together to preserve replication of treatments. Thus, three composite samples (each consisting of 6 to 8 soil samples) were sampled per treatment. Samples were preserved in transport and storage as described above.

Microbial biomass C (C_{mic}) was assessed each month from February 2001 to December 2002 by the chloroform fumigation-incubation (CFI) method (Jenkinson and Powlson, 1976*a,b*, Vance et al., 1987*a*; Luizao et al., 1992). A 10-day pre-incubation was carried out prior to fumigation of soil samples in order to allow the influence of soil disturbance to subside and living fragments of roots to die (Sparling et al., 1985; Jenkinson, 1988). C_{mic} was determined by fumigating soil samples with alcohol-free $CHCl_3$ vapor for 24 h, incubating soil samples at 25°C for 10 days, collecting respired CO_2 in NaOH, measuring CO_2 by titration, and using a proportionality constant of 0.45 to convert CO_2-C to C_{mic} after subtracting the CO_2-C produced by a non-fumigated control. All results are expressed on an oven-dry soil basis (105°C, 24 h).

The ratio of C_{mic} to C_{org} was determined for each plot throughout the study since this ratio is indicative of the quality of the organic matter for supporting microbial populations, with substrate adversity increasing as the C_{mic} to C_{org} ratio declines (Priess and Fölster, 2001). C_{mic} and C_{org} were expressed in kg ha^{-1} in determination of the C_{mic}/C_{org} ratio; this conversion was made possible by soil bulk density samples taken with a bulk density auger in the top 15 cm of all plots in August 2001 and August 2002.

To provide an estimate of the N sequestered in microbial biomass, C_{mic} values were multiplied by a conversion factor of 0.15 (Anderson and Domsch, 1980). Diaz-Raviña (1993) utilized the same conversion factor to estimate microbial biomass N from C_{mic} measurements in their study of a wide range of temperate forest soils. This conversion factor assumes a microbial biomass C to microbial biomass N ratio of 6.7%. Périé and Munson (2000) quantified both microbial biomass C and microbial biomass N in a 5-year-old lodgepole pine (*Pinus contorta* Dougl. ex Loud.) plantation and likewise found an average microbial C:N ratio of approximately 6.7%. It has been noted that microbial biomass C:N ratios are relatively constant in the absence of large quantities of freshly added plant material with a wide C:N ratio (Jenkinson, 1988; Ross et al., 1999).

Microbial activity was also estimated monthly from February 2001 to December 2002 by determining dehydrogenase activity (Lenhard, 1956; Alef, 1995). Dehydrogenase, which is only present in viable living cells, plays an integral role in the initial stages of the oxidation of soil organic matter by transferring electrons or hydrogen ions from substrates to acceptors. Therefore, activity of dehydrogenase serves as a good indicator of total microbial oxidative activity in soils, i.e., the dehydrogenase enzyme assay provides the average activity of microbial populations (Tabatabai, 1994; Camiña et al., 1998). To quantify dehydrogenase, triphenyltetrazolium chloride (TTC) was used as an artifical electron acceptor since microorganisms reduce TTC into red-colored formazans that can be extracted and quantified colorimetrically (Thalmann, 1968). All results are expressed on an oven-dry soil basis (105°C, 24 h).

Statistical Analysis

Analyses of all treatment effects were conducted by analyses of variance (ANOVA's) using the MIXED procedure of the SAS System. When an ANOVA indicated significant treatment effects, treatment means were calculated and separated by the DIFF and SLICE options of the LSMEANS procedure. The DIFF option provided multiple comparisons of treatment means by invoking t-tests to determine significant differences between all possible treatment combinations. The SLICE option provides t-tests of treatment means in which the effect of one treatment is evaluated at each level of another treatment. The SLICE option was used to investigate treatment main effects when significant 2-way interactions were found. In order to rectify heterogeneous variances revealed by the null model likelihood ratio test, C_{mic}, dehydrogenase activity, and C_{mic} to C_{org} ratio values of both 2001 and 2002 were log transformed.

Monthly measurements of C_{mic}, dehydrogenase activity, pH, organic matter, and the C_{mic} to C_{org} ratio taken in 2001 were analyzed as a one-way treatment with one level (UDBC) plus two controls (CONT, BC). The CONT, BC, and UDBC data were pooled, and ANOVA procedures were performed on a model with treatment (CONT, BC, UDBC) as a fixed effect. CONTRAST statements that compared responses to the UDBC treatment to responses to the CONT and BC treatments were used to identify significant differences between control and active treatments. This comparison of controls to active treatments was conducted for each month of 2001 to identify when C_{mic}, dehydrogenase activity, pH, organic matter, and the C_{mic} to C_{org} ratio of plots receiving the CONT and BC treatments differed from that of plots receiving the UDBC treatment.

Measurements of C_{mic}, dehydrogenase activity, pH, organic matter, and the C_{mic} to C_{org} ratio taken in 2002 were analyzed with similar procedures. Each of these variables was analyzed as a one-way treatment with 2 levels (UDBC, CUFBC) plus 4 controls (CONT, BC, NP, NPBC). Due to this treatment structure, it was necessary to conduct the analyses in two steps. First, the UDBC and CUFBC treatments were analyzed with a repeated measures model with an autoregressive correlation structure with: (1) fertilizer/brush control treatment, (2) month, and (3) the interaction between fertilizer/brush control and month as fixed effects. Next, the controls were compared to fertilizer/brush control treatments using CONTRAST statements. The fertilizer/brush control and control treatments were pooled and analyzed using ANOVA procedures performed on a model with treatment (CONT, BC, NP, NPBC, UDBC, CUFBC) as a fixed effect. Contrast statements that compared responses associated with control treatments to that of the fertilizer/brush control treatments were used in conjunction with ANOVA procedures to identify significant differences between control and active treatments. This comparison of controls to active treatments was conducted for each month of 2002.

The correlations between C_{mic}, dehydrogenase activity, soil organic matter concentration, pH, soil NO_3^- as measured by a nitrate meter, volumetric soil moisture, and average monthly soil temperature were quantified using the PROC CORR procedure of the SAS System. This procedure generates Pearson correlation coefficients and the probabilities associated with these statistics.

RESULTS

Microbial biomass C

In 2001, C_{mic} associated with CONT, BC, and UDBC treatments followed similar general trends (Figure 1). C_{mic} declined in March and April, and then increased sharply in May. C_{mic} declined somewhat during fall and winter, with the most pronounced decrease occurring in response to the UDBC treatment. In March, following the February fertilizer application, mean C_{mic} of the UDBC treatment was 30% and 39% higher than that of the CONT and BC treatments, respectively. In all other months after fertilization, mean C_{mic} of the UDBC treatment was lower than that of the CONT and BC treatments, with mean C_{mic} frequently 30% and 20% lower than the CONT and BC treatments, respectively. The UDBC treatment was associated with significantly lower (P=0.005) C_{mic} than the CONT and BC treatments in December. In July and September, the lower C_{mic} means of the UDBC treatment were marginally non-significant (P=0.10±0.02) when compared to the CONT treatment. No significant differences were detected when the C_{mic} of the BC treatment was compared to the CONT and UDBC treatments.

The fertilizer and brush control treatments induced significant differences in the C_{mic} to C_{org} ratio in 2001 (Figure 2). In March, the C_{mic} to C_{org} ratio was significantly greater (P=0.02) in UDBC plots than in CONT and BC plots; the ratio of the UDBC treatment was ~30% greater than that of the CONT and BC treatments. In June, the BC treatment was associated with a significantly higher (P=0.02) C_{mic} to C_{org} ratio than the CONT treatment, and the UDBC treatment had a somewhat higher (P=0.08) ratio than the CONT treatment. In December, the CONT treatment yielded a C_{mic} to C_{org} ratio significantly greater (P=0.04) than the UDBC treatment.

In 2002, the tree removal treatments significantly affected C_{mic} (Figure 3A). Mean C_{mic} of the CONT treatment gradually increased from February through August, then remained somewhat stable for the remainder of the season. Mean C_{mic} of the NP treatment followed a similar trend, but it was frequently ~25% lower than the CONT treatment for much of the year. C_{mic} of the NP treatment was significantly lower (P=0.03±0.02) than that associated with the CONT and BC treatments in July, September, and November. The NP treatment also produced C_{mic} significantly lower

(P=0.03±0.02) that of the UDBC treatment in April and November and the CUFBC treatment in November. However, C_{mic} of the plots receiving the NP treatment significantly exceeded that of the UDBC treatment (P=0.04±0.01) in August and October and of the CUFBC treatment (P=0.03) in August. Mean C_{mic} of the NPBC treatment was relatively stable until June, increased in July, and then remained relatively stable for the remainder of the year. C_{mic} of the NPBC treatment was typically ~ 30% lower than that of the CONT treatment for much of the year. C_{mic} of the NPBC treatment was significantly lower (P=0.02±0.02) than that of the CONT treatment in August, October, and December. The NPBC treatment was also associated with significantly lower (P=0.02±0.02) C_{mic} than (1) the BC treatment in April, August, and December, and (2) the UDBC and CUFBC treatments in April.

The fertilizer and brush control treatments significantly affected C_{mic} in 2002 (Figure 3B). The CONT treatment was consistently associated with the highest mean C_{mic}. C_{mic} of the BC treatment followed a pattern similar to that of the CONT treatment until late summer, but declined relative to the CONT treatment in the fall. C_{mic} of the BC treatment was significantly lower (P=0.04) than that of the CONT treatment in October. From April through July, C_{mic} trends associated with the UDBC treatment deviated substantially from that of the CONT treatment. As C_{mic} in response to the CONT treatment increased from mid-spring through mid-summer, C_{mic} of the UDBC treatment declined. After this decline, C_{mic} in response to the UDBC treatment remained relatively stable at a level ~45% lower than C_{mic} of the CONT treatment for the remainder of the year. The UDBC treatment was associated with C_{mic} significantly lower (P=0.01±0.02) than that of the CONT treatment from July through October and in December. In addition, C_{mic} of the UDBC treatment was significantly lower (P=0.03±0.02) than that of the BC treatment in July, August, October, and December. C_{mic} in response to the CUFBC treatment followed a trend similar to that of the CONT treatment for much of the year, but in June and November C_{mic} decreased relative to the CONT treatment. After June, C_{mic} of the CUFBC was typically ~30% lower than that of the CONT treatment. In October, C_{mic} in response to the CUFBC treatment was significantly lower than the CONT (P=0.049) treatment.

The tree removal treatments affected the C_{mic} to C_{org} ratio in 2002 (Figure 4A). The C_{mic} to C_{org} ratio associated with the NP treatment followed a trend similar to that of the CONT treatment throughout much of the year, but it was significantly lower (P=0.02) than the CONT C_{mic} to C_{org} ratio in September and November. The C_{mic} to C_{org} ratio of the NP treatment was similar to that of the BC treatment in all months except November, wherein it was significantly lower (P=0.01). In July, August, and October 2002, the NP treatment yielded a C_{mic} to C_{org} ratio significantly greater (P=0.02±0.02) than the UDBC treatment, and the C_{mic} to C_{org} ratio of the NP treatment was significantly lower (P=0.045) than that of the CUFBC treatment in November. The NPBC treatment produced C_{mic} to C_{org} ratios frequently ~40% lower those yielded by the CONT treatment; in May and October the C_{mic} to C_{org} ratios of the NPBC were significantly lower (P=0.03±0.03) than those of the CONT treatment. Relative to the NP treatment, the C_{mic} to C_{org} ratios associated with the NPBC treatment were significantly lower (P=0.03±0.02) in April, May, and August. However, the C_{mic} to C_{org} ratio of the NPBC treatment exceeded (P=0.01) that of the NP treatment in November. The NPBC treatment generated lower (P=0.02±0.03) C_{mic} to C_{org} ratios than the BC and UDBC treatments in August and May, respectively.

The fertilizer and brush control treatments also affected the C_{mic} to C_{org} ratio in 2002 (Figure 4B). In April, the C_{mic} to C_{org} ratios of BC, UDBC and CUFBC treatments were significantly greater (P=0.02±0.02) than that of the CONT treatment. The C_{mic} to C_{org} ratios associated with the UDBC treatment were frequently lower than those of other treatments. From May through October, the C_{mic} to C_{org} ratio of the UDBC treatment was significantly less (P=0.02±0.02) than that of the CONT treatment. In July and August, the UDBC treatment had lower (P=0.02±0.01) C_{mic} to C_{org} ratios than the BC treatment. In October, the CONT treatment yielded higher (P=0.02±0.01) C_{mic} to C_{org} ratios than the BC, UDBC, and CUFBC treatments.

The 2001 and 2002 C_{mic} measurements were significantly correlated with several edaphic variables. C_{mic} was positively correlated with soil organic matter concentration (r=0.30, P<0.0001), pH (r=0.43, P<0.0001), and soil temperature (r=0.29, P<0.0001). C_{mic} was negatively correlated with soil NO_3^- (r=-0.28, P<0.0001) and volumetric soil moisture (r=-0.19, P=0.002).

Microbial activity

In 2001, dehydrogenase activity differed to some extent between the CONT, BC, and UDBC treatments (Figure 5). The CONT and BC treatments were characterized by similar trends in dehydrogenase activity throughout the year, but dehydrogenase activity in response to the BC treatment was frequently ~25% lower than that of the CONT treatment. Dehydrogenase activity trends of the UDBC treatment markedly differed from that of the CONT and BC treatments in the spring. As mean microbial activity declined somewhat from February to March in plots receiving CONT and BC treatments, activity increased in UDBC plots. This increased mean activity persisted though April, then declined by May. After May, average dehydrogenase activity of the UDBC treatment followed a pattern similar to that of the CONT and BC treatments, but activity was frequently ~40% and 25% lower than that of the CONT and BC treatments, respectively. In September, microbial activity in response to the UDBC treatment was significantly lower (P=0.04) than activity of the CONT treatment, and microbial activity of the UDBC treatment was somewhat lower (P=0.11) than that of the CONT treatment in July and August.

The tree removal treatments significantly affected microbial activity in 2002 (Figure 6A). Mean dehydrogenase activity in response to the NP treatment closely followed that of the CONT treatment until August; activity of the NP treatment declined to 30% of the CONT treatment by September. In September, October, and December, dehydrogenase activity of the NP treatment was significantly lower (P=0.04±0.01) than that associated with the CONT treatment. However, activity of the NP treatment significantly exceeded (P=0.03±0.02) activity associated with the UDBC treatment in July and August. The NPBC treatment yielded the lowest microbial activities for most of 2001; the activity in response to this treatment was typically 60% less than that of the CONT treatment. Activity of the NPBC treatment was significantly lower (P=0.02±0.02) than that of the (1) CONT treatment from June through December, (2) NPBC treatment from June through August, (3) BC treatment in August, (4) UDBC treatment in August through November, and (4) CUFBC treatment from July through September and December.

The fertilizer/brush control treatments significantly influenced microbial activity in 2002 as well (Figure 6B). The BC, UDBC, and CUFBC treatments each reduced dehydrogenase activity relative to the CONT treatment, with the greatest reduction in activity occurring in response to the UDBC treatment. The BC treatment produced dehydrogenase activities lower (P=0.04±0.01) than the CONT treatment from July through September and in December, and the UDBC treatment generated dehydrogenase activities lower (P=0.02±0.01) than those of the CONT treatment from July through October and in December. The CUFBC treatment reduced (P=0.03) microbial activity relative to the CONT treatment in August and September, but had significantly higher (P=0.047) microbial activity than the UDBC treatment throughout 2002. Activity of the CUFBC treatment was comparable to that of the BC treatment each month of 2002.

Significant correlations between the 2001 and 2002 dehydrogenase activity measurements and edaphic variables were found. Dehydrogenase activity was positively correlated with soil organic matter concentration (r=0.17, P=0.004), pH (r=0.18, P=0.003), and soil temperature (r=0.13, P=0.04). In addition, dehydrogenase activity was positively correlated with C_{mic} (r=0.43, P<0.0001).

DISCUSSION

The C_{mic} values observed in this study, which ranged from ~120 to 800 mg C kg^{-1} (Figures 1 and 3) in the top 15 cm of soil, were somewhat lower than ranges of C_{mic} measured using the CFI method in other studies of temperate forest soils. However, studies of C_{mic} have not typically been conducted in young pine forests with a history of multiple intensive forest management practices (tillage, vegetation suppression, fertilization) as in our study. Diaz-Raviña et al. (1993) found a range of 282 to 1614 mg C kg^{-1} in the top 15 cm of soil in various humid temperate forest soils of Spain using the CFI method. Vance et al. (1987*b*) utilized the CFI method for determining C_{mic} of diverse broadleaf and coniferous forests in the U.K. and found a range of 720 to 1900 mg C kg^{-1} in the top 10 cm of soil, with an average of 1248 mg C kg^{-1}. Gallardo and Schlesinger (1994) found that microbial biomass increased as temperature increased; similar trends were observed in our study.

There has also been scant exploration of microbial activity as measured by dehydrogenase enzyme activity in forest soils with an intensive management history. Camiña et al. (1998) measured dehydrogenase activity of the upper 5 cm of acidic oakwood (*Quercus robur* L.) soils and found 98 to 141 μg INTF g^{-1} when methanol was used as a formazan extractant as in our study. Those activities were somewhat higher than the range of activities measured in our study (Figures 5 and 6), but their forest conditions differed from those of this study, they sampled from a higher depth, and 2-(*p*-iodophenyl)-3-(*p*-nitrophenyl)-5-phenyltetrazolium chloride was used as an artificial electron acceptor in their assay instead of triphenyltetrazolium chloride.

The clearcut and site preparation operations (bedding/subsoiling, windrowing of logging slash, vegetation suppression) done 3 years prior to the beginning of this study likely reduced C and N capital of the site. Huntington et al. (1988) determined that within the first 5 to 15 years after timber harvest up to 50% of preharvest forest floor N and C is lost due to mechanical mixing of organic matter into the soil that occurs during logging, accelerated rates of decomposition after overstory removal, and dramatically decreased rates of woody litter deposition. Tree removal exposes mineral soil to direct sunlight, which substantially increases soil temperatures. The elevation in soil temperature can lead to increased N mineralization and nitrification soon after harvests (Piatek and Allen, 1999; Thibodeau et al., 2000). C_{mic} tends to be lower in clearcut soils (Barg and Edmonds, 1999), which can decrease N immobilization. Stark and Hart (1997) theorized that N losses that occur after vegetation removal are largely due to decreased microbial assimilation of NO_3^-, which occurs as a result of reduced C inputs and increased NH_4^+ availability. Bedding has been shown to accelerate microbial activity and N mineralization within bedded soil due to increased soil aeration; soil organic C, mineralizable N, and total N are thus decreased shortly after bedding (Carter et al., 2002). Windrowing of logging slash has been shown to displace nutrients and produce N losses via increased N mineralization rates (Pye and Vitousek, 1985; Burger and Pritchett, 1988). The vegetation suppression that accompanied the bedding/subsoiling site preparation in our study likely reduced soil C reserves as well. Vegetation control has been shown to significantly reduce total soil C, C_{org} and C_{mic} in forest soils over time (Busse et al., 1996; Périé and Munson, 2000; Carter et al., 2002). However, Busse et al. (2001) noted that the effects of timber harvests and tillage on soil dynamics could sometimes overshadow effects of vegetation control.

Given the organic matter losses that may have occurred in the first years of the rotation, microbial populations were likely highly dependent on C sources supplied by vegetation. The effects of brush control treatments on microbial biomass and activity in this study were indicative of this dependence. In addition to organic matter quantity, organic matter quality is often an important controlling factor for forest soil microorganisms due to the high lignin content of forest organic matter (Vance and Chapin, 2001). Roots serve as the major importers of high-quality C sources into the soil system; these C sources are essential in sustaining soil life processes (Tate et al., 1991). Root exudates (highly labile substances such as simple carbohydrates, amino acids, and fatty acids) have been shown to stimulate microbial growth and division (Tate et al., 1991; Qualls, 2000). An abundance of root exudates compensates for low organic matter quality (Vance and Chapin, 2001). Forests with greater plant species diversity support higher microbial populations due to a more varied supply of root exudates (Donegan et al., 2001). Furthermore, residues from understory vegetation are higher quality substrates than pine residues since they are less recalcitrant and therefore encourage more rapid decomposition and nutrient turnover (Polglase et al., 1992).

The presence of herbaceous vegetation in CONT plots supported more robust microbial populations in both years of this study. All treatments in which herbaceous vegetation was eliminated reduced C_{mic} and dehydrogenase activity for much of the year relative to the CONT treatment (Figures 1, 3, 5, and 6). C_{mic} and dehydrogenase activity were frequently significantly lower in plots without herbaceous vegetation than in CONT plots in late summer through winter in both years of this study. In late summer and early fall, herbaceous vegetation biomass reached its maximum (Manuscript I), and in middle and late fall herbaceous biomass was deposited to the forest floor as plants perished. This buildup and deposition of herbaceous vegetation biomass likely promoted C_{mic} and dehydrogenase activity in CONT plots. Furthermore, as loblolly pine roots (the sole source of exudates in BC, UDBC, and CUFBC plots) went into dormancy in autumn,

C_{mic} and activity in plots without herbaceous vegetation biomass significantly decreased relative to the CONT treatment. The significantly lower C_{mic} to C_{org} ratios in response to the UDBC treatment in December 2001 (Figure 2) and the NPBC, BC, UDBC, and CUFBC treatments in October 2002 (Figure 4) suggest lower quality substrates were available to soil microbes in fall and winter where herbaceous vegetation was eliminated. Another example of the importance of deposition of herbaceous biomass was the finding that C_{mic} to C_{org} ratios of all plots that received glyphosate exceeded that of the CONT treatment in April 2002 (Figure 4). The initial application of glyphosate in March 2002 killed the panicum grass (*Panicum dichotomiflorum* L.) and broomsedge (*Andropogon* spp.) that was predominate in plots in early spring. This deposition of herbaceous biomass may have then provided some readily available C substrate for microbes. The declines in C_{mic} in response to brush control found in this study were consistent with decreases in microbial biomass found in response to vegetation control in other studies of forest vegetation suppression (Busse et al., 1996; Périé and Munson, 2000).

