DEAN MEASON
The nutrient dynamics of intensively managed *Pinus taeda* stands of different ages
(Under the direction of RODNEY WILL)

Litter layer nitrogen flux in Lower Coastal Plain and nutrient pools of above ground tree components on Lower Coastal Plain and Piedmont were measured for *Pinus taeda* L. stands of three ages that received complete interspecific competition control and annual fertilization. Nitrogen fertilization increased foliar N concentration with the upper canopy having the highest concentration and this effect increased with stand age. Previously established critical concentrations for NPK did not correspond with the growth response to treatments. Fertilized treatments retained less litter layer nitrogen than the unfertilized treatments. Fertilization increased throughfall organic N and increased the litter layer retention of organic N. The amount of inorganic nitrogen in the litter leachate was low but a return of an additional 100 kg N ha^{-1} yr^{-1} with fertilization to the mineral soil over 20 years could have a large impact on available N. Approximately 60% of fertilized N could be accounted in above ground biomass.

INDEX WORDS: Fertilization, Competition control, Litter layer, *Pinus taeda*, Nitrogen, Organic Nitrogen, Throughfall, Litter leachate, Piedmont, Coastal Plain.

THE NUTRIENT DYNAMICS OF INTENSIVELY MANAGED *PINUS TAEDA* STANDS OF DIFFERENT AGES

by

DEAN FRANCIS MEASON

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Approved:

Major Professor: Rodney Will

Committee: Daniel Markewitz
Charles Jaeger III

Electronic Version Approved:

Gordhan L. Patel
Dean of the Graduate School
The University of Georgia
December 2000

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INTRODUCTION

Nutrient availability is an important factor controlling pine productivity in plantations in the southeastern United States as the majority of plantations are located on nutrient poor soils (Neary *et al.* 1990, Zhang and Allen 1996). Many Piedmont soils are advanced weathered clays that were heavily eroded from previous farming practices and have little organic matter remaining. A number of Coastal Plain soils are formed from nutrient poor marine sediments with a small accumulation of organic matter.

Pinus taeda L. (loblolly pine) responds to silvicultural treatments that increase water and nutrient availability (Zhang and Allen 1996, Zutter *et al.* 1994, Borders and Bailey 2001, Samuelson *et al.* 2001). Various treatments used at establishment and during the rotation to increase growth, survival and volume include herbicide, burning and fertilization (Smith *et al.* 1971). Timing of treatments is important; for example, competition control is very important for growth and survival in the first several years after establishment while fertilization may be more beneficial later in stand development when nutrient demand is greater. Treatment needs vary with location; for example, phosphorus (P) is can be more limiting than nitrogen (N) in some Coastal Plain and vice versa for the Piedmont. The mechanisms of how *P. taeda* respond to treatments that increase nutrient availability are poorly understood. For example, does fertilization increase chlorophyll per unit of canopy, or increase biomass allocation from root to shoot, or does it just increase the amount of foliage per unit of area. Additionally, there is no consensus on the magnitude of *P. taeda's* response to the treatments and if the response will change over the stand's development (Dalla-Tea and Jokela 1994, Switzer and Nelson 1966). This lack of understanding is highlighted in commercial forestry operations where competition control and fertilizer treatments are applied to increase tree survival and growth. These applications can be hit or miss, the exact gains are unpredictable and the amounts and timing of fertilizer are based on crude “rules of thumb”. An understanding of how trees and stands respond to competition control and fertilizer would remove the uncertainty of applying silvicultural treatments to stands. This could make silvicultural treatments cheaper and more efficient by enabling managers to apply site-specific treatments with the correct dosage and timing.

This study investigated how *P. taeda* stands respond to increased nutrient availability by examining the changes in nutrient dynamics when interspecific competition was completely controlled, and yearly fertilizer was applied. The study includes the examination of the aboveground distribution, resource-use efficiency, internal and external cycling and interactions of macro and important micronutrients. A unique aspect of this study was the replication over several sites in Georgia and among stands at different ages, thus giving a detailed look at nutrient dynamics in Piedmont and Coastal Plain soils at different stages of stand development. In the Piedmont, plots were measured at ages five, ten and twelve while in the Coastal Plain, plots were measured at ages six, ten and twelve. At each site, the plots were replicated twice except for the five-year-old age group at the Piedmont sites, which had only one replication. Every age group at the Piedmont and Coastal Plain locations had the factorial combination of interspecific competition control (none vs. complete control) and fertilization (none vs. yearly). These extreme treatments pushed trees to the upper limits of growth for the region, which increased the range of responses to better examine treatment responses.

CHAPTER ONE:

LITERATURE REVIEW

Previous Research

Considerable research has examined how treatments that increase nutrient availability and reduce interspecific competition affect growth of plantation species. Most research has concentrated on how trees respond in terms of height, volume, leaf area and increased growth, to different timing and rates of herbicide and/or fertilizer (e.g. Fortson *et al.* 1996, Miller *et al.* 1991, Zutter *et al.* 1994). For example, *P. taeda* aged 5 to 16, responded positively to complete interspecific competition control in terms of diameter at breast height, height, basal area per hectare, total volume per hectare and merchantable volume per hectare (Fortson *et al.* 1996). With complete interspecific competition control during the first three years, 11-year-old *P. taeda* increased in volume by 217% (an average of 10 m^3 ha^{-1}) (Zutter and Miller 1998). Measurements made 8 years after 37 kg N ha^{-1} and 9 kg P ha^{-1} were applied over two consecutive years to mid rotation *P. taeda* revealed a 39% (7 m^3 ha^{-1}) increase in volume (Jokela and Stearns-Smith 1993). After 11 growing seasons, *P. taeda* with complete interspecific competition control and two fertilizer treatments (18 kg N ha^{-1}, 8 kg P ha^{-1}, 15 kg potassium (K) ha^{-1} at year one and 8 kg P ha^{-1} at year six) had 9 m^3 ha^{-1} more volume than the control (Haywood and Tiarks 1990). In the plots used for this study, the combined treatment of complete control of competing vegetation and the annual application of an average of 70 kg N ha^{-1} yr^{-1} increased volume growth at age eleven from 101 to 260 m^3 ha^{-1} in the Piedmont and from 122 to 380 m^3 ha^{-1} in the lower Coastal Plain (Borders and Bailey 2001).

Although these studies give important information on the overall response of trees to particular treatments at particular sites for particular species; they do not identify the underlying internal mechanisms which would explain how and why trees responded to increased nutrient availability, or even if the tree was directly responding to higher nutrient levels. For treatments like weed control, measuring the overall response does not indicate if a tree was responding to increased nutrients, or increased soil water, more root space e.t.c.

Nutrient dynamics of the above ground tree components

Tree nutrient research in the southeastern United States began in the 1950's as plantations were established to replace harvested southern pines that colonized abandoned farms (Wahlenberg 1960, Allen 1987). The majority of tree nutrient research on *P. taeda* has concentrated on recording the nutrient pools in trees, the sources of nutrients and the amount of nutrient recycling within trees at particular ages (Dalla-Tea and Jokela 1994, Fortson *et al.* 1996, Hodges and Lorio 1969, Margolis and Brand 1990, Matson *et al.* 1992, McNulty *et al.* 1991, Metz and Wells 1967, Miller *et al.* 1991, Neary *et al.* 1990, Pehl *et al.* 1984). Wells and Metz (1963) did one of the first comprehensive studies of *P. taeda* nutrients. They investigated N, P, K, Ca and Mg content in the crown of 5-year-old *P. taeda* over a 17 month period and found that the content of individual nutrients varied with canopy location, season and soil type. The concentration of NPK in the canopy in December was 1.00% for N, 0.11% for P and 0.45% for K. They were some of the first researchers to discover that a large amount of N, P and K was translocated from needles that were about to be abscised back into the tree. The photosynthesis apparatus have a large demand for nutrients, especially N, thus the highest concentration of plant important nutrients are located in the canopy. For example, at age five, 80% of *P. taeda's* above ground tree components components N content was in the current foliage (Smith *et al.* 1971). Switzer and Nelson (1972) discovered that *P. taeda* nutrient sources for N, P, K, Ca, Mg and S were unique to each nutrient and by age 20, the mineral soil horizons were not the single most important nutrient source. Rather, *P. taeda* heavily relied on leaf litter and retranslocation for much of its nutrients.

In the last 30 year's, silvicultural treatments such as various types of fertilizer and competition control have become increasingly important in *P. taeda* plantations. Several studies have examined changes of *P. taeda* nutrient dynamics due to various silvicultural treatments and how this varies over time. One such study investigated foliar nutrient levels of N, P, K, Ca, and Mg for 10-to-20 year old *P. taeda* five years after various N, P and K fertilizer treatments (Adams and Allen 1985). Foliar P:N ratio decreased in response to N fertilization indicating the N level in the foliage was still high five years after the treatment because of the internal recycling of N (Adams and Allen 1985). Dalla-Tea and Jokela (1994) investigated the effects of fertilizer containing N, P, K, Ca, Mg, Manganese (Mn), Zinc (Zn), Iron (Fe), Copper (Cu) and Boron (B) on 5-to-7 year old *P. taeda* and *P. elliottii* (Engelm. var. *elliottii*) in northern Florida. The amount of N and P cycling by the tree, was greater for the complete weed control and fertilizer treatments than stands that did not receive any treatment (Dalla-Tea and Jokela 1994). With complete interspecific competition control from establishment, *P. taeda* foliar N, P and K concentration increased at age two but by age six, the treatment had no effect on N, P and K concentration because of the higher nutrient demands of a larger tree (Zutter *et al.* 1999). Therefore, the positive effect of competition control on nutrient concentrations may be shortlived.

Zhang and Allen (1996) investigated the nutrient response of 11-year-old *P. taeda* to N added as urea fertilizer in the Georgia Piedmont with irrigation used to minimize water stress. Foliar weight and N and Ca concentration increased while P and Mg concentration decreased and K concentration stayed the same with the application of fertilizer. This indicated that extra N from the fertilizer was taken up by the tree and might have directly or indirectly increased Ca uptake (since Ca was not mobile within *P. taeda*). They hypothesized that "because Ca was [naturally] abundant on the site, it was continuously absorbed up from the soil . . . with the transpiration stream" (Zhang and Allen 1996). The concentration of P and Mg decreased, indicating that the tree did not increase P and Mg uptake to compensate for the higher N concentration in the canopy nor the larger canopy area. Because K concentration remained the same in the canopy size increased, the amount of K entering the canopy must have increased. The source of the extra K could have been from other parts of the tree or from some external source like leaf litter or soil. In the same year, 75% of N, 73% of P, 83% of K and 28% of Mg was retranslocated out of one-year-old foliage before absiccion while the amount of these nutrients increased in the current foliage. This suggested the movement of nutrients from older parts of the canopy to the developing parts of the canopy (Zhang and Allen 1996). The effect of fertilization on nutrient cycling has been reported in other conifers. In one study, various levels of N ammonium sulphate fertilizer (150 to 600 kg N ha^{-1}) was applied to 6-to-11 year old *Pinus radiata* D. Don (radiata pine) in South Australia. The concentration of foliar N remained high for two years after the fertilizer applications were finished (fertilizer was applied annually over two consecutive years) while an increase in basal area continued for five years. They concluded that the majority of foliar N cycling was from retranslocation rather than from the uptake of N released from litterfall (Fife and Nambiar 1997).

Various productivity measures have been used extensively in agricultural research to understand changes in productivity from fertilization (Ågren and Ingestad 1987, Ingested 1979, Hirose 1988, Lambers *et al.* 1990). Measurements include nutrient use per unit of growth, amount of foliage to the total tree biomass (leaf weight ratio), rate of photosynthesis per unit nitrogen (photosynthesis use efficiency). These measures have been used to see if changes in various measures of productivity from treatments used to enhance growth were in proportion to changes in plant nutrients. These are called measures of nutrient use efficiency where an increase in efficiency usually means that that measure of productivity has increased per unit of a nutrient (usually N) in that particular part of the tree. Some nutrient use measures are correlated to one-another. For example, higher photosynthetic nutrient use efficiency in C_3 grasses and herbs was correlated with higher leaf nitrogen productivity (leaf biomass per unit canopy N content) and plant nitrogen productivity (plant growth per unit of plant N content) (Garnier *et al.* 1995). Measures of nutrient use efficiency have been limited in tree research to laboratory work on seedlings while measures have been used in the field has been limited, with variable results. For example, applications of fertilizer on *Pinus strobus* L. (white pine) seedlings did not affect plant nutrient use efficiency (Margolis and Brand 1990).

As the stands age and grow and nutrient demand increases, the sources of tree nutrients change. Nutrient recycling (i.e. from retranslocation and leaf litter decomposition) was more important for older trees than younger trees of the same species, including *P. taeda* (Shoulders and Tiarks 1980, Switzer *et al.* 1966, Switzer and Nelson 1972, Van Lear *et al.* 1984, Wells and Metz 1963). Some nutrients (e.g. N, P and K) are more mobile than others (e.g. Ca) and mobile nutrients can move from less metabolically active to more active areas of the tree throughout the year (Cameron and Appleman 1933, Kramer and Kozlowski 1997, Metz and Wells 1967). Kramer and Kozlowski (1997) concluded from other research that the internal movement of nutrients was the case for most woody species. For example; "in perennial plants, nitrogen is stored both as soluble amino compounds and protein . . . The relative proportions of soluble verses insoluble nitrogen compounds vary with season, within different parts of the tree, with fertilization . . . and with changing environmental conditions" (Dickson 1991).

Nutrient release from the litter layer

Previous research investigated the effect of the litter layer on the cycling of nitrogen in non-fertilized conifer systems. For a typical 25-year rotation of a unfertilized southern pine stand, the difference between nitrogen inputs from the atmosphere and nitrogen outputs from biomass removal and leaching can range from a deficit of 180 kg ha^{-1} to a surplus of 300 kg ha^{-1}. (Richter and Markewitz 1996). At age 15, an unthinned *P. taeda* stand in the Piedmont produced 4,100 kg ha^{-1} yr^{-1} of litterfall, of which, 171 kg ha^{-1} was nitrogen (Van Lear and Goebel 1976). At age 40, the litter layer can contain 400 kg ha^{-1} of N (Jorgenson *et al.* 1980). The prevailing consensus of decomposition was that the litter layer immobilizes C:N until a critical N level of 20 to 25:1 is reached. The majority of net N release[1] from the litter layer was from the latter stages of decomposition (Berg and Staaf 1981, Polglase *et al.* 1992). The litter layer in unfertilized stands of *P. taeda* acted as net inorganic (nitrate and ammonium) N sink[2] throughout the life of a *P. taeda* stand. However, the retention of inorganic N decreased with stand age (Jorgensen *et al.* 1980, Switzer and Nelson 1972, Richter *et al.* 2000). The amount of nitrogen released from the litter layer does become a more important for *P. taeda* with older stands as the majority of the trees N supply comes from decomposition of its own leaf litter rather than from mineral soil N pools (Jorgensen *et al.*, 1980). However, during the length of a 30 year rotation, the litter layer of a *P. taeda* forest remains a net N and P sink (Piatek and Allen 2001)

Research on the effects of the addition of N fertilizer on nutrient release from the litter layer was inconclusive. A literature review by Fog (1988) found N addition to soil often had no or increased N immobilization. However, a few recent studies have found a significant increase in N mineralization with increased N deposition while the C:N ratio remained unchanged (Gundersen *et al.* 1998, Tietema 1993, McNulty *et al.* 1991). Seasonality plays a role; mineralization can occur during certain periods of the year like the spring where temperature and moisture conditions are ideal for microbe growth. Despite periods of net mineralization, the litter layer in the fertilized treatments can remain an annual net N sink (Matson *et al.* 1992, Casals *et al.* 1995). One study used a ^{15}N tracer in the fertilizer to determine its fate in *Pseudotsuga menziesii* ((var. *glauca* (Beissn.) Franco) stands. There was low recovery of ^{15}N in the microbe biomass and high recovery of the isotope in the form of nitrate despite a high C:N ratio. They concluded that N availability exceeded microbe demand, which resulted in nitrifiers consuming the fertilized N (Matson *et al.* 1992).

Few studies have directly examined the effect of competition control on nitrogen release from the litter layer. However, previous research has examined the effect of the proportions of

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[1] Net N release: N leaving the litter layer less the amount of N entering the litter layer.
[2] Net N sink: the demand for N in the litter layer was greater than the supply. Immobilization.

broadleaf and conifer species on litter mineralization and decomposition. As competition control effects the litter composition of broadleaf and conifer species, those studies are particularly relevant. As with fertilizer research, the results from the change of litter composition can increase, decrease or have no effect on mineralization (Gustafson 1943, Thomas 1968, Finzi and Canham , 1998, Piatek and Allen 2001). Piatek and Allen (2001) found *P. taeda* needles decomposed faster in a hardwood mix only when the ratio of hardwood leaves to *P. taeda* needles was 5:1. In contrast, Finzi and Canham (1998) found high-quality litter stimulated decomposition of low quality litter when the proportion of high quality litter was greater than 70%.

The majority of these studies used incubations of the litter layer either *in situ*, or in the laboratory. Although these methods can give very good information about whether the litter layer was a nutrient source or sink, they do not give accurate information of the flux of nitrogen over time under field conditions. Previous research found litter layer incubations were a good measure of the potential net mineralization of nitrogen. However, incubations do overestimate N flux since they were not affected by temperature and moisture fluxes that occur in the field (Tietema *et al.* 1993, Raison *et al.* 1987). Incubation measures were further confounded by the sieving, drying and rewetting of the organic matter, which can change the mineralization rate from the field (Tietema *et al.* 1993, Raison *et al.* 1987, Foster 1989). "In undisturbed forest floor, changes in root production, root exudation, N uptake, and litter production may also contribute to a change in the seasonality of N mineralization and nitrification" (Foster 1989).

The problem in studying nutrient dynamics

A critical factor in nutrient dynamics is that the response of trees depends strongly on age, species and location. There was considerable variability in the results from different studies on nutrient dynamics. For example, the results of previous studies on the plant uptake of nitrogen and phosphorus released from its own litter (resorption) showed it can increase, decrease, or not change in response to increased soil fertility and plant nutrient status (Dalla-Tea and Jokela

1994). While some of this variability can be attributed to poor study design or analysis, much was due to the variation between species, region and age group (Munson *et al.* 1995, Smith *et al.* 1971, Wells and Metz 1963, Tietema 1993, White *et al.* 1970). Hodges and Lorio (1969) concluded "no universal agreement as to the influence of moisture on the various [nutrient] fractions . . . The results seem to depend on the plant species and sampling procedure". The response to fertilization by different species was well documented by Dalla-Tea and Jokela (1994). They found *P. taeda* had a greater growth response and accumulated more nutrients from N, P, K, Ca, Mg, Mn, Zn, Fe, Cu, B fertilizer and weed control than *P. elliottii*. They proposed that as *P. elliottii* was adapted to low nutrient sites, it probably had no mechanism to use or accumulate more nutrients than it needs to survive. *P. taeda* responded well because it could exploit more nutrients than the site normally provides (Dalla-Tea and Jokela 1994). An important caveat about investigating nutrient dynamics to silvicultural treatments was summed up by Sheriff *et al.* (1995). "A decrease or increase in the availability of a [nutrient] resource may or may not result in changes in the use efficiency of that resource, because other resources may have an overriding effect" (Sheriff *et al.* 1995).

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CHAPTER TWO:

THE EFFECT OF INTENSIVE MANAGEMENT ON NITROGEN CYCLING FROM *PINUS TAEDA* LITTER LAYER OF DIFFERENT AGED STANDS

Introduction

The litter layer of *Pinus taeda* L. stands often contains a large pool of nitrogen in relation to nitrogen in the standing biomass. At age sixteen, the litter layer of a *P. taeda* stand that has received no silvicultural treatments can accumulate 300 kg ha^{-1} of nitrogen (Wells and Jorgensen 1975). The majority of soils in the southeastern United States are nitrogen poor with little surplus nitrogen available in the ecosystem. Thus nitrogen cycling within the ecosystem is critical to supply nutrient needs to *P. taeda*. Soil nitrogen pools can be depleted in the long term if the majority of nitrogen is immobilized in the litter layer (Richter *et al.* 2000). In general, the growth of nitrogen limited *P. taeda* stands will increase if more litter layer nitrogen were mineralized and accessible for tree uptake as additions of N via fertilization almost always increases *P. taeda* stand growth (Allen 1987).

Fertilization is frequently applied to managed forests in the southeastern United States to improve growth and yield. However, application rates and timing are based on “rules of thumb”. Previous research has concentrated on the growth of the tree from treatments rather than investigating the mechanisms of the response. One uncertain issue in fertilizer research is the impact of fertilization on the litter layer nitrogen pool. Previous research that has investigated litter decomposition rates after fertilization and have found fertilization either had no effect or a positive effect on decomposition (Fog 1988, Gundersen *et al.* 1998, Piatek and Allen 2001). A majority of the research only examined fresh litter decomposition and its nitrogen release, not the nitrogen flux from the entire organic horizon (Wells and Jorgensen 1975, Berg and Staaf 1981, Piatek and Allen 2001). As nitrogen release is more likely to occur in the later stages of decomposition, the fermentation and humus horizons need to be included to estimate litter layer nitrogen flux due to fertilization. Further, the entire litter layer must be measured *in situ* so the mineralization process is affected by field moisture and temperature conditions.

Competition control has had mixed results on litter layer mineralization rate. The major effect of competition control was the change to the species composition of the litter layer. As *P. taeda* needles are harder to decompose, the reduction of broadleaf species in the litter layer can decrease or have no effect on the mineralization rate (Gustafon 1943, Piatek and Allen 2001).

The objective of this study was to investigate how fertilization, competition control and stand age affects the amount and form of nitrogen being released from the litter layer. If the litter layer is changed from a net sink to a net source of nitrogen by fertilization, this N source could become an important contributor to sustained tree growth. This would provide an important feedback loop for the trees and maintain the positive effect of fertilization long after the fertilizer has passed through the litter layer. If such a feedback were self-sustaining or occurs once a threshold is reached, then the implications for management could be for less fertilizer applications once the litter layer becomes a nitrogen source.

The first hypothesis for this study was that annual nitrogen fertilization will stimulate nitrogen mineralization and decomposition in the litter layer, thus increasing nitrate, ammonium and organic nitrogen content in litter leachate. The second hypothesis was that complete competition control would have no effect on the nitrate, ammonium and organic nitrogen flux from the litter layer. The third hypothesis was that older stands would have greater rates of mineralization. The organic horizon deepens as the forest ages, with fermentation and humus horizons developing in the lower organic horizon. Thus, the litter layer in older stands is more likely to have greater mineralization rates from older, thicker and more fully decomposed litter.

Site Description and Methodology

The study was located at two sites in the Dixon Memorial Forest, 16 km southeast of Waycross Georgia, USA (31° 10' N, 82° 18' W). All sites were established on recently clear cut stands that had previously supported *P. taeda*. The remaining vegetation on the sites was piled and burned, leaving the sites relatively clear of vegetation. The sites were then bedded with an average bed height of 53 cm and an average width between rows of 6.4 m. These site preparation techniques were typical for the lower Coastal Plain. The genetically improved (1-0) seedlings used for this study were from half-sib family 7-56 (North Carolina State Tree Improvement Cooperative) and hand planted at a density of 823 trees per ha (Borders and Bailey 2001). Plots of 0.15 ha in size were established in 1987, 1989 and 1993 at two sites designated as Waycross Wet and Waycross Dry. At each site, the treatments assigned to plots were a factorial combination of annual fertilization and complete interspecific competition control. The Waycross Wet site usually experienced standing water during the winter months while the Waycross Dry site did not.

The specific treatments were as follows:

- Control (C): no treatments after the intensive mechanical site preparation.
- Herbicide (H): At ages' one, two and three, 292 ml ha^{-1} of sulfomethuron methyl was broadcast evenly over the sites. Follow-up treatments of directed sprays of glyphosate were applied in mid-summer. From age three, directed sprays of glyphosate were applied annually where needed to keep plots clear of competing woody and herbaceous vegetation (Borders and Bailey 2001). All of the herbicides were non-soil active.
- Fertilization (F): annual fertilizer additions were applied at the following rates; years one and two had 78 kg ha^{-1} of nitrogen (N) in the form of ammonium nitrate plus 58 kg ha^{-1} of potassium (K) in spring in the form of potassium chloride, followed by 59 kg ha^{-1} of phosphorus (P) and 19 kg ha^{-1} of N in mid-summer in the form of diammonium phosphate.

From year three to year ten, ammonium nitrate was applied each spring, adding 59 kg N ha^{-1} yr^{-1}. At age eleven, the annual nitrogen application rate increased to 118 kg N ha^{-1} of nitrogen and 36 kg P ha^{-1} of phosphorus (as triple super phosphate) was added (Borders and Bailey 2001). At age thirteen, the amount of N applied was reduced to 92 kg N ha^{-1} and an application of Super Rainbow® fertilizer in the same year added 179 kg P ha^{-1} and 45 kg K ha^{-1} and approximately 6 kg ha^{-1} of magnesium (Mg), 17 kg ha^{-1} of calcium (Ca), 17 kg ha^{-1} of sulfur (S), 3 kg ha^{-1} of boron (B), 0.6 kg ha^{-1} of copper (Cu), 2 kg ha^{-1} of manganese (Mn) and 5 kg ha^{-1} of iron (Fe). Appendix D lists the application rates of the various fertilizers for each year.

- Herbicide + Fertilization (HF): Herbicide and Fertilizer treatments combined.

The Waycross Dry site had well drained to moderately well drained soils. The dominant soil series was Bonifay. The Bonifay series was described as a loamy, siliceous, subactive, thermic, Grossarenic Plinthic Paleudult. Bonifay series was associated with Blanton series. The Waycross Wet site was a poorly to somewhat poorly drained soil. The dominant soil series was Pelham. The Pelham series was described as a loamy, siliceous, subactive, thermic Arenic Paleaquult. Pelham series was associated with Rigdon series. The Waycross Dry and Waycross Wet sites had slopes of less than one percent. Typical annual rainfall for the region was 1270 mm while typical mean annual temperature was 19 °C (Soil Survey Division, 2001).

Within each plot, three throughfall collectors and four zero tension lysimeters were installed in the first row of the three-tree row plot buffer zone. The throughfall collectors were placed at random within each plot in March 2000. Each throughfall collector used a 160 mm diameter funnel with a high density polyethylene screen set 50 mm from the top to prevent debris from entering the collection vessel. Each funnel was sealed to the collection vessel with a neoprene stopper. The funnel extended 100 mm into the vessel. High-density polyethylene containers (3.75 l) were used as the throughfall collection vessel. Each vessel was wrapped in aluminium tape to discourage algae growth and to prevent the solute temperature from rising due to solar radiation.