The effects of tree removal treatments (NP, NPBC) implemented in 2002 on C_{mic} and dehydrogenase activity (Figures 3 and 6) further highlight the dependence of microbial populations on vegetation C sources. The primary source of C for microorganisms in plots receiving the NPBC treatment was the root systems of harvested trees, which can serve as a readily decomposable source of C for microbes (Thibodeau et al., 2000). However, the lack of living vegetation in NPBC plots dramatically reduced the C_{mic} and dehydrogenase activity in NPBC plots relative to all other treatments. Dehydrogenase activity of the NPBC treatment was the lowest of all treatments for most of 2002. C_{mic} in response to the NPBC treatment was also lower than that of the CONT and BC treatments in summer and fall. The significantly lower C_{mic} to C_{org} ratios (Figure 4) of NPBC plots relative to that of CONT, BC, and NP treatments in summer and fall may demonstrate the greater recalcitrance of dead pine root systems as microbial substrates. K-strategist microorganisms, which reproduce relatively slowly, tend to become predominant when substrates are more recalcitrant (Pianka, 1970; DeLeij, 1993); such a microbial community shift could have contributed to the lower microbial biomass and activity observed when all living vegetation was removed. Soil microbes in plots receiving the NP treatment had herbaceous vegetation and dead pine roots as C sources. As a result, C_{mic} and dehydrogenase activity (Figures 3 and 6) in response to the NP treatment were comparable to treatments in which trees were retained until the substantial reduction of actively growing herbaceous vegetation in autumn. In September through December, dehydrogenase activity of the NP treatment (Figure 6) was lower than that of the CONT treatment, and C_{mic} of the NP treatment (Figure 3) was significantly lower than all treatments with pine retention in November. The C_{mic} to C_{org} ratio of the NP treatment (Figure 4) was also lower than that of the CONT, BC, and CUFBC treatments in November. This lower ratio may indicate the more recalcitrant substrates available to soil microorganisms as herbaceous vegetation senesced. The shift in living vegetation abundance in NP plots in late fall may have caused a shift in microbial community composition from r-strategist microorganisms (which thrive in more substrate-rich environments) to K-strategist microbes (Pianka, 1970).

After the February 2001 urea/DAP application, C_{mic}, C_{mic} to C_{org} ratio, dehydrogenase activity (Figures 1, 2, and 5) increased relative to the control treatments in the following month. However, as the year proceeded the UDBC treatment was associated with the lowest C_{mic}, C_{mic} to C_{org} ratios, and dehydrogenase activity. Nitrogen added as urea has produced short-term increases in microbial respiration and biomass in several studies (Salonius and Mahendrappa, 1975; Ettema et al., 1999; Thirukkumaran and Parkinson, 2000; Homann et al., 2001). The protonation of ammonia that occurs during urea hydrolysis consumes protons, which causes a transient increase in soil pH (Homann et al., 2001). This brief increase in pH can improve microbial substrate availability by increasing cellulase activity, mobilizing organic compounds, and increasing microbial access to inorganic nutrients sequestered at lower pH (Thirukkumaran and Parkinson, 2000; Homann et al., 2001; Vance and Chapin, 2001; Jandl et al., 2002). No significant increases in soil pH were observed after our fertilizer treatments, but the soonest post-fertilization soil pH sampling occurred one month after fertilization. It is possible that a brief increase in soil pH in the uppermost soil occurred between sampling dates. The transient increases in C_{mic}, dehydrogenase activity, and the C_{mic} to C_{org} ratio observed in March 2001 suggest that microbial populations temporarily increased as a result of improved microbial substrate palatability shortly after fertilization.

The short-term increase in substrate availability after fertilization produces a shift in microbial communities to r-strategists, which reproduce quickly and consume substrates quickly due to a metabolism less efficient than that of K-strategists (Thirukkumaran and Parkinson, 2000). Easily utilizable organic C compounds are consumed quickly, and soil microorganisms become suppressed after the compounds are exhausted (Thirukkumaran and Parkinson, 2000; Homann et al., 2001). Suppressed microbial respiration, biomass, and activity in response to urea addition have been found when microbial assessments were made after longer durations (Bååth et al., 1981; Nohrstedt et al., 1989; Vesterdal, 1998; Homann et al., 2001). Ettema et al. (1999) observed that soil microbial communities become more C limited after N inputs. The decreased C_{mic}, dehydrogenase activity, and C_{mic} to C_{org} ratios of the UDBC treatment observed later in 2001 were consistent with a possible faster expenditure of organic C compounds occurring in fertilized plots. Another factor noted to promote faster decreases in microbial biomass and activity after fertilization is an increase in predation by microphytophagus organisms (protozoa, nematodes) that occurs in tandem with increases in bacteria and fungal populations (Groffman, 1999; Joergensen and Scheu 1999; Ettema et al., 1999). This phenomenon may have contributed to our results as well.

Although the fertilizer treatments applied in April 2002 did not produce a short-term increase in C_{mic}, C_{mic} to C_{org} ratio, or dehydrogenase activity (Figures 3, 4, and 6) as in 2001, there was some evidence that microbial biomass and activity declined more markedly in UDBC plots due to faster substrate exhaustion and/or declining substrate quality. In 2002, the decrease in C_{mic} in UDBC plots relative to CONT and BC treatments began in the month following fertilization (Figure 3). In summer through winter, C_{mic} of the UDBC treatment was typically lower than that of the CONT and BC treatments. Dehydrogenase activity of the UDBC treatment was significantly lower than that of the CONT, BC, and CUFBC treatments through much of the year (Figure 6). The UDBC treatment was associated with lower C_{mic} to C_{org} ratios (Figure 4) than CONT and BC treatments in the summer and fall, indicating poorer substrate quality in the plots fertilized with urea/DAP after fertilization. The greater C_{mic}, C_{mic} to C_{org} ratio, and dehydrogenase activity of the NP treatment than both the UDBC and CUFBC treatments in late summer further indicates that substrate quality of herbaceous vegetation biomass and residue was greater than that in plots receiving glyphosate and fertilizers. The higher exposure of soil to sunlight also likely contributed to the greater microbial biomass and activity of the NP treatment. It is possible that differences in soil organic matter concentration reduced the potential for short-term increases in microbial populations. Soil organic matter concentration was 5% lower when fertilizer was applied in April 2002 than in February 2001. It has been noted that microbial responses to N inputs are more pronounced with greater soil organic matter abundance (Vance and Chapin, 2001). In addition, short-term uptake of fertilizer N by loblolly pine was much greater in response to the April 2002 application than the February 2001 application (Manuscript I). This increased pine N immobilization may have reduced the potential for short-term increases in microbial populations.

The CUFBC treatment did not impact C_{mic}, C_{mic} to C_{org} ratio, and dehydrogenase activity as greatly as did the UDBC treatment (Figures 3, 4, and 6). C_{mic}, C_{mic} to C_{org} ratios, and dehydrogenase activity in response to the CUFBC treatment were significantly lower than the CONT treatment with less frequency than in response to the UDBC treatment. C_{mic}, C_{mic} to C_{org} ratios, and dehydrogenase activity of the CUFBC treatment were consistently comparable to the BC treatment, and dehydrogenase activity of the CUFBC treatment was significantly greater than that of the UDBC treatment throughout 2002. CUF, due to its lower solubility, did not release bioavailable N in concentrations as high as did the urea/DAP mixture (Manuscript I). Thirukkumaran and Parkinson (2000) found that N and P addition in a closed environment suppressed microbial respiration due to buildup of osmotic potential to toxic levels. It is possible that the lesser impact of CUF on microbial biomass and activity relative to the more soluble urea/DAP mixture observed in our study was attributable in part to its lower osmotic potential.

The reductions in C_{mic} resulting from brush control and fertilizer treatments likely have implications for N availability. Microbial biomass has been positively correlated with potentially mineralizable N (Stockdale and Rees, 1994). Nitrogen and other nutrients are released as microbial cells die and surviving microbes mineralize their content, i.e., mineralization of nutrients increases as microbial biomass declines (Stockdale and Rees, 1994; Aggangan et al., 1999). The significant inverse correlation between C_{mic} and soil NO_3^- in our study suggests that N availability was greater with reduced C_{mic}.

When estimates of microbial biomass N were integrated with loblolly pine and herbaceous biomass N (Manuscript I) and soil NO_3^- (Manuscript III) measurements taken in September 2001 and 2002 (dates at pine and understory vegetation biomass was at its peak), it is observed that microbial biomass comprises a relatively small portion of the total biomass N budget for the site (Figure 7). The size of the microbial N pool slightly increased from 2001 to 2002. The higher microbial biomass observed in studies of older forests (Vance et al., 1987*b*; Diaz-Raviña et al., 1993) suggest that microbial biomass may become an increasingly significant sink for N as the stand ages. Stark and Hart (1997) suggested that the accumulation of soil C and N that occurs in conjunction with the rapid growth of younger forests leads to microbial biomass becoming net sinks for inorganic N. Given the management history (bedding/subsoiling site preparation, vegetation suppression) of the young plantation observed in this study, soil C and N has had little opportunity to accumulate. As such, microbial biomass has not yet become a substantial sink for N. Herbicide treatments have been demonstrated to increase soil N availability via reduction in N competition and increases in N mineralization (Zutter et al., 1999, NCSFNC, 2001; Busse et al., 2001). In both years of this study, elimination of herbaceous vegetation in the BC treatment led to increased soil NO_3^-, decreased microbial biomass N, and increased loblolly pine N immobilization (Figure 7). Fertilization, when done in conjunction with continuous brush control, led to a decrease in microbial biomass N, increased soil NO_3^-, and higher loblolly pine N immobilization. Ettema et al. (1999) similarly found that forest fertilization decreased microbial biomass and did not lead to microbial N immobilization. Our findings suggest that microbial biomass does not serve as a significant competitor for applied N when young, intensively managed loblolly pine forests are fertilized.

CONCLUSIONS

The juvenile loblolly pine plantation assessed in this study was treated with several silvicultural practices that continue to become commonplace in forest management due to the efforts of foresters to meet global demand for forest products. When herbaceous vegetation was suppressed, microbial biomass and activity declined, and microbial biomass and activity decreased further when brush control treatments were combined with N and P fertilization. Given the vast importance of soil microorganisms in the processes of litter decomposition and the cycling of nutrients, declines in microbial biomass and activity may have longer-term ramifications for forest growth. Future research on the ability of microbial communities to adapt to frequent brush control and fertilization treatments or to recover from occasional brush control and fertilizer applications seems a worthwhile endeavor. In addition, the low capacity of soil microorganisms to sequester the applied N and the elevated soil NO_3^- levels measured several months after fertilization (particularly after fertilization done at stand age 3), warrants further exploration of the leaching potential associated with fertilization of young stands. The sustainability of management practices is contingent upon the minimization of long-term disruptions in essential soil processes and negative environmental impacts.

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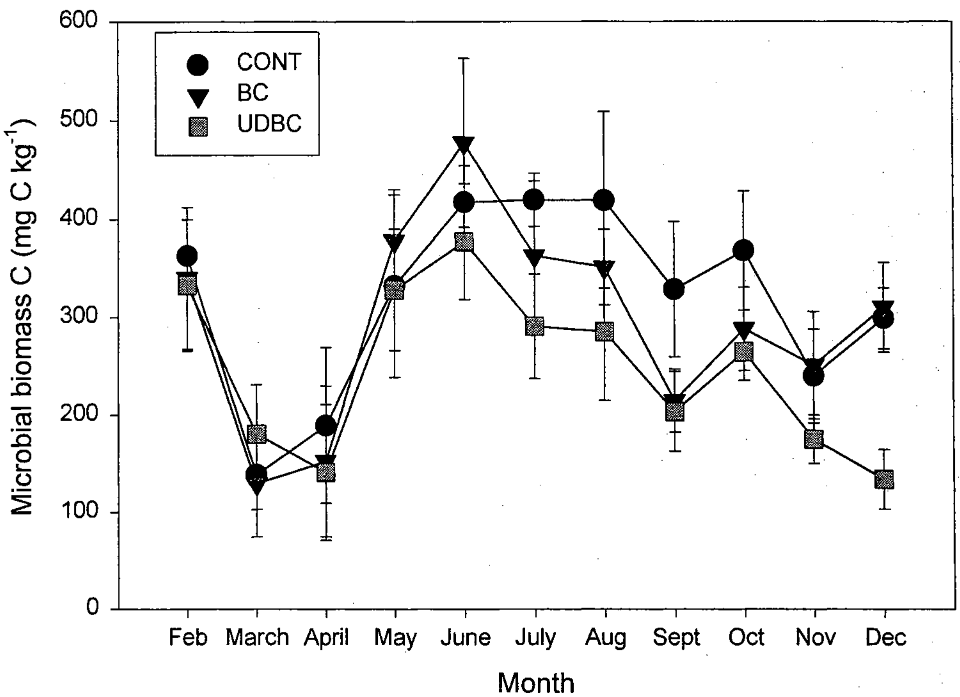


Figure 1. Microbial biomass C in response to control (CONT), continuous herbaceous vegetation suppression by glyphosate (BC), and continuous vegetation suppression by glyphosate and application of urea/diammonium phosphate mixture in February 2001 (UDBC). Treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars represent 1 SE.

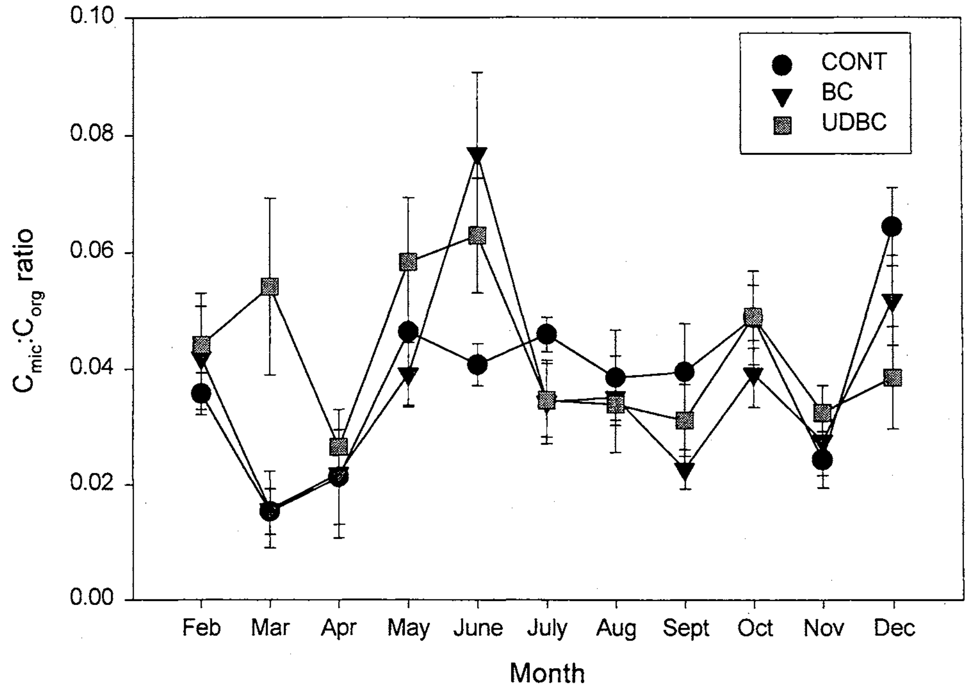
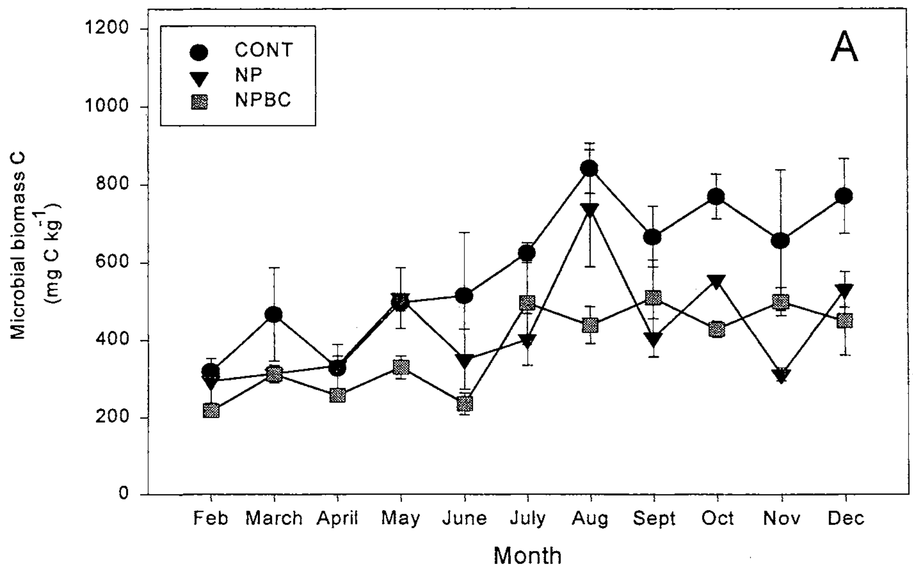


Figure 2. Ratio of microbial biomass C to soil organic C in response to control (CONT), continuous herbaceous vegetation suppression by glyphosate (BC), and continuous vegetation suppression by glyphosate and application of urea/diammonium phosphate mixture in February 2001 (UDBC). Treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars represent 1 SE.



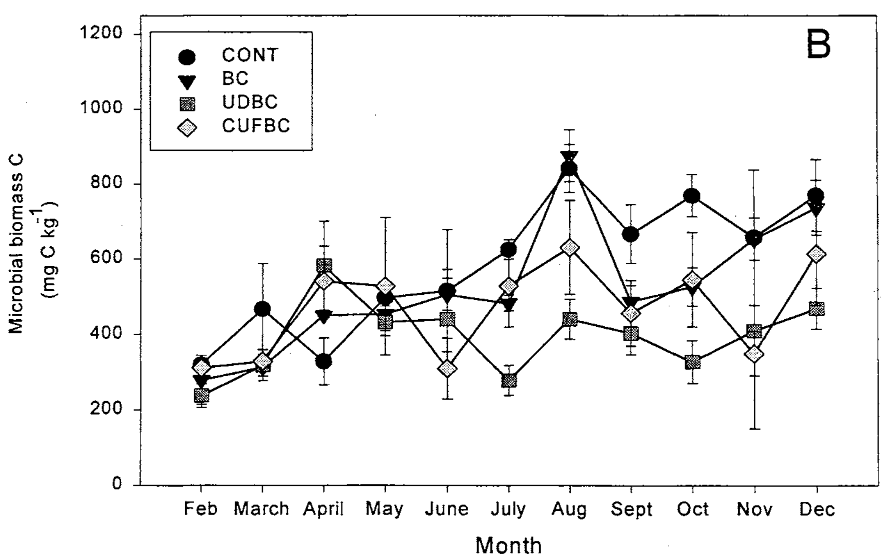
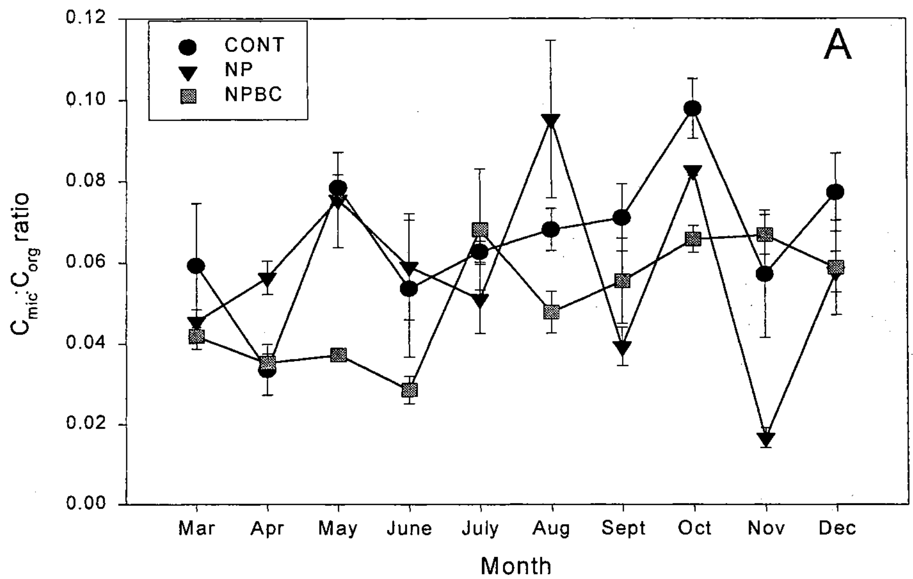


Figure 3. Microbial biomass C in response to: (A) untreated control (CONT), loblolly pine removal (NP), and loblolly pine removal in conjunction with continuous brush control (NPBC); (B) untreated control (CONT), brush control (BC), brush control and application of urea/diammonium phosphate mixture in April 2002 (UDBC), and brush control and application of slow-release coated urea fertilizer (CUFBC) in April 2002 . Treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars represent 1 SE.



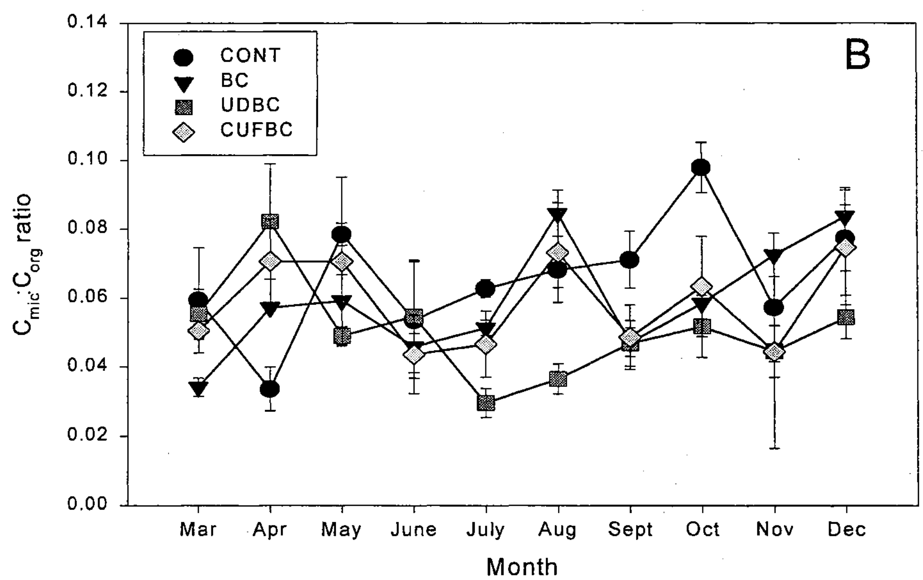


Figure 4. Ratio of microbial biomass C to soil organic C in response to: (A) untreated control (CONT), loblolly pine removal (NP), and loblolly pine removal in conjunction with continuous brush control (NPBC); (B) untreated control (CONT), brush control (BC), brush control and application of urea/diammonium phosphate mixture in April 2002 (UDBC), and brush control and application of slow-release coated urea fertilizer (CUFBC) in April 2002 . Treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars represent 1 SE.

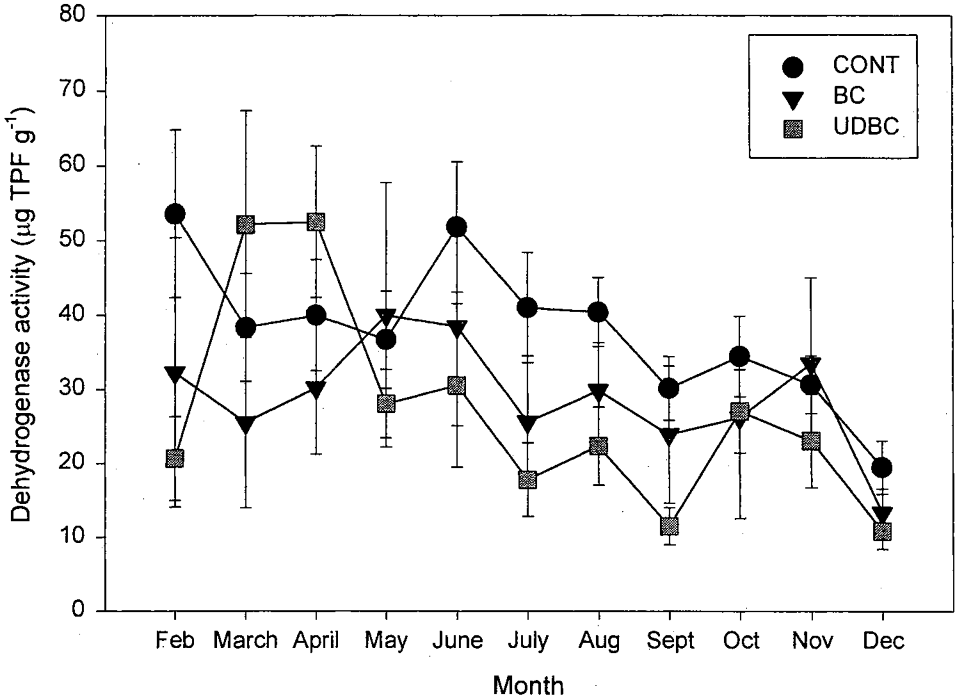
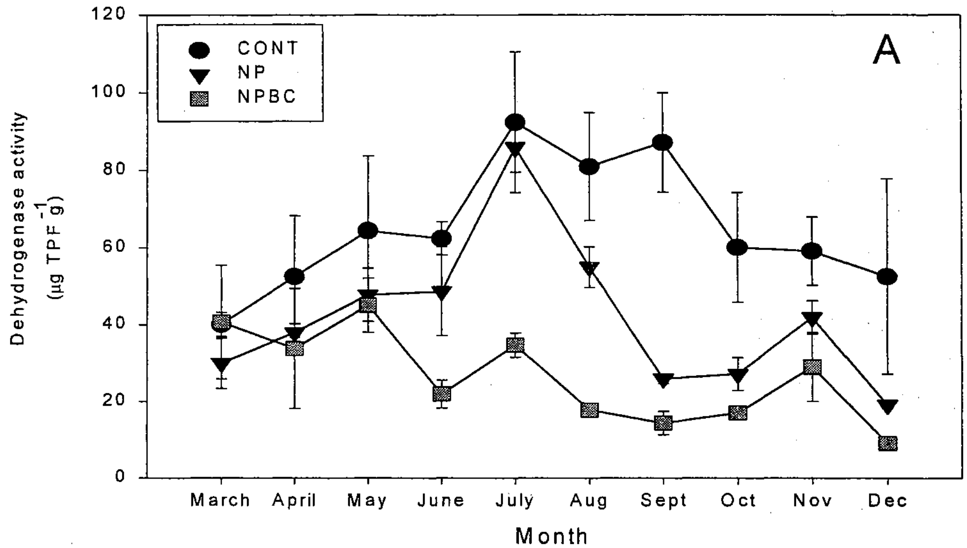


Figure 5. Dehydrogenase activity in response to control (CONT), continuous herbaceous vegetation suppression by glyphosate (BC), and continuous vegetation suppression by glyphosate and application of urea/diammonium phosphate mixture in February 2001 (UDBC). Treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars represent 1 SE.



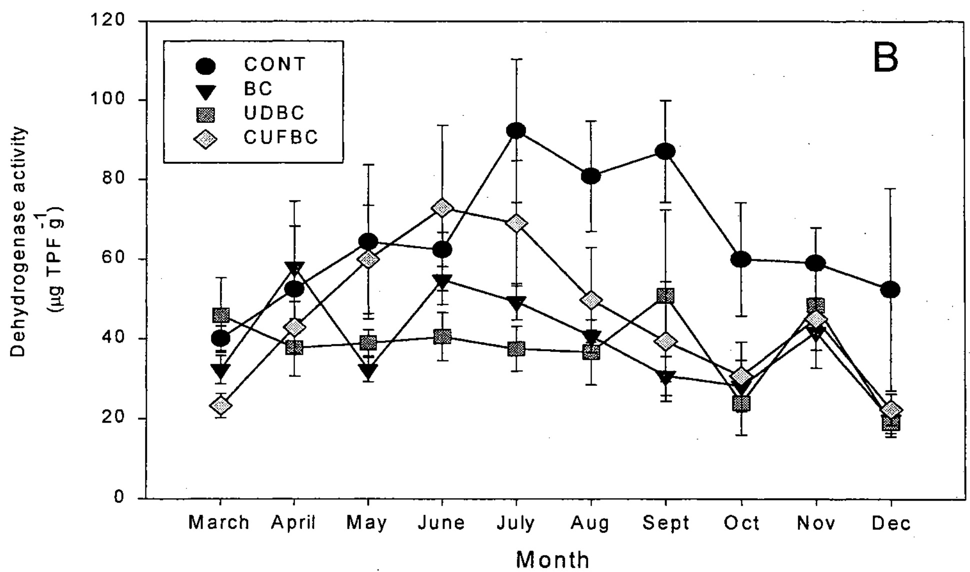


Figure 6. Dehydrogenase activity in response to: (A) untreated control (CONT), loblolly pine removal (NP), and loblolly pine removal in conjunction with continuous brush control (NPBC); (B) untreated control (CONT), brush control (BC), brush control and application of urea/diammonium phosphate mixture in April 2002 (UDBC), and brush control and application of slow-release coated urea fertilizer (CUFBC) in April 2002 . Treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Error bars represent 1 SE.

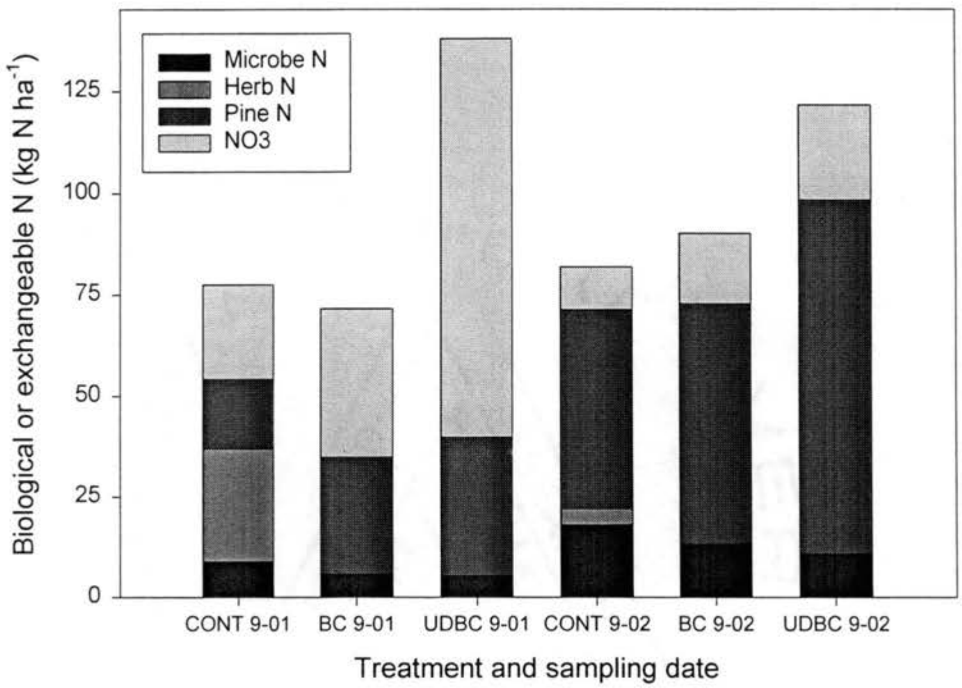


Figure 7. N sequestered in loblolly pine, herbaceous vegetation, and microbial biomass and soil NO_3^- in response to control (CONT), brush control by glyphosate (BC), and a combination of brush control by glyphosate and application of an urea/diammonium phosphate mixture. The fertilizer mixture was applied to a 3-year-old loblolly pine plantation in February 2001 and to a 4-year-old loblolly pine plantation in April 2002. September 2001 measurements are of trees treated in 2001, and September 2002 measurements are of trees treated in 2002. Haworth, OK.

Manuscript III

Effects of fertilization and vegetation control on soil and foliage nutrient dynamics of a young loblolly pine plantation

Abstract

Effectiveness and sustainability of forest nutrition improvement practices can be enhanced through a better understanding of seasonal soil and nutrient dynamics in response to brush control and fertilization treatments. Soil and foliage concentrations of five macronutrients (N, P, K, Ca, Mg) and five micronutrients (B, Cu, Fe, Mn, Zn) were measured in a juvenile loblolly pine plantation in southeastern Oklahoma on a monthly basis in response to: (1) untreated control, (2) continuous herbaceous vegetation suppression, (3) urea/diammonium phosphate (DAP), (4) urea/DAP in conjunction with continuous herbaceous vegetation suppression, and (5) slow-release coated urea fertilizer (CUF) in conjunction with continuous herbaceous vegetation suppression. Transient changes in several soil macro- and micronutrients were produced by the treatments, but no persistent changes in soil nutrient concentrations were found. Soil NO_3^- and foliage N concentrations were increased by the fertilization treatments, but the increases persisted longer when herbaceous vegetation was suppressed in conjunction with fertilization. Fertilizer formulations tested produced similar foliage and soil N levels when herbaceous vegetation was controlled. Understory vegetation was also a significant competitor for K during summer months. Available soil P was increased by all fertilization treatments, whereas foliage P concentrations were decreased by fertilization treatments due to growth dilution. Foliage P:N ratios indicate the 10:1 fertilizer ratio of N to P did not provide enough P to match gains in N. Transient increases in soil and foliage B were yielded by the B-containing CUF; the brush control and urea/DAP+brush control treatments also increased foliar B concentrations. Foliage K:N ratios suggest pest susceptibility was increased by fertilization treatments, particularly when herbaceous vegetation was

suppressed. Short-term changes in soil and/or foliage K, Ca, Mg, and Zn were induced by the brush control and fertilizer treatments, but the changes were not likely dramatic enough to affect loblolly pine growth.

1. Introduction

A large body of research has demonstrated the effectiveness of vegetation control and fertilization for increasing forest productivity. These practices have been integral in the efforts of forest managers to balance timber and fiber production with preservation of biological diversity and long-term site productivity (Velazquez-Martinez et al. 1992). Limitations to tree growth are routinely alleviated on approximately 13% of U.S. forests, and these amended forests produce ~40% of domestic forest products. Productivity of these intensively managed forests, which are frequently plantations, is 200% greater than unamended forests (Fox 2000, Vance 2000). Currently ~ 15 million acres of forestland, predominantly planted in loblolly pine (*Pinus taeda* L.), have been fertilized each year in the southeastern United States, making the forests of the region among the world's most productive (Fox 2000, NCSFNC 2001). Continued increases in forest productivity are feasible with improvements to nutrient addition and reallocation practices. Maintenance of optimal forest nutrition throughout the rotation has become a management objective of forest managers. As such, fertilization and understory vegetation control are becoming more prevalent in younger plantations. However, few investigations of the influence of vegetation control and fertilization on the nutrient dynamics of juvenile loblolly pine forests have been conducted.

Knowledge of soil nutrient dynamics has proven useful in assessing the sensitivity of forested areas to anthropogenic disturbances and in ascertaining interactions between fertilizer, nutrient availability, and acidification of forest soils (Johnson et al. 2000, Schroth et al. 2000). Vegetation control may alter the cation-exchange capacity (CEC) of forest soils since there is a strong positive correlation between soil organic matter and CEC (Johnson et al. 2000), but studies on the effects of vegetation control on forest soil chemistry are lacking. Effects of nutrient additions to forest soils have been variable in previous studies, depending on the intensity of fertilization, soil properties, climate, and forest composition and age. Jandl et al. (2002) proposed that fertilization mobilized the recalcitrant nutrient pool of forest floor material in 75- and 90-year-old mixed pine forests by turning soil organic matter into a more attractive substrate for microbial populations. In their study of the influence of fertilization on soil chemistry of a tropical multi-strata agroforestry system, Schroth et al. (2000) found pronounced fluctuations of soil nutrients, increases in Al concentrations, and decreased pH due to exchange reactions between added N and P fertilizer cations and sorbed acidity. In contrast, no lasting effects of short-term N additions on soil nutrients and pH were found in a study of 30- to 60-year-old Norway spruce (*Picea abies*) forests (Nohrstedt 2002). Smethurst et al. (2001) similarly found no long-term effects of N fertilization on nutrients in soil solution in young eucalypt (*Eucalyptus nitens*) plantations.

Foliage nutrient concentrations have been used in numerous studies to assess nutrient uptake in response to fertilization and interspecific competition (McNeil et al. 1988, Bockhem and Leide 1991, Malik and Timmer 1996, Sung et al. 1997). Foliage is useful in monitoring tree responses to nutrient amendments since it is the major site of nutrient storage (Zhang and Allen 1996). Elimination of competing vegetation has been shown to increase foliage nutrient concentrations (Morris et al.1993, Malik and Timmer

1996). Several studies have demonstrated increases in foliar concentrations of nutrients supplied via fertilization (Valentine and Allen 1990, Sung et al. 1997, Zhang and Allen 1996). When several nutrients were added to Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests, significant increases in foliage concentrations of added nutrients occurred. In that study, foliage Mg (which was not supplied by fertilizer) concentrations increased as well, implying that fertilization also enhanced root and mycorrhizal activity, thereby increasing the ability of trees to sequester water and nutrients (Velaquez-Martinez et al. 1992). However, a study of loblolly pine seedling responses to fertilization showed that foliage N concentrations increased in response to N fertilization, while concentrations of other macronutrients were unaffected (Sung et al. 1997). Since foliage nutrient concentrations fluctuate throughout the season, it has been proposed that following foliage nutrient dynamics over time is required for thorough investigations of tree vigor (Sung et al. 1997). A few studies of temporal distribution of foliar nutrients have been pursued (Adams et al. 1987, Rathfon et al. 1993, Murthy et al. 1996, Sung et al. 1997). In a study of the temporal patterns of several foliage nutrients in response to fertilization of a Scots pine (*Pinus sylvestris* L.) forest, Helmisaari (1992) found that fertilization altered the amounts but not the patterns of nutrient dynamics.

Nitrogen is the predominant nutrient added to forest soils (Reich and Schoettle, 1988). However, further increases in forest productivity may necessitate addition of nutrients other than N that limit productivity (Velaquez-Martinez et al. 1992). Macronutrients have typically been observed in studies of soil and foliar nutrient dynamics, but few comprehensive studies of seasonal fluctuations of micronutrients have been conducted in response to intensive forest management. Observation of all nutrients may help identify nutrient limitations other than N, which would help improve forest fertilization recommendations. In addition, loblolly pine response to fertilizer may possibly be affected by the rate of dissolution and transformation of the fertilizer in the soil after application. Slow-release fertilizers may improve foliage nutrient concentrations more than conventional fertilizer formulations. Such fertilizers have been successfully used in agriculture, and have been tested for forestry use on monterey pine (*Pinus radiata* D.Don) (Mead et al. 1975), slash pine (*Pinus elliotti* Engelm.) (Fisher and Pritchett 1982), and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) (Radwan and DeBell 1989).

Garrison et al. (2000) found that foliage K concentrations increased in response to ammonium-based fertilizers, while foliage N concentrations did not increase as much as anticipated. These results were attributed to competition between the fertilizer-derived NH_4^+ ions and K^+ for exchange sites. The NH_4^+ ions may have been bound on exchange sites while K^+ ions were made available for tree uptake. Radwan and DeBell (1989) found reductions in Ca, Mg, K, and S ions in response to several urea formulations. Their results were attributed to possible changes in the availability of these elements in the rooting zone due to the direct or indirect action of the fertilizers or their transformation products. Inferences about soil nutrition changes in response to fertilization in such studies have been made in the absence of empirical evidence of such changes. Pairing observations of foliage nutrient dynamics with soil chemistry measurements may bolster understanding of soil nutrient changes that underlie foliar nutrient responses to fertilizer and vegetation control treatments. For example, a study of the soil and vegetation nutrient responses of bromegrass (*Bromus inermis* Leyess.)

pastures to N fertilization revealed that changes in soil Al, Fe, and Mn were manifested in hay as well (Malhi et al. 2000).

The objectives of this study are to characterize the seasonal foliage and soil macro- and micronutrient dynamics in response to two formulations of urea fertilizers and vegetation control treatments applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Few studies of this nature have been pursued in the northwestern portion of its range, where moisture limitations can impact responses to fertilization and competing vegetation suppression treatments.

2. Materials and Methods

2.1. Site description

A complete description of the study site is given in Manuscript 1; key characteristics of the site will be described here. The site is a 15-hectare (37-acre) loblolly pine plantation in southeastern Oklahoma planted on a 1.8 m × 5.5 m (6.0 ft. × 18.0 ft.) spacing with a single coastal North Carolina family in February 1999. Prior to planting, the site was prepared via a bedding/subsoiling operation, and a mixture of sulfometuron methyl (Oust®) and imazapyr (Arsenal®) herbicides was applied to control competing vegetation. The soil is a nutrient-poor, acidic, sandy loam (USDA-SCS, 1974). The average annual rainfall of the region is 125 cm (49 in.), and the average annual temperature is 17°C (63°F).

The plantation was developed into a loblolly pine fertility research area in January 2001. Trees of average height in January 2001 were selected as study trees. The experimental units for this study were 24-m^2 (254-ft^2) plots each containing a single study tree, and each plot was separated by a buffer space of at least 3.7 m (12 ft.) within each row and 5.5 m (18.0 ft.) between rows to prevent contamination of study trees via lateral flow of applied nutrients.

2.2. Treatments

The following treatments (each replicated 10 times) were randomly applied to plots in 2001 and 2002 to investigate the effects of vegetation control and fertilization on foliage nutrient dynamics and soil chemistry:

1. No brush control, no fertilizer (CONT)
2. Brush control, no fertilizer (BC)
3. Urea and diammonium phosphate mixture, no brush control (UD)
4. Brush control, urea and diammonium phosphate mixture (UDBC)
5. Brush control, coated urea fertilizer (CUFBC)

These treatments were applied to 50 plots (10 per treatment) in February 2001 and to 50 separate plots in April 2002. The CONT treatment served as a control, and the BC treatment isolated the influences of vegetation control on foliage and soil nutrient dynamics. The UD treatment was applied to investigate the effects of competing vegetation on loblolly pine nutrient uptake and soil nutrition, and the UDBC treatment provided information about pine nutrient uptake and soil nutrient dynamics in response to fertilization in the absence of competing vegetation. The coated urea fertilizer was a slow-release fertilizer coated with a P- and B-containing coating that delayed release of urea until a significant precipitation event. Thus, the CUFBC treatment provided information about the influences of the rate of fertilizer dissolution on foliage and soil nutrient dynamics.

Fertilizers were applied to a 24-m^2 (254-ft^2) area around study trees using hand spreaders in February 2001 and April 2002. Nitrogen was applied at 202 kg ha^{-1} (180 lb ac^{-1}); phosphorus was applied at 20 kg ha^{-1} (18 lb ac^{-1}). In addition, the coated urea fertilizer contributed 0.65 kg ha^{-1} (0.58 lb ac^{-1}) of B to the soil.