Polyvinyl chloride (PVC) piping was used to construct the zero tension lysimeters; the piping was cut into sections 300 mm long by 100 mm wide (inside arc), which created a lysimeter 25 mm deep. A PVC cap was attached at one end and the lysimeter was left open at the other end creating a collection area of 300 cm^2. The lysimeter design is based on lysimeters used by Jordan (1968) and Haines *et al.* (1982). Each plot had 4 lysimeters with 2 lysimeters connected to one collection vessel. Thus, two lysimeters formed a surface area of 600 cm^2 for each collection vessel. For each collection vessel, one lysimeter was place on or near the top of the bed while the other was placed between the beds. At least 1.5 m was between the two-paired lysimeters with the bed and interbed lysimeters at an angle of at least 90^o. The collection vessels were placed underground to ensure a negative flow of the solute. High-density polyethylene containers (3.75 l) were used as the lysimeter collection vessel with an air hole pierced under the top of the handle. The lysimeter tubing from the bed and interbed were connected with a Y connector and one tube ran through a neoprene stopper into the collection vessel. The lysimeter collection vessels were painted black and the pits holding the collection vessels were covered to discourage algae growth and to prevent the solute temperature from rising due to solar radiation.

The water table rose to near the surface at the Waycross Wet site during September 2000, which contaminated samples the lysimeters collected during the sixth collection. A new lysimeter collection vessel was installed for the eighth collection (November 2000) at the Wet site to keep the collection vessel sealed from ground water. Qorpak™ (Qorpak, Bridgeville, Pennsylvania, USA) 4 l high density polyethylene containers were placed in 100 mm (inside diameter) PVC piping with a small diameter tubing installed near the top of the container to act as an air hole. The small tubing was sealed to the container with silicone caulk and tubing was kept above the ground with a stake. Lysimeter tubing entered the container as above except the neoprene stopper was sealed with silicone. Because the interbed lysimeter could be contaminated with ground water if ground water rose to the surface, the interbed lysimeters were disconnected from the container at the Wet site until the twelfth collection. To keep the sites consistent, the interbed lysimeters were also disconnected at the Waycross Dry site. Concrete blocks weighing 5 kg were placed on top of the PVC piping to make sure the container did not move when the water table rose. The top of the container and associated tubing were placed below the lip of the PVC piping so the block would not pinch the tubing. This set-up was used successfully for the Waycross Wet site until the end of the experiment. Interbed lysimeters were reconnected in March 2001 for collections twelve and thirteen.

The lysimeters were inserted horizontally between the humus of the organic layer and the mineral A horizon, leaving the litter layer above the lysimeters mostly intact. If a fine root mat was present in the litter layer, it was left in place. Root mats occurred most often in the F and HF plots. Some of the younger C and H plots had only small amounts of litter, so to minimize the disturbance to the thin litter layer, five of the lysimeters were inserted with a thin layer of mineral soil. The layer of mineral horizon in the lysimeter had no significant effect on the overall net mineralization rates, as there was no deviation in net mineralization from other lysimeter measurements with the same stand age and treatment application. Tubing running from the lysimeters to the collection vessels was supplied with enough downward slope to ensure a good flow. The first collection was made after a seven week settling period. No preservatives were used in the collectors as it was assumed that nitrogen loss would be negligible and it would not affect tests for treatment effects (see below).

Collections were from 16 May 2000 until 9 May 2001. Collections were made on an average of 23 days after the first rain event. Collections one to seven and twelve and thirteen collected solution from all lysimeters. Collections eight to eleven only used the bed lysimeter collectors. For collection six, the majority of the lysimeter collection vessels at the Wet site were disturbed by ground water, which disconnected the tubing such that only a partial sample was made for the collection period. Water samples were undisturbed so a least squares regression was calculated for lysimeter volume for that collection. For the regression, throughfall values were correlated with the lysimeter volumes for each plot over the previous five collections. For collection seven, lysimeter samples were only collected for the Dry site.

At the end of a particular collection, the throughfall and lysimeter collection vessels were exchanged with empty collectors in the field and the collected samples were taken to the laboratory. When changing collection vessels, the tube entering the collection vessel was rinsed with de-ionized water and if necessary, cleaned with a brush to remove algae growth or debris clogging the tubing. Unimpeded water flow from the lysimeter to the collection vessel was periodically checked with de-ionized water while collectors were disconnected. Volumes were measured for each collection vessel and for each plot. The three throughfall samples were combined as were the two lysimeter samples. A subsample was taken from throughfall and lysimeter collections of each plot and was filtered using a 0.20 µm Nuclepore® track-etch membrane (Corning Costar Corporation, Acton, Massachusetts, USA). The filtered subsamples were refrigerated at 4 ^{o}C until nitrogen analysis was completed. Nitrogen analyses were conducted within 30 days after filtering.

The weather station used by this study was located at the Waycross office of the Georgia Forestry Commission. This was 3 km southwest of the Waycross Dry site and 5 km south of the Waycross Wet site. Two locations were used to collect precipitation, a clearing at the Waycross Wet site and at the Georgia Forestry Commission. Collections from the two sites were combined to estimate the amount of nitrate, ammonium and organic N in precipitation.

Nitrogen Analysis

Three smaller subsamples from each filtered sample were separated; one for ammonium, one for nitrate and one for total N. The concentration of ammonium was determined by the automated phenate method (Clesceri *et al.*, 1998). The ammonium reacted with alkaline phenol and hypochlorite reagents to form indophenol blue, which was proportional to the ammonium concentration. The blue colour was intensified with sodium nitroferricyanide. The absorbtion at a wave length of 660 nm was measured with an Alpkem EnviroFlow 3000™ (Alpkem, O.I. Corporation, College Station, Texas, USA). A Disodium EDTA (Ethylenediaminetetraacetate) complexing reagent was added to eliminate any precipitates of calcium and magnesium hydroxides that occur in the reaction (Annon 1994b).

The concentration of nitrate was determined by the automated cadmium reduction method (Clesceri *et al.*, 1998). Nitrate was reduced to nitrite by a cadmium column. Both the nitrite organelle in the sample and the reduced nitrite were diazotized with sulfanilamide. Then these forms of nitrogen were coupled with N-1-naphthylethylenediamine dihydrochloride. The resulting azo dye was measured at 540 nm with an Alpkem EnviroFlow 3000™. EDTA complexing reagent was added to eliminate any precipitates of iron, copper or other metals during the reaction (Annon 1994a). The Ph of the samples was measured to ensure they were between a Ph of 5 to 9 and if necessary, adjusted.

To quantify total N, all forms of nitrogen were converted into nitrate using a persulphate oxidizing technique to measure total N (Koroleff 1983, Yu *et al.*, 1994). The oxidizing reagent was prepared using the Everglades recipe as described by Qualls (1986). An 8 ml aliquot was used for each sample. Throughfall samples were not diluted for digestion, as carbon content was usually less than 20 mg l^{-1}. Lysimeter samples were diluted to 2:1 or more if the dissolved organic carbon content was greater than 30 mg l^{-1}; this was estimated either by sample color (i.e. dark indicating high N) or by incomplete digestion (i.e. the color remaining after oxidation). If there was an incomplete digestion, a new aliquot was taken from the sample and it was diluted further. Persulfate was added at 1.6 ml to 8 ml of sample, shaken and autoclaved for 30 minutes. The persulfate oxidizer acted in two ways while being autoclaved; it digested all carbon in the sample and oxidized all forms of nitrogen to nitrate. The digested samples then were tested for nitrate as above except the persulphate was added to the standard matrix.

Preservation test

In July 2001, a sub-experiment was established to compare the stability of throughfall nitrogen using the collection method with two other techniques. Five replicates of three preservative methods were set up in a 12-year-old control plot in Whitehall forest, 11 km south of Athens, Georgia. Each replication was placed randomly in the plot. Within each replication, the three methods were grouped together. The first method was collecting samples after every rainfall event over the 21 day period (Set A). The second method was like the main experiment with the collectors remaining in field for the entire 21-day period (Set B). For the last method, samples were left out for the entire period with a 10 ml preservative of 2 M sulfuric acid (Set C). The Ph was tested at the end of the collection to confirm it was less than 2. After collection, the samples were processed using the same method for throughfall in the main experiment. However, the third rain event was low. Therefore all of the replicates from Set A were combined to have enough sample for analysis. Organic nitrogen and ammonium were analyzed using the same method as the main experiment. Nitrate was run using ion chromatography method with a Dionex DX500 Ion Chromatograph (Dionex Corporation, Sunnyvale, California, USA). The acid used for Set C's preservative was added to the standard and carriers used for the automated phenate method for ammonium measurements and automated cadmium reduction method for total nitrogen measurements.

Volume weighted concentrations

Volume weighted concentrations were calculated to test the effect of solute volume collected on N content. Collections two to eleven and thirteen were used for reasons explained in the results section. The data for nitrate, ammonium, organic N and total N concentration were collapsed as the main experiment had no significant site or age effects (see the results below). Mean throughfall volume for each collection was divided by the sum of the throughfall volume from all collection periods. This resulted in a weighted throughfall volume for each collection period. The weighted throughfall volume for each collection period was then multiplied by the mean nitrate, ammonium and total N concentration for each treatment (C, H, F and HF) for the particular collection period. The volume weighted concentration of all collection periods were then summed to calculate volume weighted concentration for the experiment. Volume weighted N concentrations were estimated in the same way for litter leachate. The weighted concentrations were converted to a hectare basis with the same method as the main experiment. Collections two to eleven and thirteen were added up to give the weighted concentrations on an annual basis.

Estimation of N flux

Nitrogen content in the throughfall and litter leachate was calculated by multiplying N concentration in the throughfall and litter leachate by the throughfall volume or litter leachate volume collected per unit area and scaled up to the kg ha^{-1} basis. Organic nitrogen was estimated by subtracting nitrate and ammonium content from total nitrogen content in throughfall or litter leachate. If the difference was negative, it was assumed that the organic component was so small that it was below the detection limits of the Alpkem EnviroFlow 3000™ and treated as zero. The nitrogen flux from the forest floor was estimated by subtracting the amount of nitrate, ammonium, organic nitrogen and total nitrogen in throughfall from the amount of nitrate, ammonium, organic nitrogen and total nitrogen in litter leachate. A positive figure meant that there was more nitrogen leaving the litter layer than what entered, thus causing a release of nitrogen in the litter layer. A negative figure meant that there was less nitrogen leaving the litter layer than what entered, thus causing a retention of nitrogen in the litter layer.

Statistical Analysis

The Waycross Wet and Waycross Dry sites served as replicates. The experimental unit was the plot with the three throughfall collectors and the two lysimeter collectors bulked before anaylsis. The General Linear Model (GLM) procedure from the statistical program package, Statistical Analysis System (SAS®, SAS Institute, Cary, North Carolina, USA) was used for the analysis. The model used for the GLM procedure was a split, split plot design whose whole plot factor was age, the first split being fertilizer, herbicide and associated interactions, and the second split being time (the collection dates) and associated interactions. Duncan's Multiple Range Test was used to test for treatment differences where applicable. For collection seven, there were no collections of litter leachate at the Wet site. Therefore, release of the three forms of nitrogen from the litter layer could not be estimated at the Wet site and were treated as missing values.

Results

Volume weighted concentrations

The fertilizer and competition control treatments had no significant effect on volume weighted nitrate and ammonium concentration in throughfall at the p=0.05 level (Table 2-1). Fertilizer and competition control had no significant effects on volume weighted nitrate and ammonium concentrations in litter leachate. Competition control had no significant effect on organic or total N volume weighted concentrations in throughfall or litter leachate. Fertilizer significantly increased volume weighted organic N concentration in throughfall (p=0.05) while there was no treatment effect on volume weighted organic N concentration in litter leachate (Table 2-1). There was no treatment effect on volume weighted total N concentration in throughfall while fertilizer significantly increased litter leachate volume weighted total N concentration (p=0.01) (Table 2-1).

The effect of the annual fertilizer application litter layer N flux

Fertilizer was applied as ammonium nitrate to the F and HF plots twice during the collection period, 25 days before the end of first collection period (16 May 2000) and twelve days before the end of twelfth collection period (3 April 2001). This created two fertilizer pulses. The first was during collection one (2 April to 16 May 2000). The second pulse occurred during the twelfth collection (12 March to the 3 April 2001) and possibly continued into the thirteenth (and last) collection (15 April to 9 May 2001). Release of nitrate and ammonium from the litter layer was far greater in the first collection than the other collections (Figure 2-1). Three rainfall events occurred between the fertilizer application and the end of the first collection, totaling about 80 mm (Appendix A). This fertilizer pulse was restricted to the first collection, as the following collections did not approach that level of release of inorganic[3] nitrogen. Further, almost all the other collection dates have a retention of nitrate rather than a release. There was no fertilizer pulse effect on organic nitrogen (Figure 2-1).

The second fertilizer pulse was not as distinct as the first. Fertilizer for the 2001 growing season was applied during the twelfth collection period. Three rainfall events occurred after the second fertilizer application, totaling about 20 mm (Appendix A). This created a partial fertilizer pulse, most clearly seen for the release of ammonium at age twelve (Figure 2-2). However, there was a retention of nitrate during this collection period. Assuming the response to the fertilizer applied in 2001 would be similar to the previous year, all the fertilizer applied during the twelfth collection was probably not dissolved. The large fertilizer pulse during the first collection was associated with a large amount of rainfall, including a 60 mm rain event. During the thirteenth collection, there was a retention of nitrate in the fertilized plots and a moderate release of ammonium was consistent with the other collection periods. It was assumed that any influence of fertilizer during the thirteenth collection was minimal and it had little impact on the release or retention of nitrogen. Three rainfall events totaling about 26 mm occurred during the thirteenth collection, which could account for a low fertilizer release (Figure 2-2, Appendix A). To account for the rest of the fertilizer, it was assumed that fertilizer continued to enter the litter layer after the thirteenth collection when heavier rainfall occurred or that some of the fertilizer was volatilized when wetted during the light rain events or dew.

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[3] Inorganic nitrogen: nitrate and ammonium.

To test if fertilizer affected the flux of the different forms of nitrogen from the litter layer, the collections with a fertilizer pulse were dropped from the analysis. Therefore, the first and twelfth collections were dropped but the thirteenth collection was retained as it was assumed the effect of the 2001 fertilizer application was minimal during the thirteenth collection. The treatment effects and interactions were the same as the results presented below if the thirteenth collection was dropped from the analysis as well.

Treatment effects on litter layer N flux between fertilizer applications

When the three forms of nitrogen are expressed as total nitrogen, all three treatments and the control had an annual retention of nitrogen (Figure 2-2). Herbicide had no treatment effect on net nitrate or ammonium flux (Table 2-2). The fertilized treatments had significantly less retention of nitrate than the non-fertilized treatments (Table 2-2, Figure 2-2). Similarly, the flux of ammonium had significantly greater release or smaller retention in the fertilized treatments than the non-fertilized treatments (Table 2-2, Figure 2-2). For nitrate and ammonium, the date effect and the date x fertilizer interaction were significant because the nitrogen flux and the effects of fertilization varied with sampling date (Table 2-2). The majority of ammonium release occurred during the growing season (Figure 2-2). However, the difference between summer and winter months were less clear for nitrate (Table 2-2, Figure 2-2).

In contrast to nitrate and ammonium, fertilization increased retention of organic nitrogen. In particular, heavy rainfall during the third collection greatly increased retention of organic nitrogen in the fertilized treatments (fertilizer x date interaction) (Table 2-2, Figure 2-2). Within a seven day period, 71 mm of rainfall occurred, which exceeded the capacity of the collection vessels and shortened the collection period to twelve days. Throughfall contained significantly higher organic nitrogen during the third collection than the other periods in the fertilized treatments, while litter leachate was consistent with the other collection periods (not shown). If the third collection was removed from the organic nitrogen analysis, there would be no treatment effect. Without the third collection, there was no clear pattern of seasonality in the flux of organic nitrogen (Figure 2-2). There was also a significant herbicide and herbicide x fertilizer interaction for organic nitrogen. Retention of organic nitrogen was the greatest in the F treatment, followed by HF treatment, then the H treatment and finally C (Figure 2-2). While retention nitrate in of both non-fertilized and fertilized plots seem to increase with age, the trend was not significant (Table 2-3, Figure 2-3). No pattern of annual flux of ammonium occurred with age (Table 2-3, Figure 2-3).

There was no significant difference in throughfall nitrate and ammonium content at the p=0.10 level due to fertilization or competition control (Table 2-4). There were significant H (p=0.003), F (p=0.0002) and H x F interaction (p=0.002) in throughfall organic nitrogen. Throughfall organic nitrogen content was the highest in the F treatment while the HF treatment throughfall organic nitrogen was substantially lower and much more similar to the C and H treatments (Table 2-4). Fertilized treatments had significantly higher nitrate and ammonium content (p= 0.0003 and 0.007 respectively) in the litter leachate (Table 2-4). There was no herbicide or fertilizer treatment effect for litter leachate organic nitrogen content (Table 2-4). Over the collection period, precipitation contained 3.2 kg ha^{-1} yr^{-1} of nitrate-N, 5.2 kg ha^{-1} yr^{-1} of ammonium-N and 5.2 kg ha^{-1} yr^{-1} of organic nitrogen-N. Net canopy N flux[4] of nitrate and ammonium from the fertilized plots was not significantly greater than the non-fertilized treatments (Table 2-5). The retention of organic nitrogen was significantly greater ($p<0.0001$) in the fertilized treatments (Table 2-5). A significant H x F interaction (p=0.0006) occurred because of a large release of organic nitrogen form the canopy was the highest in the F treatment while the HF was substantially lower and similar to the C and H treatments (Table 2-5).

[4] Net canopy N flux: subtracting N content in precipitation from N content in throughfall. Positive number, release of N from canopy. Negative number, retention of N by the canopy.

Throughfall preservative test

In the preservation study, no statistical difference between the three collection methods for nitrate, ammonium and total throughfall N content C (Table 2-6). No significant difference was found between the Set A method (collecting rainfall samples after each event) and Set B method (collectors left at the site for the 21 day period) for organic throughfall nitrogen (Table 2-6). The Set C method (collectors left at the site for the 21 day period with an acid preservative) had significantly greater (p=0.007) organic throughfall nitrogen (Table 2-6). No significant difference was found in the volumes collected between the three methods (not shown).

Discussion

The dominant form of inorganic nitrogen in the litter leachate was ammonium in both the non-fertilized and fertilized treatments (Table 2-4). This was consistent with previous research, as nitrifying bacteria do poorly in conditions with a Ph 4 or less (Haynes 1986); the Ph of the soils in this experiment has been measured as 4 by other researchers[5]. Although nitrate and ammonium have an overall retention, the amount retained was lower in the fertilized treatments than in the non-fertilized treatments. The fertilizer effect continued throughout the year, although at lower rates during winter. Thus, the treatment effect occurred long after the fertilizer had passed through the soil, which was consistent with previous research (Crane 1992, Fife and Nambiar 1997). At age fourteen, the retention of inorganic nitrogen-N in the unfertilised treatments was 6 kg N ha^{-1} yr^{-1} while the fertilized treatments had a retention of 2 kg N ha^{-1} yr^{-1} (Table 2-3). Because the fertilized and non-fertilized treatments had similar throughfall concentrations of inorganic nitrogen, the fertilized treatments had a higher inorganic nitrogen N litter leachate content. Litter leachate inorganic nitrogen content in the fertilized treatments ranged from 5.4 kg ha^{-1} yr^{-1} at age eight to 8.4 kg ha^{-1} yr^{-1} at age fourteen. With an annual uptake of nitrogen in the fertilized treatments of this study averaging about 58 kg ha^{-1} yr^{-1} at age fourteen, litter leachate

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[5] Daniel Markewitz, University of Georgia, Athens, Georgia, USA.

would contribute only 14% of annual uptake compared with litter leachate in the non-fertilized treatments contributing 6% of annual uptake. However, the accumulative effect of the release of inorganic nitrogen over the length of a rotation could be far greater. Assuming annual inorganic nitrogen content in litter leachate remains constant after age fourteen, total release of inorganic nitrogen from age 10 to age 30 would be 25 kg ha^{-1} for the non-fertilized treatments and 142 kg ha^{-1} for the fertilized treatments. An additional 100 kg ha^{-1} could be returned to the mineral soil over twenty years without additional application of fertilizer. After a 25 rotation for a unfertilized *P. taeda* stand, the effect of N additions from atmospheric deposition and fixation and nitrogen losses from stem removal and leaching could change the soil available N budget from a N surplus of up to 300 kg N ha^{-1} to a N to deficit of up to 250 kg N ha^{-1} (Richter *et al.* 2000). Therefore, if over 100 kg ha^{-1} was returned to the mineral soil over a rotation, this would have a significant impact in replacing nitrogen lost from the site by the previous harvest of trees. How long the fertilizer effect would continue if annual fertilization were to be stopped is unknown. Previous research found the effect of fertilizer additions to nitrogen cycling to continue as long as five to twelve years after the last application (Crane 1992, Fife and Nambiar 1997). The length of the fertilizer response, however, was dependent of the amount applied and the number of years it was applied. With a high amount of annual fertilization in this study, it’s reasonable to assume that the fertilizer effect on the flux inorganic nitrogen would continue until the end of the rotation if fertilization stopped at age fourteen.

An important difference between the fertilized and non-fertilized treatments was the amount of nitrogen in the system. The fertilized treatments were able to produce a larger amount of plant biomass than the non-fertilized treatments, which increased the amount of nitrogen cycling in the ecosystem. For example, at age fourteen the amount of organic nitrogen in the litter leachate was 7.5 kg N ha^{-1} in the non fertilized treatments and 12.3 kg N ha^{-1} in the fertilized treatments while ammonium in litter leachate was 1.5 kg N ha^{-1} in the non-fertilized treatments and 6.3 kg N ha^{-1} in the fertilized treatments. The larger amount of N cycling in the fertilized stands magnified the response of mineralization to fertilization. It is not clear if the higher amount of N cycling was in proportion to the increased biomass. The only indication of a change in proportion of N cycling to biomass was that at age fourteen, where the amount of inorganic N in litter leachate to supply the trees N demand increased from 6% to 14%. Thus, the increase in mineralization was small when compared to the N demand of the biomass in the fertilized treatments.

Litter layer processes caused the lower retention of inorganic nitrogen in the fertilized treatments because throughfall nitrogen contents were was similar between the fertilized and non-fertilized treatments. Nitrate and ammonium in throughfall from the non-fertilized treatments had a greater percentage immobilized in the litter layer (81% and 64% respectively) than the fertilized treatments (41% and 10% respectively). Thus, the higher mineralization from the fertilized treatments could have occurred because the majority of microbe nitrogen demand was met by litter decomposition or, throughfall moved fast enough through the fertilized treatment litter layer to prevent higher immobilization rates. As there was enough time to immobilize organic nitrogen, in the litter layer of the fertilized treatments, there would have been enough time to immobilize nitrate and ammonium, which are easier forms of nitrogen for microbes to ingest. Also, the litter layer of fertilized treatments was deeper than the non-fertilized treatments and water would have taken longer to pass through. Therefore, the additional litter leachate nitrate and ammonium was from a higher mineralization rate in the litter layer.

Gunderson *et al.* (1998) hypothesized the greater release in ammonium from the litter layer in the fertilized treatments they found was not caused by a change in the mineralization rate. The fertilizer may have changed the release of ammonium from the litter layer by saturating ammonium immobilization processes (Gunderson *et al.* 1998). This would have caused a greater release of ammonium even though the actual mineralization of litter layer ammonium had not changed (Gunderson *et al.* 1998). The conifer species involved with this study were *Pinus abies*, *Pinus sitchensis*, *Pseudotsuga menziesii* and *Pinus sylvestris* (Gunderson *et al.* 1998).

Gunderson's theory was not highly applicable for this study. As the fertilizer was constantly applied to Gunderson's study, it would be possible to keep ammonium immobilizing processes saturated. However, fertilizer was applied once a year in this study of *P. taeda*. It is unlikely that all the ammonium immobilizing processes would stay saturated for 365 days from one application.

Microbe type and activity, C/N ratio and other litter quality measures or actual decomposition rates of fresh litter were not measured in conjunction of this project. Therefore, the following explanations concerning the effect of fertilization on the mineralization of litter layer is based on previous research and conjecture. Three factors probably influenced the fertilizer effect on inorganic nitrogen release:

1. Canopy nitrogen concentrations were significantly higher in the fertilized treatments and translated to a significantly higher (1 mg g^{-1}) nitrogen concentration in fresh litterfall (Daniel 2001). The increase in nitrogen concentration combined with greater litterfall from a larger canopy created higher litter nitrogen content. At age twelve, the non-fertilized treatments had an average of 146 kg N ha^{-1} in the litter layer while the fertilized treatments had 378 kg N per hectare (Unpublished data[6]). The increase in nitrogen did not approach the critical C:N ratio of 30:1, therefore fertilization was not enough to change the system from nitrogen limited to carbon limited system as the C:N ratio decreased from 125:1 to 100:1 with fertilization (Unpublished data[7]). However, the higher litter layer nitrogen concentration and content per hectare provided a higher mineralization potential in the fertilized treatments.
2. The fertilized treatments had better developed litter horizons. Neither the control nor the herbicide treatment had nearly as well developed fermentation and humus horizons as the fertilizer and herbicide x fertilizer treatments. Nitrogen release during decomposition has

[6] Daniel Markewitz, University of Georgia, Athens, Georgia, USA.

[7] Daniel Markewitz, University of Georgia, Athens, Georgia, USA.

been described to occur in three stages, leaching, accumulation and release, although each of these stages does not always occur in particular ecosystems (Berg and Staaf 1981, Haynes 1986, Polglase *et al.* 1992). The fermentation and humus horizons probably had a greater mass in the fertilized plots where the majority of the release stage occurs. Previous research found that nitrogen content was higher in the fermentation and humus horizons (Jorgensen *et al.* 1980). However, any increase in decomposition caused by improved litter quality from fertilization would not necessarily off-set the increase in litterfall due to an increase in leaf area (McNulty *et al.* 1991). Indeed, litter in the HF treatment was thickest. Conversely, the litter horizon appeared to dominate the litter layer in the non-fertilized treatments. Thus the accumulation stage and therefore immobilization probably played a larger role in the nitrogen flux of the litter layer in the non-fertilized treatments.

3. Organic nitrogen in throughfall was significantly greater in the F treatment with 8.8 kg ha^{-1} yr^{-1} more organic nitrogen than the non-fertilized treatments. The difference in throughfall organic nitrogen resulted from greater leaching of organic nitrogen from the F treatment canopies. No significant difference was found between the treatments in litter leachate organic nitrogen; therefore the majority of throughfall organic nitrogen was retained in the litter layer. Throughfall Dissolved Organic Nitrogen (DON) was available to be consumed by microbes and with the extra nitrogen available, DON could contribute to the net mineralization of inorganic nitrogen from the litter layer. Vestgarden (2001) found the dominant forms of throughfall DON were amides and free amino groups. Therefore microbes could digest these forms of dissolved organic matter (DOM) which could be preferable to nitrogen in plant matter which is contained in hard to digest cells like lignin (Qualls and Haines 1992, Michakik *et al.* 2001). It is not clear from previous research if it would be possible for microbes to preferably consume DON in the DOM without consuming Dissolved Organic Carbon (DOC). Qualls and Haines (1992) argued that because DON did not decompose faster than DOC in the mineral soil, they were linked and it was not possible for

microbes to preferably decompose DON. In contrast, Michakik and Matzner (1999) found a significant but only a weak correlation between DOC and DON, which indicated different decomposition pathways. Thus, previous research has indicated that it could be possible for microbes to preferably choose DON over DOC. Although the increased throughfall DON in the fertilized treatments was not the only factor that increased inorganic nitrogen litter leachate, it probably was a major contributor to the increased mineralization.

Results from previous studies on the effect of fertilization on the amount of DON in litter leachate have ranged from no treatment difference to an increase in DON (Gunderson *et al.* 1996, Kalbitz *et al.* 2000, Fog 1988, McDowell *et al.* 1998, Qualls *et al.* 1991, Vestgarden 2001). The majority of these studies, did not examine throughfall DON so the flux of DON from the litter layer could not be estimated. A contrast with this study and previous research was the dominance of litter leachate DON. Qualls *et al.* (1991) for example, found 94% of litter leachate nitrogen was DON in *Quercus* dominated Appalachian forest in the southeastern United States. Quall's study found for the non-fertilized treatments, 57% of litter leachate nitrogen was DON while 32% was DON in the fertilized treatments. The results of this study are confirmed by other research, which found DON in throughfall was not related to DON in litter leachate (Michakik and Matzner 1999, Michalzik *et al.* 2001). In the canopy from twelve forest ecosystems throughout North America, the canopy was a net source of organic nitrogen (Lovett 1992). The difference between this study and previous research could by due to the *P. taeda* ecosystem and that the measurements were made in the field. Laboratory conditions can cause higher DON release than in the field due to the high, constant temperature and moisture conditions kept during incubation (Kalbitz *et al.* 2000).

The canopy made little contribution to throughfall inorganic nitrogen in the fertilized and non-fertilized treatments since there was either a small release or small retention of nitrate and ammonium from the canopy. Thus, the largest source of inorganic nitrogen entering the litter layer as throughfall was atmospheric. Previous research found an average atmospheric input of nitrogen in the southeastern United States to be between 10 to 12 kg N ha^{-1} yr^{-1} (Johnson and Lindberg 1992). These studies corresponded well with this study where precipitation contained 14 kg N ha^{-1} yr^{-1} of nitrogen. The canopy of the non-fertilized treatments added a small amount to throughfall organic nitrogen. However, the canopy in the fertilized treatments added significantly more organic nitrogen (Table 2-5). For the F treatment, the canopy added 64% of throughfall organic nitrogen (15 kg N ha^{-1} yr^{-1}). Past studies have not reported this phenomenon. The F treatment had significantly more DON leaching from the canopy than the HF treatment. This would indicate that leaching of DON was less from the *P. taeda* canopy and more from the other species. The leaf structure of the other species could be more susceptible to loss of organic compounds through abrasion, leakage during leaf development, stomata and pathogen attack.

The effect of interspecific competition control and litter quality

Differences in flux of litter leachate inorganic nitrogen were not significant between the treatments that did not receive herbicide treatments. Previous research found a difference in decomposition between conifers and broadleaf species (Piatek and Allen 2001). A reasonable assumption was that adding litter of other species growing in the non-herbicide treatments (e.g. *Liquidambar styruciflua* L.) would increase litterfall quality and therefore increase mineralization. However, this was not the case. No effect from the hardwood litter on inorganic N release may have occurred for several reasons; the hardwoods could have effectively retranslocated leaf nitrogen before abscission, or the hardwoods could have been too small proportion of the litter layer to have much influence. Studies in mixing conifer needles with broadleaf species without adding fertilizer have ranged from no effect to an increase in mineralization (Gustafson, 1943, Thomas, 1968). For example *P. taeda* needles decomposed faster in a hardwood mix only when the ratio of hardwood leaves to *P. taeda* needles was 5:1 (Piatek and Allen 2001). Another study found high-quality litter stimulated decomposition of low quality litter only when the proportion of high quality litter was greater than 70% (Finzi and Canham 1998).

The effect of age

The flux of nitrogen did not vary with age. Previous research with litter decomposition found conflicting results with the effect of age; stand age could increase, decrease or have no effect on mineralization (Gholz *et al.* 1985, Jorgensen *et al.* 1980, Van Lear and Goebel 1976). There were trends showing retention of nitrate and organic nitrogen could be increasing with age (Figure 2-3, Table 2-3). An age effect may have been masked by the low power of the age tests. The split-split plot design meant age was a whole plot factor; therefore the test of age had less power than the tests for fertilizer and herbicide effects. Another reason could have been the small difference (six years) between the ages of the study. A wider age interval may be needed to detect an age effect.

The seasonality of the nitrogen flux from the litter layer

The seasonality of the inorganic nitrogen flux over the year is consistent with previous research where temperature, water flux, or temperature and water flux were the primary factors controlling the mineralization rate (Casals *et al.* 1995, Foster 1989, Michalzik and Matzner 1999, Nadelhoffer *et al.*1984, White *et al.* 1988). However, the seasonality was the clearest for net ammonium release while nitrate seem to respond to the amount of precipitation during a collection period. Studies that found no difference in flux over the seasons have generally been incubation experiments where temperatures and moisture were stable. Incubation experiments provide a good measure of the potential leaf litter mineralization rate but not the actual fluxes of nitrogen release under field conditions (Nadelhoffer *et al.* 1984, Raison *et al.* 1987, Tietema *et al.* 1993).

The inconsistency of the fertilizer pulse effect

The 2000 fertilizer pulse corresponded with previous research, however the fertilizer pulse ended faster than previously documented (Sogn and Abrahmsen 1998, Matson *et al.* 1992, Seely and Lajtha 1997). The lack of a large fertilizer pulse in 2001 was surprising. The lack of a 2nd fertilizer pulse could be attributed to low rainfall. If the fertilizer granules were not completely dissolved, the fertilizer pulse may have continued beyond the last collection. Another possibility was that microbes, fine roots and exchangeable sites were able to take up a majority of the fertilizer. With small rainfall events in the last two collections, dissolved fertilizer would not have moved as quickly through the litter layer as during the first collection. This would have given extra time for biotic factors to immobilize the fertilizer and more time for fertilizer to be volatilized, thus creating a smaller fertilizer pulse.

Factors affecting the study

The experimental error associated with the measurements was large. The reason is two fold. Firstly, spatial heterogeneity was large compared to the four lysimeters and three throughfall collectors used to measure net nitrogen release for the 0.15 ha plots. Secondly, data was lost from the Wet site for the sixth and seventh collections. At the end of the sixth collection, some of the lysimeters at the Wet site were contaminated with ground water. As the majority of the lysimeter collection vessel holes were filled with ground water in the sixth collection, it made it impossible to install the collection vessels for the seventh collection. From the eighth collection to the eleventh collection, interbed lysimeters were disconnected for the Waycross Wet and Dry sites. Thus, the lysimeter collectors were halved during the winter months. Although the affected individual dates halved the number of lysimeters, it was assumed this would not have an adverse effect on the annual estimates because microbe activity during winter was low. Problems with spatial heterogeneity and sampling are a common problem in lysimeter research. In a review of lysimeter systems, Titus and Mahendrappa (1996) found large variability in collections of water volumes and nitrogen concentration across a research site as with nitrogen. "Nutrients whose mobility's are largely a function of biological activity are likely to be most variable" (Titus and Mahendrappa 1996).

Interception of throughfall by the litter layer ranged from 20% to 100%. Over the collection period, 1264 mm of precipitation was collected while 911 mm of throughfall and 267 mm of litter leachate were collected. Previous research calculated average interception of the litter layer in natural *P. taeda* forests of 5% of annual precipitation and that litterfall storage capacity would not normally exceed 50 mm yr^{-1} (Hewlett 1982). Either the litter layer in these plots was far more efficient in intercepting throughfall, even in the control plots, or the volume collected in the vessels underestimated the volume of the water passing through. Water uptake of root mats in the litter layer also could reduce litter leachate. The potential effects of root mats are discussed below. Rainfall intensity could have been a factor; Kittredge (1948) found the forest floor in natural southeastern forests could retain all throughfall if it was less than 5 ml per rainfall event. Low solute collection efficiency and variance between lysimeters continue to be an issue in using lysimeters for research (Titus and Mahendrappa 1996, Russell and Ewel 1985, Jemison and Fox 1992). Collection efficiency at a depth of 10 cm from one study increased from 10 to 26% when the tray size was increased from 162 cm^2 to 2500 cm^2. The largest tray (2500 cm^2) was 36% efficient under grass and 17% efficient under forest (Radulovich and Sollins 1987). In contrast, Haines *et al.* (1982) estimated lysimeter collection efficiency (with an area of 162 cm^2) at 82%. The small area (300 cm^2) of the collectors plus the limited number of collectors probably underestimated the volume of solute passing through the litter layer. However, the samples collected are a good measure of the nitrogen concentration. The assumption used for this study was a certain volume of solute would bypass the lysimeters but the nitrogen concentration in the water collected would be representative of the total volume passing through the litter layer and that the bias in sample volume collected would be consistent across the treatments. These assumptions were consistent with previous lysimeter research (Titus and Mahendrappa 1996). As no water budget was estimated for the sites, there was no reasonable way to approximate the actual annual volume of litter leachate. The volume weighted nitrogen concentrations were calculated to see if the low litter leachate volumes affected the estimated net nitrogen flux. The estimated rates of N flux could be a function of the low lysimeter volumes rather than actual net N release. If the litter leachate N concentration was inflated by low volumes collected from the fertilized treatments, this could exaggerate the effect of fertilization on the litter layer N flux. The N flux of volume weighted concentrations were in the same magnitude with what was estimated in Table 2-3. The treatment effects on throughfall and litter leachate were also the same. Although the litter leachate volumes collected were probably conservative in that they underestimated flux if a large amount of litter leachate bypassed the lysimeters. The litter leachate volumes were probably enough to measure the general effect of the treatments on the flux of nitrogen from the litter layer.

A potential confounding factor was extensive root mats in the fermentation and humus horizons of the litter layer in some of the plots. At installation, approximately half of the plots had fine root mats. As most of the nutrients in Coastal Plain soils are located in the A horizon or the litter layer, this is a normal occurrence for *P. taeda* forests. Extensive root mats occurred mainly in the older plots. Root mats where left in place for two reasons. Firstly, removing the root mat would have disturbed and removed part of the F and H horizons. Secondly, root mats would probably have grown back after installation. Root mats could have confounded the experiment by removing inorganic nitrogen from the solute before entering the lysimeter and altering the hydrology of the litter layer by reducing volume collection by absorbing water. Alternatively, turnover of fine roots could have contributed to nitrogen release from the litter layer. However, from observation at installation and volumes collected afterwards, there seemed to be no correlation between the occurrence of the root mat and flux of particular forms of nitrogen. Previous research on nutrient release of root mats is limited, although some research does indicate that extensive root mats could have an important impact on nitrogen release from the litter layer (Parsons *et al.* 1994, Perez *et al.* 1991, Stark and Jordan 1978).

Testing the stability of the forms of nitrogen in throughfall nitrogen

Various methods have been used to preserve nitrogen in the field (Titus and Mahendrappa 1996). Studies that leave samples in the field balance the time between collections and loss of nitrogen through volatilization, decomposition and consumption as well as switching from one form of nitrogen to another (Titus and Mahendrappa 1996). For example, Harr and Fredriken (1988) found a 17% loss of nitrate concentration of stream water samples after 3 weeks. To obtain a measure of nitrogen losses from this flux experiment, a throughfall preservative test was set-up in July 2001 using three sample preservation techniques. It was generally believed that samples taken after each rainfall event are the most accurate form of sampling as no nitrogen would be lost or transformed nor solute lost by evaporation. The study site for the main study was 400 km from the University of Georgia. Thus, collections after each rainfall event were impracticable. In the preservation study, no significant difference was found between Set A (samples collected after each rainfall event) and Set B (no preservative, left out for the entire collection period of 21 days) for all types of nitrogen, although ammonium content in Set B was 1.8 times greater than Set A (Table 2-6). Thus for inorganic nitrogen concentration in throughfall solute, there was no significant difference in leaving the solute out for 21 days. However, there was high variability in the data. With more samplers and replication over a year, the difference in ammonium content between Set A and Set B could be significant. Organic nitrogen was estimated by subtracting inorganic nitrogen from total nitrogen. The high organic nitrogen content in Set C was from the high total nitrogen content. It was not clear the cause of total nitrogen being higher in Set C. The sulfuric acid preservative could have affected the persulphate digest. This was not tested in the sub-experiment. The results do show that throughfall organic nitrogen content measured in the main experiment was not overestimated. More importantly, there was no significant difference between Set A and Set B. Throughfall was chosen for this sub-experiment as the solute was exposed to high temperature fluxes and light, thus it was more likely to have nitrogen loss and transformations. Litter leachate solute was less vulnerable to nitrogen loss and transformations as it was kept cool underground and was not exposed to light. Therefore, it was unlikely that there was a large difference in litter leachate nitrogen solutes if Set A method was used.

Summary and Conclusions

Annual fertilizer applications caused a significant pulse of N in the litter leachate solution shortly after fertilization. The fertilized treatments had significantly less retention of nitrate and ammonium compared to the non-fertilized treatments. Fertilization had no impact on organic nitrogen content in litter leachate, however fertilizer doubled organic N in throughfall, which significantly increased the retention of organic nitrogen in the litter layer. The effect of fertilizer on N retention in the litter layer was sustained after the initial fertilizer pulse had passed through the litter layer. The decrease in retention of inorganic N in the litter layer was not due to a change in throughfall, but from a greater amount of inorganic N in litter leachate. The increased retention of organic N in the fertilized treatments was associated with a large retention of organic N was due to greater throughfall and no change in litter leachate. The large increase in throughfall DON associated with fertilization applications had not been reported in previous research. Competition control had no effect on the flux of nitrate or ammonium from the litter layer. The lower retention of organic nitrogen in the competition control treatments resulted from the lower amount of organic nitrogen leached from the canopy. The flux of inorganic N did vary seasonally. No significant age effect was found for any form of N. The fertilizer accelerated stand development with, deeper, more developed litter layers and increased N concentration in fresh litterfall.

The N fluxes indicate that mineralization occurred at a greater rate in the fertilized treatments likely due to better litter quality, better developed litter layer and the high amount of throughfall DON being available for microbe consumption. Although inorganic nitrogen content in the litter leachate increased for the fertilized treatments, the litter layer was still a net sink of N as microbes were still N limited. The amount of inorganic N leaving the litter layer in the litter leachate in the fertilized treatments (8 kg ha^{-1}) would be 14% of the annual tree uptake of 58 kg N ha^{-1} yr^{-1}. In contrast, the amount of inorganic N leaving the litter layer in the litter leachate from the non-fertilized treatments contributed 6% of the annual N uptake. The N flux from in the litter layer has changed in response to fertilizer inputs, although not enough to approach the amount of N that was applied annually. However, the total amount of inorganic N released from age fourteen to age 30 could be over 100 kg ha^{-1} which would have an important impact on N supply in plantation forests of the southeastern United States.

Table 2-1: Annual volume weighted concentration for annual nitrate, ammonium and organic N content in throughfall and litter leachate by the control (C), herbicide (H), fertilizer (F) and herbicide and fertilizer (HF) treatments at Waycross, GA. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen). Concentrations and volumes from collections two to eleven and thirteen were used.

	Treatment	Nitrate mg l^{-1}	Ammonium mg l^{-1}	Organic mg l^{-1}	Total mg l^{-1}
Throughfall	C	0.127	0.167	0.218	0.509
	H	0.123	0.210	0.247	0.576
	F	0.133	0.239	0.791	1.162
	HF	0.145	0.252	0.324	0.727
Litter Leachate	C	0.043	0.101	0.133	0.280
	H	0.034	0.073	0.152	0.261
	F	0.178	0.275	0.162	0.525
	HF	0.092	0.199	0.135	0.435

Table 2-2: p-values of the nitrate, ammonium and organic N flux from the litter layer by age, treatment and collection date for *P. taeda* stands at Waycross, GA. Samples were collected on average every 23 days for a one year period. Treatment effects tested were a factorial combination of fertilization and competition control. Fertilization treatments consisted of annual fertilization with an average of 70 kg N ha^{-1} yr^{-1} and no fertilization. Herbicide treatments consisted of complete elimination of interspecific competition and no control of competing vegetation. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen).

	p-values			
Variable	Nitrate	Ammonium	Organic N	Total N
Age	n.s.	n.s.	n.s.	n.s.
Site	n.s.	0.030	n.s.	0.040
Fertilizer	0.013	0.047	0.004	n.s.
Herbicide	n.s.	n.s.	0.027	n.s.
Herb x Fert	n.s.	n.s.	0.021	n.s.
Age x Fert	n.s.	n.s.	n.s.	n.s.
Age x Herb	n.s.	n.s.	n.s.	n.s.
Age x Fert x Herb	n.s.	n.s.	n.s.	n.s.
Date	>0.0001	>0.0001	>0.0001	>0.0001
Date x Age	n.s.	n.s.	n.s.	n.s.
Date x Fert	>0.0001	>0.0001	>0.0001	>0.0001
Date x Herb	n.s.	n.s.	>0.0001	>0.0001
Date x Age x Fert	n.s.	n.s.	n.s.	n.s.
Date x Age x Herb	n.s.	n.s.	n.s.	n.s.
Date x Fert x Herb	n.s.	n.s.	>0.0001	>0.0001
Date x Age x Fert x Herb	n.s.	n.s.	n.s.	n.s.

n.s: not significant.

Table 2-3: Annual nitrate, ammonium and organic N flux from the litter layer by non-fertilized (NF) and fertilized (F) treatments and age for *P. taeda* stands at Waycross, GA. Samples were collected on average every 23 days for a one year period. Annual flux for the three types of nitrogen was the average daily flux over collections two to eleven and thirteen multiplied by 365 days. Treatment effects tested were a factorial combination of fertilization and competition control. Fertilization treatments consisted of annual fertilization with an average of 70 kg N ha^{-1} yr^{-1} and no fertilization. Herbicide treatments consisted of complete elimination of interspecific competition and no control of competing vegetation. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen). Standard error in parenthesis.

Stand Age	Treatment	Nitrate kg N ha^{-1} yr^{-1}	Ammonium kg N ha^{-1} yr^{-1}	Organic Nitrogen kg N ha^{-1} yr^{-1}
8 yrs	NF	-2.12 (0.21)	-2.60 (1.26)	-3.09 (0.32)
	F	-1.20 (0.55)	-0.28 (0.18)	-9.68 (4.03)
12 yrs	NF	-2.91 (0.29)	-2.79 (0.61)	-1.68 (0.98)
	F	-1.62 (0.44)	-0.35 (1.61)	-7.14 (3.56)
14 yrs	NF	-3.31 (0.63)	-2.70 (0.92)	-5.27 (1.51)
	F	-2.03 (0.51)	0.28 (1.62)	-9.46 (2.82)

Table 2-4: Annual nitrate, ammonium and organic nitrogen content in throughfall and litter leachate by the control (C), herbicide (H), fertilizer (F) and herbicide and fertilizer (HF) treatments for *P. taeda* stands at Waycross, GA. Annual N content for the three types of nitrogen in throughfall and litter leachate was the average daily N content over collections two to eleven and thirteen multiplied by 365 days. There was no significant age effect, therefore the three age groups for each treatment were collapsed. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen). Standard error in parenthesis.

		Nitrate	Ammonium	Organic N
	Treatment	kg N ha^{-1} yr^{-1}	kg N ha^{-1} yr^{-1}	kg N ha^{-1} yr^{-1}
Throughfall	C	3.25 (0.39)	4.11 (0.61)	5.87 (0.30)
	H	3.05 (0.30)	4.92 (1.02)	6.52 (0.90)
	F	3.32 (0.25)	5.90 (0.43)	15.04 (2.02)
	HF	3.62 (0.29)	5.29 (0.87)	8.11 (0.79)
Litter Leachate	C	0.70 (0.11)	1.92 (0.34)	2.89 (0.33)
	H	0.50 (0.13)	1.34 (0.19)	3.03 (0.38)
	F	2.33 (0.30)	5.67 (1.33)	3.70 (0.75)
	HF	1.78 (0.37)	4.39 (0.77)	3.03 (0.35)

Table 2-5: Annual net canopy N flux (Throughfall N – Precipitation N) of nitrate, ammonium and organic N content in by the control (C), herbicide (H), fertilizer (F) and herbicide and fertilizer (HF) treatments for *P. taeda* stands at Waycross, GA. Annual flux for the three types of nitrogen in throughfall and litter leachate was the weighted average daily flux over collections two to eleven and thirteen multiplied by 365 days. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen). Standard error in parenthesis.

Treatment	Nitrate kg N ha^{-1} yr^{-1}	Ammonium kg N ha^{-1} yr^{-1}	Organic N Kg N ha^{-1} yr^{-1}
C	0.11 (0.35)	-1.14 (0.59)	0.53 (0.31)
H	-0.09 (0.29)	-0.50 (1.10)	0.96 (1.01)
F	0.15 (0.24)	0.57 (0.44)	9.64 (2.10)
HF	0.42 (0.26)	0.26 (0.97)	2.97 (0.80)

Table 2-6: Throughfall nitrate, ammonium and organic N concentration and content with 2 collection methods and a preservative method at Athens, GA. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen). Standard error in parentheses.

Nitrogen concentration

Collection Method	Nitrate $mg\ l^{-1}$ $x\ 10^{-3}$	Ammonium $mg\ l^{-1}$ $x\ 10^{-3}$	Organic $mg\ l^{-1}$ $x\ 10^{-3}$	Total $mg\ l^{-1}$ $x\ 10^{-3}$
Collection after each rainfall event (Set A)	0.32 (0.04)	0.35 (0.15)	0.27 (0.10)	1.13 (0.12)
Collected after 21 day's (Set B)	0.32 (0.05)	0.79 (0.15)	0.16 (0.05)	1.78 (0.22)
Preservative (Set C)	0.026 (0.04)	0.61 (0.14)	0.60 (0.07)	2.12 (0.25)

Nitrogen content

Collection Method	Nitrate $g\ N\ ha^{-1}$	Ammonium $g\ N\ ha^{-1}$	Organic $g\ N\ ha^{-1}$	Total $g\ N\ ha^{-1}$
Collection after each rainfall event (Set A)	117 (13)	125 (25)	196 (37)	439 (60)
Collected after 21 day's (Set B)	98 (19)	260 (64)	216 (53)	574 (114)
Preservative (Set C)	93 (10)	232 (72)	451*** (**54)	776 (132)

*****Significantly larger ($p<0.05$) than the other method's for the particular form of nitrogen.

Figure 2-1: Nitrate, ammonium and organic N flux per day by each collection period for collection periods one to thirteen at different aged stands for non-fertilized (NF) and fertilized (F) treatments for *P. taeda* stands at Waycross, GA. Treatment effects tested were a factorial combination of fertilization and competition control. Fertilization treatments consisted of annual fertilization with an average of 70 kg N ha^{-1} yr^{-1} and no fertilization. Herbicide treatments consisted of complete elimination of interspecific competition and no control of competeing vegetation. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen). Vertical bars represent one standard error from the mean. No flux was estimated for the Wet site for collection seven, therefore no standard error was calculated.

Collection 1 = 4/23/00 to 5/16/00, collection 2 = 5/21/00 to 6/13/00, collection 3 = 6/15/00 to 6/22/00, collection 4 = 6/27/00 to 7/18/00, collection 5 = 7/24/00 to 8/14/00, collection 6 = 8/29/00 to 9/19/00, collection 7 = 9/21/00 to 10/26/00, collection 8 = 11/13/00 to 12/8/00, collection 9 = 12/13/00 to 1/14/01, collection 10 = 1/16/01 to 2/9/01, collection 11 = 2/10/01 to 3/6/01, collection 12 = 3/12/01 to 4/3/01 and collection 13 = 4/15/01 to 5/9/01.

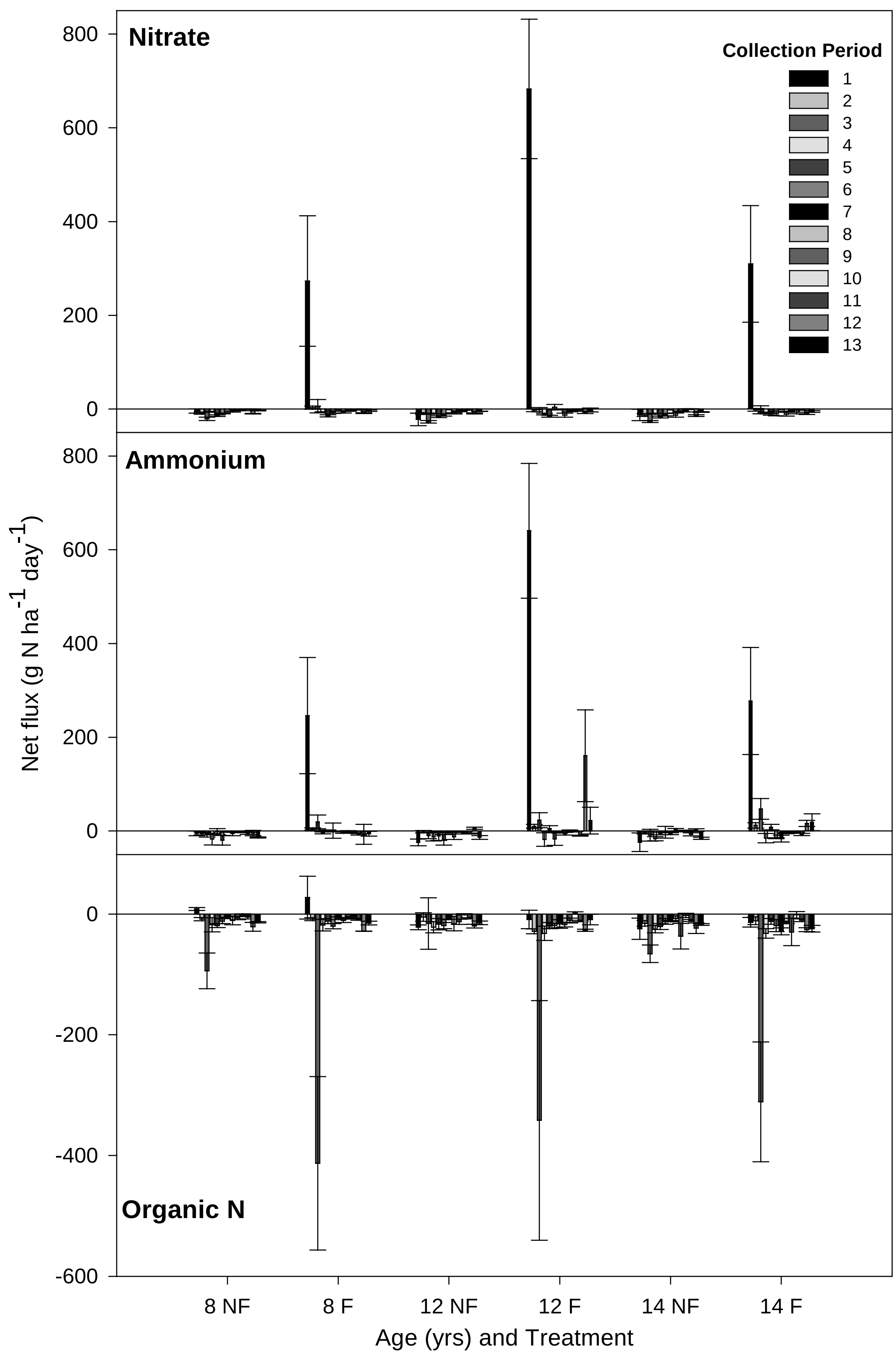

Nitrate
Ammonium
Organic N
Collection Period
1
2
3
4
5
6
7
8
9
10
11
12
13
800
600
400
200
0
-200
-400
-600
Net flux (g N ha^{-1} day^{-1})
8 NF
8 F
12 NF
12 F
14 NF
14 F
Age (yrs) and Treatment

Figure 2-2: Nitrate, ammonium and organic N flux per day by each collection period for collection periods two to thirteen at different aged stands for non-fertilized (NF) and fertilized (F) treatments for *P. taeda* stands at Waycross, GA. Treatment effects tested were a factorial combination of fertilization and competition control. Fertilization treatments consisted of annual fertilization with an average of 70 kg N ha^{-1} yr^{-1} and no fertilization. Herbicide treatments consisted of complete elimination of interspecific competition and no control of competing vegetation. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen). Vertical bars represent one standard error from the mean. No flux was estimated for the Wet site for collection seven, therefore no standard error was calculated.