Brush control consisted of elimination of herbaceous and woody vegetation. A 10% solution of glyphosate (Accord®) was applied periodically throughout the 2001 and 2002 growing seasons to prevent any herbaceous understory vegetation from growing. Woody vegetation was controlled with triclopyr (Garlon®) applied in February 2001. Since the competitive ability of herbaceous vegetation to acquire applied nutrients in a young loblolly pine plantation was of interest in this study, woody vegetation was eliminated from the entire study site. Herbaceous vegetation was eliminated from a 16-m^2 (168-ft^2) area around study trees chosen for BC, UDBC, and CUFBC treatments.

2.3. Foliage sampling and analysis

Foliage was sampled from all study trees throughout this study. In both years of this study, foliage sampling commenced immediately prior to fertilization and proceeded monthly throughout the remainder of the year. In 2001, foliage from the second flush of 2000 was collected from February to October, and foliage from the first flush of 2001 was sampled from May to December. In 2002, foliage from the first flush of 2001 was collected from April to October, and foliage from the first flush of 2002 was sampled from May to December. Each foliage sample consisted of four fascicles of needles drawn from the mid-crown position (Zhang and Allen 1996). These fascicle samples were then composited to produce three foliage samples per treatment. To preserve replication of treatments, each composite sample consisted of fascicles collected from three or four study trees; foliage from the same three or four study trees was composited from month to month. To minimize respiratory losses of nutrients, samples were refrigerated immediately after collection and dried to constant weight at 70°C within 48 h. Dried foliage samples were milled to pass a 20-mesh sieve.

Macronutrient (N, P, K, Ca, Mg) concentrations were obtained by dry ashing of foliage samples followed by analysis with inductively coupled plasma atomic emission spectroscopy (Beck 2002). Micronutrient (B, Cu, Fe, Mn, Zn) contents were obtained using microwave/nitric acid digestion of foliage samples followed by nutrient measurement by plasma atomic emission spectroscopy (Beck 2002). Due to laboratory constraints, monthly micronutrient measurements were carried out only in 2002, and micronutrients in response to the UD treatment were not observed.

2.4. Soil sampling and analysis

Bioavailable soil nutrients were sampled concurrently with the foliage samples in response to the February 2001 and April 2002 treatments. Soil samples were collected from the top 15 cm of soil using a soil auger. In each plot, a single sample was collected approximately 1 m from the base of the study tree, within the bedded/subsoiled area. Soil samples were collected from ten plots per treatment; these samples were then composited as described above for foliage samples to create three composite samples per treatment.

A Mehlich III solution (Mehlich 1984) was used to extract bioavailable P, K, Ca, Mg, B, Cu, Fe, Mn, and Zn. Each element was measured by inductively coupled plasma emission. Several measurements of these nutrients were correlated with bioavailable nutrient values that would be yielded by methods commonly used in the central U.S. region, and the values reported here are the results of those correlations. Measurements of P were correlated to available P that would be yielded with the Bray P1 method (Bray and Kurtz 1945). Measurements of B were correlated to hot water soluble B (Keren 1996), and Mn and Zn were correlated to available Mn and Zn as extracted by 0.1 N HCl solution (Reed and Martens 1996).

Nitrate was measured using a nitrate meter (Horbia Cardy nitrate meter, Spectrum Technologies, Inc.). Soil samples were dried at 105°C to constant weight and pulverized to pass a 10-mesh sieve. An extractant/standard solution developed for the Cardy meter was used to remove nitrate from the soil; the meter was then used to measure nitrate (Spectrum Technologies 1990).

Cation exchange capacity (CEC) and base saturation (BS) were also assessed for each soil sample. CEC was determined as the sum of K, Ca, Mg, and H^+ in the soil sample. Soil H^+ was extracted using the Shoemaker-McLean-Pratt single buffer method (Sims 1996), and H^+ was quantified using a pH electrode (ROSS® Sure-Flow™ pH Electrode, Orion Research). BS was calculated as the sum of K, Ca, and Mg divided by the CEC.

2.5. Statistical Analysis

Analyses of all treatment effects were conducted by analyses of variance (ANOVA's) using the MIXED procedure of the SAS System (SAS Institute Inc., Cary, NC). When the null model likelihood ratio test revealed heterogeneous variances in a dataset, the GROUP option of MIXED was utilized to perform ANOVA's using different variances for all treatment combinations. When an ANOVA indicated significant treatment effects, treatment means were calculated and separated by the DIFF and SLICE options of the LSMEANS procedure. The DIFF option provided multiple comparisons of treatment means by invoking t-tests to determine significant differences between all possible treatment combinations. The SLICE option provides t-tests of treatment means in which the effect of one treatment is evaluated at each level of another treatment. The SLICE option was used to investigate treatment main effects when significant two-way interactions were found.

Monthly measurements of foliage macronutrients, soil nutrients, CEC, and base saturation in response to the February 2001 and April 2002 fertilizer applications were analyzed as a one-way treatment (fertilizer/brush control) structure with 3 levels (UD, UDBC, CUFBC) plus 2 controls (CONT, BC). Foliage micronutrients were analyzed as a one-way treatment with 2 levels (UDBC, CUFBC) plus 2 controls. Due to these treatment structures, it was necessary to conduct the analyses in two steps. First, the fertilizer/brush control treatments were analyzed with a repeated measures model with an autoregressive correlation structure with: (1) fertilizer/brush control treatment, (2) month, and (3) the interaction between fertilizer/brush control and month as fixed effects. Next, the controls were compared to fertilizer/brush control treatments using CONTRAST statements. The fertilizer/brush control and control treatments were pooled and analyzed using ANOVA procedures performed on a model with treatment (CONT, BC, UD, UDBC, CUFBC) as a fixed effect. Contrast statements that compared responses associated with CONT and BC treatments to those of the fertilizer/brush control treatments were used in conjunction with ANOVA procedures to identify significant differences between control and active treatments. This comparison of controls to active treatments was conducted for each month of the study to identify when foliage and/or soil nutrients in response to CONT and BC treatments were significantly different from those of trees receiving fertilizer/brush control treatments.

3. Results

3.1. Nitrogen

In 2001, soil NO_3^- increased dramatically from February to March in all plots (Figure 1, Table 1). The increases in NO_3^- coincided with sharp declines in microbial biomass (Manuscript II). As such, a period of N mineralization likely occurred in the same period in which fertilizer was applied. Thus, the increases in NO_3^- in CONT and BC plots were likely attributable to N mineralization, and the increases in NO_3^- in fertilized plots was from a combination of applied N and N mineralization. After the early-spring increase, NO_3^- in all plots gradually declined through mid-summer. The BC treatment never produced NO_3^- significantly higher than that found in CONT plots; all fertilization treatments increased soil NO_3^-. However, NO_3^- in response to the UD treatment was comparable to that of the CONT and BC treatments by August, whereas NO_3^- in UDBC and CUFBC plots remained significantly higher than that in control plots through November. The UDBC treatment produced the highest soil NO_3^- means in 2001, but the NO_3^- of UDBC and CUFBC treatments were statistically similar throughout the year. By December, soil NO_3^- was similar in all plots.

Similar differences in soil NO_3^- were found in response to the April 2002 fertilizer treatments (Figure 1, Table 1). The CONT and BC treatments had comparable NO_3^- throughout the majority of the year. All fertilizer treatments increased NO_3^-, but NO_3^- of the UD treatment was statistically comparable to CONT and BC treatments sooner than in plots receiving UDBC and CUFBC treatments. The UDBC and CUFBC produced the highest soil NO_3^-, and NO_3^- was statistically similar in response to these two treatments throughout the year.

In 2001, foliage N concentration trends of the previous-season foliage were similar to the soil NO_3^- trends (Figure 2, Table 2). The CONT treatment was consistently associated with the lowest N concentrations, and the BC treatment never significantly increased foliage N over that of the CONT treatment. The CUFBC treatment produced the highest mean foliage N concentrations, and foliage N in response to this treatment was significantly greater than all treatments in June and September. Foliage N of the UDBC treatment was comparable to that of the CUFBC treatment in most months post-fertilization. The UD treatment significantly increased foliage N over that of the two control treatments, but this significant increase in foliage N over controls did not persist as long as in response to the two fertilizer+brush control treatments. After April, foliage N in response to the UD treatment was statistically equivalent to that of the BC treatment. Foliage N of the UD treatment was also frequently lower than that of the UDBC and/or CUFBC treatments after April. N concentrations of previous-season foliage of all treatments increased from March to April, with the greatest increases occurring in response to the fertilizer treatments. N concentrations of previous-season foliage declined during the summer, and then plateaued in the fall.

In 2001, foliage N concentration trends of the current-season foliage were similar to the previous-season foliage N trends (Figure 2, Table 2). The CONT and BC treatments consistently had the lowest foliage N; the BC treatment did not significantly increase foliage N over that of the CONT treatment. The CUFBC treatment yielded the highest foliage N means; in May and June, foliage N of the CUFBC treatment was significantly higher than all other treatments. The UD treatment significantly increased foliage N over the control treatments until June. After June, foliage N of the UD treatment was always significantly less than the control treatments and frequently less than that of the UDBC and CUFBC treatments. N concentrations of current-season foliage slightly decreased during early and middle summer months, with the steepest decreases occurring in response to the fertilizer treatments (particularly the UD treatment). For the remainder of the year, foliage N concentrations remained relatively stable.

In 2002, N concentrations of the previous-season foliage in response to CONT and BC treatments decreased throughout the year (Figure 3, Table 3). Foliage N of all fertilizer treatments increased following the April applications then decreased for the remainder of the year. The BC treatment significantly increased foliage N over the CONT treatment throughout the summer, but this increase in N was not as substantial as those yielded by the fertilizer treatments. All fertilizer treatments produced statistically comparable increases in foliage N.

The current-season foliage N concentrations in 2002 (Figure 3, Table 3) followed a general trend similar to that of the current-season foliage N in 2001 (Figure 2, Table 2). The CONT treatment was associated with the lowest foliage N concentrations throughout the year (Figure 3, Table 3). The BC treatment increased foliage N over that of the CONT treatment in September. All fertilizer treatments increased foliage N; increases in N in response to the UD treatment did not persist as long as in response to the UDBC and CUFBC treatments. Foliage N of the two fertilizer+brush control treatments were comparable throughout the year.

3.2. Phosphorus

In 2001 and 2002, the fertilizer treatments produced the highest available soil P means (Table 4). In early summer 2001 and late summer/early fall 2002, all fertilizer treatments significantly increased soil P relative to that of CONT and BC treatments. Soil P was comparable for the fertilizer/brush control treatments in 2001 and 2002 with the exception in August 2002, wherein the UDBC treatment had greater soil P than the UD treatment. In both years, the BC treatment was associated with the lowest soil P.

In 2001, P concentrations of both previous- and current-season foliage did not significantly differ between the UD, UDBC, and CUFBC treatments (Figure 4). P concentrations of previous-season foliage slightly declined from February until July, and then remained stable for the rest of the year. Foliage P similarly decreased until late summer in current-year foliage, and then slightly increased for the remainder of the year. In previous-season foliage, P concentrations of the CONT treatment were significantly greater than that of the UD, UDBC, and CUFBC treatments in June and October (P=0.03±0.02). Previous-season foliage P concentration of the CONT treatment also exceeded (P=0.02) that of the BC treatment in October. In current-year foliage, P concentrations of the CONT treatment were significantly greater than the (1) UDBC treatment in May, June, and November (P=0.048±0.001), (2) UD treatment in June (P=0.01), and (3) CUFBC treatment in November (P=0.049). Current-year foliage P of the BC treatment exceeded (P=0.02), the UDBC treatment in May.

In 2002, P concentrations of both previous- and current-season foliage did not significantly differ between the UD, UDBC, and CUFBC treatments (Figure 5). The UD treatment increased (P=0.03±0.02) previous-season foliage P over that of the CONT treatment in May and June. In previous-season foliage, the BC treatment frequently had the highest mean foliage P. Foliage P of the BC treatment was significantly greater than that of the (1) CONT treatment from May through July (P=0.02±0.02), (2) UDBC treatment in May and August (P=0.04), (3) UD treatment in August (P=0.04), and (4) CUFBC treatment in July, September, and October (P=0.02±0.01). The BC treatment also frequently had the highest foliage P concentrations in current-year foliage. The BC treatment was associated with foliage P significantly greater than that of the (1) CONT treatment in May (P=0.04), (2) UD in July and August (P=0.03±0.02), (3) UDBC in August and October (P=0.03±0.01), and (4) CUFBC in July through October (P=0.02±0.02).

In 2001, the ratio of foliage P to N (P:N ratio) of previous-season foliage, which ranged from 0.04 to 0.11 with a mean of 0.07, differed significantly (P=0.01) among the fertilizer treatments. The UD and UDBC treatments both had significantly greater P:N ratios than the CUFBC treatment. The P:N ratios of current-season foliage, which ranged from 0.04 to 0.13 with a mean of 0.07, also differed significantly (P=0.001) among the fertilizer treatments. In current-season foliage, the UD treatment had P:N ratios greater than the UDBC and CUFBC treatments; the P:N ratios of UDBC and CUFBC treatments were similar.

In 2002, previous-season foliage P:N ratios, which ranged from 0.04 to 0.11 with a mean of 0.07, did not differ significantly among the fertilizer treatments. A significant fertilizer × month effect (P=0.004) was found in the analysis of current-season foliage P:N ratios (which ranged from 0.05 to 0.09 with a mean of 0.07); significant fertilizer effects were found from July though November. The UD treatment had significantly higher P:N ratios (*P*=0.01±0.01) than the CUFBC treatment from July through November. The UD treatment had P:N ratios significantly (*P*=0.01±0.02) greater than that of the UDBC treatment in August through October, and the UDBC treatment had P:N ratios greater (*P*=0.02±0.02) than the CUFBC treatment in July and October.

3.3. Calcium

In 2001, exchangeable soil Ca content, which ranged from 336 to 2349 kg ha^{-1} with a mean of 739, differed among treatments only in June. In June, the CONT treatment was associated with soil Ca significantly greater (*P*=0.02±0.01) than that of BC, UD, and UDBC treatments. In 2002 soil Ca content, which ranged from 359 to 1692 kg ha^{-1} with a mean of 884, differed among treatments in August and November. In August, the UDBC and CUFBC treatments were associated with soil Ca greater (*P*=0.03±0.01) than that of the UD treatment. In November, the CONT treatment produced significantly higher (*P*=0.002±0.001) Ca than the BC, UDBC, and CUFBC treatments.

In 2001 the CONT treatment was associated with the highest previous-season Ca concentrations in February (prior to any brush control or fertilizer applications), and this higher foliage Ca persisted throughout much of the year (Figure 6). The CONT treatment had significantly greater previous-season foliage Ca than the: (1) BC and UD treatments in all months (*P*=0.02±0.02), (2) UDBC treatment in February and March (*P*=0.01±0.001), and (3) CUFBC treatment in all months except August (*P*=0.02±0.02). No significant differences in current-year foliage Ca concentrations were observed in 2001.

In 2002, previous-year foliage Ca differed among treatments only in June, in which the BC treatment had greater (P=0.02±0.02) foliage Ca than the CONT and UDBC treatments. In the same month, the CONT treatment was associated with higher (P=0.01) foliage Ca than the UDBC treatment. The CONT treatment also had significantly greater (P=0.01±0.01) current-season foliage Ca concentrations than the UDBC, and CUFBC treatments in May and June of 2002. In May 2002, the current-season foliage Ca of the CONT treatment was also greater (P=0.01±0.01) than that of the BC and UD treatments. In both years of this study, foliage Ca concentrations constantly increased in both observed foliage flushes in response to all treatments.

3.4. Magnesium

Few significant differences in exchangeable soil Mg were found in either year of this study, and soil Mg remained relatively stable throughout the year. Soil Mg ranged from 74.0 to 580.6 kg ha^{-1} (with a mean of 219.6) in 2001 and from 86.3 to 319.4 kg ha^{-1} (with a mean of 172) in 2002. In 2001 and 2002, soil Mg did not significantly differ among the UD, UDBC, and CUFBC treatments. In April 2002, plots receiving the BC treatment had higher (P=0.04) soil Mg those receiving the CONT and UDBC treatments. In September 2002, the BC treatment produced higher (P=0.04) soil Mg than the UD treatment.

In 2001, Mg concentrations of previous-season foliage declined through mid-summer, then remained stable for the remainder of the year (Figure 7). Current-season foliage Mg concentrations remained relatively stable throughout the year, with a slight decrease occurring from May through July. The CONT treatment was frequently associated with the highest Mg concentrations in both foliage flushes. In previous-year foliage, foliage Mg concentrations of the CONT were significantly higher (P=0.03±0.02) than the fertilizer treatments in June, August, and October. In foliage produced in 2001, the CONT treatment yielded foliage Mg higher than that of the: (1) UDBC treatment in all months except August and November (P=0.02±0.01), (2) CUFBC treatment in all months except September (P=0.03±0.02), (3) UD treatment in June (P=0.02), and (4) BC treatment in October (P=0.01). Foliage Mg concentrations of 2001 foliage in response to the BC treatment were higher than that of the fertilizer treatments in May and June (P=0.04±0.01). In both foliage flushes, the UD treatment was associated with significantly greater (P=0.03±0.02) foliage Mg than the CUFBC treatment; the UD treatment also produced higher (P=0.02) Mg concentrations than the UDBC treatment in foliage produced in 2001.

In 2002, previous-season foliage Mg concentrations followed a trend similar to that of the previous-season foliage in 2001 (Figure 8). Mg concentrations of current-season foliage gradually declined from May though November in all treatments. The BC treatment frequently produced the highest Mg concentrations in foliage produced in 2001. From May through October, the BC treatment yielded foliage Mg significantly higher (P=0.02±0.01) than that of the CONT treatment. Previous-season foliage Mg of the BC treatment also exceeded that of the UD treatment from July through September (P=0.03±0.02) and that of the UDBC treatment in August and September (P=0.03±0.01). In foliage produced in 2002, the CONT treatment yielded higher Mg concentrations than the UDBC and CUFBC treatments in May and June (P=0.03±0.02). In May, the CONT treatment was also associated with significantly greater current-season foliage Mg concentrations than the UD and BC treatments (P=0.02±0.01).

3.5. Potassium

In both years of this study, there were few differences among the treatments in available soil K. In 2001, soil K ranged from 24.7 to 334.0 kg ha^{-1} (with a mean of 159), and soil K ranged from 22.4 to 201.7 kg ha^{-1} (with a mean of 75.3) in 2002. Soil K never differed significantly among the UD, UDBC, and CUFBC treatments. In March 2001, the CONT and BC treatments were associated with soil K greater (P=0.047) than that of the UDBC treatment. Soil K of the CONT and UD treatments exceeded (P=0.01±0.01) that of the BC treatment in May 2001. In August 2002, the plots receiving UDBC treatment had higher soil K than those receiving CONT and BC treatments. In December 2002, the BC treatment was associated with higher (P=0.02±0.01) soil K than the UDBC and CUFBC treatments.

In 2001, K concentrations of previous-year foliage differed significantly among the fertilizer treatments (Figure 9). In previous-year foliage, K concentrations of the fertilizer treatments differed significantly (P=0.004); K concentrations of the UDBC and CUFBC treatments were greater than those of the UD treatment. Previous-year foliage K concentrations of the UDBC and CUFBC treatments were comparable. In May, foliage K concentrations in previous-year foliage in response to the CONT treatment were greater (P=0.03±0.02) than that of the fertilizer treatments. However, in July foliage K of the UDBC and CUFBC treatments were greater (P=0.01±0.01) than that of the CONT treatment. In August, foliage K of the CONT and BC treatments exceeded (P=0.02±0.03) that of the UD treatment; the BC treatment also yielded foliage K higher (P=0.01±0.01) than the CUFBC treatment. In general, foliage K concentrations of previous-year foliage decreased through early spring, increased from March through

May, and then remained relatively stable for the remainder of the year.

Significant differences (P=0.01) in foliage K concentrations of foliage produced in 2001 were detected among the fertilizer/brush control treatments in June through August 2001 (Figure 9). The UD treatment produced foliage K significantly lower than that of the UDBC and CUFBC treatments from June through August, and the UDBC treatment yielded foliage K lower than that of the CUFBC treatment in June and July. The CONT and BC treatments had greater current-season foliage K concentrations than the fertilizer/brush control treatments in summer. The CONT and BC treatments were associated with current-season foliage K greater (P=0.01±0.01) than that of the UD treatment from May through August. In May, current-season foliage K in response to the CONT and BC treatments were also significantly higher (P=0.01) than that of the UDBC treatment. Foliage K concentrations in foliage produced in 2001 declined from May through October, and then remained stable until December.

In August and September 2002, K concentrations of foliage produced in 2001 were greater (P=0.02±0.003) in response to the BC treatment than the CONT and UD treatments (Figure 10). In August, foliage K of previous-year foliage was higher (P=0.04) in response to the UD, UDBC, and CUFBC treatments than the CONT treatment. K concentrations of foliage produced in 2002 were greater in response to the BC treatment than the CONT treatment in July, August, and October 2002 (P=0.04±0.01) and the UD treatment in August and September (P=0.03±0.01). In June and July, the UDBC treatment yielded current-year foliage K concentrations greater (P=0.03) than that of the CONT treatment. K concentrations of foliage produced in 2002 significantly differed (P=0.03) among the fertilizer treatments throughout the year. The UD treatment had significantly lower foliage K than the UDBC treatment, and the CUFBC treatment was associated with foliage K concentrations comparable to that of the UD and UDBC treatments. In general, previous-season foliage K concentrations followed a trend similar to those of previous-season foliage in 2001. K concentration trends of foliage produced in 2002 declined slightly each month from May through September, and then moderately increased through November.