Collection 2 = 5/21/00 to 6/13/00, collection 3 = 6/15/00 to 6/22/00, collection 4 = 6/27/00 to 7/18/00, collection 5 = 7/24/00 to 8/14/00, collection 6 = 8/29/00 to 9/19/00, collection 7 = 9/21/00 to 10/26/00, collection 8 = 11/13/00 to 12/8/00, collection 9 = 12/13/00 to 1/14/01, collection 10 = 1/16/01 to 2/9/01, collection 11 = 2/10/01 to 3/6/01, collection 12 = 3/12/01 to 4/3/01 and collection 13 = 4/15/01 to 5/9/01.

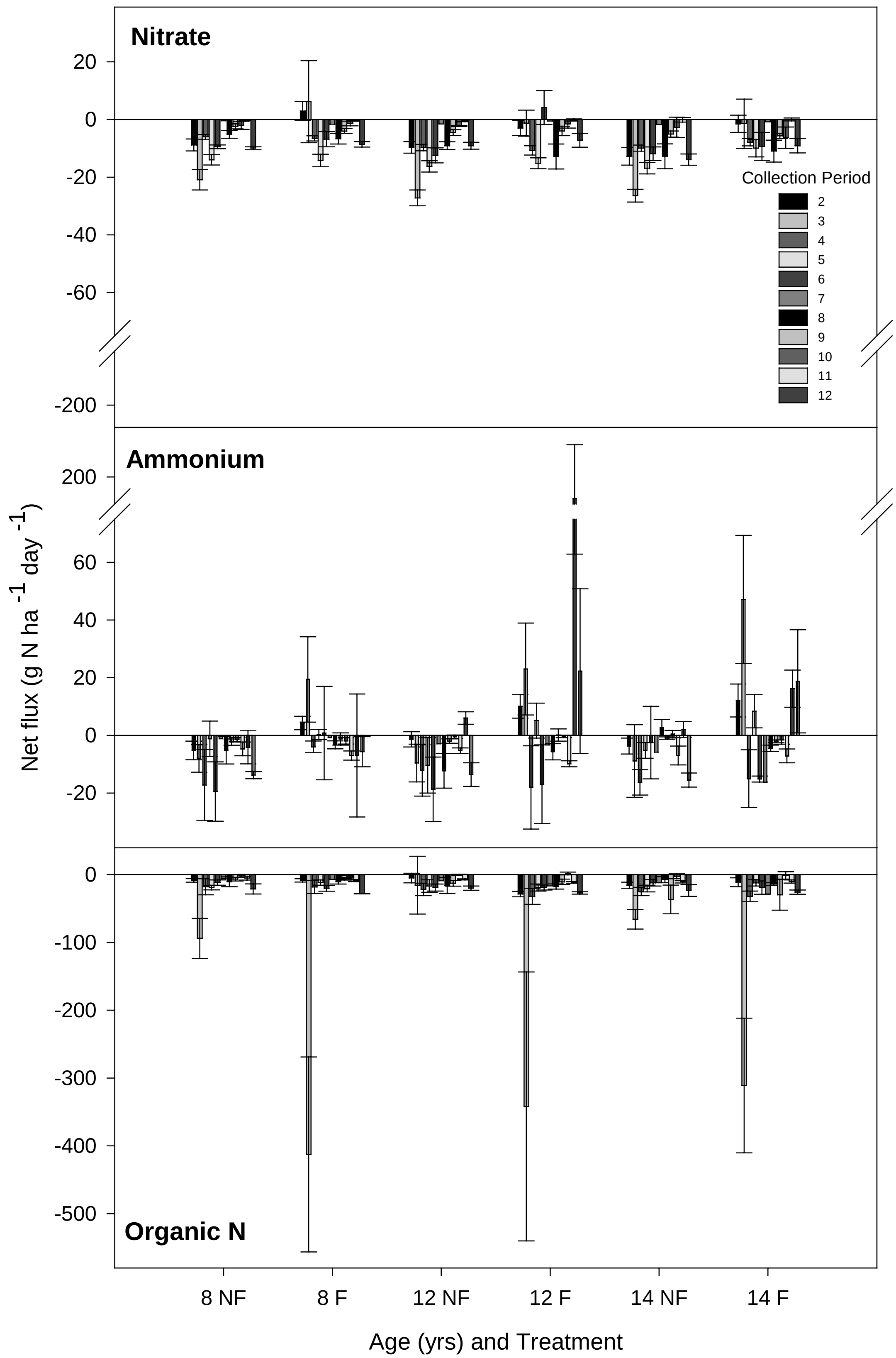
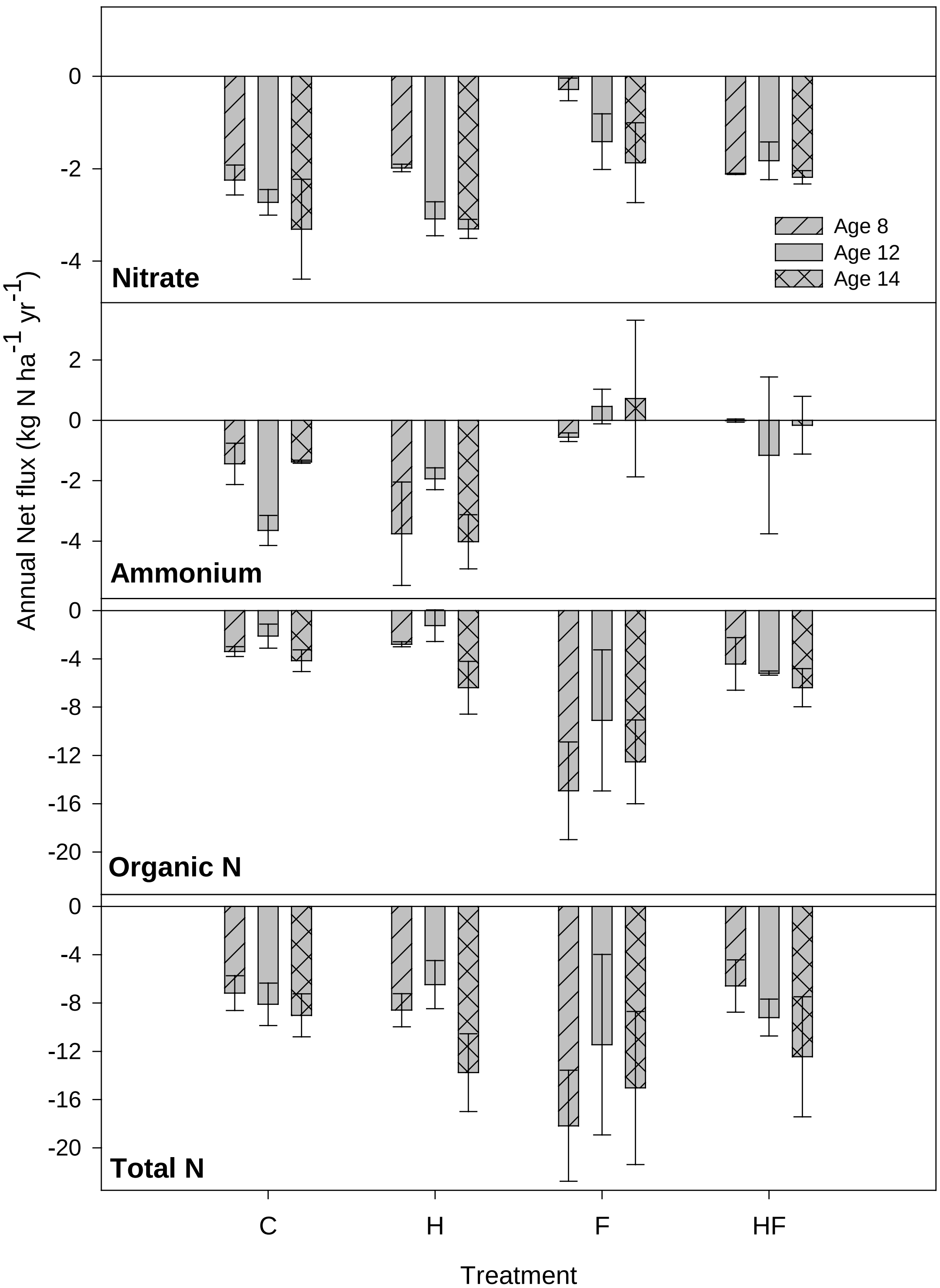

Nitrate
Ammonium
Organic N
Collection Period
2
3
4
5
6
7
8
9
10
11
12
20
0
-20
-40
-60
-200
200
60
40
20
0
-20
0
-100
-200
-300
-400
-500
Net flux (g N ha -1 day -1)
8 NF
8 F
12 NF
12 F
14 NF
14 F
Age (yrs) and Treatment

Figure 2-3: Annual nitrate, ammonium, organic and total N flux for the control (C), herbicide (H), fertilizer (F), and herbicide x fertilizer (HF) treatments by age for *P. taeda* stands at Waycross, GA. Fertilization treatments consisted of annual fertilization with an average of 70 kg N ha^{-1} yr^{-1} and no fertilization. Herbicide treatments consisted of complete elimination of interspecific competition and no control of competing vegetation. The mean for the ages eight, twelve and fourteen was taken for each treatment. Annual flux for each type of nitrogen was the sum of fluxes from collections two to eleven and thirteen. Stands were established in 1993 (age eight), 1989 (age twelve) and 1987 (age fourteen). Vertical bars represent one standard error from the mean.



Nitrate
Ammonium
Organic N
Total N
Age 8
Age 12
Age 14
Annual Net flux (kg N ha-1 yr-1)
Treatment
C
H
F
HF
0
-2
-4
2
-8
-12
-16
-20

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CHAPTER THREE:

THE EFFECT OF INTERSPECIFIC COMPETITION CONTROL AND ANNUAL NITROGEN FERTILIZATION ON NUTRIENT DYNAMICS OF ABOVE GROUND TREE COMPONENTS OF DIFFERENT AGED *PINUS TAEDA* STANDS

Introduction

In the last 30 years, fertilization has become an important management tool to increase productivity of plantation species in the southeastern United States (Dangerfield and Hubbard 1998). In the early 1990’s fertilizer was applied to 150,000 ha per year of *Pinus taeda* (L.) forest throughout the southeast (Zhang and Allen 1996). Research has repeatedly demonstrated the positive effects of fertilization on growth; however, the mechanisms of how *P. taeda* respond to treatments that increase nutrient availability are poorly understood. For example, does fertilization increase chlorophyll per unit of canopy, or increase biomass allocation from root to shoot, or does it just increase the amount of foliage per unit of area. This has lead to hit or miss applications and unpredictable productivity gains. A better understanding of the mechanisms of the tree’s response to fertilization should improve stand management because prescriptions could be tailored to sites using process rather than site specific empirical data.

Determining the mechanisms of competition control and fertilization is difficult. Results from experiments in the laboratory are limited by tree age and inference is limited. The results from operational treatments in the field are often confounded by other environmental factors. Using extreme treatments like annual application of fertilizer and complete interspecific competition control push the tree to the upper limits of growth. By doing so, the mechanisms of the tree’s response to the treatments can be more readily examined. Nutrient pools change during the growing season (Wells and Metz 1963), therefore, nutrient samples need to be collected in the dormant season to ensure a stable picture of nutrient pools throughout the tree. Sampling in winter removes the confounding effects associated with active growth.

The objective of this study was to investigate changes in the nutrient pools of the above ground tree components due to fertilization, competition control and stand development. Previous work examining nutrient changes with stand development has concentrated on changes in nutrient pools and their respective ratio's to nitrogen (N) for stands that have not received intensive treatments. Research that has examined treatment effects (i.e., fertilization) on tree nutrients has generally only looked at one age. It is not clear from these studies if the treatment response at one stage of stand development would be the same at another stage.

The hypotheses were:

1. Fertilizer will increase foliar and total above ground tree components NPK content and concentration, but decrease nutrient use efficiency. Trees will exhibit luxury uptake of fertilized NPK and store the extra nutrients throughout the tree, increasing NPK concentration in all parts of the tree. Measures of nutrient use efficiency will decrease as not all of surplus nutrients will be used for growth or physiological processes related to growth.
2. The control of competing vegetation will increase foliar and above ground tree components NPK content while concentration and measures of nutrient use efficiency will not be affected by competition control. Without interspecific competition, more nutrients contained in the soil are available for tree uptake. Therefore, tree growth increases in response to removal of competition, but the increase in growth rate is maintained only as long as additional nutrient are available. As the stands develop, the trees fully take up the available nutrients. Therefore concentrations and efficiencies will become similar after the first several years of stand development.

3. With increasing age, NPK content will increase, NPK use efficiency will decrease and NPK concentration will remain the same. Nutrient concentration in all parts of the tree will be the same over time. Therefore, any increase in nutrient content as the stand develops will be proportional to tree growth. Canopy closure will slow growth and reduce nutrient use efficiency.
4. For the fertilized treatments, foliar concentrations for nutrients not added will decrease compared to N but remain the same for the competition control treatments. There is no evidence in previous research of active uptake of non-fertilized nutrients to compensate for fertilized nutrients. Either the tree is able to redistribute nutrients not added by fertilizer from other parts of the tree or these nutrients will be diluted in the foliage of the fertilized treatments. Conversely, competition control will not have the same effect because any increase in growth will be proportional to the natural soil nutrient pools.

To answer these questions, *P. taeda* trees were sampled from stands established at three different times with the factorial combination of annual fertilization and complete interspecific competition control. The factorial design meant that not only the individual treatment effects could be tested, but also treatment and age interactions could be clearly examined. Two replications of the above experiment were established at two sites in the Piedmont and two sites in the Lower Coastal Plain, which gave insight into any treatment differences in two physiographic regions. Important plant marco and micro nutrients were sampled from all sections of the above ground tree components to give a clear comprehensive understanding of nutrient dynamics under such widely differing treatments.

Site Description and Methodology

The study was established at two locations in the State of Georgia, USA; the BF Grant Forest on the Piedmont and Dixon Memorial Forest on the Coastal Plain. BF Grant Forest is located 20 km south of Madison (33° 24' N, 83° 30' W). Dixon Memorial Forest is located 16 km southeast of Waycross (31° 10' N, 82° 18' W). Both locations were established on recently clear-cut areas that had previously supported *P. taeda* stands. Before planting, the plots at BF Grant forest were sheared, raked and then the remaining vegetation was piled and burned. When the site was cleared of vegetation, it was disked. Raking, piling and disking were typical intensive site preparation techniques in the Piedmont. At the plots in the Dixon Memorial Forest, remaining vegetation on the sites was piled and burned, leaving it relatively clear of vegetation. The sites were then bedded with an average bed height of 53 cm and an average width between rows of 6.4 m. The site preparation technique was typical for the Lower Coastal Plain. The genetically improved (1-0) seedlings used for this study were from half-sib family 10-25 for BF Grant Forest and 7-56 for Dixon Memorial Forest (North Carolina State Tree Improvement Cooperative). Seedlings at both sites were hand planted at a density of 823 stems per hectare (Borders and Bailey 2001).

At each location, two research sites were installed, each containing three stand ages. For each age, a complete factorial combination of fertilization and interspecific competition control treatments were installed in plots of 0.15ha. At BF Grant Forest, the two sites were designated as Powerline and Monitor with plots established in 1988, 1990 and 1995. The youngest age at BF Grant Forest was only replicated once at Powerline and once at Monitor while the older ages were replicated twice at each site. Replicates of a particular stand age within a site were not randomly located, but installed adjacent to each other. The slope at the Monitor site was steeper than the Powerline site; however, slopes were no steeper than 15%. At Dixon Memorial Forest, the two sites were designated as Waycross Wet and Waycross Dry with plots established in 1987, 1989 and 1993. Each age was replicated twice at Waycross Wet and Waycross Dry. Waycross Wet usually experiences standing water during the winter months while Waycross Dry does not. The slope at Waycross Wet and Dry was <1%.

The specific treatments were as follows:

- Control (C): no treatments after the intensive mechanical site preparation.
- Herbicide (H): At ages one, two and three, 292 ml ha^{-1} of sulfomethuron methyl was broadcast evenly over the sites. Follow up treatments of directed sprays of glyphosate were applied in mid-summer. From age three, directed sprays of glyphosate were applied annually where needed to keep plots clear of competing woody and herbaceous vegetation (Borders and Bailey 2001). All of the herbicides were non-soil active.
- Fertilization (F): annual fertilizer additions were applied at the following rates; years one and two had 78 kg ha^{-1} of nitrogen (N) in the form of ammonium nitrate plus 58 kg ha^{-1} of potassium in spring in the form of potassium chloride, followed by 59 kg ha^{-1} of phosphorus and 19 kg ha^{-1} of nitrogen in mid-summer in the form of diammonium phosphate. From year three to year ten, ammonium nitrate was applied each spring, adding 59 N kg ha^{-1} yr^{-1}. At age eleven, the annual N application rate increased to 118 kg N ha^{-1}. In addition, 36 kg P ha^{-1} (as triple super phosphate) was added (Borders and Bailey 2001). At age twelve and thirteen, the fertilizer applications at BF Grant Forest and Waycross differed. At BF Grant, ammonium nitrate was applied at 92 kg N ha^{-1} at age twelve and 118 kg N ha^{-1} at age thirteen. Application of Super Rainbow® fertilizer at age twelve added 179 kg P ha^{-1} and 45 kg K ha^{-1} and approximately 6 kg ha^{-1} of magnesium (Mg), 17 kg ha^{-1} of calcium (Ca), 17 kg ha^{-1} of sulfur (S), 3 kg ha^{-1} of boron (B), 0.6 kg ha^{-1} of copper (Cu), 2 kg ha^{-1} of manganese (Mn) and 5 kg ha^{-1} of iron (Fe). At Waycross the amount of N applied at age thirteen was reduced to 92 kg N ha^{-1} and an application of Super Rainbow® fertilizer in the same year added 179 kg P ha^{-1} and 45 kg K ha^{-1} and approximately 6 kg ha^{-1} of Mg, 17 kg ha^{-1} of Ca, 17 kg ha^{-1} of S, 3 kg ha^{-1} of

B, 0.6 kg ha^{-1} of Cu, 2 kg ha^{-1} of Mg and 5 kg ha^{-1} of Fe. Appendix C and D list the application rates of the various fertilizers for each year.

- Herbicide + Fertilization (HF): Herbicide and Fertilizer treatments combined.

Soils at Powerline and Monitor were well drained with Cecil being the dominant soil series. Cecil series is defined as fine, kaolinitic, thermic Typic Kanhapludults. Cecil series soils on these sites were associated with Pacolet, Appling and Davidson series. A number of the plots had visible surface erosion. Annual rainfall for the region was 1220 mm while mean annual temperature was 15 °C. Waycross Dry has well drained to moderately well drained soils. The dominant soil series was Bonifay. The Bonifay series was described as a loamy, siliceous, subactive, thermic, Grossarenic Plinthic Paleudult. Bonifay series was associated with Blanton series. The Waycross Wet site was a poorly to somewhat poorly drained soil. The dominant soil series was Pelham. The Pelham series was described as a loamy, siliceous, subactive, thermic Arenic Paleaquult. Pelham series was associated with Rigdon series. Annual rainfall for the region was 1270 mm while mean annual temperature was 19 °C (Soil Survey Division, 2001).

Sampling and Analysis

Measurements in each plot were from trees within a buffer that was three rows deep. To sample trees from both forests at similar ages, tree harvests were done in December 1998 and January 1999 at Waycross and January 2000 at BF Grant. However, the youngest age at Powerline and Monitor were one year younger at harvest than the Waycross sites as it was established two years later. Therefore, the ages at harvest were five, ten and twelve at BF Grant and six, ten and twelve at Waycross. Trees were harvested in winter during the period when nutrient concentrations are most stable. Four trees were harvested per plot; the belowground biomass was not harvested. Foliar samples were randomly taken from six locations from the upper and middle canopy at Waycross and upper, middle and lower canopy at BF Grant. Each sample was 3 to 5 g, with only current year foliage sampled. Within each canopy position, samples were bulked for individual trees. For branch bark and branch wood, three 75 mm branch lengths were cut from branch sections of the upper, middle and lower canopy and branch bark was separated by using a potato peeler at the site. Branch bark was only collected from trees at Waycross. Composite samples of branch bark and branch wood from each tree were stored in separate paper bags. Needles were placed on ice in the field and stored at 4 °C in the laboratory until they were processed. Stem bark and stem wood samples were taken from a disk sampled from each tree at 122 cm height. Foliage, branch bark, branch wood, stem bark and stem wood were dried for several weeks at 64 °C in paper bags before they were ground. All branch wood and stem samples were first coarse ground with a Wiley mill. Then all tissue samples were finely ground with a Wiley mill to pass through a 40-mesh sieve. Samples were stored in air-tight plastic bags until the nutrient concentrations were determined. Final composite samples from each tree for nutrient analysis were lower foliage (BF Grant only), middle foliage, upper foliage, branch bark, branch wood (BF Grant only), stem bark and stem wood.

Before nutrient analysis, one tree was dropped from the four trees sampled per plot for financial reasons. Nutrient concentrations were measured separately for each tree. All nutrients (B, Ca, Cu, Fe, K, Mg, Mn, Mo, P and Zn) except for N were analyzed using the inductively coupled plasma technique. Samples (4 mg) were dried for four hours at 500 °C before being cooled. Then 10 ml of an aqua regia solution was added to each sample (containing 30% 12.1 M HCl and 10% 15.7 M HNO_3^-). Samples were allowed to settle; then the liquid from each sample was extracted and placed in a Model 965 Plasma Atomcorp (Thermo-Jarrel Ash, Franklin, MA). The liquid was burned in an argon flame at 3000 °C. The light wavelengths produced were split by defraction grading and passed through a photo multiplier to intensify the wavelength measured for each nutrient. The absorption of the wavelength was proportional to the nutrient concentration.

For N concentration, the Waycross samples were run on a NC2100 CNS analyzer and the BF Grant samples were run on a NA 1500 nitrogen/carbon analyzer (CE Elantech Inc, Lakewood, NJ, USA). Both machines used the same N measuring technique. Calibration curves were developed using a 2,5-Bis-(5-tert.-butyl-benzoxazol-2-yl)-thiophen (BBOT) standard. A 5 to 10 mg sample was used for the Waycross samples while the BF Grant samples used between 1 to 2 mg. Samples were dropped into a 900 °C combustion tube where a measured amount of oxygen was added to combust the sample at 1,800 °C. The combusted gases were driven through an oxidative catalyst layer to complete the oxidation of N. The gases were then forced through a copper-reducing column (kept at 780 °C) to reduce nitrate to elemental N. Helium carried the gases through an anydrone water trap and a gas chromatograph column to remove impurities before passing across a thermal conductivity detector. The electrical signal produced was proportional to the concentration of N in the sample. Twenty randomly selected samples run through the first machine were later run through the second machine in February 2001 to test if there was a significant difference in measurements due to machine. No difference was found.

Estimation of nutrient content

To calculate nutrient content, nutrient concentrations from the three trees harvested in each plot were averaged and then multiplied by the biomass (in kg ha^{-1}) of that particular part of the tree for each plot. Stem bark, stem wood, branch bark and branch wood biomass were calculated from measurements made during the above ground tree component harvests. Stem biomass was estimated by height and diameter measurements taken at regular intervals along the stem while the stem sections were taken to a laboratory for density and moisture content measurements. Taper equations were developed using the stem measurements by Dr Yujia Zhang[8]. All branches of each harvested tree were weighed at the site while a random sample of branches was taken to a laboratory for density and moisture measurements. Hector de Los Santos-Posadas[1] developed equations for branch biomass. Stem and branch biomass of individual trees were calculated to a hectare basis. Foliar biomass was calculated on a hectare basis from the

[8] Warnell School of Forest Resources, University of Georgia, Athens, Georgia, USA.

amount of litterfall collected by five 750 cm diameter round litter traps randomly placed in each plot. Litter was collected approximately every six weeks from March 1999 to March 2000 at Waycross and March 2000 to March 2001 at BF Grant (Munger 2001). Samples were dried at 64 °C before being weighed. Litterfall from the C and F treatments were separated into *P. taeda* and all other species. As foliage biomass based on litter trap measurements could not be separated into upper, middle and lower canopy, an arithmetic mean was taken for the overall foliar concentration of the canopy of each nutrient to calculate content. Table XII and XIII in Appendix B contain biomass (kg ha^{-1}) calculated for each part of the above ground tree components of BF Grant and Waycross respectively.

Only the branch biomass (outside bark) was calculated for BF Grant and Waycross. Therefore estimates of branch wood and bark were needed. Block two (est. 1988) and block five (est. 1995) at the Monitor site were sampled in July 2001 to determine this ratio. A branch from the upper and middle canopy was randomly sampled from two trees per plot. A 75 mm sample was taken from the upper, middle and lower part of each branch; the branch bark was removed by a peeler and the branch wood and bark were placed into separate paper bags. Samples were then dried for seven days at 64 °C before being weighed. The percentage bark to branch wood was calculated for each sample and no significant differences between the treatments and age were found. Total above ground tree components nutrient content was calculated by adding the nutrient content from the different parts of the tree.

Nutrient concentration was not measured for Waycross branch wood; thus the branch wood nutrient concentration from BF Grant was used to estimate content. There was no significant difference in branch bark nutrient concentration between BF Grant and Waycross sites; therefore it was assumed that there was no difference in branch wood concentration.

Calculation of measures of efficiency

Leaf weight ratio (LWR kg kg^{-1}):

Foliar biomass / Above ground tree components biomass

This efficiency measure examines if the investment in foliar biomass changed relative to the above ground tree components.

Previous research has shown an increase in leaf biomass in response to fertilization. However, an important question to ask is if increases in foliar biomass are proportional to increases in the biomass of the above ground tree components.

Stem growth nutrient use efficiency (SNUE kg kg^{-1}):

Stem growth for one year period / Foliar nutrient content during that year

SNUE is a measure of stem growth per unit of foliar nutrient. As the canopy is the driving force of tree growth, the question was if an increase in foliar NPK was proportional to an increase in stem growth. For this test, the growth of stem biomass was compared to nutrient content of the previous year's foliage cohort. This cohort is on the tree for the majority of the subsequent growing season and is the primary source of carbon for stem biomass growth during its second year on the tree.

Statistical Analysis.

Powerline and Monitor served as replicates for BF Grant forest while Waycross Wet and Dry served as replicates for Dixon Memorial forest. The locations were tested separately. Ages were not randomized at each site, therefore trees within plots as well as plots of the same age at a given site were averaged before analysis. The General Linear Model (GLM) procedure from the statistical program package, Statistical Analysis System (SAS®, SAS Institute, Cary, North Carolina, USA) was used for the analysis. The model used to test nutrient concentration by canopy location was a split-split plot design. Stand age was the whole plot factor. The first split tested the factorial combination of treatments and associated interactions. The second split was used to test nutrient concentration of the treatments by canopy location. Canopy position was not randomized, therefore canopy position was first tested using the error term consisting of replication x canopy position x variable(s) being tested. If this test was not significant, the term was tested using the normal error term. If this test was significant, the term was not tested further. When canopy location was not included, i.e. stem and branch measurements, a split plot design were used with age as the whole units and the factorial combination of treatments as the sub-units. Duncan's Multiple Range Test was used to test for treatment differences where applicable.

Results

Foliar NPK concentration

Fertilizer effects

Fertilizer significantly increased foliar N concentration at BF Grant and Waycross (Table 3-1, Figure 3-1). At both locations, there was also a significant age x fertilizer interaction because the effect of fertilizer increased with age (Table 3-1). Fertilizer had no effect at age five at BF Grant. However, fertilizer increased foliar N concentration from 12.8 to 15.0 g kg^{-1} at age ten ($p=0.03$) and from 12.8 to 17.1 g kg^{-1} ($p<0.0001$) at age twelve (Figure 3-1). A similar pattern occurred at Waycross with only a slight impact at age six, but with fertilizer increasing N concentration at age ten from 13.2 to 15.1 g kg^{-1} ($p=0.01$) and age twelve from 12.8 to 17.0 g kg^{-1} ($p<0.0001$) (Figure 3-1).

The effect of fertilization on foliar P concentration was inconsistent. Fertilizer did not affect foliar P concentration at Waycross while fertilization increased foliar P at BF Grant (Table 3-1, Figure 3-2). There was an age x fertilizer interaction at BF Grant, because fertilizer only had a large effect on P concentration at age twelve ($p<0.0001$), increasing foliar P from 1.14 to 1.40 g kg^{-1} (Figure 3-2).

Fertilizer significantly increased foliar K concentration at both sites while there was an age x fertilizer interaction only at BF Grant (Table 3-1, Figure 3-3). At Waycross, fertilizer increased K concentration from 3.22 to 3.88 g kg^{-1} (Figure 3-3). At BF Grant, the fertilizer effect was only significant at age twelve where K concentration increased from 4.56 to 5.82 g kg^{-1} ($p<0.0001$) (Figure 3-3).

Competition control effects

Competition control increased BF Grant foliar N concentration from 14.3 to 15.0 g kg^{-1} while it had no effect at Waycross (Table 3-1). Competition control did not affect foliar P concentration at Waycross while it decreased P from 1.24 to 1.19 g kg^{-1} at BF Grant (Table 3-1). However, there was a significant age x herbicide effect at BF Grant for foliar P (Table 3-1). When the analysis was done for each separate age, the smallest p value was $p=0.053$ at age five where competition control decreased P concentration by 0.13 g kg^{-1} (Figure3-2).

Competition control had no overall impact on foliar K concentration either at BF Grant or Waycross (Table 3-1). There was a significant age x herbicide interaction for Waycross because foliar K concentration decreased with competition control at age six ($p=0.001$) from 4.50 to 3.54 g kg^{-1} but was not affected at the other stand ages (Figure 3-4). At BF Grant, there was a significant age x herbicide x fertilizer interaction for foliar K (Table 3-1) due to large variability between treatments at different ages.

The effect of canopy position on foliar NPK

At Waycross, there was a significant canopy location effect where foliar N concentration was higher in the upper canopy regardless of the treatment (Table 3-1, Figure 3-5). No overall canopy location effect on foliar N at BF Grant occurred (Table 3-1). However, there was a canopy location x fertilizer interaction because foliar N concentration increased from lower (14.8 g kg^{-1}) to upper foliage (16.3 g kg^{-1}) for the fertilized treatments, but the highest concentration for the unfertilized treatments was in the middle canopy (Figure 3-5). There was a significant canopy effect for foliar P concentration at both sites (Table 3-1, Figure 3-6). Phosphorus concentration was the highest in the upper canopy (Figure 3-6).

At BF Grant, foliar K concentration in the upper canopy (6.3 g kg^{-1}) was greater than the lower (5.0 g kg^{-1}) and middle (4.8 g kg^{-1}) canopy (Table 3-1). There was no overall canopy location effect at Waycross, however there was a significant herbicide x fertilizer x canopy location interaction (Table 3-1). Despite this interaction, foliar K concentration was greater in the upper canopy for all treatments (Figure 3-7). BF Grant and Waycross had significant age x herbicide x canopy location interaction for foliar K for different reasons. For BF Grant, upper canopy K concentration at age five was greater in the competition control treatments (8.7 g kg^{-1}) than the non-competition control treatments (7.1 g kg^{-1}) but similar at other ages (Figure 3-8). Potassium concentration at Waycross at age five was significantly less in the competition control treatments while the upper canopy had a higher K concentration (3.6 g kg^{-1}) than the middle canopy (3.4 g kg^{-1}) (Figure 3-8). Thus the response of foliar K concentration to fertilizer varied with age and site.

NPK concentration in the other parts of the above ground tree components

Concentrations for different age and treatment combinations for NPK concentrations of branch bark, branch wood, stem bark and stem wood are presented in Table 3-3, 3-4, 3-5 and treatment p-values are presented in Table 3-2.

Fertilizer effects

Fertilizer consistently increased N concentration in the branches. Fertilizer increased N concentration in branch bark and branch wood at BF Grant and branch bark at Waycross (Waycross branch wood was not measured) (Table 3-2, 3-3). There was no overall age effect on branch N concentration. However, there was a significant age x fertilizer interaction for branch bark N concentration at both sites (Table 3-2). Fertilizer had no effect at the youngest age at either site. At age ten, branch bark N concentration increased from 4.6 to 5.3 g kg^{-1} at BF Grant ($p=0.02$) and from 4.7 to 5.4 g kg^{-1} at Waycross ($p=0.005$). At age twelve, the fertilizer effect was even greater. Branch bark N concentration increased from 4.7 to 5.8 g kg^{-1} at BF Grant ($p=0.004$)

and from 4.9 to 6.0 g kg^{-1} at Waycross (p=0.001) (Table 3-3). Unlike the branches, fertilization had no effect on N concentration in the stem except for Waycross stem wood (Table 3-2) where it increased N concentration from 0.63 to 0.89 g kg^{-1}. Waycross stem wood N had a significant age effect where N concentration was higher at age six than at age’s ten and twelve (Table 3-2, 3-3).

The response of P concentration to fertilizer was inconsistent between BF Grant and Waycross. Fertilizer increased P concentration in the stem bark at BF Grant and increased P concentration in the branch bark, stem bark and stem wood at Waycross (Table 3-2, 3-4). Although there was not a significant main effect of fertilization on branch bark P concentration at BF Grant, there was a significant age x fertilizer interaction (Table 3-2). The interaction occurred because fertilizer decreased P concentration at age five (p=0.001) from 0.50 to 0.43 g kg^{-1}, had no effect at age ten, and increased P at age twelve (p=0.003) from 0.44 to 0.55 g kg^{-1} (Table 3-4). In contrast, fertilizer increased branch bark P concentration at Waycross for all ages (Table 3-4). There was also an age x fertilizer interaction for BF Grant stem bark P concentration (Table 3-2). Fertilizer had no effect at age five and ten, while at age twelve, fertilizer increased stem bark P concentration (p=0.01) from 0.14 to 0.24 g kg^{-1}.

Unlike the N and P concentrations, fertilizer had no effect on K concentrations in other parts of the above ground tree components except at BF Grant where stem bark K concentration increased (Table 3-2, 3-5). However, an age x fertilizer interaction also occurred because the fertilizer effect was only significant at age twelve (p=0.03) with K concentration increasing from 0.86 to 1.38 g kg^{-1}, possibly as a response to K fertilizer applied earlier that year.

Competition control effects

Competition control had no effect on branch wood, stem bark or stem wood N concentrations at BF Grant nor the N concentrations in branch bark, stem bark or wood at Waycross (Table 3-2). However, competition control did significantly decrease N concentration in the branch bark at BF Grant from 5.40 to 5.10 g kg^{-1} (Table 3-2).

Competition control had little effect on P concentration at Waycross while it decreased P throughout the above ground tree components at BF Grant (Table 3-2, 3-4). At Waycross, the only competition control effect was in the stem bark where it decreased P concentration from 0.095 to 0.072 g kg^{-1} (Table 3-2). At BF Grant, competition control decreased P concentration in the branch wood from 0.09 to 0.07 g kg^{-1} and stem bark from 0.17 to 0.14 g kg^{-1} (Table 3-2). Branch bark and stem wood P concentration also decreased with competition control treatments at BF Grant (Table 3-2, 3-4). However, significant age x herbicide interactions also occurred for these sections of the tree. At age five, competition control significantly decreased branch bark P concentration (p=0.002) from 0.53 to 0.41 g kg^{-1} while it did not affect P concentration at ages ten and twelve (Table 3-2). The age effect was similar for BF Grant stem wood with competition control decreasing P concentration at age five (p=0.02) from 0.15 to 0.09 g kg^{-1} (Table 3-2) but having little effect on older stands.

Competition control had an inconsistent effect on K concentrations at various locations of the above ground tree components at BF Grant and Waycross. Competition control had no overall effect on branch bark K concentration at BF Grant or Waycross (Table 3-2). However, at Waycross, there was a significant age x herbicide and age x herbicide x fertilizer interaction where competition control generally decreased branch bark K concentration but was highly variable between the treatments at different ages (Table 3-5).

At BF Grant, competition control decreased K concentration in the branch wood and stem wood and had no effect on K concentrations at those locations at Waycross (Table 3-2, 3-5). However at Waycross, competition control interacted with fertilizer to reduce the fertilizer effect on K concentration in stem bark (Table 3-2). The fertilizer treatment had the highest K concentration (0.17 g kg^{-1}) while HF treatment had the same concentration as C (0.10 g kg^{-1}). The overall competition control effect decreased BF Grant branch wood concentration from 1.24 to 1.10 g kg^{-1}. At BF Grant, competition control decreased stemwood K concentration and there was an age x herbicide interaction (Table 3-2). The competition control effect was only significant at age five ($p=0.03$) where it decreased from 1.26 to 1.02 g kg^{-1}.

There were two three-way interactions for K concentrations that were difficult to explain. Waycross branch bark K concentration had a significant age x herbicide x fertilizer interaction (Table 3-2) where the difference between the H and HF treatments was the largest at age six. Both treatments had a K concentration less than the control. However, the HF treatment K concentration was less by 0.36 g kg^{-1}while the H treatment was less by 0.16 g kg^{-1}. Stem bark K concentration at BF Grant also had an age x herbicide x fertilizer interaction. The three-way interaction was difficult to interpret except that at age five and twelve, the F treatment K concentration was higher than the control.

Above ground tree components NPK content.

Fertilizer effects

Above ground N content significantly increased with fertilization at Waycross and BF Grant (Table 3-6). There was a significant age x fertilizer interaction at both sites where fertilization had little effect at the youngest age (Table 3-6, Figure 3-9, 3-10). At BF Grant, the fertilizer effect was significant at age twelve where it increased above ground N content ($p=0.002$) from 204 to 337 kg ha^{-1}. At Waycross, fertilizer increased above ground N content at age ten ($p=0.02$) from 174 to 258 kg ha^{-1} and age twelve ($p=0.003$) from 194 to 403 kg ha^{-1} (Figure 3-10).

For the individual tree components, fertilizer significantly increased N content in the branch bark, foliage and stem bark at both sites, branch wood at BF Grant and stem wood at Waycross at the $p=0.05$ level (Figure 3-9, 3-10). There was a significant age x fertilizer interaction for branch bark, foliage and stem bark at BF Grant and foliage, stem bark and stem wood at Waycross at the $p=0.05$ level. The largest fertilizer effect on N content for these components was at age fourteen (Figure 3-9, 3-10).

Fertilizer increased above ground P content at both sites (Table 3-6, Figure 3-11, 3-12). Like N, there was a significant age x fertilizer effect on P content (Table 3-6). Fertilizer had little effect at the youngest two ages at both sites, while at age twelve, fertilizer increased above ground P content from 13 to 22 kg ha^{-1} at BF Grant (p=0.003) and from 15 to 29 kg ha^{-1} at Waycross (p=0.02).

For the individual tree components, fertilizer significantly increased P content in the branch bark, foliage, stem bark and stem wood at both sites and branch wood at BF Grant at the p=0.05 level (Figure 3-11, 3-12). There was a significant age x fertilizer interaction for branch bark, foliage, stem bark and stem wood at BF Grant and stem bark at Waycross at the p=0.05 level. The largest fertilizer effect on P content for these components was at age fourteen (Figure 3-11, 3-12).

The impact of fertilization on above ground K content was similar to P. Fertilizer increased above ground K content at both sites (Table 3-6, Figure 3-13, 3-14). As with N and P, there was a significant age x fertilizer interaction at BF Grant (Table 3-6). Fertilization was significant at age twelve (p=0.04) where ground K content increased from 103 to 146 kg ha^{-1} (Figure 3-3).

For the individual tree components, fertilizer significantly increased K content in the foliage and stem wood at both sites and branch bark, branch wood and stem bark at BF Grant at the p=0.05 level (Figure 3-13, 3-14). There was a significant age x fertilizer interaction for branch bark, foliage and stem bark at BF Grant and foliage and stem bark at Waycross at the p=0.05 level. The largest fertilizer effect on K content for these components was at age fourteen (Figure 3-13, 3-14).

Competition control effects

Competition control only had an impact on above ground NPK content at BF Grant. Competition control increased N content from 145 to 202 kg ha^{-1}, P content from 10.5 to 14.6 kg

ha^{-1} and K content from 65.2 to 101.0 kg ha^{-1} (Table 3-6). Competition control had no interaction with age or fertilizer for these nutrients (Table 3-6).

When the individual above ground tree components were examined, the impact of competition control was more varied. Competition control increased N content in the branch bark, branch wood, foliage and stem bark at BF Grant while the treatment only increased N content in the stem bark at the p=0.05 level (Figure 3-9, 3-10). There was an age x herbicide interaction at BF Grant for branch wood and foliage where the largest treatment effect on N content was at age fourteen at the p=0.05 level (Figure 3-9). Competition control significantly (at the p=0.05 level) increased P and K content in every above ground tree component at BF Grant while the treatment had no impact on P and K content at Waycross (Figure 3-11, 3-13). There was no age x herbicide interactions for P content at BF Grant. There was significant age x herbicide interactions for BF Grant K content in the foliage and stem bark at the p=0.05 level. The largest competition control effect was the largest for both components was at age fourteen (Figure 3-13).

Nutrient use efficiency in the canopy and the above ground tree components

Fertilizer had no effect on LWR at either site while LWR declined with age (Table 3-7). Competition control had no overall effect on LWR at BF Grant, however, it decreased at Waycross (Table 3-7, 3-8). For both sites, there was an age x herbicide interaction for LWR because competition control decreased LWR the most at the youngest age (Table 3-8).

Fertilizer had no effect on N SNUE at either site (Table 3-7). However, there was a significant age and age x fertilizer interaction for Waycross N SNUE. At age twelve, fertilizer decreased SNUE from 187 to 134 (p=0.01). Competition control decreased N SNUE at BF Grant and Waycross (Table 3-7, 3-8). There was an age x herbicide interaction for BF Grant N SNUE (Table 3-7). The biggest decreased due to competition control was at age five (p=0.06).

Fertilizer had no effect on P SNUE at either site (Table 3-7). Competition control had no effect on P SNUE at Waycross while at BF Grant, competition control caused significant herbicide effect and herbicide and age x herbicide interaction (Table 3-7). Like the interaction effect for N SNUE, the biggest difference was at age five (p=0.06).

K SNUE responded to different treatments at different sites. There was no fertilizer effect at BF Grant while there was a significant fertilizer and age x fertilizer effect at Waycross (Table 3-7). For age twelve at Waycross, fertilizer increased K SNUE from 385 to 438 (Table 3-8). In contrast, competition control had no effect at Waycross while there was a herbicide effect and age x herbicide interaction at BF Grant (Table 3-7). As above, the biggest difference was at age five (p=0.05) where herbicide decreased K SNUE from 1416 to 435.

Ratios between foliar nutrients

Fertilizer effects

The response of the foliar P:N and K:N ratios varied greatly between BF Grant and Waycross. Fertilizer significantly decreased (p=0.0004) the P:N ratio at BF Grant from 9.0 to 8.1 % (Table 3-9). There was no significant fertilizer effect at Waycross (Table 3-9). There was a significant age effect at BF Grant where the P:N ratio increased with age (p=0.01) (Table 3-9). Despite a 2% difference in the Waycross P:N ratio at age twelve, there was no significant fertilizer effect. This was due the large variation in the P:N ratio between Waycross Dry and Waycross Wet. There was a small fertilizer effect (<1%) at Waycross Wet while at Waycross Dry the P:N ratio in the non-fertilized treatments were 4% greater than the fertilized treatments. There was no significant site effect. The K:N ratio was not affected by fertilizer or age at either site.

The majority of the N ratios to nutrients that were not added decreased in response to fertilization. Fertilization had no effect on the B:N, Cu:N and Mo:N ratio at either site or on the Fe:N ratio at BF Grant. Fertilizer significantly decreased the ratio at BF Grant and Waycross for Ca:N, Mg:N, Mn:N and Zn:N at the p=0.005 level (Table 3-9). There were significant age x fertilizer interactions for Waycross Fe:N ratio and BF Grant Mg:N ratio where the above fertilizer effect occurred at age twelve at the p=0.05 level, but not at younger stand ages.

Competition control effects

The response of P:N and K:N ratio to competition control were similar to the fertilizer effects (Table 3-9). Competition control had no effect on the P:N ratio at Waycross while it had a significant herbicide (p=0.001) and age x herbicide (p=0.0006) interaction at BF Grant. The herbicide effect was largest at age five (p=0.04), where the P:N ratio decreased from 8.9 to 7.4%. Competition control had no effect on K:N ratio at BF Grant or Waycross sites.

Competition control had little effect on foliar N ratios at either site when compared to nutrients not added with fertilization (Table 3-9). Only the Mg:N ratio at BF Grant had a significant overall herbicide effect. There were two age x herbicide interactions (at the p=0.05 level); at BF Grant for Mg:N and Mn:N where competition control decreased the ratio at age five but less so at older ages. However, the age x herbicide interaction was more complex for Mn:N ratio because at age twelve Mn:N in the competition control treatments was higher than the control. There was a significant age x herbicide x fertilizer interaction at the p=0.05 level at Waycross. At age six, the F treatment had the lowest B:N ratio while the fertilizer x herbicide interaction was able to keep B concentration from being diluted by N, thus the ratio was similar to the control (Table 3-9).

Discussion

Fertilizer effects on NPK

The results generally agreed with hypothesis one, which stated that fertilization would increase NPK content and concentration in above ground tree components. Nitrogen concentration increased due to fertilization with the increase generally becoming larger as stands aged. Previous studies measured higher concentration of foliar N from the additional uptake of fertilized N (Zhang and Allen 1996, Fife and Nambiar 1997). Apparently annual fertilization was increasing the amount of available N taken up and stored in the tree.

Foliar critical concentration is defined as the concentration below which growth is limited. The critical concentration for N in *P. taeda* in the southeastern United States has been described as 12 g kg^{-1} (Jokela *et al.* 1991). Nitrogen concentration in all treatments and ages were higher than this; at BF Grant at age twelve, foliar N concentration for the non-fertilized treatments was 13 g kg^{-1} and 16 g kg^{-1} for the fertilized treatments. Therefore, the concept of critical concentration did not correspond to the increases in growth found in this study due to fertilization.

The majority of additional N uptake was preferentially stored in the canopy with the fertilizer effect increasing with age for foliage and branch N concentrations, which agrees with previous research (Sheriff and Nambiar 1991, Zhang and Allen 1996). There are several reasons for this; firstly, there could be no active mechanism to redistribute N to the bole. Secondly, forests are, in general, N limited. Therefore the response of the tree to any increase in available N is probably to store it where it is needed the most, in this case the canopy. Finally, despite higher N concentrations in the foliage and other parts of the tree, stand growth was still N limited. Fertilization had little effect on the measures of N use efficiency, which disagreed with hypothesis one. The only indication of a surplus of N was the decrease SNUE at age twelve for Waycross. The decrease in N SNUE at Waycross was from either growth slowing due to other factors or the accumulative effect of annual uptake of fertilized N. Otherwise foliar N content was fairly proportional to stem growth.

The N concentration in needles during the dormant season is probably greater than during the growing season as a significant amount of N is moved from older foliage to new needles grown in the spring. However, measurement of foliar N at the same sites found elevated N concentrations throughout the growing season due to fertilization (Munger 2001), which agrees with previous research (Zhang and Allen 1996). However, Zhang and Allen (1996) found no fertilizer effect in N concentration in any part of the canopy in November. Fertilizer was only applied once in Zhang and Allen's study, thus it might take repeated fertilizer applications before there is a fertilizer effect in the dormant season.

The increased foliar N concentrations in the canopy due to fertilization did not enhance photosynthetic capacity. Munger (2001) found no difference between treatments in saturated net photosynthesis (A_{SAT}) at BF Grant and Waycross. Therefore, the increase in N concentration in the middle and upper foliage seems to be associated with N storage. As the majority of stored N would be used for new growth in the following growing season, it would be advantageous to store additional N where it is most needed. This storage of additional N and subsequent use for new needle development may be why there was a good correlation between N content and bole growth even though critical concentration was exceeded in all plots. This brings into question the importance of critical concentration for evaluating growth potential. Although critical concentration may correspond to leaf level physiology, it does not seem to correspond well with potential leaf area development, which in this case, was well correlated to growth (Munger 2001).

Over twelve years, greater than 800 kg ha^{-1} of N was applied to the fertilized treatments. The annual fertilization regime was extreme compared to fertilizer regimes in managed stands where *P. taeda* may receive up to three applications over a rotation. To see how much N fertilizer was lost from the forest ecosystem, the amounts of fertilized N in the above ground components were estimated by subtracting N content of the non-fertilized treatments from that of fertilized treatments. At age twelve at BF Grant and Waycross, 27% and 32% of fertilized N respectively were stored in the above ground tree components. Dr Markewitz[9] estimated for Waycross, 30% of fertilizer inputs over twelve years were returned to the litter layer as litterfall. Despite an average N application of 70 kg N ha^{-1} yr^{-1}, 60% of fertilized N can be accounted in *P. taeda* aboveground biomass litter at Waycross. The rest of the fertilizer probably can be accounted by the lost of N through volatilization and leaching, the immobilization of N in the soil and additional N taken up

[9] University of Georgia, Athens, Georgia, USA.

by the tree that accumulated in roots. It is important to note that despite the extreme N fertilization regime, over half of the N applied stayed within the forest ecosystem.

The response of foliar P concentration to fertilization was only clear for BF Grant at age twelve. This seems to be a direct response to the application of 179 kg P ha^{-1} fertilizer earlier in spring of that year. This indicated that *P. taeda* will take up extra available P from the soil. However, despite fertilizer being applied in years one and two, there was no fertilizer effect at the youngest age at BF Grant and Waycross. This was probably because at ages one and two, trees could not to take up much fertilized P. Later during stand development, P from the first application that was still in the soil was taken up in proportion to growth. Critical foliar concentration of P in *P. taeda* was described in previous research as 1.0 g kg^{-1} (Jokela *et al.* 1991) which all treatments exceeded at both sites.

The response of other above ground components besides foliage to applications of P is harder to explain. Phosphorus concentration increased in the branch and stem but not in the foliage. There was a trend in foliar P concentration where fertilized treatments had a higher concentration at ages ten and twelve. The lack of significance of this trend could be a reflection in the variability of the data since the lower canopy was not sampled at Waycross. Another possibility was from the fact that foliar P concentration at BF Grant was lower than Waycross. At a lower concentration, a small increase in P concentration due to P fertilization would be more statistically significant than the same increase at a higher concentration. Therefore at Waycross, there was a proportional increase in P concentration throughout the tree, not a redistribution of P away from the canopy.

Stands at Waycross show the effect of K fertilization at ages one and two with a higher K concentration at ages ten and twelve. The age x fertilizer interaction at age twelve at BF Grant was a response to K applied earlier that year (Appendix C). As with P, this seems to indicate that the tree has the ability to take up additional K. Jokela et al. (1991) considered the critical concentration of K to be 4.0 g kg^{-1}. The concentration of K was above the critical concentration for all treatments and ages at BF Grant. However, K concentration at Waycross dropped below the critical concentration at age ten and twelve for all treatments. This made Waycross more responsive to K at all ages and is probably why fertilizer increased K SNUE only at the Lower Coastal Plain site.

As with N concentration in the canopy, foliar P and K concentrations were higher in the upper canopy than in the lower canopy in both the fertilized and non-fertilized treatments (except for Waycross K). Therefore, the upper canopy seems to have a higher NPK demand than the other parts of the canopy. The amount of P and K in the foliage was substantially less than N. Canopy position effects for N, P and K were similar to previous studies for non-fertilized and fertilized treatments (Wells and Metz 1963, Zhang and Allen 1996).