Ratios of foliage K to foliage N (K:N ratios) were decreased by fertilizer treatments in 2001 (Table 5). In previous-year foliage, K:N ratios of all fertilizer treatments were significantly lower than those of the CONT and BC treatments from March through September. As of October, the K:N ratios of all treatments were statistically similar. The previous-season foliage K:N ratios increased throughout the year in response to the CONT and BC treatments and decreased in response to the UD, UDBC, and CUFBC treatments in the two months following the February fertilizer applications. In foliage produced in 2001, the CONT and BC were associated with the highest K:N ratios, and the UDBC treatment frequently yielded the lowest K:N ratios. Current-season foliage K:N ratios of the CUFBC treatment were comparable to those of the control treatments in June and July, and ratios of the UD treatment were comparable to those of the control treatments by September. By November, all treatments had similar K:N ratios. Foliage K:N ratios of current-year foliage declined until October in response to all treatments.

Foliage K:N ratios were also decreased by fertilizer treatments in 2002 (Table 6). Previous-season foliage K:N ratios followed general trends in 2002 similar to those observed in 2001. In foliage produced in 2001, K:N ratios of the CONT and BC treatments significantly exceeded those of the fertilized treatments in the two months following the April fertilizer applications. UD and CUFBC treatments frequently produced the lowest K:N ratios, whereas ratios of the UDBC treatment were typically comparable to those of the control treatments. By October, previous-season foliage K:N ratios were similar for all treatments. In foliage produced in 2002, K:N ratios decreased in all treatments through September. The BC treatment typically yielded the highest K:N ratios, and the UD and CUFBC treatments commonly produced the lowest ratios.

3.6. Boron

The fertilizer treatments significantly affected available soil B in 2001 and 2002. Soil B ranged from 0.6 to 1.7 kg ha^{-1} in 2001, with a mean of 0.81. In 2002, soil B ranged from 0.6 to 2.5 kg ha^{-1} with a mean of 0.61. In 2001, the CUFBC treatment produced significantly greater ($P=0.02\pm0.01$) soil B than the BC treatment from March through May. In April 2001, the CUFBC treatment was associated with greater ($P<0.0001$) B than the UD and UDBC treatments, and in May the CUFBC had greater ($P=0.03$) B than the CONT treatment. In 2002, the CUFBC treatment had higher ($P=0.04$) soil B than the CONT treatment in August.

The fertilizer treatments also affected foliage B concentrations in 2002 (Figure 11, Table 7). In the month following the April fertilizer applications, the CUFBC treatment was associated with the highest B concentrations in previous-season foliage. The CUFBC treatment also produced the highest B concentrations in foliage produced in 2002 in June, August, and September. In August and September, current-season foliage B concentrations of the CUFBC treatment were markedly greater than those of all other treatments. Throughout the year, the BC, UDBC, and CUFBC treatments frequently had

B concentrations in both foliage flushes that significantly exceeded that of the CONT treatment. In September and October, the B concentrations of previous-season foliage increased substantially in trees receiving the UDBC treatment.

3.7. Copper

In 2001 and 2002, no consistent differences in available soil Cu among the treatments were found. In 2001, soil Cu ranged from 0.7 to 1.5 kg ha^{-1}, with a mean of 1.1. Soil Cu ranged from 0.7 to 1.3 kg ha^{-1} in 2002, with a mean of 1.0. In 2001, the CONT treatment was associated with soil Cu greater than that of the BC treatment in May (P=0.048) and the CUFBC treatment (P=0.03) in September. The UDBC treatment produced higher soil Cu than the BC treatment in May 2001 (P=0.04). In 2002, the CONT treatment was associated with greater (P=0.03±0.01) Cu than the UDBC and CUFBC treatments in May and September. However, soil Cu of the UDBC and CUFBC treatments exceeded (P=0.003) that of the CONT treatment in August. The BC treatment produced soil Cu higher than that of all fertilizer treatments in September 2001 (P=0.01±0.03) and the CONT treatment in December 2002 (P=0.04).

Few differences in foliage Cu concentrations were found in 2002. Cu concentrations of the foliage produced in 2001 ranged from 0.5 to 22.6 mg g^{-1} with a mean of 3.0, and Cu concentrations of foliage produced in 2002 ranged from 0.6 to 36.2 with a mean of 4.4. The BC treatment was associated with higher previous-season foliage Cu than the CONT treatment (P=0.01) in June and the CUFBC treatment (P=0.04) in September. Previous-season foliage Cu of the CONT treatment exceeded those of the BC and UDBC treatments (P=0.04±0.01) in July, but the UDBC treatment had higher (P=0.05) Cu than the CONT treatment in September. In foliage produced in

2002, Cu concentrations of the CONT treatment exceeded (P=0.03±0.02) those of the BC and UDBC treatments in June. In August, current-season foliage Cu concentrations yielded by the UDBC treatment were greater (P=0.04±0.01) than those of the CONT and CUFBC treatments.

3.8. Manganese

In 2001, no significant differences in soil Mn were observed. Soil Mn of the CONT treatment was significantly higher (P=0.04±0.01) than that of the BC treatment in July, August, November, and December 2002. In July 2002, soil Mn of the CONT treatment was also greater (P=0.047) than that of the CUFBC treatment. In 2001, soil Mn ranged from 5.6 to 147.9 kg ha^{-1} (with a mean of 24.8), and soil Mn ranged from 14.6 to 276.8 kg ha^{-1} (with a mean of 101.2) in 2002.

Although the CONT treatment frequently produced soil Mn higher than that of the BC treatment in 2002, the BC treatment was frequently associated with the highest Mn concentrations in previous-season foliage in 2002. Previous-season foliage Mn of the BC treatment exceeded that of the CONT treatment in March and June (P=0.02±0.01) and the UDBC treatment in October (P=0.01). In June, Mn concentrations of foliage produced in 2002 were greater (P=0.03±0.02) in response to the BC treatment than the UDBC and CUFBC treatments. Mn concentrations ranged from 392 to 1326 mg g^{-1} (with a mean of 795) in previous-season foliage and ranged from 313 to 637 mg g^{-1} (with a mean of 451) in the first foliage flush of 2002.

3.9. Zinc and Iron

Significant differences in soil Zn were seldom observed in either year of this study. In April 2001, the CONT treatment was associated with greater (P=0.01) soil Zn than the BC treatment. In the same month, soil Zn contents of the UDBC and CUFBC treatments were significantly higher (P=0.01±0.002) than that of the BC treatment. No other differences in soil Zn were observed in 2001, and no differences were found in 2002. In 2001, soil Zn ranged from 1.3 to 10.6 kg ha^{-1} (with a mean of 2.84), and soil Zn ranged from 1.8 to 7.8 kg ha^{-1} (with a mean of 3.7) in 2002.

In 2002, the previous-season foliage Zn concentrations (Figure 12) in response to the BC treatment were greater than those of the UDBC treatment in June and July (P=0.004±0.01) and the CONT and CUFBC treatments in June (P=0.005±0.001). Foliage Zn concentrations of the first flush of 2002 in response to the BC treatment also exceeded that of the UDBC treatment in October. Zn concentrations ranged from 2.2 to 99.1 mg g^{-1} (with a mean of 33.8) in foliage produced in 2001 and from 25.7 to 110.5 mg g^{-1} (with a mean of 45.9) in foliage produced in 2002.

Soil and foliage Fe were unchanged by the fertilization treatments. No significant differences in soil and foliage Fe were observed in either year of this study.

3.10. Cation exchange capacity and base saturation

Soil CEC seldom differed among the treatments in 2001 and 2002. In June 2001, CEC of the CUFBC treatment was greater (P=0.02) than that of the CONT treatment. In 2002, the BC treatment was associated with greater (P=0.03) CEC than the CONT treatment in October. The UDBC and CUFBC treatments had higher (P=0.03±0.02) CEC than the CONT treatment in July 2002. In 2001, CEC ranged from 4.7 to 17.2 meq 100 g soil^{-1} (with a mean of 10.5), and CEC ranged from 2.0 to 12.8 meq 100 g soil^{-1} (with a mean of 8.9) in 2002.

In 2001, base saturation differed among the treatments in only March, wherein the base saturation of the UDBC treatment was significantly lower (P=0.02±0.02) than those of the CONT and BC treatments. In 2002, the CONT and BC treatments frequently produced the highest base saturations (Figure 13). The BC treatment was associated with base saturations higher (P=0.04±0.01) than those of the CUFBC treatment in May and June. Base saturation of the CONT treatment was significantly greater than that of the BC treatment in October through November (P=0.03±0.01), the CUFBC treatment in June, October, and November (P=0.01±0.01), and the UD and UDBC treatments in October and November (P=0.03±0.02). Base saturation ranged from 12.0 to 56.0 with a mean of 24.7 in 2001 and ranged from 17.0 to 68.0 with a mean of 30.7 in 2002.

4. Discussion

The seasonal patterns of foliage nutrient concentrations were consistent with those observed in other studies of seasonal pine nutrient dynamics (Bockheim and Leide 1991, Helmisaari 1992, Zhang and Allen 1996, Son et al. 2000). Concentrations of each mobile nutrient (N, P, K, Mg) decreased through the year, whereas those of immobile nutrients (Ca, B, Cu, Fe, Mn, Zn, Fe) either increased throughout the year or remained relatively stable. Nutrient concentrations tend to be highest for all nutrients in young needles due to their high metabolic activity. As new shoot growth begins, mobile nutrient concentrations decrease due to growth dilution and retranslocation to younger tissues (Helmisaari 1992, Zhang and Allen 1996). Immobile nutrients, which are poorly retranslocated, will accumulate in foliage throughout the year provided there is sufficient capital of the nutrient in the soil (Zhang and Allen 1996).

Several soil and/or foliage nutrients were affected by the brush control and fertilizer treatments. Each of the applied nutrients (N, P, B) altered the nutrient levels in the soil and foliage. It has been documented that foliage nutrient concentrations of added nutrients, whether limiting or not, tend to increase after fertilization (Valentine and Allen 1990, Zhang and Allen 1996, Piatek and Allen 2000). No consistent changes in Mn, Fe, Cu, or CEC were produced by the brush control and fertilizer treatments. Radwan and DeBell (1989) similarly found that Mn, Fe, and Cu concentrations were not significantly affected by N fertilization of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). Richter et al. (1994) found that CEC remained relatively unchanged by nutrient additions to forest soils. In regard to Mn, the significant differences between the BC and other treatments in foliage Mn were likely due to pretreatment biases, i.e. the trees receiving the BC treatment had higher mean foliage Mn prior to treatment. The significant difference in exchangeable soil Mn between the CONT and BC treatments appeared to be due to pretreatment biases as well. Such pretreatment biases have been observed in a study of ponderosa pine nutrient dynamics (*Pinus ponderosa* Dougl. ex Laws.) (Johnson et al. 2000). Other nutrients assessed in this study (Ca, Mg, K, Zn) experienced transient changes in either foliar or soil nutrients.

Nitrogen dynamics in soil and foliage were most profoundly affected by the fertilizer/brush control treatments (Figures 1-3, Tables 1-3). Changes in NO_3^- induced by the treatments were similar to the changes in foliage N concentrations in both years of the study. The BC treatment did not significantly raise soil NO_3^- above levels observed in

CONT plots in either year of the study (Figure 1, Table 1). The BC treatment did not significantly raise foliar N concentrations in 2001 (Figure 2, Table 2), but its foliage N accumulation was higher that of the CONT treatment (Manuscript I). In 2002, the BC treatment significantly increased foliage N concentrations over that of the CONT treatment (Figure 3, Table 3). Furthermore, foliage N accumulation was increased by the BC treatment in 2002 (Manuscript I). These increases in foliage N concentrations and accumulation and concomitant lack of increases in soil N suggest that the N liberated by suppression of herbaceous vegetation was effectively buffered by loblolly pines (Manuscript I). When herbaceous vegetation was maintained, it proved to be an effective competitor for applied N. The UD treatment produced significant increases in both NO_3^- and foliage N concentrations in both years of this study, but these increases subsided sooner than in response to the UDBC and CUFBC treatments. Interference of N uptake attributable to competing vegetation has been demonstrated in other studies of loblolly pine (Cain 1999, Zutter et al. 1999). The highest foliage N concentration means and longest periods of elevated NO_3^- availability throughout this study were achieved by the UDBC and CUFBC treatments. The increase in soil N availability did not persist; by the end of each year NO_3^- levels of all treatments were similar. Forest fertilization does not tend to produce sustained increases in N availability; N additions temporarily increase N availability but do not alter site factors that govern productivity (Mitchell et al. 1996, Chappell et al. 1999). Most applied N is taken up or lost within one year of application (Mitchell et al. 1996). The CUFBC treatment yielded the highest foliage N concentrations in both foliage flushes in some months of 2001, which may indicate a modest benefit to the slower dissolution rate of CUF. Ingestad (1991) proposed that application of smaller, sustained doses of fertilizer are more efficient in promoting tree nutrient uptake and more environmentally sound than single large doses.

The UD, UDBC, and CUFBC treatments were all associated with foliage P concentrations less than that of the CONT treatment in portions of 2001 and 2002 (Figures 4, 5). The lack of significant differences in foliar and available soil P between the UD, UDBC, and CUFBC treatments suggests that herbaceous vegetation did not serve as a significant competitor for applied P. Cain (1999) found that herbaceous vegetation in a young loblolly pine plantation did not influence loblolly pine foliage P uptake. Decreases in foliage P concentrations in response to N and P fertilizer treatments have been noted in several studies (Radwan and DeBell 1989, Zhang and Allen 1996). However, increases in foliage P concentrations have been observed in response to N and P fertilization as well (Adams et al. 1987, Son et al. 2000). Depressions in foliar P concentrations in response to fertilization have been attributed to: (1) immobilization of P by stimulated soil microbes, (2) adverse effects of high NH_4^+ concentrations on surface roots and mycorrhizae, (3) changes in amount or availability of P in the rooting zone affected by the direct or indirect action of the fertilizers or their transformation products, and (4) dilution of P by foliage growth (Radwan and DeBell 1989). Microbial biomass and activity were decreased by fertilizer and brush control treatments (Manuscript II), suggesting microbial P immobilization may not have been stimulated. All fertilizer treatments were associated with transient increases in available soil P (Table 4). The fertilizer and brush control treatments significantly increased foliage biomass growth (Manuscript I); dilution of P by growth likely occurred. However, the possibility of negative effects of high NH_4^+ concentrations on root and mycorrhizae functioning cannot be discounted.

The transient increases in available soil P (Table 4) in response to the fertilizer treatments relative to the control treatments contrast with the foliage P concentration trends. Other studies have also revealed increases in extractable P in response to P fertilization (Smethurst et al. 2001, Nohrstedt 2002). Longevity of elevations in soil P in response to fertilization is variable; P increases persist for several years on some sites and are never evident on others (Nohrstedt 2002). The short-term increases in available P in our study may have been due to the relatively low amount of P added.

Through much of both 2001 and 2002, the UD treatment had significantly higher P:N ratios than the UDBC and CUFBC treatments. The UD treatments produced significantly less foliage biomass than the UDBC and CUFBC treatments (Manuscript I), so foliage of trees receiving the UD treatments had a lower potential for P dilution. In addition, trees receiving the UD treatment had lower foliage N concentrations than the trees receiving the fertilizer+brush control treatments. Thus, the higher P:N ratios of the UD treatment were attributable to a combination of higher P and lower N concentrations than the UDBC and CUFBC treatments. Decreases in P:N ratios in response to N fertilization of loblolly pine have been noted in the eastern portion of its range (Zhang and Allen 1996). Adams and Allen (1985) proposed an optimum P:N ratio range of 0.095 to 0.105 for N- and P-fertilized loblolly pine in the Piedmont and Coastal Plain. Below this range, P was perceived to be limiting to pine growth. The P:N ratios observed in this study were often below this range, implying that a fertilizer ratio of N to P lower than 10:1 would have provided a better balance of these nutrients to the juvenile loblolly pines on our site, particularly when competing vegetation was controlled in conjunction with fertilization. However, Adams and Allen (1985) developed the P:N ratio range for mid-rotation trees in the eastern portion of the loblolly pine range and did not explore seasonal fluctuations in PN ratios. Further exploration of optimum P:N ratios for juvenile loblolly pine in diverse environments would likely improve efficiency of N and P fertilization of young plantations.

CUF proved to be an effective vector for B. In both years of this study, the CUFBC treatment was associated with transient increases in B levels in both soil and foliage. In 2001, elevated soil B levels in response to CUF application were observed in early summer, and in 2002 increased soil B was evident in late summer. When foliage B concentrations were measured in 2002, the CUFBC treatment was associated with short-term increases in foliage B (Figure 11, Table 7). The increased foliage B status of trees was more evident in current-year foliage; the CUFBC treatment produced the highest B concentrations from mid-summer through early fall. No clearly-defined critical foliar B levels have been developed for loblolly pine, but a critical range of 6 to 14 mg g^{-1} has been developed for radiata pine (*Pinus radiata* D. Don) in New Zealand (Will and Fitzgerald 1985). All foliage B concentrations observed in our study either met or exceeded this range, and biomass growth of trees receiving the CUFBC treatment did not significantly exceed that of the UDBC treatment (Manuscript I). The increases in foliage B concentrations without a concomitant increase in growth over that of the UDBC treatment (which added only N and P) suggest luxury consumption of B occurred. These findings could indicate that B was not limiting on our site, even when substantial N was added. Inadequate B can limit responses to N fertilizer (Blake et al. 1990), but B capital appeared to be sufficient on our site. The BC and UDBC treatments also produced significant increases in foliage B concentrations in late fall and early winter of 2002. These increased B concentrations and lack of increases in soil B in plots receiving BC and UDBC treatments may suggest that the B liberated by elimination of competing vegetation was effectively buffered by loblolly pine.

In March 2001 (the month following fertilizer treatments), exchangeable soil K was higher in response to CONT and BC treatments than to the fertilizer/brush control treatments. It is possible that the substantial influx of NH_4^+ from urea created a short-term reduction in K availability. N fertilization can induce downward flushes of K in soil; NH_4^+ and K^+ compete for exchange sites (Garrison et al. 2000, Bengtsson and Bergwall 2000, Nohrstedt 2002). An alternative reason for post-fertilization exchangeable K declines may be increased K uptake after fertilization (Nohrstedt 2002). No consistent trends in exchangeable K were observed in 2002.

In both years of this study, herbaceous vegetation influenced foliage K concentrations in summer months, when it was at its peak biomass. In summer 2001, the UD treatment was associated with foliage K concentrations lower than all other treatments in both measured foliage flushes (Figure 9). Since fertilization significantly increased herbaceous vegetation biomass and N accumulation (Manuscript I), its K uptake likely increased as well. Nevertheless, by the end of the year mean foliage K concentrations of trees receiving the UD treatment were 0.40, which is well above the critical foliage K range of 0.25 to 0.30 for loblolly pine (Moorhead 2002). In 2002, foliage K concentrations of the BC treatment significantly exceeded those of the CONT and UD treatments in both foliage flushes in several summer and fall months (Figure 10).

The UDBC treatment also yielded foliage K concentrations higher than those of the CONT treatment in late summer. Suppression of herbaceous vegetation appeared to have produced benefits in K uptake.

Since excess N in relation to K can make trees more susceptible to insects and disease, the K:N ratio provided a measure of tree vitality (Ouimet and Fortin 1992, Moore et al. 1994, Garrison et al. 2000). The fertilization treatments significantly reduced foliar K:N ratios in both years of this study (Tables 5 and 6). Zhang and Allen (1996) also noted that N fertilization of loblolly pine decreases K:N ratios. Ingestad (1967, 1979) suggested that for all conifers a foliar K:N ratio of 0.50 is critical and a ratio of 0.65 is optimal. All K:N ratios observed in this study were below the critical level, and fertilization treatments prompted significant reductions in K:N ratios. The critical level of 0.50 was developed with Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) seedlings; as such, its applicability to loblolly pine may not be appropriate. However, given the prevalence of pests such as Nantucket tip moth (*Rhyacionia frustrana* (Comstock)) in the northwestern portion of loblolly pine's range, further exploration of juvenile plantation fertilization and pest susceptibility seems warranted.

Although the fertilizer/brush control treatments did not produce any persistent differences in exchangeable Ca and Mg, they were associated with significantly lower foliage Ca and Mg concentrations than the CONT treatment for portions of 2001 and 2002. In early summer of both 2001 and 2002, the CONT treatments yielded the highest current-year foliar Mg concentrations (Figures 7 and 8). The CONT treatment was also associated with the highest current-year Ca concentrations in early summer 2002. Due to the greater foliage growth of trees receiving the brush control and fertilizer treatments, the potential for dilution of Ca and Mg was greater in response to these treatments. Concentrations of Ca and Mg have been noted to decrease in larger fascicles (Zhang and Allen 1996). Zutter et al. (1999) found that Ca and Mg concentrations decreased in response to vegetation control treatments due to rapid expansion of crown biomass. Despite the relatively lower foliar Ca and Mg concentrations of trees receiving brush control and/or fertilizer treatments in early summer, Mg and Ca concentrations of all trees were well above critical levels (Moorhead 2002) by the end of the growing season.