Fertilization increased N content in most above ground tree components at both sites. There was a more even distribution of additional uptake of P and K to above ground tree components. Unlike N, an increase in P or K content did not necessarily mean an increase in concentration the above ground tree components. There were also site differences. Fertilization increased P content in all above tree components at both sites and P concentration increased in all above ground tree components at Waycross. BF Grant P concentration only increased in the foliage and stem bark. In contrast, fertilization increased BF Grant K content in the foliage and bark components, while K concentration only increased in the stem bark. Fertilization at Waycross increased K content in the foliage and stem bark while concentration remained unchanged. The site difference for K could reflect the amount of available K at BF Grant and Waycross. If fertilizer adds more K to a large pool of the available K in the soil, the resulting increase in the available K pool may be enough to met most of *P. taeda's* nutrient demands. Thus, content and concentration increase throughout the above ground tree components. However, if fertilization has not increased the total available K pool enough to meet the majority of *P. taeda's* nutrient demands, any increase in concentration from additional uptake was in components that were more sensitive to change in uptake.

The fertilizer effect seems to be pronounced in the bark compared to the wood. This was consistent with previous research, which found nutrient concentration fluctuates more in the bark throughout the year than in the wood (Hodges and Lorio, 1969, White *et al.* 1970, White et *al*. 1972). The response to fertilization in branches could have been more pronounced as branch bark and branch wood have a larger proportion of living cells than in the stem. Nutrient concentrations in stem bark and stem wood are less responsive to changes in fertilization than branch bark and branch wood. Stem samples were taken from a cross section of bark and stem tissue thus, nutrient concentrations were from cellular growth over a large period of years and for stem wood, the entire life of the tree. So unlike branch wood and branch bark, it would be harder to measure a direct P or K fertilizer response in the stem.

Competition control effects on NPK

Hypothesis two postulated that competition control would have little effect on NPK concentration in the foliage and the above ground tree components. There seemed to be a difference between sites, with competition control having a large impact on N and P at BF Grant and on K at Waycross. The lack of competition increased foliar N concentration at BF Grant, which seems to indicate that interspecific competition for nutrients was more aggressive in the Piedmont. With competition control, there was comparatively more available nitrogen at BF Grant than at Waycross and the additional N uptake by *P. taeda* caused a significant competition control effect. Competition control reduced P concentration at age five, which indicated a shortage of available P early in stand development at BF Grant. Also, available soil K seems to be lower in Waycross, thus the elimination of interspecific competition increased tree uptake of K in the Coastal Plain but not in the Piedmont.

The majority of competition control effects for NPK SNUE and P concentration at BF Grant and K concentration at Waycross were at the youngest age. The increase in NPK SNUE at age five at BF Grant was probably due to the small, open canopies in the C and F treatments. The open canopy increased light interception per unit leaf area and therefore photosynthesis per unit leaf area, which accelerated growth per unit leaf biomass and foliar nutrient content proportionally more than the older ages. The only herbicide x canopy location interaction was for K where competition control increased K concentration in the upper canopy. Thus additional K was stored in the upper canopy like the fertilizer x canopy location interaction. This lends support that given enough P and K, the tree will store additional nutrients in the upper canopy.

The herbicide x fertilizer effect for Waycross K stem bark was harder to explain; one possibility was the increased growth in the HF treatment during the first six years could have outstripped the applied fertilizer and soil K. By age ten, fertilized K in labile pools could have become available, which increased plant available K and increased stem bark K concentration.

Effect on Age of NPK content and concentration

Aside from interactions involving age discussed above, the overall age effect on NPK content, concentration and nutrient use efficiency generally agreed with hypothesis three. Hypothesis three stated that as the stand aged, NPK concentration would remain the same. Foliar N concentration in the non-fertilized treatments was fairly constant over time with an increase in N content proportional to an increase in biomass. However, annual N fertilization increased foliar N concentration over time as additional N uptake was accumulated and stored in the canopy. Foliar P and K concentration changed little with stand age. However, there was a downward trend in foliar K concentration in the control with stand age (though not significant). There were no age main effects on NPK concentration in other parts of the above ground tree components.

Above ground tree components NPK content increased with age, which agreed with hypothesis three. BF Grant P and K and Waycross N content increased with age and BF Grant N and Waycross P content had an age x fertilizer interaction in response to fertilizer applied at age eleven. Thus, content generally increased with age in all treatments, while the increases were greater with fertilization. For Waycross P and K content however, the lack of an overall age effect may reflect nutrient deficiencies in the soil since stand biomass was increasing and P and K content was not. At age six, P and K contents for the control were 15 and 47 kg ha^{-1} respectively. Waycross P and K content actually decreased at age twelve with P and K content equal to 13 and 43 kg ha^{-1} respectively. Low plant available P and K would help explain why there was a fertilizer effect for K at Waycross at all ages. It seems that an amount of the fertilized K was made unavailable at application and released in later years for the tree uptake. Fertilized K that entered the fixed K pool (partly available K) could be released into the exchangeable K pool, which would readily interact with the soil solution. Weathered clays and mica do have the ability to fix K and slowly release K into the soil solution (McLaren and Cameron 1990). Another source of K in later years was the recycling of K from litterfall.

LWR declined with age at BF Grant and Waycross indicating that at youngest age, a large amount of above ground tree components biomass was invested in the canopy. As the stands developed and canopies closed, the proportion of stem biomass increased while the foliage biomass remained relatively stable. Although LWR agreed with hypothesis three, the response of NPK SNUE was more site specific. N SNUE declined with age at Waycross while BF Grant N SNUE did not. There were age x herbicide interactions at BF Grant for P and K SNUE while there was an age x fertilizer interaction with Waycross K SNUE. Soil pools of N and K at Waycross and P at BF Grant could be smaller than the N and K pools at BF Grant and P pool at Waycross; hence any treatment differences would be more easily measured at these sites. The age x herbicide effect at BF Grant probably resulted from decreases in SNUE that occurred with canopy closure.

Treatment effects on the foliar N ratio

The ratios of other nutrients to N in the control treatments at both sites are comparable to previous research on *P. taeda* in the Piedmont and Coastal Plain (Adams and Allen 1985). Fertilizer increased N relative to other nutrients. This agrees with hypothesis four, which stated that *P. taeda* would not be able to increase its uptake of non-fertilized nutrients proportional to N. Phosphorus and K fertilizer were used to counter balance additional N uptake from annual N fertilizer. The applications of P and K largely worked with no fertilizer effect on the K:N ratio and the decrease in P:N ratio at age twelve was small. The results for the K:N ratio agrees with Adams and Allen (1985) in that N fertilizer alone decreased the K:N ratio as the tree was not able to increase foliar K concentration. Therefore in the terms of the foliar K:N ratio, the amount and timing of applied K was enough to correct for any foliar imbalances of K relative to N. Fertilization did not affect foliar N ratio's for Cu, Mo and B at BF Grant. This is could be a reflection of the low concentrations and the large variance in measurements, which make it hard to measure a significant treatment effect or an adequate supply of these particular micro nutrients at BF Grant (Appendix B). Despite a fertilizer application of macro and micro nutrients at age twelve at BF Grant, there was no change in the foliar ratio's of nitrogen to B, Ca, Cu, Fe, Mg, Mn, Mo and Zn. This could be reflection of interspecific competition for nutrients or the amount of those nutrients applied were not enough to change foliar concentration with the large surplus of N contained in the foliage. A simpler explanation was that there was lag time between application and uptake, thus an increase in foliar N ratios could occur several years after application.

Nutrient ratios are important measures to see if uptake of nutrients not added as fertilizer increased in proportion to the fertilized nutrients or, weather deficiencies in other non-fertilized nutrients might occur. If there is an imbalance of nutrients in the foliage, biological processes like photosynthesis and enzyme production could be affected. The apparent storage of foliar N does bring into question the measurement of foliar nutrient ratios. The ratio of N to other nutrients involved with foliar biological processes may not be affected by fertilization if the additional foliar N not used in biological processes is kept separate. Thus, measuring the foliar N ratios by the method used in this study may not be accurate measure of any dilution effects caused by N fertilization. It is not clear if the entire stored N is used for growth in the next growing season or if there is a separation of stored N from N used in biological processes. Further investigation would be needed.

Unlike the fertilizer effect, all of the competition control effects occurred at the youngest age. The results agree with hypothesis four where almost all of the nutrient ratio's to N were not affected by competition control. Like the fertilizer effect, P:N ratio was not affected by the competition control while P:N ratio at BF Grant increased at age five. As discussed above, the response was probably from the low available P for the respective growth rate. The decrease in the Mg:N and Mn:N ratio's with competition control was from the increased N availability caused by complete competition control..

Comparison with previous research

Nutrient concentrations and content from this study were comparable to previous work with *P. taeda* and other conifer species (Well and Metz, 1962, Switzer and Nelson, 1972, Fife and Nambiar, 1997, Zhang and Allen 1996). Table 3-10 showed that although there was some variation with other studies, foliar concentration and content of all the studies were in the same range. The application of the fertilizer and competition control did change nutrient concentrations and content of various parts of the above ground tree components for this study. However, the general distribution of those nutrients remained in most cases similar to the above studies. Other research with fertilizer applications on *P. taeda* had similar findings with NPK (Zhang and Allen 1996, Samuelson *et al.* 2001).

Conclusion

Above ground *P. taeda* NPK pools were affected by annual fertilization. The canopy dominated the above ground tree components nutrient pools with the majority of additional NPK taken up in association with the herbicide and fertilizer treatments ending up in the canopy. Fertilization reduced the majority of nutrients relative to N. This is a strong indication that the tree cannot readily change the rate of uptake of other nutrients to compensate for increased N supply in the canopy. The effects of age generally did not affect foliar NPK concentrations.

The current foliage in the upper canopy acted as a store of additional nutrients. The comparison of critical foliar NPK concentrations with foliar NPK concentrations and measures of efficiency from the different treatments in this study showed that traditional inferences from critical concentrations may be not correct because growth increased in proportion with increased nutrient concentration. Although NPK critical concentrations may correspond to leaf physiology, they did not correspond well with potential leaf area development and growth.

Table 3-1: p-values from the statistical analysis of foliar nutrient concentration of *Pinus taeda* for Nitrogen (N), Phosphorus (P) and Potassium (K) by treatment and canopy position at BF Grant and Waycross, GA. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross. Fert represents annual fertilization verses no fertilization. Herb represents complete control of interspecific competition verses no control. Canopy position represents upper, middle and lower canopy at BF Grant and the upper and middle canopy at Waycross.

	BFGrant			Waycross		
Variable	N	P	K	N	P	K
Site	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age	n.s.	n.s.	n.s.	n.s.	n.s	n.s.
Herb	0.01	0.003	n.s	n.s.	n.s.	n.s.
Fert	<0.0001	0.0003	0.001	<0.0001	n.s.	0.0009
Herb x Fert	n.s.	n.s.	n.s.	n.s.	n.s	n.s.
Age x Herb	n.s.	0.02	n.s.	n.s.	n.s.	0.01
Age x Fert	0.0002	<0.0001	0.003	0.006	n.s.	n.s.
Age x Herb x Fert	n.s.	n.s.	0.002	n.s.	n.s.	n.s.
Canopy	n.s.	<0.0001	<0.0001	<0.0001	<0.0001	n.s.
Site x Canopy	0.004	n.s	n.s.	n.s.	n.s.	<0.0001
Canopy x Age	n.s.	n.s.	0.0004	n.s.	n.s.	n.s.
Site x Canopy x Age	n.s.	n.s.	n.s.	n.s.	n.s.	0.002
Canopy x Herb	n.s	n.s	n.s	n.s	n.s	n.s
Canopy x Fert	0.02	n.s.	n.s.	n.s.	n.s.	n.s.
Herb x Fert x Canopy	n.s	n.s	n.s	n.s	n.s	0.01
Age x Herb x Canopy	n.s.	n.s.	0.02	n.s.	n.s.	0.02
Age x Fert x Canopy	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age x Herb x Fert x Canopy	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

n.s. non significant

Table 3-2: p-values from the statistical analysis of above ground tree components concentration of *Pinus taeda* for Nitrogen (N), Phosphorus (P) and Potassium (K) by treatment for branch bark, branch wood, stem bark and stem wood at BF Grant and Waycross, GA. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross. Fert represents annual fertilization verses no fertilization. Herb represents complete control of interspecific competition verses no control.

BF Grant p-values

	Branch Bark			Branch Wood			Stem Bark			Stem Wood		
Variable	N	P	K	N	P	K	N	P	K	N	P	K
Site	n.s.	n.s.	n.s.	0.02	n.s.	n.s.	n.s.	n.s.	n.s.	0.03	n.s.	n.s.
Age	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Herb	0.04	<0.0001	n.s.	n.s.	0.005	0.003	n.s.	0.02	n.s.	n.s.	0.001	0.009
Fert	0.001	n.s.	n.s.	0.001	n.s.	n.s.	n.s.	0.02	0.04	n.s.	n.s.	n.s.
Herb x Fert	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age x Herb	n.s.	0.008	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.003	0.005
Age x Fert	0.01	<0.0001	n.s.	n.s.	n.s.	n.s.	n.s.	0.001	0.03	n.s.	n.s.	0.05
Age x Herb x Fert	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.04	n.s.	n.s.	n.s.

Waycross p-values

	Branch Bark			Branch Wood			Stem Bark			Stem Wood		
Variable	N	P	K	N	P	K	N	P	K	N	P	K
Site	n.s.	n.s.	0.04	n.a	n.a	n.a	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age	n.s.	n.s.	n.s.	n.a	n.a	n.a	n.s.	n.s.	n.s.	0.04	n.s.	n.s.
Herb	n.s.	n.s.	n.s.	n.a	n.a	n.a	n.s.	0.008	n.s.	n.s.	n.s.	n.s.
Fert	0.0001	0.001	n.s.	n.a	n.a	n.a	n.s.	0.04	n.s.	0.008	0.02	n.s.
Herb x Fert	n.s.	n.s.	n.s.	n.a	n.a	n.a	n.s.	n.s.	0.03	n.s.	n.s.	n.s.
Age x Herb	n.s.	n.s.	0.03	n.a	n.a	n.a	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age x Fert	0.002	n.s.	n.s.	n.a	n.a	n.a	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age x Herb x Fert	n.s.	n.s.	0.04	n.a	n.a	n.a	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Table 3-3: *Pinus taeda* Nitrogen (N) concentrations in the branch bark, branch wood, stem bark and stem wood by treatment and age at BF Grant and Waycross GA. Treatments were control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide + fertilizer (HF) treatments. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross. Concentration values given are: mean ± one standard error.

Stand Age	Treatment	BF Grant N concentration (g kg^{-1})			
		Branch Bark	Branch Wood	Stem bark	Stem wood
5	C	5.79 ± 0.36	3.36 ± 0.65	2.9 ± 0.95	1.17 ± 1.17
	H	5.19 ± 0.55	3.61 ± 0.64	3.26 ± 0.03	0.9 ± 0.9
	F	5.49 ± 0.29	4.07 ± 1.12	3.3 ± 0.08	1.12 ± 1.12
	HF	5.47 ± 0.24	4.21 ± 0.79	2.7 ± 0.31	1.32 ± 1.32
10	C	4.85 ± 0.32	3.48 ± 0.48	2.8 ± 0.52	0.71 ± 0.68
	H	4.5 ± 0.21	3.51 ± 0.47	2.75 ± 0.6	0.89 ± 0.73
	F	5.49 ± 0.28	4.12 ± 0.32	4.65 ± 0.89	0.27 ± 0.33
	HF	5.34 ± 0.34	3.52 ± 0.54	2.89 ± 0.54	0.42 ± 0.37
12	C	4.87 ± 0.24	3.59 ± 0.67	3.68 ± 1.06	1.08 ± 0.89
	H	4.52 ± 0.41	3.11 ± 0.66	3.24 ± 0.42	0.69 ± 0.69
	F	6.04 ± 0.22	4.03 ± 0.53	5.04 ± 0.73	1.26 ± 1.04
	HF	5.63 ± 0.35	3.67 ± 0.77	4.19 ± 0.81	0.94 ± 0.84

Stand Age	Treatment	Waycross N concentration (g kg^{-1})			
		Branch Bark	Branch Wood	Stem bark	Stem wood
6	C	5.02 ± 0.27	n.a	3.43 ± 0.3	0.82 ± 0.31
	H	5.09 ± 0.19	n.a.	3.2 ± 0.19	1.21 ± 0.29
	F	5.43 ± 0.13	n.a	3.62 ± 0.19	1.15 ± 0.2
	HF	5.06 ± 0.04	n.a.	3.23 ± 0.28	1.01 ± 0.42
10	C	4.91 ± 0.2	n.a	3.01 ± 0.16	0.25 ± 0.26
	H	4.61 ± 0.23	n.a.	2.96 ± 0.3	0.49 ± 0.25
	F	5.2 ± 0.23	n.a	3.09 ± 0.23	0.59 ± 0.18
	HF	5.51 ± 0.22	n.a.	2.98 ± 0.24	0.6 ± 0.21
12	C	4.8 ± 0.23	n.a	3.09 ± 0.1	0.49 ± 0.3
	H	4.95 ± 0.36	n.a.	3.25 ± 0.41	0.45 ± 0.39
	F	6.02 ± 0.52	n.a	3.47 ± 0.23	0.93 ± 0.19
	HF	6.01 ± 0.55	n.a.	3.29 ± 0.25	0.95 ± 0.33

n.a not available

Table 3-4: *Pinus taeda* Phosphorus (P) concentrations in the branch bark, branch wood, stem bark and stem wood by treatment and age at BF Grant and Waycross GA. Treatments were control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide + fertilizer (HF) treatments. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross. Concentration values given are: mean ± one standard error.

Stand Age	Treatment	BF Grant P concentration (g kg^{-1}) Branch Bark	Branch Wood	Stem bark	Stem wood
5	C	0.57 ± 0.01	0.208 ± 0.000	0.16 ± 0.01	0.15 ± 0.008
	H	0.43 ± 0.03	0.157 ± 0.029	0.13 ± 0.05	0.09 ± 0.022
	F	0.49 ± 0.01	0.197 ± 0.009	0.11 ± 0.01	0.14 ± 0.019
	HF	0.38 ± 0	0.151 ± 0.021	0.12 ± 0.03	0.09 ± 0.006
10	C	0.49 ± 0.03	0.185 ± 0.019	0.15 ± 0.01	0.08 ± 0.009
	H	0.43 ± 0.02	0.179 ± 0.02	0.14 ± 0.01	0.07 ± 0.01
	F	0.47 ± 0.03	0.198 ± 0.005	0.18 ± 0.01	0.08 ± 0.008
	HF	0.43 ± 0.04	0.159 ± 0.007	0.14 ± 0.02	0.06 ± 0.011
12	C	0.46 ± 0.02	0.175 ± 0.019	0.15 ± 0.02	0.06 ± 0.006
	H	0.42 ± 0.01	0.155 ± 0.011	0.14 ± 0.02	0.06 ± 0.012
	F	0.56 ± 0.04	0.196 ± 0.027	0.29 ± 0.03	0.06 ± 0.008
	HF	0.54 ± 0.02	0.187 ± 0.023	0.2 ± 0.01	0.06 ± 0.005

Stand Age	Treatment	Waycross P concentration (g kg^{-1}) Branch Bark	Branch Wood	Stem bark	Stem wood
6	C	0.55 ± 0.07	n.a	0.11 ± 0.02	0.1 ± 0.02
	H	0.54 ± 0.03	n.a.	0.09 ± 0.03	0.09 ± 0.02
	F	0.61 ± 0.01	n.a	0.14 ± 0.01	0.1 ± 0.02
	HF	0.53 ± 0.06	n.a.	0.09 ± 0.01	0.11 ± 0.03
10	C	0.51 ± 0.07	n.a	0.07 ± 0.01	0.06 ± 0.01
	H	0.45 ± 0.07	n.a.	0.06 ± 0.03	0.06 ± 0.01
	F	0.53 ± 0.08	n.a	0.09 ± 0.03	0.08 ± 0.03
	HF	0.55 ± 0.06	n.a.	0.06 ± 0.02	0.07 ± 0.03
12	C	0.46 ± 0.07	n.a	0.07 ± 0.02	0.05 ± 0.01
	H	0.48 ± 0.07	n.a.	0.06 ± 0.03	0.06 ± 0.01
	F	0.6 ± 0.08	n.a	0.11 ± 0.01	0.07 ± 0.01
	HF	0.58 ± 0.05	n.a.	0.07 ± 0.03	0.06 ± 0.01

n.a not available

Table 3-5: *Pinus taeda* Potassium (K) concentrations in the branch bark, branch wood, stem bark and stem wood by treatment and age at BF Grant and Waycross, GA. Treatments were control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide + fertilizer (HF) treatments. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross. Concentration values given are: mean ± one standard error.

Stand Age	Treatment	BF Grant K concentration (g kg^{-1})			
		Branch Bark	Branch Wood	Stem bark	Stem wood
5	C	2.96 ± 0.13	1.31 ± 0.07	0.73 ± 0.09	1.18 ± 0.02
	H	2.41 ± 0.16	1.04 ± 0.08	0.62 ± 0.32	0.98 ± 0.15
	F	2.88 ± 0.29	1.41 ± 0.12	0.38 ± 0.05	1.34 ± 0.03
	HF	2.8 ± 0.61	1.14 ± 0.05	0.8 ± 0.3	1.05 ± 0.08
10	C	2.4 ± 0.3	1.21 ± 0.13	0.81 ± 0.07	0.86 ± 0.08
	H	1.94 ± 0.26	1.01 ± 0.07	0.6 ± 0.09	0.75 ± 0.09
	F	2.13 ± 0.35	1.13 ± 0.05	0.87 ± 0.16	0.82 ± 0.03
	HF	2.36 ± 0.32	1.08 ± 0.03	0.8 ± 0.06	0.81 ± 0.08
12	C	2.64 ± 0.32	1.23 ± 0.12	0.88 ± 0.13	0.72 ± 0.07
	H	2.52 ± 0.25	1.17 ± 0.05	0.85 ± 0.16	0.77 ± 0.08
	F	3.03 ± 0.2	1.21 ± 0.1	1.68 ± 0.09	0.67 ± 0.03
	HF	2.84 ± 0.26	1.15 ± 0.05	1.08 ± 0.16	0.69 ± 0.04

Stand Age	Treatment	Waycross K concentration (g kg^{-1})			
		Branch Bark	Branch Wood	Stem bark	Stem wood
6	C	2.11 ± 0.38	n.a	0.17 ± 0.07	0.3 ± 0.13
	H	1.95 ± 0.36	n.a.	0.14 ± 0.12	0.3 ± 0.1
	F	2.33 ± 0.18	n.a	0.22 ± 0.05	0.32 ± 0.1
	HF	1.74 ± 0.15	n.a.	0.1 ± 0.05	0.34 ± 0.1
10	C	1.73 ± 0.05	n.a	0.07 ± 0.06	0.18 ± 0.08
	H	1.35 ± 0.21	n.a.	0.19 ± 0.04	0.28 ± 0.03
	F	1.4 ± 0.42	n.a	0.18 ± 0.05	0.21 ± 0.05
	HF	1.84 ± 0.39	n.a.	0.03 ± 0.04	0.22 ± 0.11
12	C	1.21 ± 0.42	n.a	0.07 ± 0.04	0.24 ± 0.09
	H	1.35 ± 0.23	n.a.	0.06 ± 0.04	0.25 ± 0.04
	F	1.53 ± 0.31	n.a	0.13 ± 0.05	0.27 ± 0.07
	HF	1.42 ± 0.28	n.a.	0.09 ± 0.05	0.24 ± 0.11

n.a not available

Table 3-6: p-values from the statistical analysis of above ground tree components content of *Pinus taeda* for Nitrogen (N), Phosphorus (P) and Potassium (K) by treatment for branch bark, branch wood, stem bark and stem wood at BF Grant and Waycross GA. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross. Fert represents annual fertilization verses no fertilization. Herb represents complete control of interspecific competition verses no control.

	BF Grant			Waycross		
Variable	N	P	K	N	P	K
Site	n.s.	n.s.	n.s.	0.02	n.s.	n.s.
Age	n.s.	0.01	0.02	0.01	n.s.	n.s.
Herb	0.0001	0.0002	<0.0001	n.s.	n.s.	n.s.
Fert	<0.0001	0.0003	0.001	0.0001	0.001	0.003
Herb x Fert	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age x Herb	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age x Fert	0.0006	0.001	0.05	0.004	0.03	n.s.
Age x Herb x Fert	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Table 3-7: p-values of the measures of *Pinus taeda* Leaf Weight Ratio (LWR) and Stem Nutrient Use Efficiency (SNUE) for Nitrogen (N), Phosphorus (P) and Potassium (K) by treatment and age at the BF Grant (BFG) and Waycross (WC), GA. Treatments comprise of the control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide + fertilizer (HF) treatments. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross.

	LWR		N SNUE		P SNUE		K SNUE	
Variable	BFG	WC	BFG	WC	BFG	WC	BFG	WC
Site	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age	0.05	0.001	n.s.	0.03	n.s.	n.s.	n.s.	n.s.
Herb	n.s.	0.006	0.03	0.05	0.04	n.s.	0.04	n.s.
Fert	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	0.05
Herb x Fert	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Age x Herb	0.0003	0.01	0.02	n.s.	0.03	n.s.	0.03	n.s.
Age x Fert	n.s.	n.s.	n.s.	0.01	n.s.	n.s.	n.s.	0.04
Age x Herb x Fert	0.01	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

Table 3-8: Measures of *Pinus taeda* Leaf Weight Ratio (LWR) and Stem Nutrient Use Efficiency (SNUE) for Nitrogen (N), Phosphorus (P) and Potassium (K) by treatment by age at the BF Grant (BFG) and Waycross (WC), GA. Treatments comprise of the control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide + fertilizer (HF) treatments. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross.

		LWR		N SNUE		P SNUE		K SNUE	
Age	Treatment	BFG	WC	BFG	WC	BFG	WC	BFG	WC
5/6*	C	3.9	9.5	885	234	9495	2035	1995	826
	H	10.6	6.6	156	219	1907	1914	343	881
	F	6.6	9.1	348	249	4116	2401	838	825
	HF	8.0	7.0	217	275	3254	2552	528	1045
10	C	8.4	5.0	126	221	1343	2074	339	913
	H	4.7	3.5	116	185	1283	1925	370	852
	F	6.0	4.2	124	212	1435	1952	417	817
	HF	4.2	3.7	183	168	2308	1750	574	669
12	C	5.5	3.5	135	202	1520	1905	405	929
	H	4.2	3.1	123	173	1470	1624	366	802
	F	4.6	2.9	180	148	2220	1560	535	668
	HF	4.4	4.2	106	120	1274	1295	342	580

*Note: Age five for BF Grant and age six for Waycross.

Table 3-9: Ratio of foliar nutrient concentration to foliar nitrogen (N) concentration by treatment and age at BF Grant and Waycross, GA. Stand ages when measured were 5, 10, 12 at BF Grant and 6, 10 and 12 at Waycross. Treatments comprise of the control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide + fertilizer (HF) treatments. Foliar nutrient ratios to N were tested for boron (B), calcium (Ca) copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), molybdenum (Mo), phosphorus (P) and Zinc (Zn).

BF Grant

Stand Age	Trt	N	B	Ca	Cu	Fe	K	Mg	Mn	Mo	P	Zn
		Nutrient Ratio (%)										
5	C	100	0.046	13.7	0.023	0.50	43.7	9.7	3.06	0.0033	9.16	0.12
	H	100	0.042	11.5	0.025	0.44	44.3	6.5	2.10	0.0025	8.07	0.11
	F	100	0.043	14.5	0.017	0.53	44.3	8.2	2.77	0.0026	8.64	0.10
	HF	100	0.062	10.3	0.021	0.39	41.6	6.1	2.16	0.0032	6.69	0.09
10	C	100	0.037	16.4	0.014	0.52	40.2	9.5	3.26	0.0024	9.49	0.13
	H	100	0.035	14.8	0.020	0.49	32.1	10.0	3.36	0.0019	9.13	0.14
	F	100	0.031	10.8	0.017	0.50	35.5	7.7	2.44	0.0023	8.95	0.11
	HF	100	0.039	11.4	0.013	0.45	34.8	7.5	2.80	0.0026	8.08	0.11
12	C	100	0.038	13.3	0.015	0.59	36.8	9.5	2.76	0.0026	9.15	0.14
	H	100	0.040	13.5	0.016	0.53	35.3	8.8	3.41	0.0022	8.88	0.14
	F	100	0.044	10.0	0.020	0.39	34.8	5.9	1.84	0.0014	8.14	0.11
	HF	100	0.042	10.6	0.013	0.39	32.0	6.7	2.47	0.0017	8.40	0.11

Waycross

Stand Age	Trt	N	B	Ca	Cu	Fe	K	Mg	Mn	Mo	P
		Nutrient Ratio (%)									
6	C	100	0.078	15.1	0.018	0.45	30.2	10.2	2.22	0.0037	11.59
	H	100	0.068	13.6	0.018	0.47	25.2	10.6	1.83	0.0032	11.42
	F	100	0.063	12.6	0.017	0.42	30.2	8.0	1.86	0.0022	10.42
	HF	100	0.079	12.8	0.017	0.47	26.3	8.3	1.74	0.0023	10.81
10	C	100	0.076	16.4	0.016	0.52	24.2	11.4	1.70	0.0035	10.70
	H	100	0.094	13.8	0.020	0.61	22.0	9.7	2.52	0.0049	10.62
	F	100	0.075	12.6	0.016	0.51	25.9	8.9	1.85	0.0031	10.82
	HF	100	0.059	8.7	0.012	0.50	25.1	7.1	1.25	0.0024	9.60
12	C	100	0.080	14.5	0.013	0.59	22.5	12.2	2.07	0.0022	11.29
	H	100	0.074	14.4	0.011	0.61	21.7	12.6	1.86	0.0024	10.89
	F	100	0.080	9.1	0.012	0.45	22.5	8.3	1.26	0.0016	9.54
	HF	100	0.071	10.2	0.009	0.43	21.1	8.2	1.77	0.0019	8.41

Table 3-10: Comparison between Waycross, GA control treatment (C – no treatment) foliar NPK concentration and content with the results of other studies on *P. taeda* that had no fertilization, competition control or any other silvicultural treatment. Waycross stand ages when measured were 6, 10 and 12.

	Concentration (kg ha^{-1})				Content (kg ha^{-1})			
	Age	N	P	K	Age	N	P	K
This Study	6	14.3	1.3	6.3	6	4.9	0.4	2.1
	10	13.0	1.2	5.1	10	50.0	4.7	20.0
	12	13.2	1.2	4.7	12	53.3	4.8	19.0
Other	4 [1]	14.6	1.1	5.6	5 [4]	46.7	5.8	21.9
Studies	5 [2]	9.5	1.0	4.1	16 [5]	55.0	6.3	31.9
	11 [3]	10.7	1.1	4.8	20 [6]	59.5	5.0	27.4

Key to other studies:

[1] Samuelson *et al.* 2001.

[2] Wells and Metz 1963.

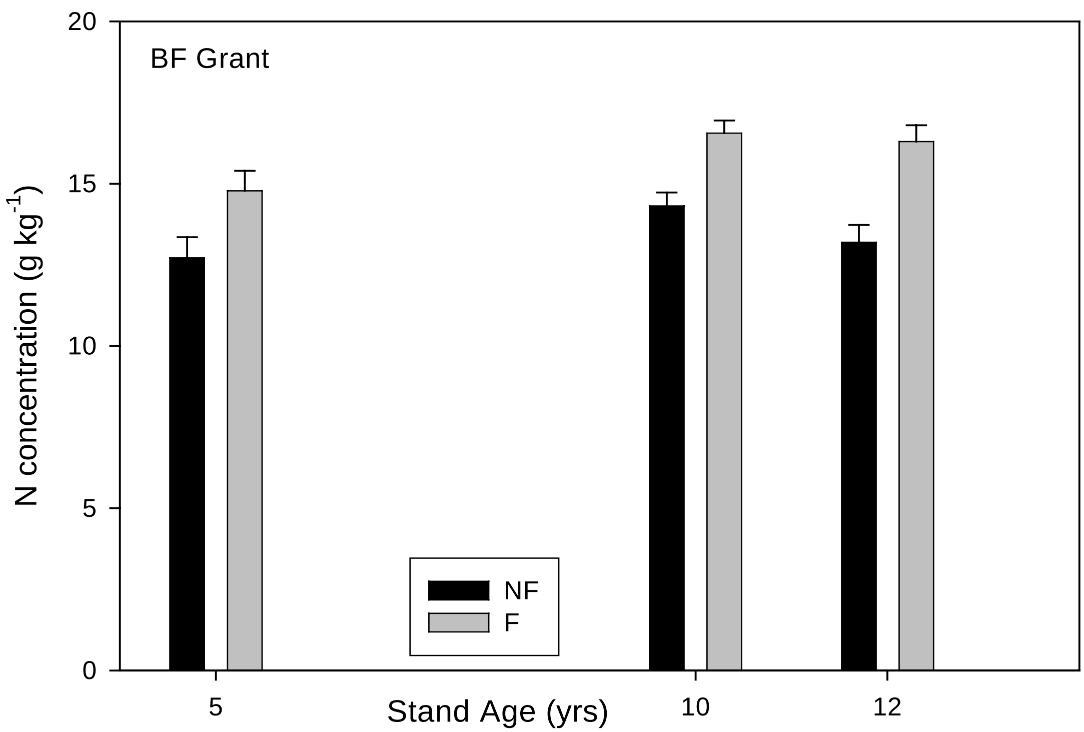
[3] Zhang and Allen 1996.

[4] Nelson *et al.* 1968.

[5] Wells and Jorgensen 1975.

[6] Switzer and Nelson 1972.

Figure 3-1: *Pinus taeda* foliar nitrogen (N) concentration for fertilized (F) and non-fertilized treatments (NF) by each age at BF Grant and Waycross, GA. Foliar concentrations represent the mean N concentration of the upper, middle and lower canopy at BF Grant and the upper and middle canopy at Waycross. Fertilized treatments represent the mean foliar N concentration of the fertilizer and herbicide + fertilizer treatments. Non-fertilized treatments represent the mean foliar N concentration of the control and herbicide treatments. BF Grant sites were established in 1995 (age five), 1990 (age ten) and 1988 (age twelve). Waycross sites were established in 1993 (age six), 1989 (age ten) and 1987 (age twelve). Vertical bars represent one standard error from the mean.


BF Grant
N concentration (g kg-1)
20
15
10
5
0
NF
F
5
10
12
Stand Age (yrs)

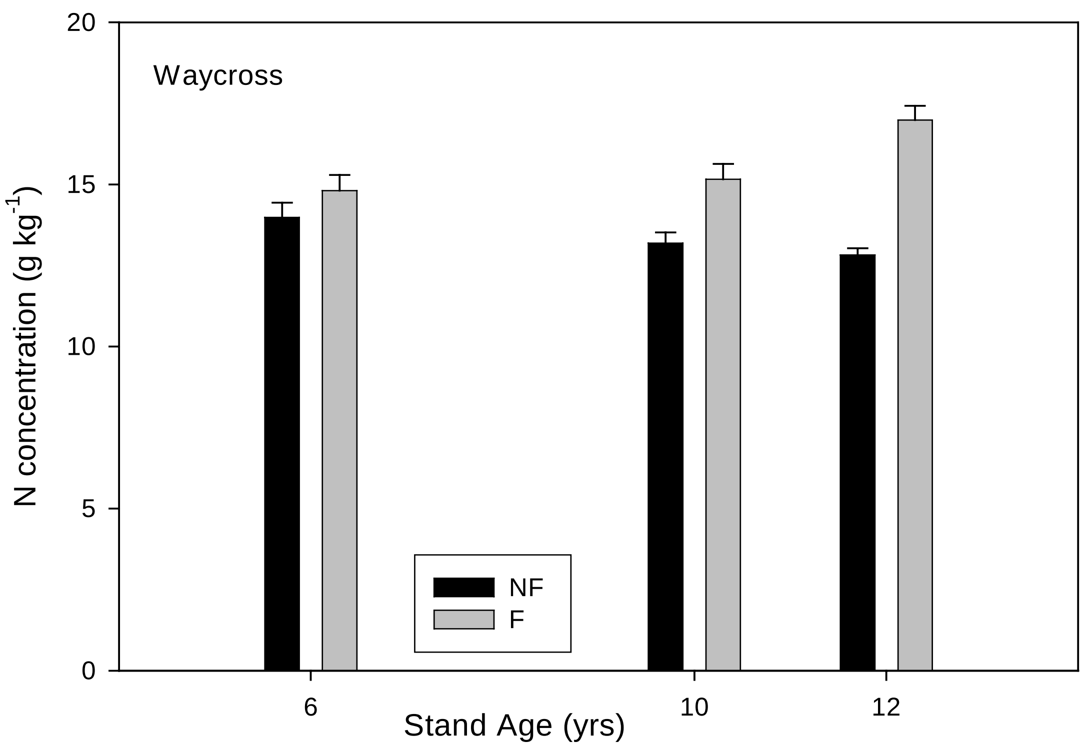
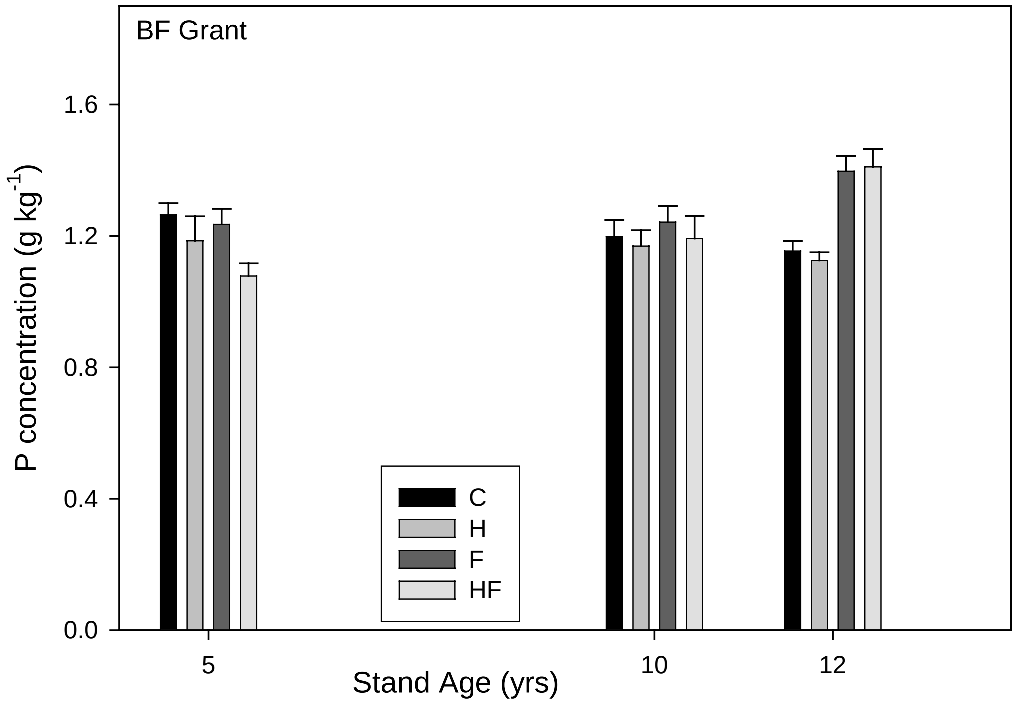

Waycross
N concentration (g kg-1)
20
15
10
5
0
NF
F
6
10
12
Stand Age (yrs)

Figure 3-2: *Pinus taeda* foliar phosphorus (P) concentration for the control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide x fertilizer (HF) treatments for each stand age at BF Grant and Waycross, GA. Foliar concentrations represent the mean P concentration of the upper, middle and lower canopy at BF Grant and the upper and middle canopy at Waycross. Vertical bars represent one standard error from the mean.


BF Grant
P concentration (g kg-1)
1.6
1.2
0.8
0.4
0.0
C
H
F
HF
5
10
12
Stand Age (yrs)

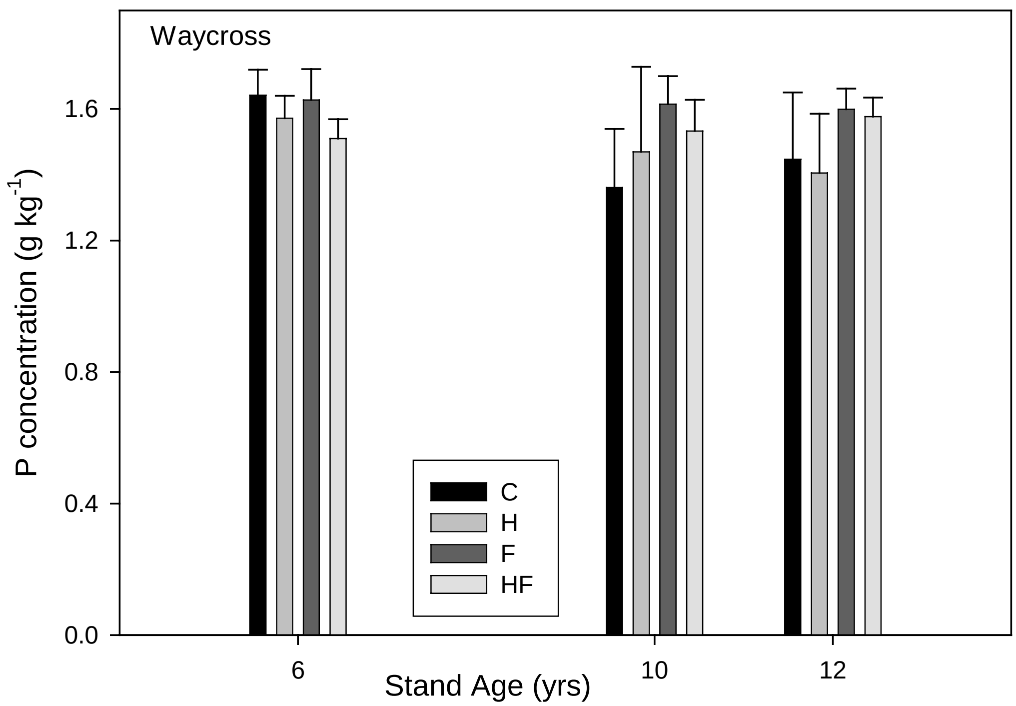
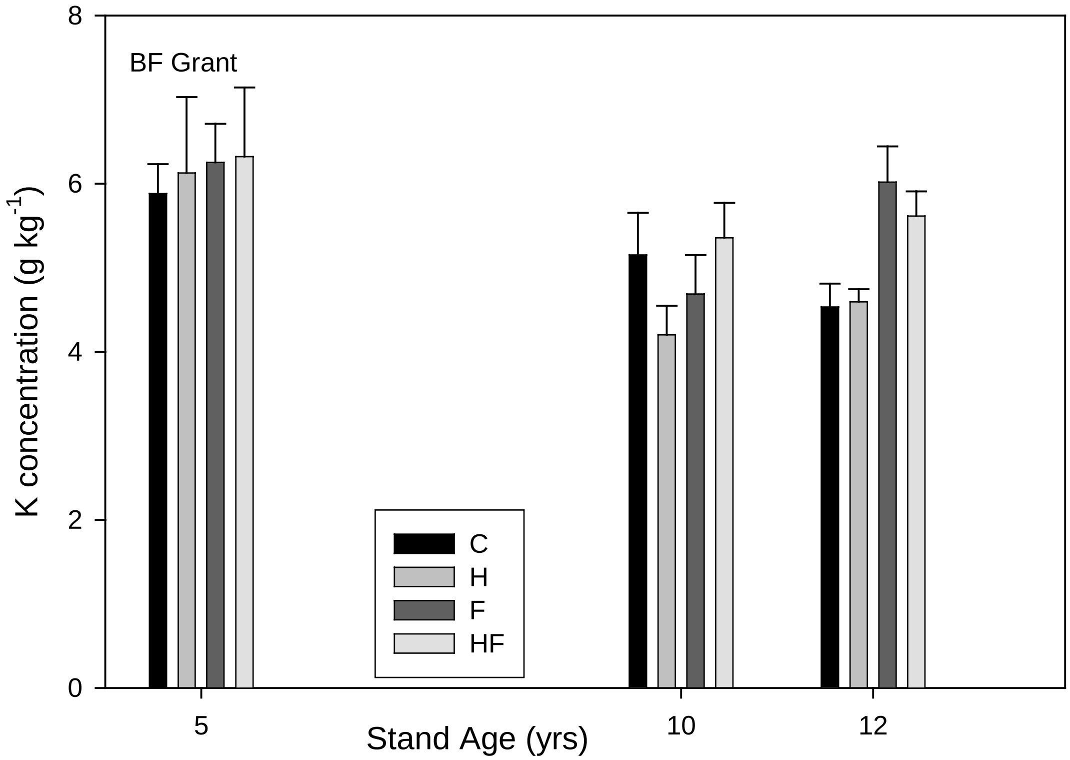

Waycross
P concentration (g kg-1)
1.6
1.2
0.8
0.4
0.0
C
H
F
HF
6
10
12
Stand Age (yrs)

Figure 3-3: *Pinus taeda* foliar potassium (K) concentration for the control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide x fertilizer (HF) treatments for each stand age at BF Grant and Waycross, GA. Foliar concentrations represent the mean K concentration of the upper, middle and lower canopy at BF Grant and the upper and middle canopy at Waycross. Vertical bars represent one standard error from the mean.


BF Grant
K concentration (g kg-1)
Stand Age (yrs)
C
H
F
HF
0
2
4
6
8
5
10
12

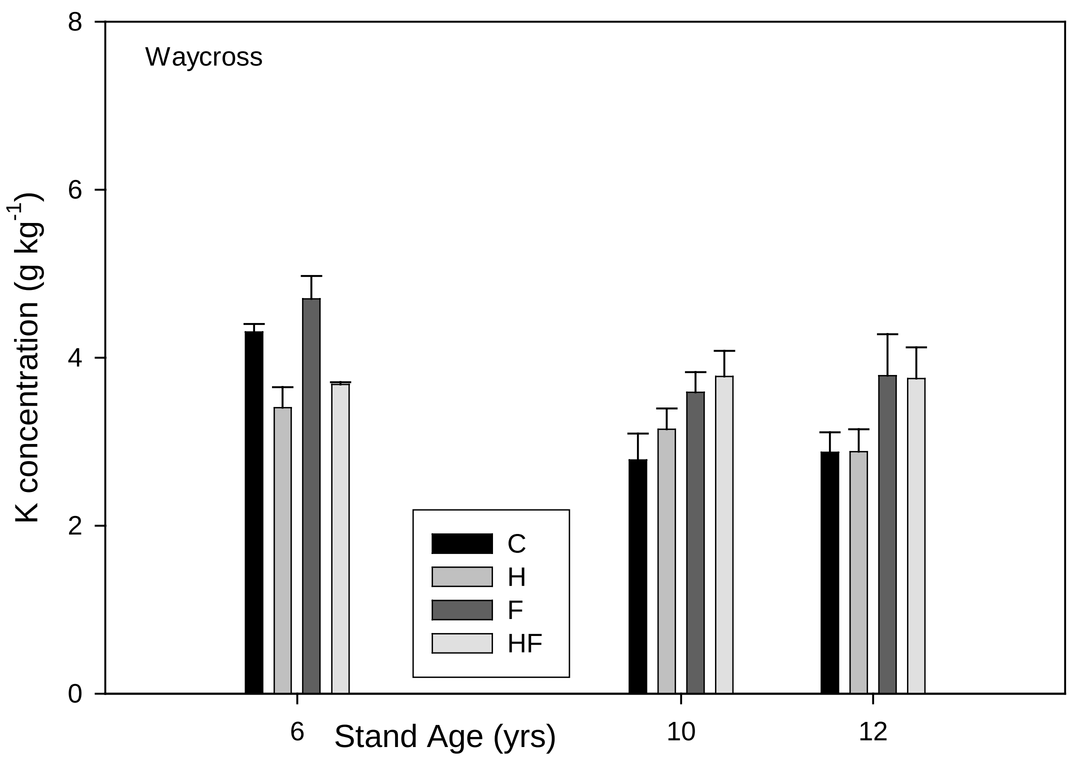

Waycross
K concentration (g kg-1)
Stand Age (yrs)
C
H
F
HF
0
2
4
6
8
6
10
12

Figure 3-4: *Pinus taeda* foliar potassium (K) concentration for herbicide (H) and non-herbicide treatments (NH) for each stand age at Waycross, GA. Foliar concentrations represent the mean K concentration of the upper and middle canopy. Herbicide treatments represent the mean foliar K concentration of the herbicide and herbicide x fertilizer treatments. Non-herbicide treatments represent the mean foliar K concentration of the control and fertilizer treatments. Vertical bars represent one standard error from the mean.

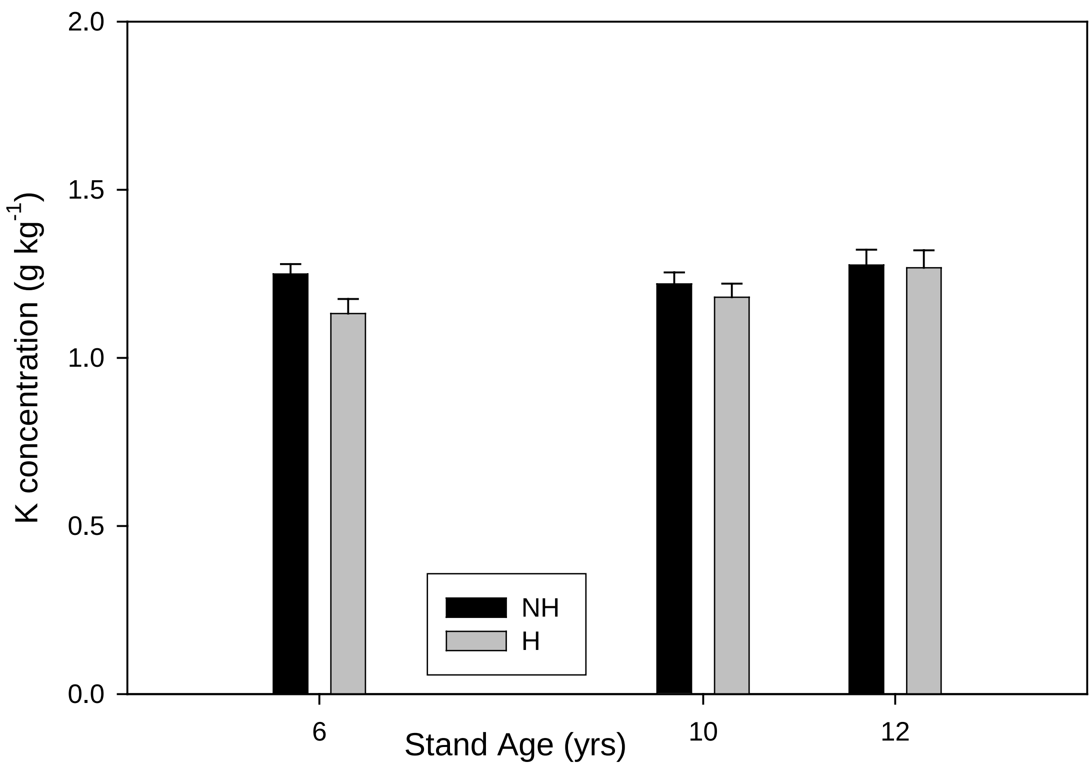
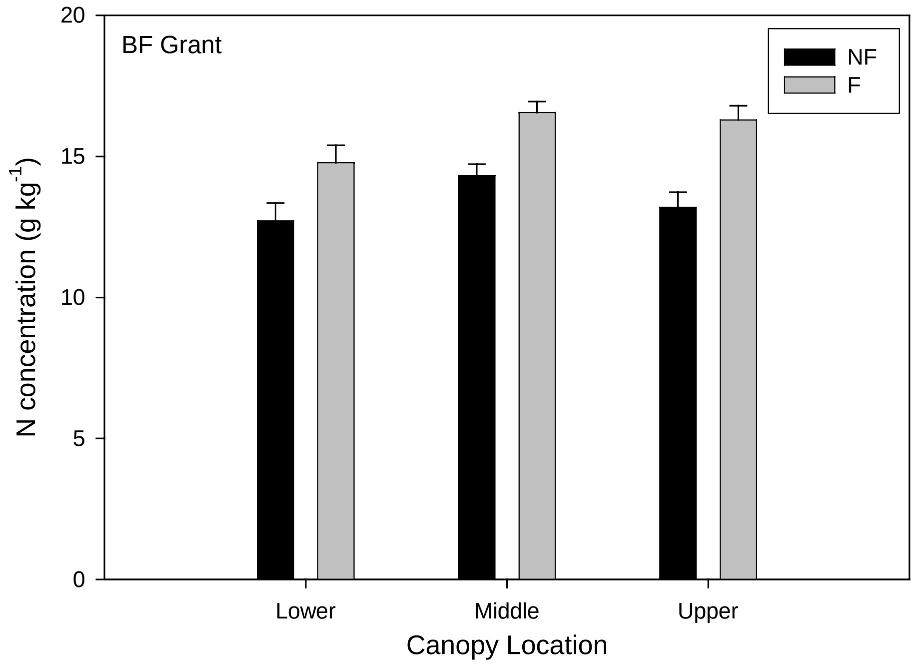


Figure 3-5: *Pinus taeda* foliar nitrogen (N) concentration for fertilized (F) and non-fertilized treatments (NF) by upper, middle and lower canopy at BF Grant and middle and upper canopy at Waycross, GA. Fertilized treatments represent the mean foliar N concentration of the fertilizer and herbicide + fertilizer treatments. Non-fertilized treatments represent the mean foliar N concentration of the control and herbicide treatments. Mean foliar nitrogen concentration was taken across the three stand age groups at BF Grant (five, ten and twelve) and Waycross (six, ten and twelve). Vertical bars represent one standard error from the mean.