Suppression of herbaceous vegetation increased foliage Zn concentrations in 2002; Zn concentrations of the BC treatment occasionally exceeded those of the CONT, UDBC, and CUFBC treatments (Figure 12). The lower Zn concentrations of UDBC and CUFBC treatments relative to the BC treatment could be attributable to phosphorus-zinc interactions. Applications of phosphorus fertilizers can depress plant zinc contents by altering either plant or soil factors (Marschner 1995). Elevated phosphorus contents in soils can decrease solubility of zinc, although such effects do not always occur (Loneragan et al. 1979, Pasricha et al. 1987). Increased phosphorus supply can reduce root growth and mycorrhizal infection, which are important factors for the acquisition of zinc (Marschner 1995). Our assessments of root growth (Manuscript I) showed that root growth was not adversely impacted by fertilization. However, foliage growth was increased by fertilization treatments (Manuscript I), and enhanced growth can cause dilution of Zn in plants (Neilson and Hogue 1986). A critical foliage level of 11 mg g^{-1} has been proposed for radiata pine (SERG 2001). If this critical level is applicable to loblolly pine, the differences in foliage Zn concentrations among treatments are likely of minimal consequence to the trees since Zn concentrations were well above 11 mg g^{-1} throughout our study.

The significantly higher base saturations of CONT and BC treatments may indicate that base cations were reduced by fertilization treatments. In 2001, base saturation of the UDBC treatment declined relative to those of the control treatments in the month following fertilization. In 2002, base saturations of the CONT and BC treatments were frequently greater than those of the UD, UDBC, and CUFBC treatments in summer and fall (Figure 13). Some base cations may have been displaced by the influx of NH_4^+; it is also possible the base saturation reductions in fertilized plots were caused by increased nutrient uptake resulting from elevated growth rates of fertilized trees.

5. Conclusions

Several key issues concerning the effectiveness of improving young loblolly pine nutrition in a plantation in the northwestern portion of the loblolly pine range were revealed in this study. The brush control and fertilizer treatments investigated in this study did not have lasting effects on soil nutrient levels, which is an important aspect in regard to the sustainability of the practices. The 10:1 fertilizer ratio of N and P did not seem to provide enough P to match the gain in N. Insect and disease susceptibility may have increased in the summer and fall following fertilizer applications given the reductions in foliar K:N ratios, particularly when competing vegetation was suppressed in conjunction with fertilization. Suppression of understory vegetation improved both N and K nutrition of crop trees. Although transient changes in several foliage nutrients were induced by fertilization and brush control treatments, the alterations were likely not dramatic enough to impact loblolly pine growth. Rate of fertilizer dissolution and provision of B in fertilizer has not yet produced any added benefits in the nutrient status of our trees relative to an urea/diammonium phosphate mixture. Nutrient dynamics of this site will continue to be studied in an effort to produce fertilization practices that optimize the nutrition of a loblolly pine plantation in a sustainable manner.

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Table 1. Soil NO_3^- content (kg ha^{-1}) in response to: untreated control (CONT), continuous brush control with glyphosate (BC), urea/diammonium phosphate (UD), urea/diammonium phosphate in conjunction with continuous brush control (UDBC), and coated urea fertilizer in conjunction with continuous brush control (CUFBC). Fertilizer treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in February 2001 and April 2002.

	2001					2002				
	Treatment					Treatment				
Month	CONT	BC	UD	UDBC	CUFBC	CONT	BC	UD	UDBC	CUFBC
Feb	9 *a*	7 *a*	9 *a*	12 *a*	12 *a*	---	---	---	---	---
Mar	137 *ab*	117 *a*	245 *bc*	185 *abc*	255 *c*	52 *a*	38 *a*	57 *a*	23 *a*	31 *a*
Apr	75 *a*	90 *ab*	141 *bc*	128 *abc*	130 *c*	38 *a*	42 *b*	19 *a*	15 *a*	14 *a*
May	64 *a*	39 *a*	134 *b*	262 *c*	144 *b*	44 *a*	36 *a*	72 *b*	52 *ab*	79 *b*
June	10 *a*	20 *a*	217 *b*	81 *a*	174 *b*	34 *b*	19 *a*	41 *b*	41 *b*	46 *b*
July	20 *a*	26 *a*	20 *ab*	64 *ab*	92 *b*	10 *a*	12 *a*	18 *a*	33 *ab*	72 *b*
Aug	66 *a*	31 *a*	21 *a*	94 *b*	93 *b*	9 *a*	10 *a*	22 *ab*	44 *b*	44 *b*
Sept	23 *a*	37 *a*	36 *a*	98 *b*	133 *b*	10 *a*	17 *a*	18 *a*	69 *b*	46 *b*
Oct	19 *a*	31 *a*	21 *ab*	34 *b*	64 *b*	26 *a*	25 *a*	43 *ab*	52 *ab*	70 *b*
Nov	7 *a*	9 *a*	12 *ab*	45 *ab*	51 *b*	25 *a*	19 *a*	26 *a*	66 *a*	31 *a*
Dec	12 *a*	10 *a*	16 *a*	21 *a*	26 *a*	10 *a*	13 *ab*	11 *ab*	13 *ab*	19 *b*

NOTE: For each year, means within a row followed by a different letter differ significantly at $P < 0.05$.

Table 2. Foliage N concentration (%) in response to: untreated control (CONT), continuous brush control with glyphosate (BC), urea/diammonium phosphate (UD), urea/diammonium phosphate in conjunction with continuous brush control (UDBC), and coated urea fertilizer in conjunction with continuous brush control (CUFBC). Fertilizer treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in February 2001.

	2nd flush 2000					1st flush 2001				
	Treatment					Treatment				
	CONT	BC	UD	UDBC	CUFBC	CONT	BC	UD	UDBC	CUFBC
Month										
Feb	1.22*a*	1.18*a*	1.27*a*	1.30*a*	1.26*a*	-----	-----	-----	-----	-----
Mar	1.21*ab*	1.15*a*	1.26*ab*	1.34*b*	1.34*b*	-----	-----	-----	-----	-----
Apr	1.40*ab*	1.32*a*	1.65*bc*	1.80*c*	1.81*c*	-----	-----	-----	-----	-----
May	1.31*a*	1.29*a*	1.50*a*	1.69*b*	1.86*b*	1.48*a*	1.54*a*	1.78*b*	1.82*b*	2.00*b*
June	1.12*a*	1.24*ab*	1.39*bc*	1.53*c*	1.74*d*	1.29*a*	1.39*a*	1.38*ab*	1.77*b*	1.85*c*
July	1.15*a*	1.26*ab*	1.30*b*	1.48*c*	1.57*c*	1.20*a*	1.41*a*	1.32*a*	1.60*b*	1.61*b*
Aug	1.08*a*	1.22*ab*	1.26*bc*	1.40*cd*	1.48*d*	1.20*a*	1.33*ab*	1.29*ab*	1.50*b*	1.39*ab*
Sept	1.06*a*	1.15*ab*	1.17*ab*	1.30*b*	1.48*c*	1.25*a*	1.43*ab*	1.32*ab*	1.57*bc*	1.65*c*
Oct	1.13*a*	1.13*a*	1.15*a*	1.30*a*	1.30*a*	1.32*a*	1.45*a*	1.37*ab*	1.63*bc*	1.62*c*
Nov	-----	-----	-----	-----	-----	1.43*a*	1.51*a*	1.48*a*	1.44*a*	1.62*a*
Dec	-----	-----	-----	-----	-----	1.42*a*	1.50*ab*	1.45*ab*	1.59*ab*	1.62*b*

NOTE: For each foliage flush, means within a row followed by a different letter differ significantly at $P < 0.05$.

Table 3. Foliage N concentration (%) in response to: untreated control (CONT), continuous brush control with glyphosate (BC), urea/diammonium phosphate (UD), urea/diammonium phosphate in conjunction with continuous brush control (UDBC), and coated urea fertilizer in conjunction with continuous brush control (CUFBC). Fertilizer treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.

	1st flush 2001					1st flush 2002				
	Treatment					Treatment				
Month	CONT	BC	UD	UDBC	CUFBC	CONT	BC	UD	UDBC	CUFBC
Mar	1.29*a*	1.34*a*	1.24*a*	1.18*a*	1.27*a*	-----	-----	-----	-----	-----
Apr	1.26*a*	1.28*a*	1.22*a*	1.16*a*	1.27*a*	-----	-----	-----	-----	-----
May	1.15*a*	1.24*a*	1.50*b*	1.44*b*	1.50*b*	1.43*a*	1.48*a*	1.74*b*	1.78*b*	1.77*b*
June	1.13*a*	1.27*b*	1.45*c*	1.49*c*	1.47*c*	1.37*a*	1.45*a*	1.68*b*	1.74*b*	1.68*b*
July	1.02*a*	1.15*b*	1.23*c*	1.27*c*	1.32*c*	1.28*a*	1.36*ab*	1.37*ab*	1.50*bc*	1.55*c*
Aug	0.94*a*	1.03*b*	1.05*bc*	1.13*c*	1.18*c*	1.13*a*	1.23*a*	1.19*a*	1.33*ab*	1.36*b*
Sept	0.88*a*	0.95*ab*	1.00*b*	1.06*b*	1.05*b*	1.14*a*	1.22*a*	1.20*a*	1.32*ab*	1.31*b*
Oct	0.90*a*	0.94*a*	1.03*ab*	1.18*b*	1.08*ab*	1.22*a*	1.35*b*	1.24*a*	1.30*b*	1.42*b*
Nov	-----	-----	-----	-----	-----	1.24*a*	1.30*ab*	1.28*ab*	1.40*b*	1.42*b*

NOTE: For each foliage flush, means within a row followed by a different letter differ significantly at $P < 0.05$.

Table 4. Soil available P concentration (%) in response to: untreated control (CONT), continuous brush control with glyphosate (BC), urea/diammonium phosphate (UD), urea/diammonium phosphate in conjunction with continuous brush control (UDBC), and coated urea fertilizer in conjunction with continuous brush control (CUFBC). Fertilizer treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in February 2001 and April 2002.

	2001					2002				
	Treatment					Treatment				
	CONT	BC	UD	UDBC	CUFBC	CONT	BC	UD	UDBC	CUFBC
Month										
Feb	12.5 *a*	11.5 *a*	10.0 *a*	14.5 *a*	12.5 *a*	-----	-----	-----	-----	-----
Mar	15.3 *a*	11.3 *a*	23.0 *a*	15.5 *a*	19.8 *a*	8.3 *a*	8.0 *a*	9.0 *a*	14.0 *a*	8.0 *a*
Apr	7.0 *a*	6.7 *a*	14.0 *a*	13.8 *a*	12.3 *a*	7.3 *a*	8.0 *a*	6.3 *a*	8.0 *a*	6.7 *a*
May	6.0 *a*	8.0 *a*	9.7 *ab*	9.0 *ab*	17.0 *b*	8.0 *ab*	6.3 *a*	15.3 *b*	12.7 *b*	11.3 *ab*
June	9.0 *a*	9.7 *a*	9.7 *ab*	15.0 *ab*	18.3 *b*	7.7 *ab*	7.0 *a*	20.7 *b*	12.0 *ab*	12.0 *ab*
July	12.0 *ab*	10.3 *a*	11.5 *ab*	18.3 *b*	19.0 *b*	9.3 *ab*	6.3 *a*	17.0 *b*	19.7 *b*	14.0 *ab*
Aug	16.0 *ab*	11.3 *a*	15.0 *ab*	22.8 *b*	22.3 *b*	9.0 *ab*	6.0 *a*	15.5 *bc*	19.5 *c*	13.5 *bc*
Sept	6.3 *a*	10.3 *ab*	8.8 *ab*	20.7 *b*	16.0 *ab*	11.3 *ab*	8.0 *a*	16.3 *ab*	19.7 *b*	18.7 *b*
Oct	7.0 *a*	9.7 *a*	8.0 *a*	12.0 *a*	11.0 *a*	9.0 *a*	6.7 *a*	15.0 *b*	15.3 *b*	11.0 *ab*
Nov	8.3 *a*	8.3 *a*	10.0 *a*	12.3 *a*	12.3 *a*	11.3 *ab*	8.3 *a*	17.0 *b*	14.0 *ab*	13.0 *ab*
Dec	6.3 *a*	7.0 *a*	8.7 *a*	9.5 *a*	11.7 *a*	12.3 *a*	16.0 *a*	17.3 *a*	19.7 *a*	15.3 *a*

NOTE: For each year, means within a row followed by a different letter differ significantly at $P < 0.05$.

Table 5. Ratio of foliage N concentration to foliage K concentration (%) in response to: untreated control (CONT), continuous brush control with glyphosate (BC), urea/diammonium phosphate (UD), urea/diammonium phosphate in conjunction with continuous brush control (UDBC), and coated urea fertilizer in conjunction with continuous brush control (CUFBC). Fertilizer treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in February 2001.

	2nd flush 2000					1st flush 2001				
	Treatment					Treatment				
Month	CONT	BC	UD	UDBC	CUFBC	CONT	BC	UD	UDBC	CUFBC
Feb	0.29 *a*	0.29 *a*	0.28 *a*	0.29 *a*	0.29 *a*	-----	-----	-----	-----	-----
Mar	0.26 *bc*	0.28 *c*	0.22 *a*	0.23 *ab*	0.23 *ab*	-----	-----	-----	-----	-----
Apr	0.23 *b*	0.26 *c*	0.19 *a*	0.19 *a*	0.18 *a*	-----	-----	-----	-----	-----
May	0.33 *b*	0.31 *b*	0.23 *a*	0.21 *a*	0.20 *a*	0.58 *b*	0.55 *b*	0.41 *a*	0.39 *a*	0.39 *a*
June	0.35 *b*	0.32 *b*	0.22 *a*	0.26 *a*	0.23 *a*	0.55 *b*	0.51 *b*	0.36 *a*	0.33 *a*	0.37 *a*
July	0.30 *b*	0.31 *b*	0.23 *a*	0.28 *ab*	0.25 *a*	0.39 *b*	0.40 *b*	0.31 *a*	0.30 *a*	0.35 *ab*
Aug	0.35 *bc*	0.36 *c*	0.24 *a*	0.28 *ab*	0.24 *a*	0.41 *b*	0.42 *b*	0.30 *a*	0.32 *a*	0.37 *b*
Sept	0.38 *b*	0.35 *b*	0.29 *ab*	0.29 *ab*	0.25 *a*	0.38 *b*	0.34 *ab*	0.29 *ab*	0.28 *a*	0.27 *a*
Oct	0.37 *a*	0.36 *a*	0.32 *a*	0.31 *a*	0.30 *a*	0.32 *b*	0.31 *b*	0.31 *b*	0.25 *a*	0.25 *a*
Nov	-----	-----	-----	-----	-----	0.34 *a*	0.33 *a*	0.31 *a*	0.32 *a*	0.30 *a*
Dec	-----	-----	-----	-----	-----	0.42 *a*	0.42 *a*	0.40 *a*	0.40 *a*	0.44 *a*

NOTE: For each foliage flush, means within a row followed by a different letter differ significantly at $P < 0.05$.

Table 6. Ratio of foliage N concentration to foliage K concentration (%) in response to: untreated control (CONT), continuous brush control with glyphosate (BC), urea/diammonium phosphate (UD), urea/diammonium phosphate in conjunction with continuous brush control (UDBC), and coated urea fertilizer in conjunction with continuous brush control (CUFBC). Fertilizer treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.

	1st flush 2001					1st flush 2002				
	Treatment					Treatment				
Month	CONT	BC	UD	UDBC	CUFBC	CONT	BC	UD	UDBC	CUFBC
Mar	0.23 *a*	0.22 *a*	0.25 *a*	0.26 *a*	0.23 *a*	-----	-----	-----	-----	-----
Apr	0.24 *a*	0.25 *a*	0.26 *a*	0.24 *a*	0.24 *a*	-----	-----	-----	-----	-----
May	0.26 *b*	0.26 *b*	0.21 *a*	0.21 *ab*	0.20 *a*	0.41 *b*	0.41 *b*	0.34 *a*	0.34 *a*	0.30 *a*
June	0.28 *b*	0.29 *b*	0.23 *a*	0.24 *a*	0.24 *a*	0.35 *ab*	0.36 *b*	0.31 *a*	0.34 *ab*	0.31 a
July	0.34 *ab*	0.37 *b*	0.29 *a*	0.34 *ab*	0.29 *a*	0.32 *ab*	0.37 *b*	0.30 *ab*	0.35 *ab*	0.29 *a*
Aug	0.38 *ab*	0.46 *b*	0.35 *a*	0.40 *ab*	0.34 *a*	0.38 *ab*	0.46 *b*	0.35 *a*	0.41 *ab*	0.36 *ab*
Sept	0.38 *ab*	0.49 *b*	0.33 *a*	0.41 *ab*	0.39 *ab*	0.34 *ab*	0.40 *b*	0.28 *a*	0.35 *ab*	0.35 *ab*
Oct	0.42 *a*	0.47 *a*	0.41 *a*	0.40 *a*	0.44 *a*	0.36 *a*	0.40 *a*	0.37 *a*	0.39 *a*	0.36 *a*
Nov	-----	-----	-----	-----	-----	0.39 *a*	0.42 *a*	0.37 *a*	0.39 *a*	0.38 *a*

NOTE: For each foliage flush, means within a row followed by a different letter differ significantly at $P < 0.05$.

Table 7. Foliage B concentration (mg g^{-1}) in response to: untreated control (CONT), continuous brush control with glyphosate (BC), urea/diammonium phosphate (UD), urea/diammonium phosphate in conjunction with continuous brush control (UDBC), and coated urea fertilizer in conjunction with continuous brush control (CUFBC). Fertilizer treatments were applied to a juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.

	1st flush 2001				1st flush 2002			
	Treatment				Treatment			
	CONT	BC	UDBC	CUFBC	CONT	BC	UDBC	CUFBC
Month								
Mar	11.2 *a*	12.6 *a*	15.9 *ab*	21.03 *b*	-----	-----	-----	-----
Apr	10.2 *a*	8.8 *a*	10.7 *a*	10.0 *a*	-----	-----	-----	-----
May	12.0 *a*	15.3 *a*	20.4 *a*	31.2 *b*	-----	-----	-----	-----
June	11.6 *a*	12.6 *a*	13.0 *a*	11.7 *a*	9.6 *a*	8.9 *a*	11.8 *b*	13.4 *b*
July	13.7 *ab*	21.8 *b*	13.7 *ab*	8.4 *a*	9.8 *a*	8.4 *a*	11.8 *a*	7.4 *a*
Aug	5.5 *a*	9.1 *ab*	9.5 *b*	9.5 *b*	11.3 *a*	8.9 *a*	13.4 *a*	22.3 *b*
Sept	14.8 *a*	20.4 *bc*	25.3 *c*	15.4 *ab*	11.6 *a*	15.9 *a*	19.1 *a*	38.0 *b*
Oct	12.1 *a*	13.0 *a*	38.0 *b*	13.4 *a*	10.4 *a*	12.0 *b*	17.9 *c*	13.7 *c*
Nov	-----	-----	-----	-----	14.4 *a*	19.8 *c*	18.1 *bc*	17.2 *b*

NOTE: For each foliage flush, means within a row followed by a different letter differ significantly at $P < 0.05$.

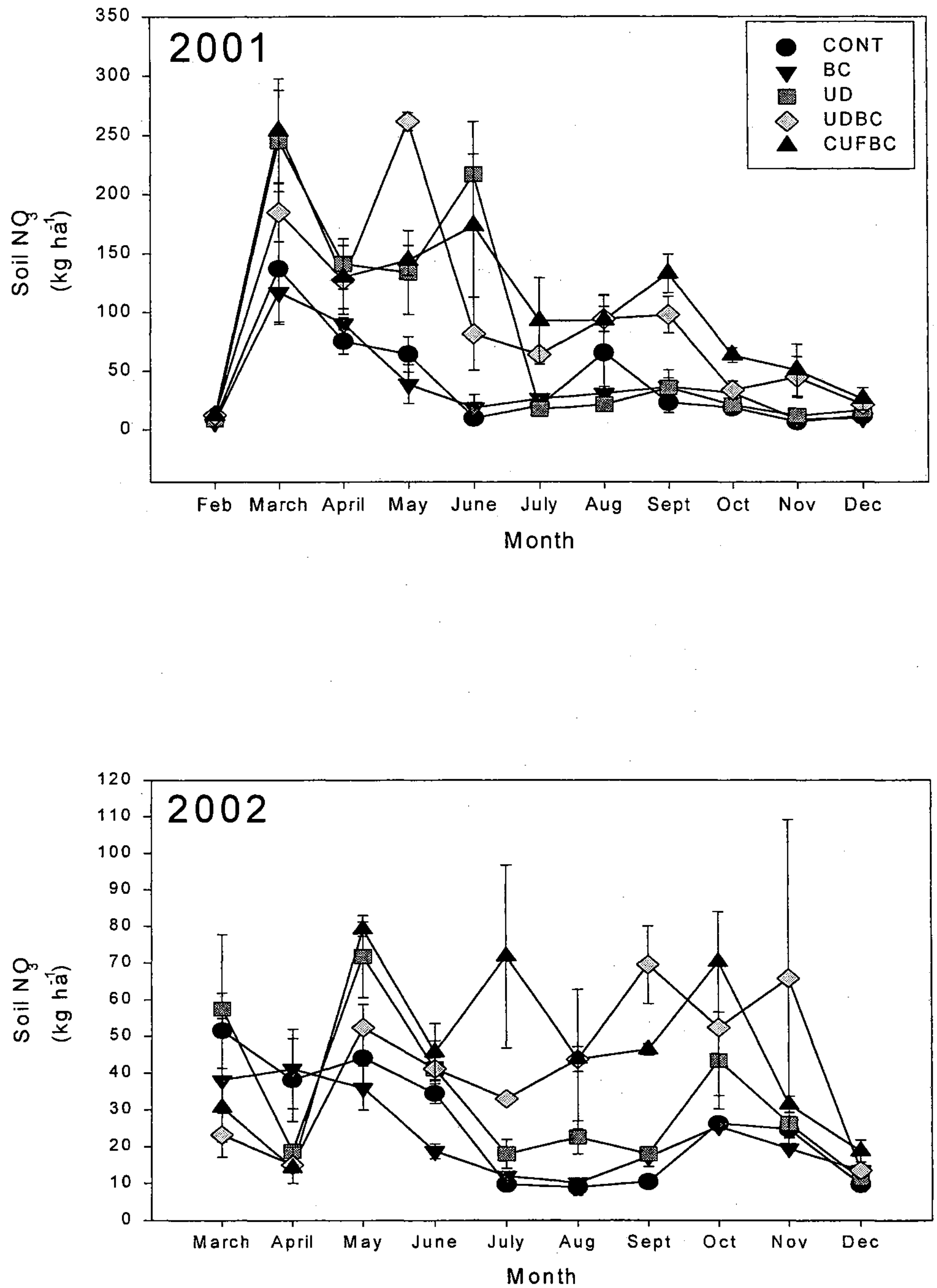
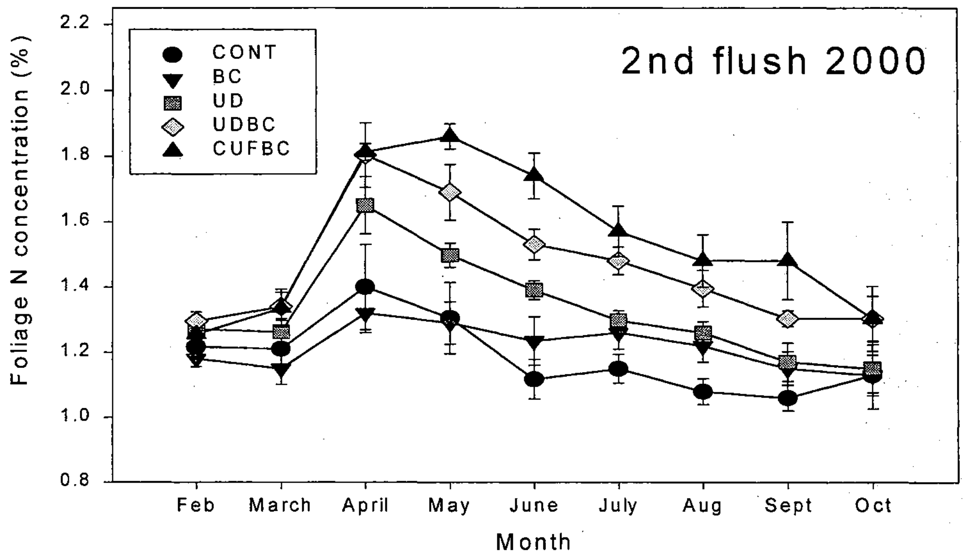


Figure 1. Soil NO_3^- in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC) treatments applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Glyphosate was used for brush control, and fertilizers were applied February 2001 and April 2002.



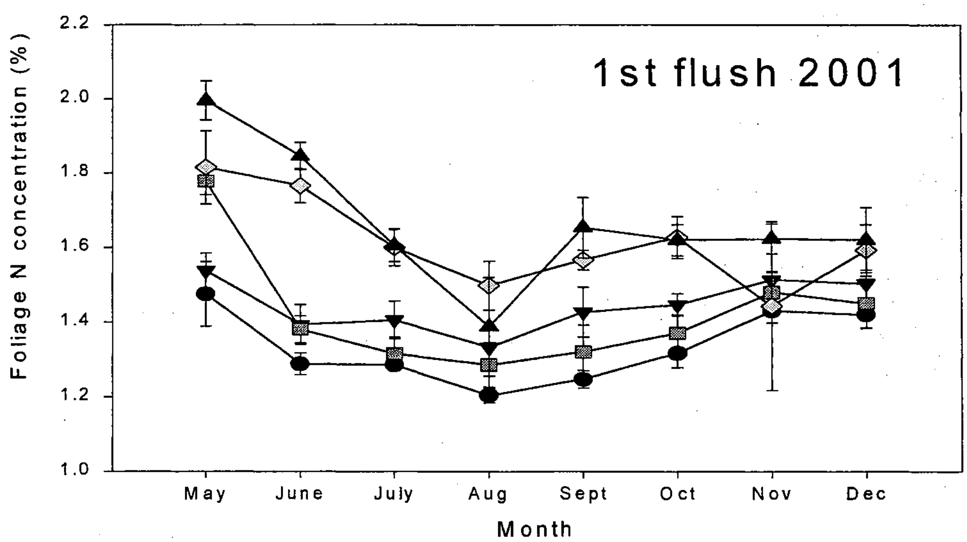


Figure 2. Foliage N concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in February 2001.

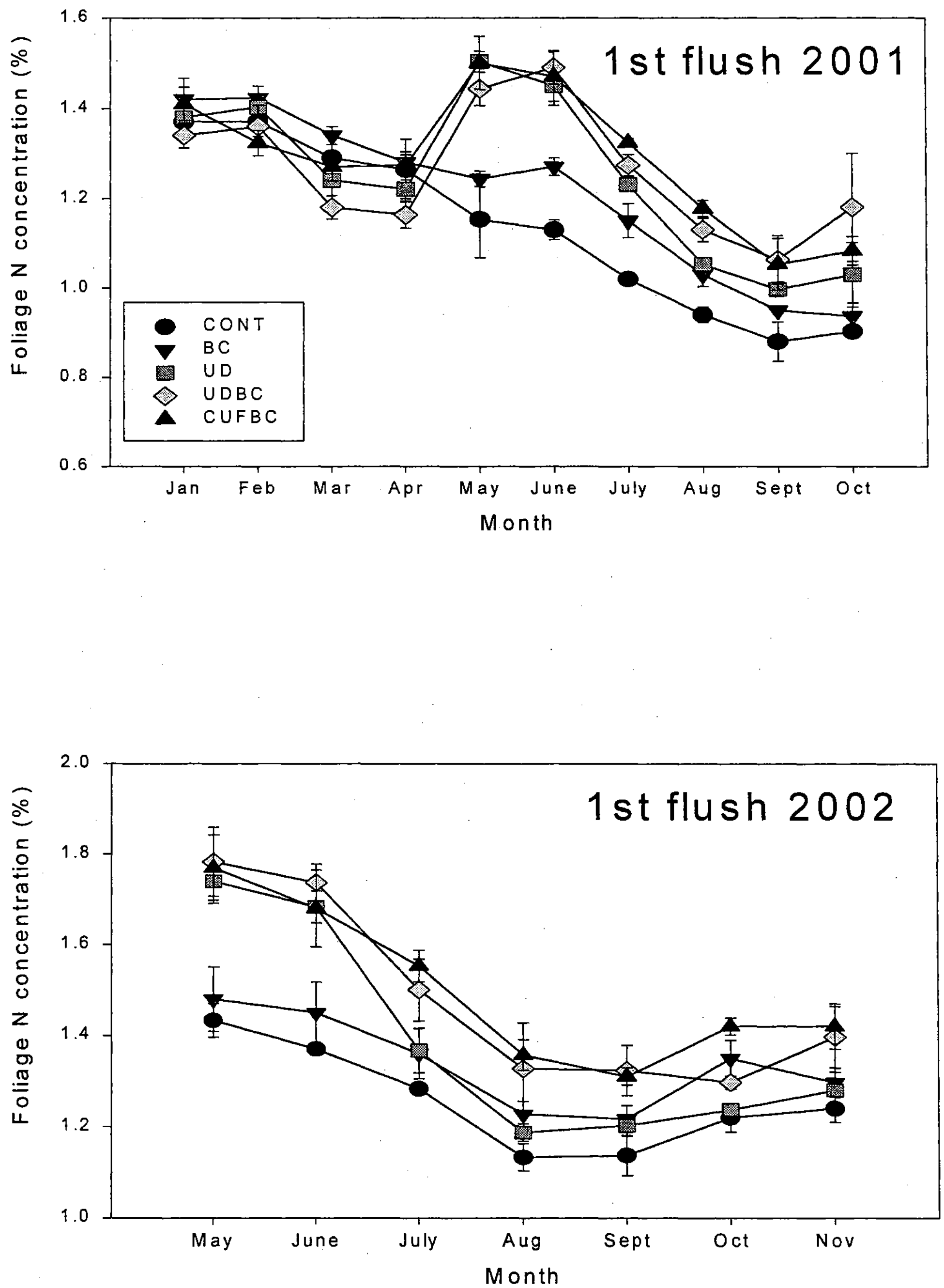
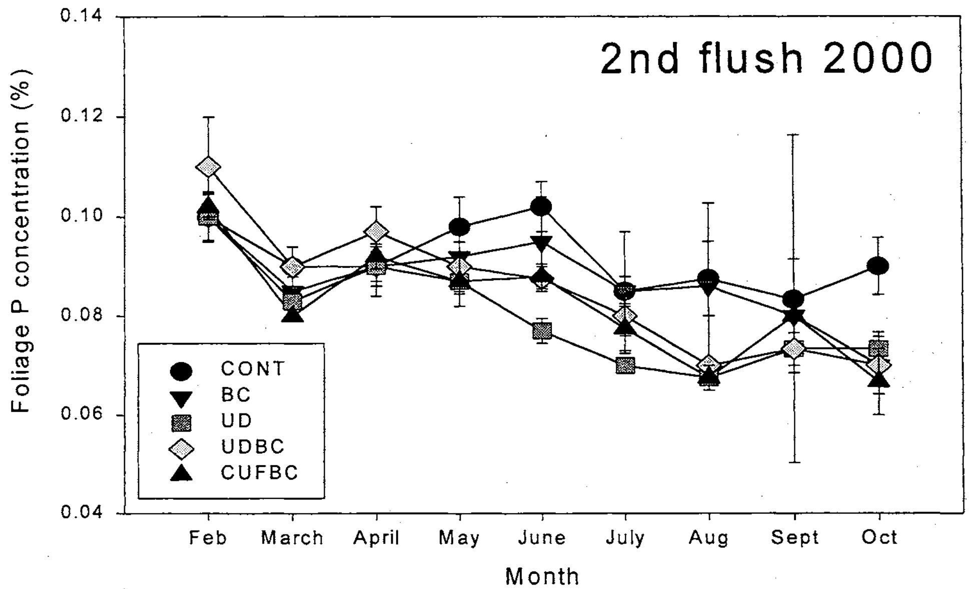


Figure 3. Foliage N concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.



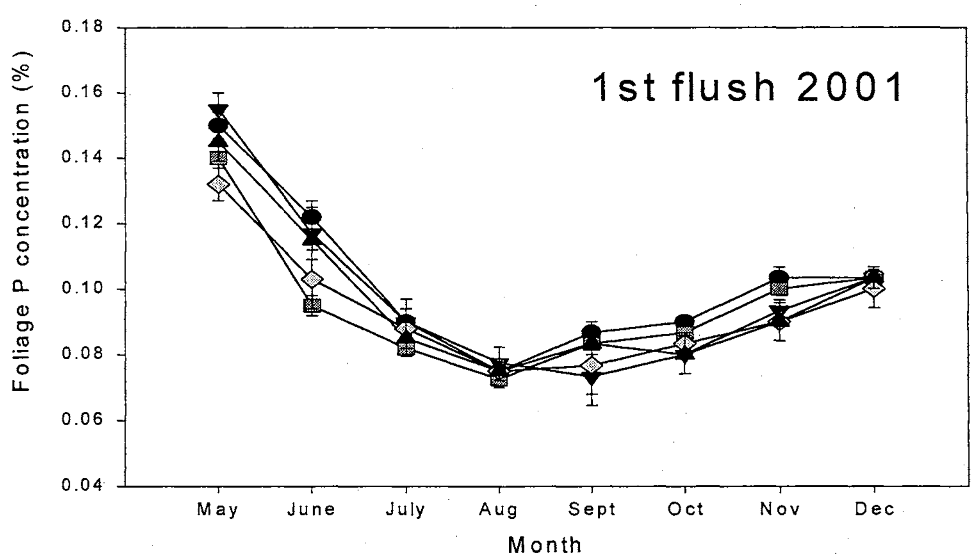
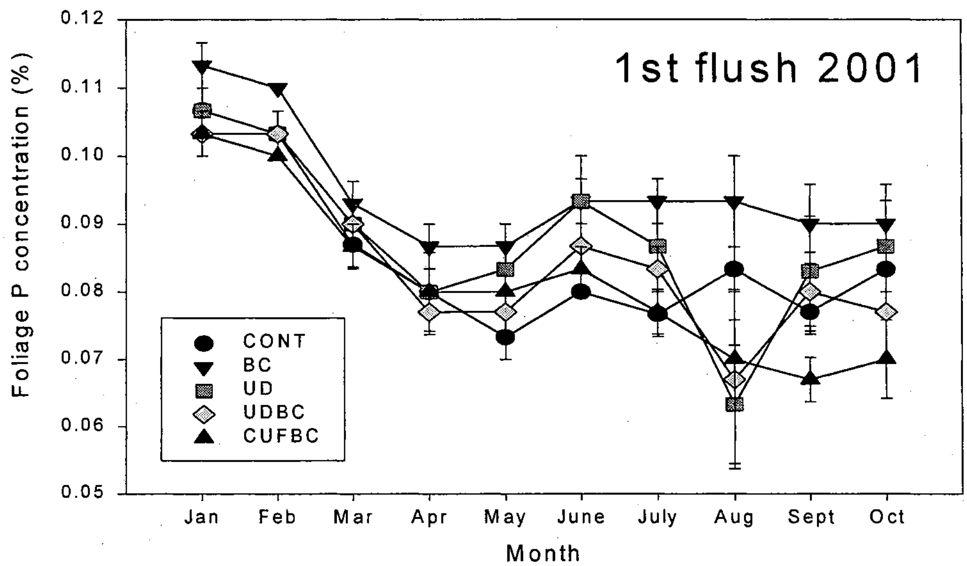


Figure 4. Foliage P concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in February 2001.



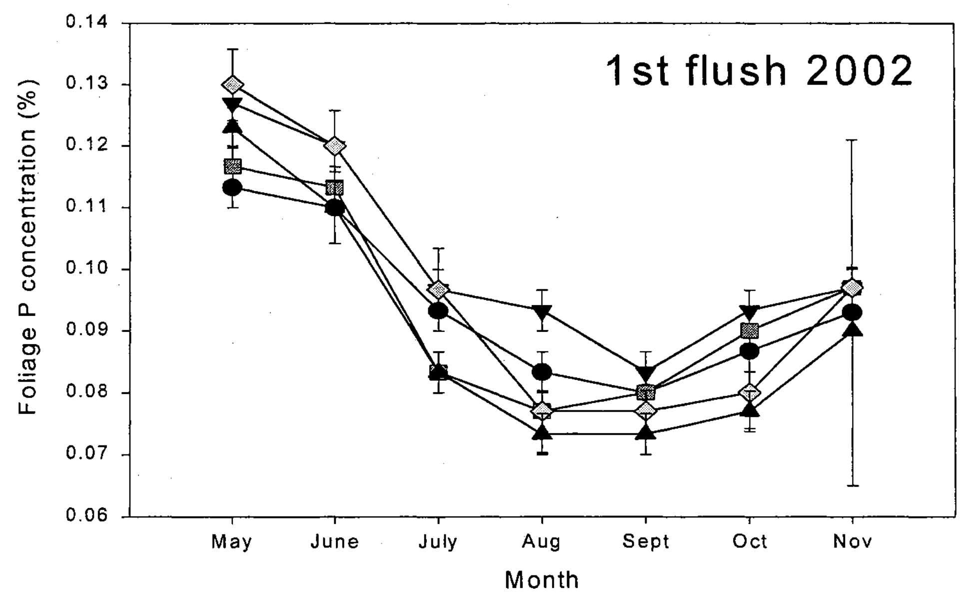


Figure 5. Foliage P concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.

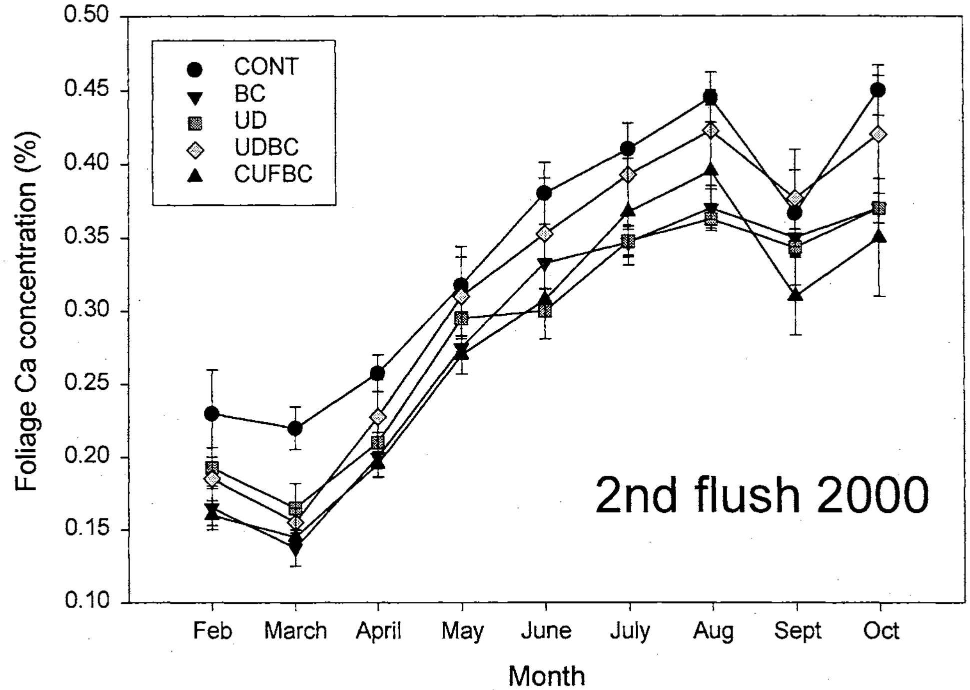


Figure 6. Foliage Ca concentration of previous-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in February 2001.

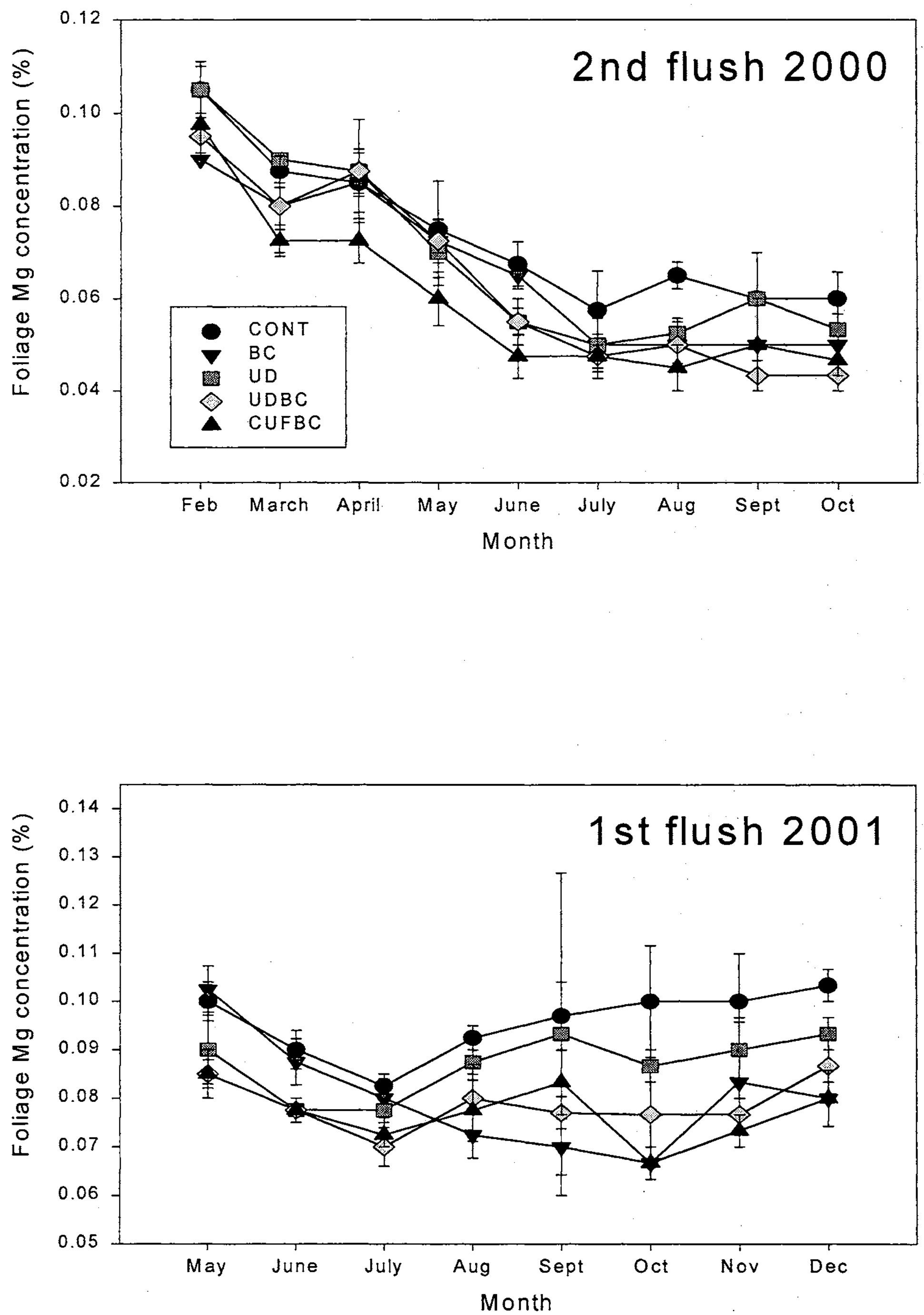
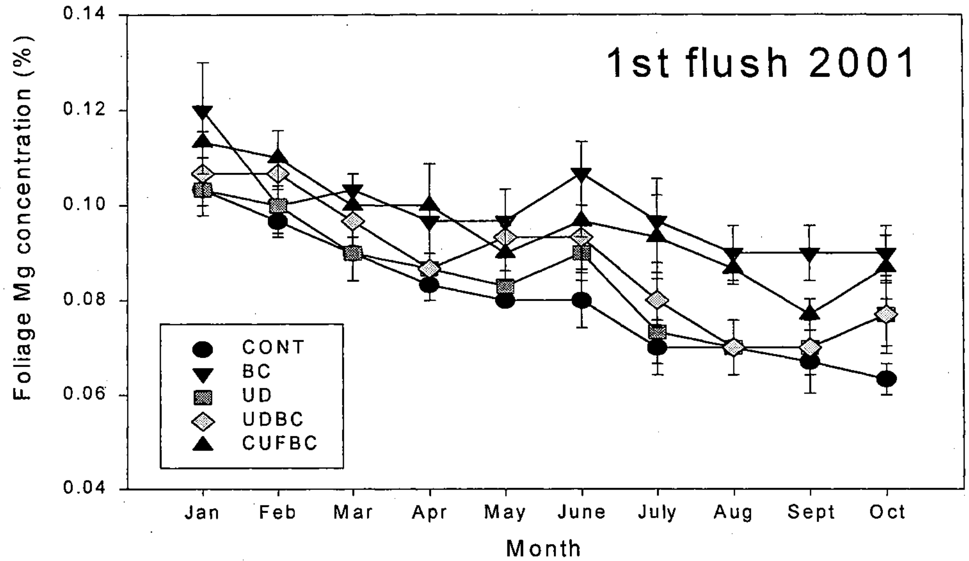


Figure 7. Foliage Mg concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in February 2001.



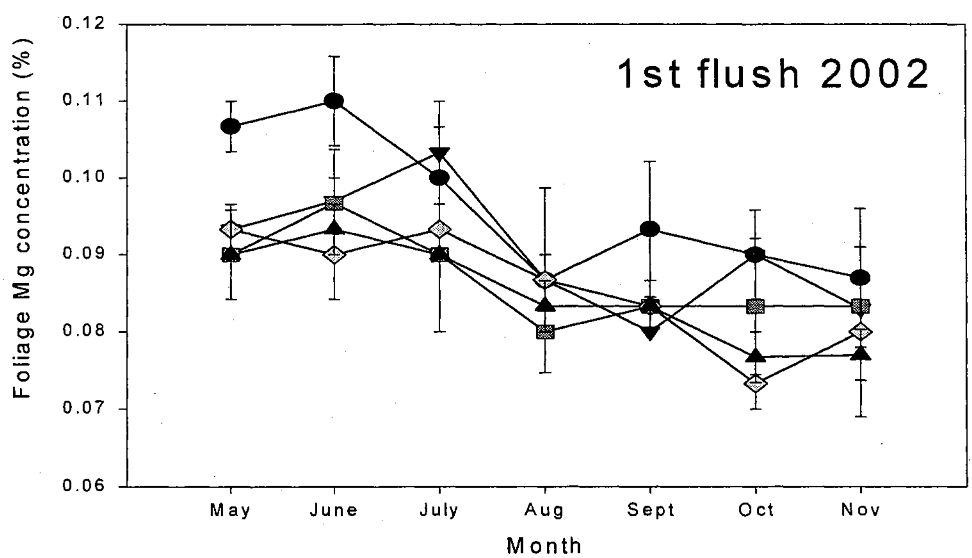
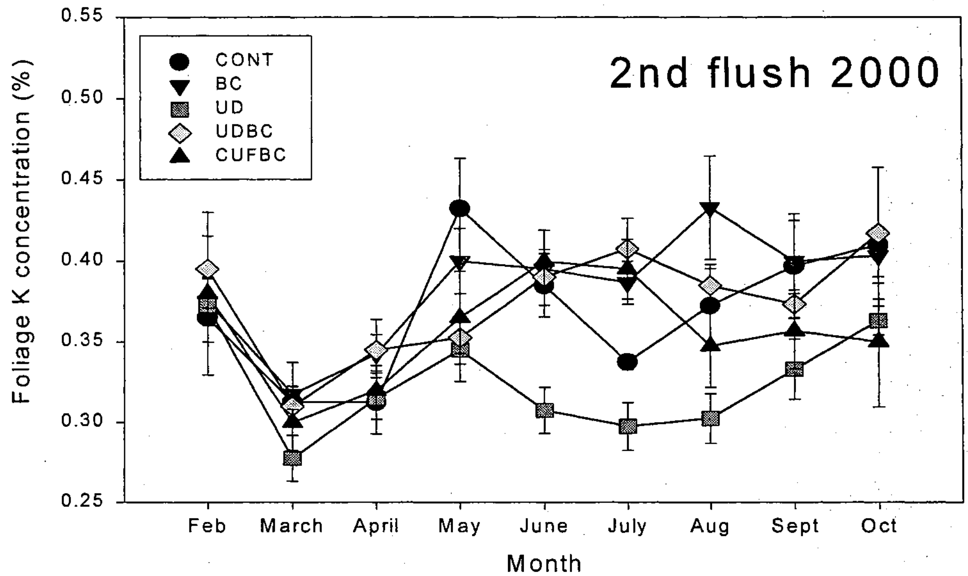


Figure 8. Foliage Mg concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.



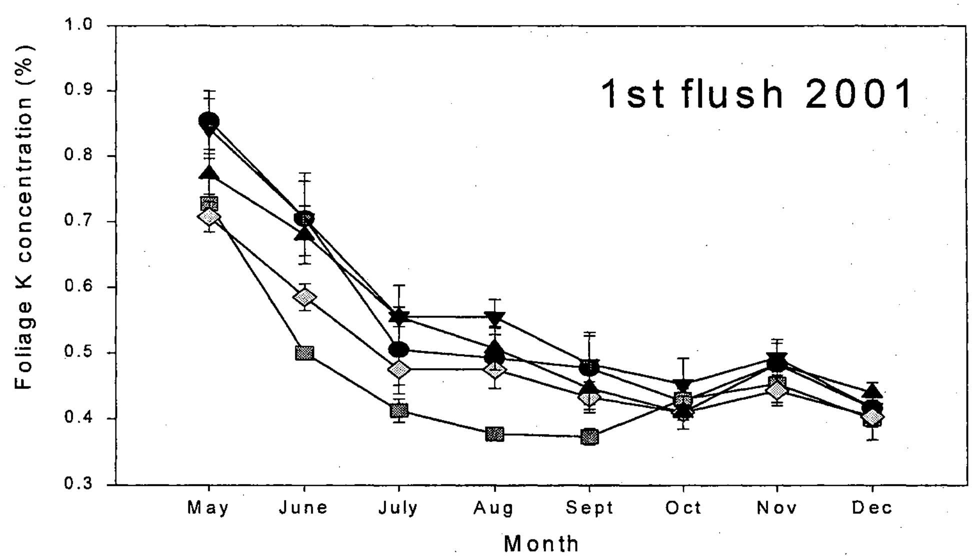


Figure 9. Foliage K concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in February 2001.

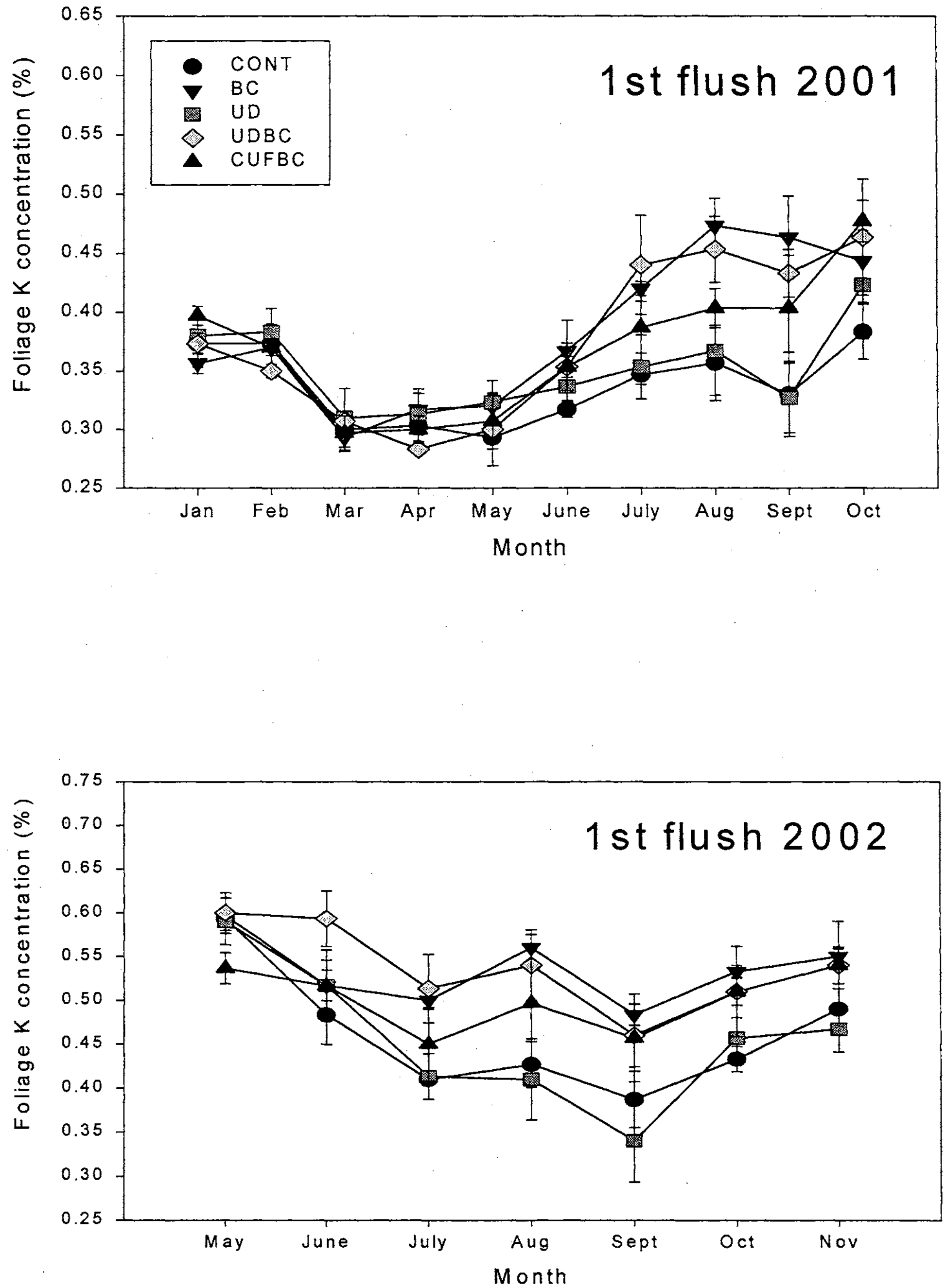
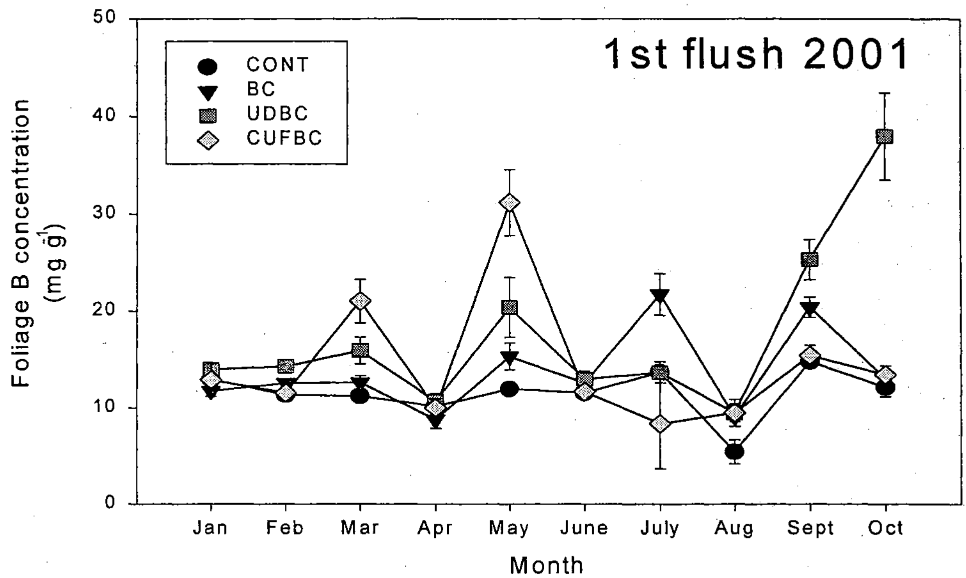


Figure 10. Foliage K concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.



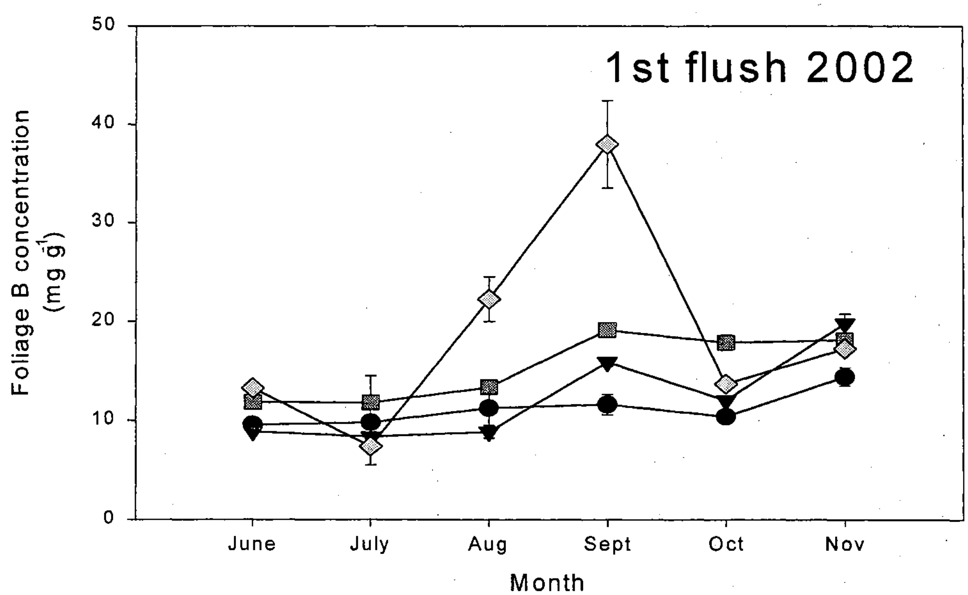
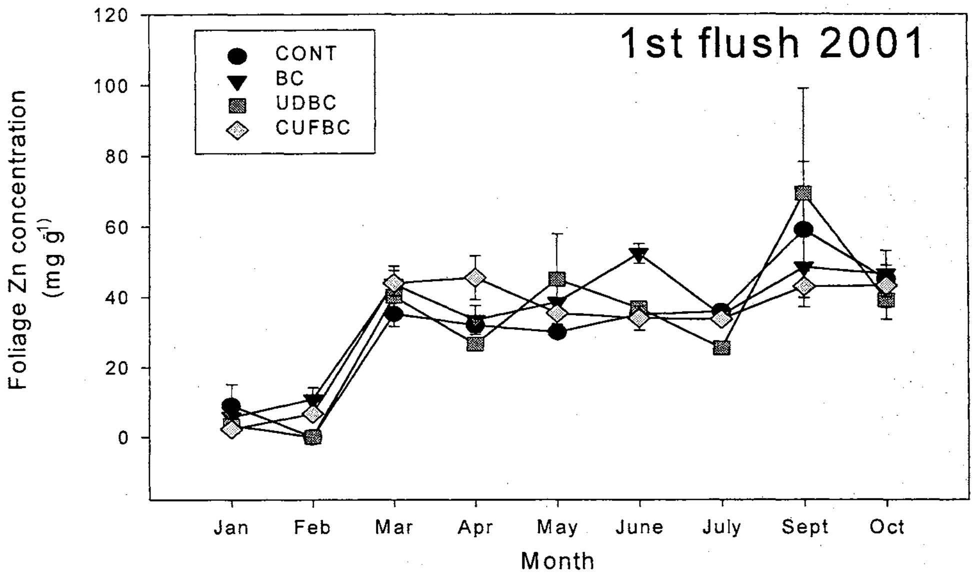


Figure 11. Foliage B content of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.



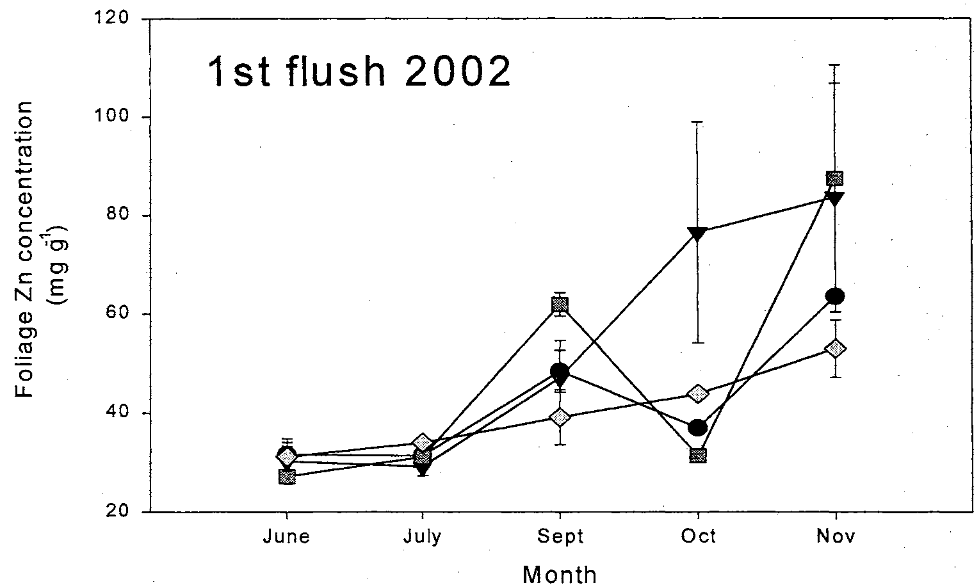


Figure 12. Foliage Zn concentration of previous- and current-year foliage in response to untreated control (CONT), continuous brush control (BC), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC). Glyphosate was used for brush control, and fertilizers were applied to the juvenile loblolly pine plantation in southeastern Oklahoma in April 2002.

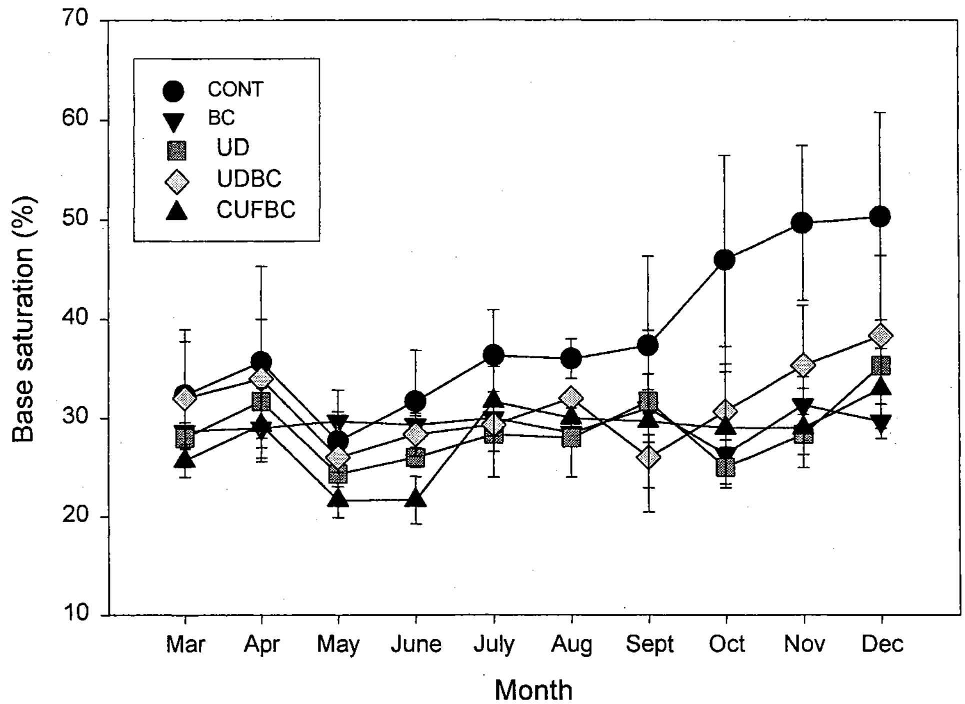


Figure 13. Soil base saturation in response to untreated control (CONT), continuous brush control (BC), fertilization with an urea/diammonium phosphate mixture (UD), fertilization with urea/diammonium phosphate and continuous brush control (UDBC), and fertilization with a coated urea fertilizer and continuous brush control (CUFBC) treatments applied to a juvenile loblolly pine plantation in southeastern Oklahoma. Glyphosate was used for brush control, and fertilizers were applied in April 2002.

VITA

Michael Allen Blazier

Candidate for the Degree of

Doctor of Philosophy

Thesis: NUTRIENT DYNAMICS OF THE SOIL/PLANT/MICROBIAL SYSTEM OF A YOUNG LOBLOLLY PINE PLANTATION: EFFECTS OF FERTILIZER DATE OF APPLICATION AND FORMULATION

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Experience: Student Research Assistant, Department of Forestry, Louisiana Tech University, August 1996 to August 1997; Graduate Research Assistant, Department of Forestry, Oklahoma State University, August 1997 to December 1999; Graduate Research Associate, Department of Forestry, Oklahoma State University, January 2001 to August 2003.

Professional Memberships: Society of American Foresters, Alpha Zeta, Xi Sigma Pi