BF Grant
NF
F
N concentration (g kg^{-1})
0
5
10
15
20
Lower
Middle
Upper
Canopy Location

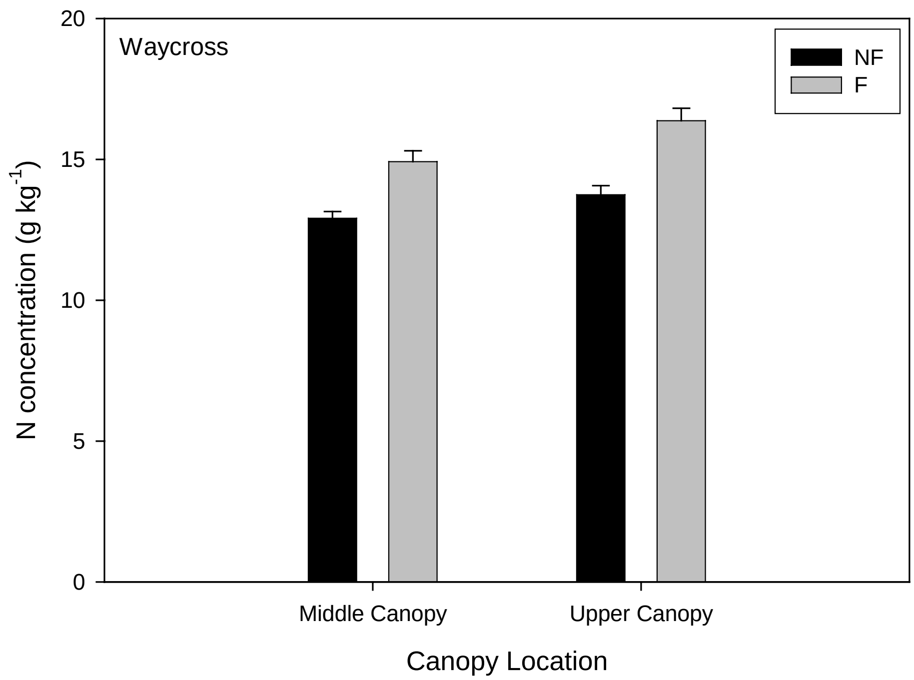
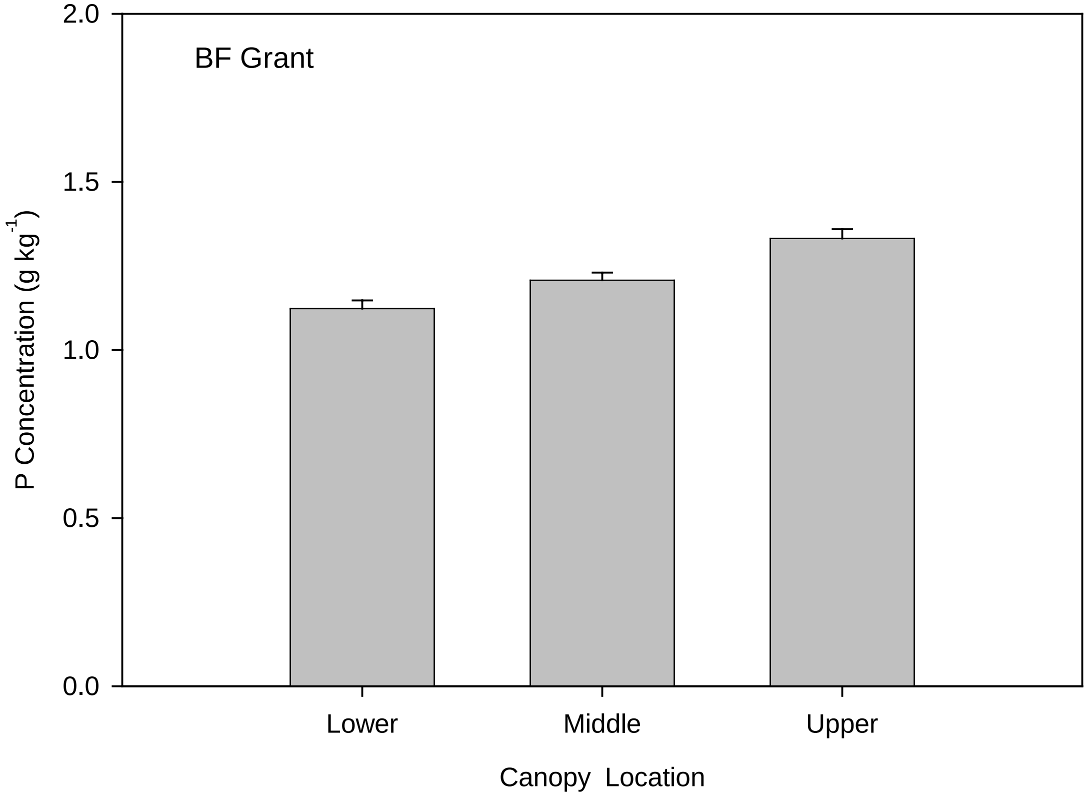

Waycross
NF
F
N concentration (g kg^{-1})
0
5
10
15
20
Middle Canopy
Upper Canopy
Canopy Location

Figure 3-6: *Pinus taeda* foliar phosphorus (P) concentration for canopy position at BF Grant and Waycross. Canopy position was the lower, middle and upper canopy at BF Grant and middle and upper canopy at Waycross, GA. Foliar concentrations represent the mean P concentration of the treatments (control, herbicide, fertilizer and herbicide + fertilizer) and the stand ages (five, ten and twelve at BF Grant and six, ten and twelve at Waycross). Vertical bars represent one standard error from the mean.


BF Grant
P Concentration (g kg-1)
2.0
1.5
1.0
0.5
0.0
Lower
Middle
Upper
Canopy Location

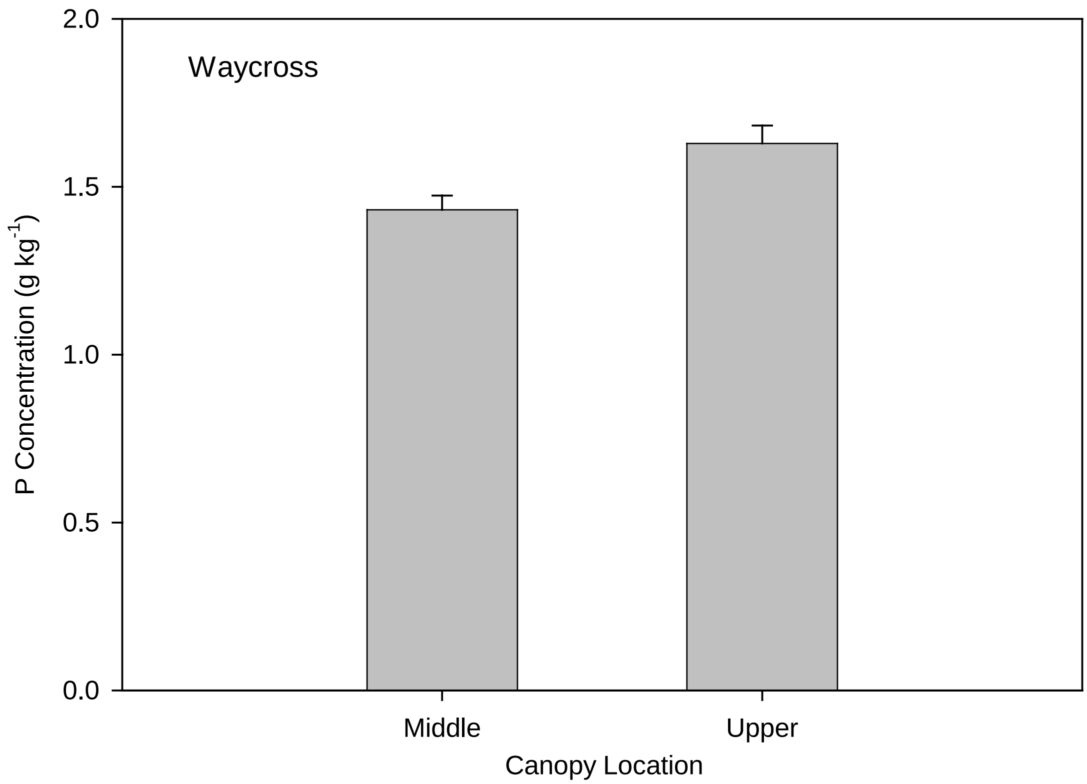

Waycross
P Concentration (g kg-1)
2.0
1.5
1.0
0.5
0.0
Middle
Upper
Canopy Location

Figure 3-7: Waycross, GA *Pinus taeda* foliar potassium (K) concentration for the control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization) and herbicide x fertilizer (HF) by canopy position. Foliar concentrations represent the mean of the stand age's six, ten and twelve. Vertical bars represent one standard error from the mean.

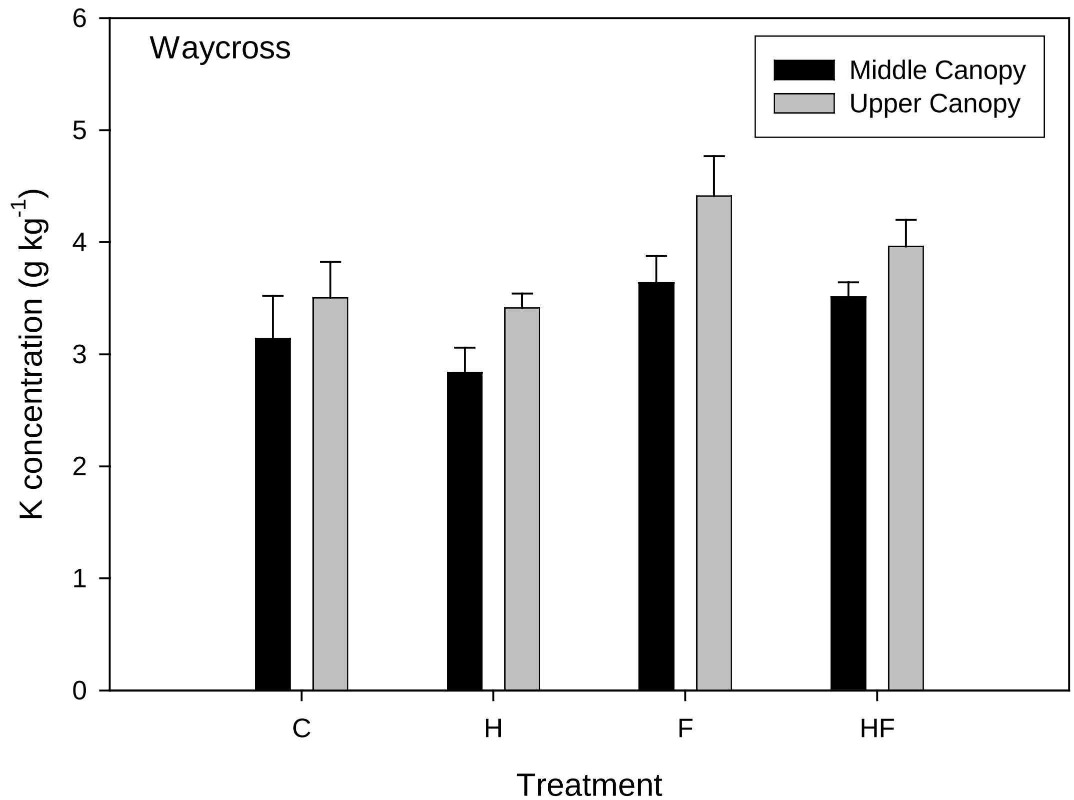
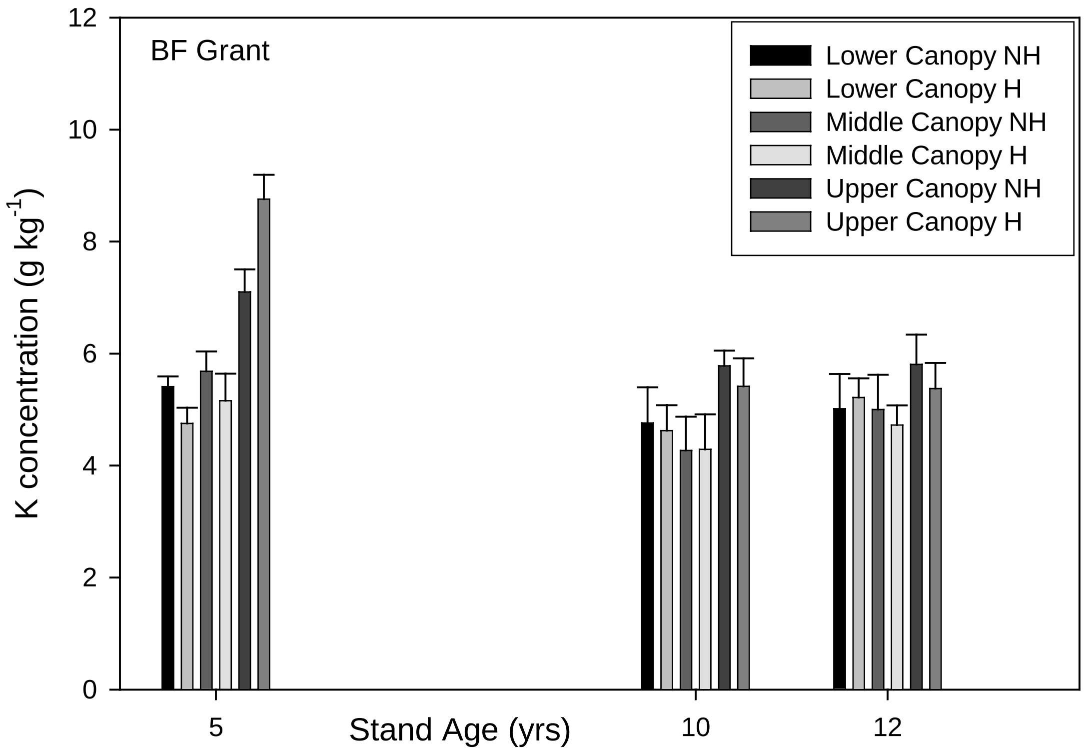

Waycross
Middle Canopy
Upper Canopy
K concentration (g kg-1)
0
1
2
3
4
5
6
C
H
F
HF
Treatment

Figure 3-8: *Pinus taeda* foliar potassium (K) concentration by canopy position for herbicide (H) and non-herbicide treatments (NH) by each age at the BF Grant and Waycross, GA. Herbicide treatments represent the mean foliar K concentration of the herbicide and herbicide x fertilizer treatments. Non-herbicide treatments represent the mean foliar K concentration of the control and fertilizer treatments. Vertical bars represent one standard error from the mean.


BF Grant
Lower Canopy NH
Lower Canopy H
Middle Canopy NH
Middle Canopy H
Upper Canopy NH
Upper Canopy H
K concentration (g kg-1)
Stand Age (yrs)
0
2
4
6
8
10
12
5
10
12

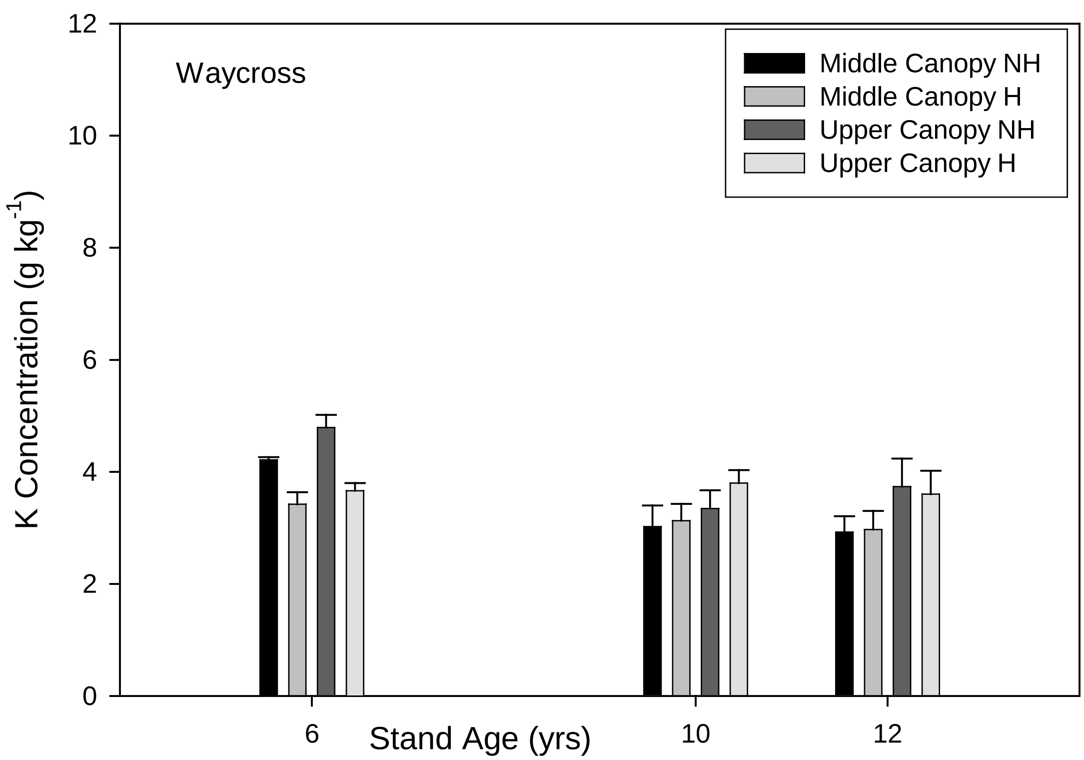
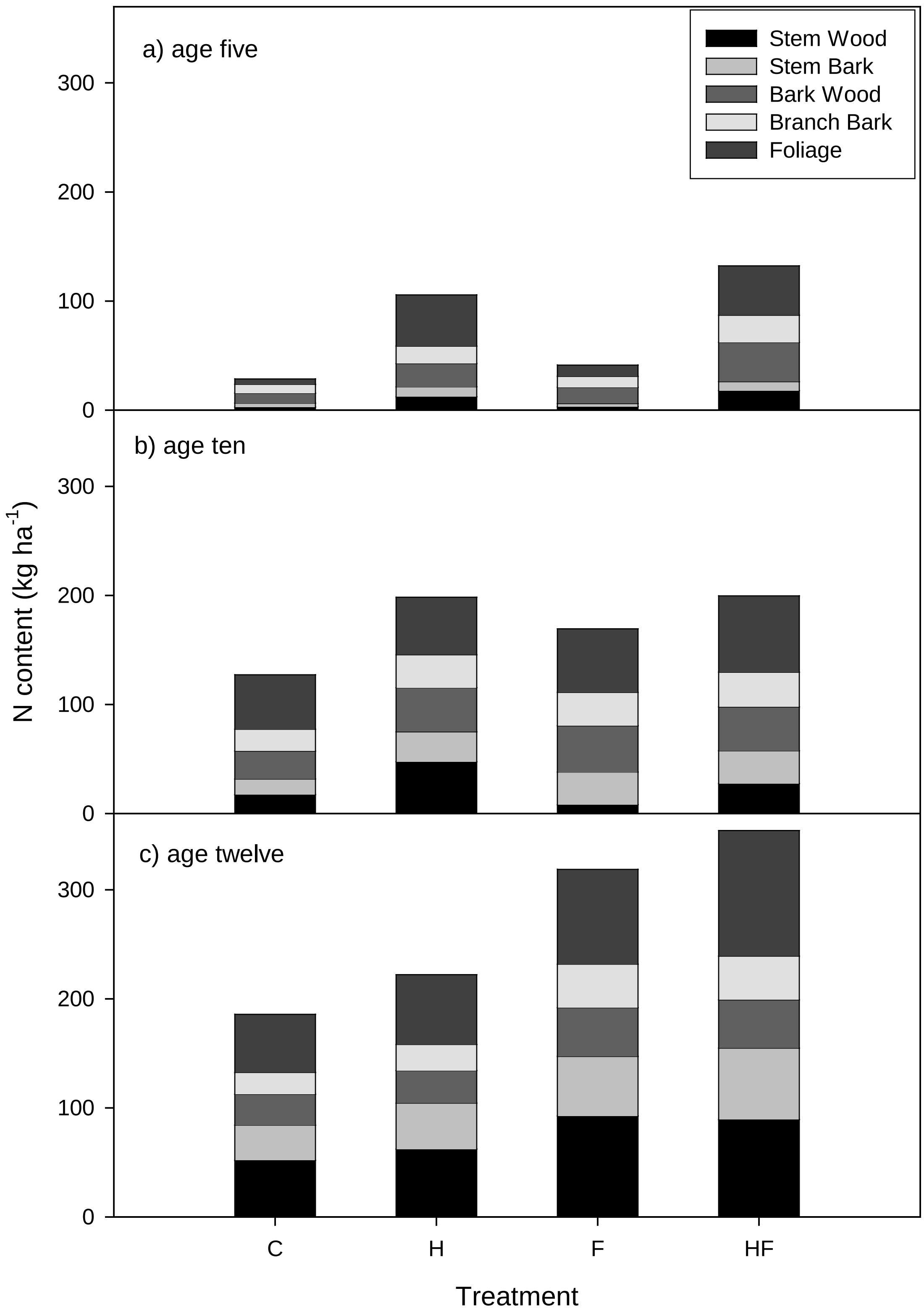

Waycross
Middle Canopy NH
Middle Canopy H
Upper Canopy NH
Upper Canopy H
K Concentration (g kg-1)
Stand Age (yrs)
0
2
4
6
8
10
12
6
10
12

Figure 3-9: BF Grant, GA *Pinus taeda* above ground tree nitrogen (N) content by tree component for control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide x fertilizer (HF) treatments for stands established in 1995 (age five), 1990 (age ten) and 1988 (age twelve). Tree components stacked in each vertical bar graph from bottom to top: stem wood, stem bark, branch wood, branch bark and foliage.



a) age five
b) age ten
c) age twelve
Stem Wood
Stem Bark
Bark Wood
Branch Bark
Foliage
N content (kg ha-1)
0
100
200
300
C
H
F
HF
Treatment

Figure 3-10: Waycross, GA *Pinus taeda* above ground tree nitrogen (N) content by tree component for control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide x fertilizer (HF) treatments for stands established in 1995 (age five), 1990 (age ten) and 1988 (age twelve). Tree components stacked in each vertical bar graph from bottom to top: stem wood, stem bark, branch wood, branch bark and foliage.

Note: branch wood concentrations from BF Grant were used for the calculation of branch wood content at Waycross.

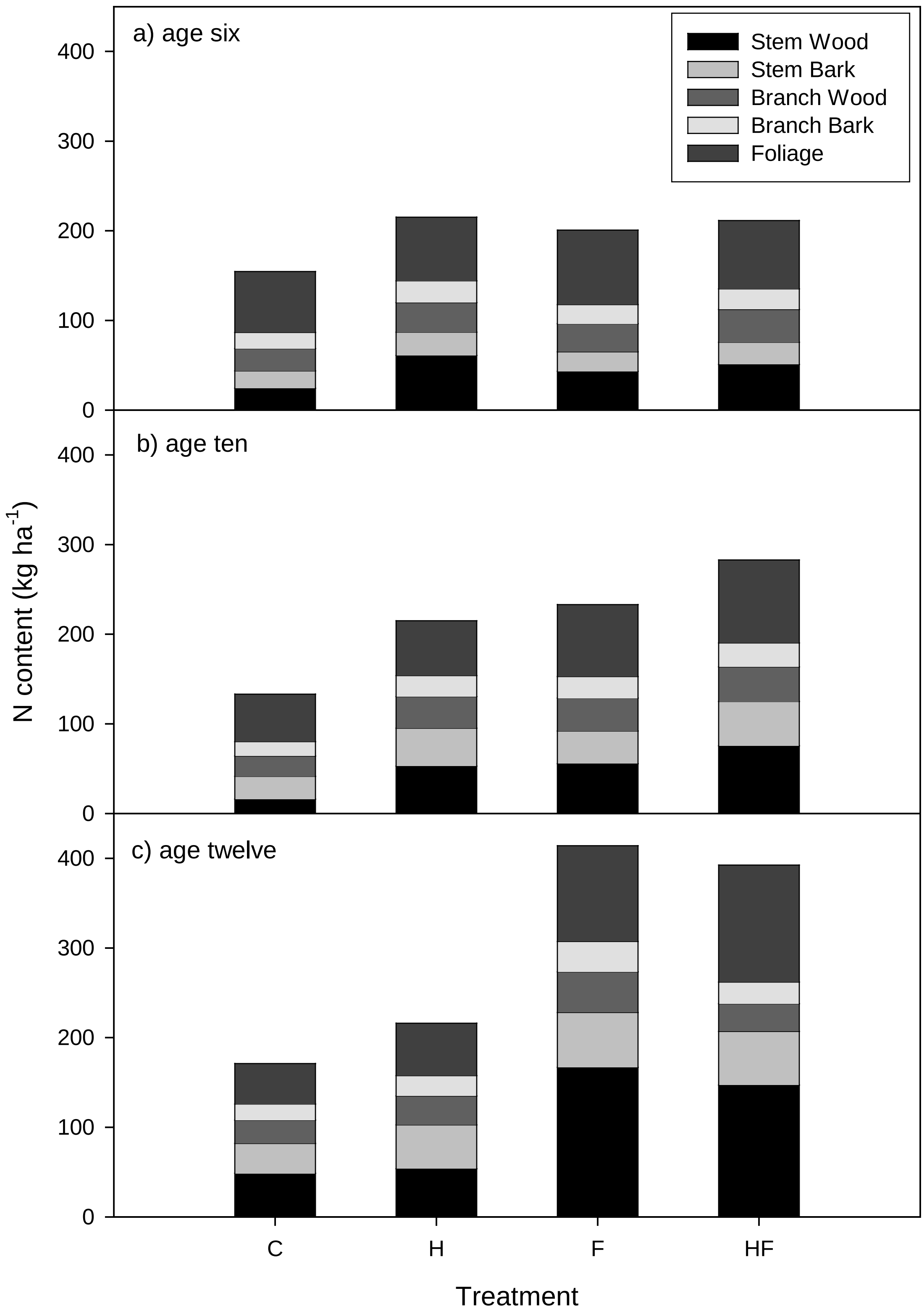
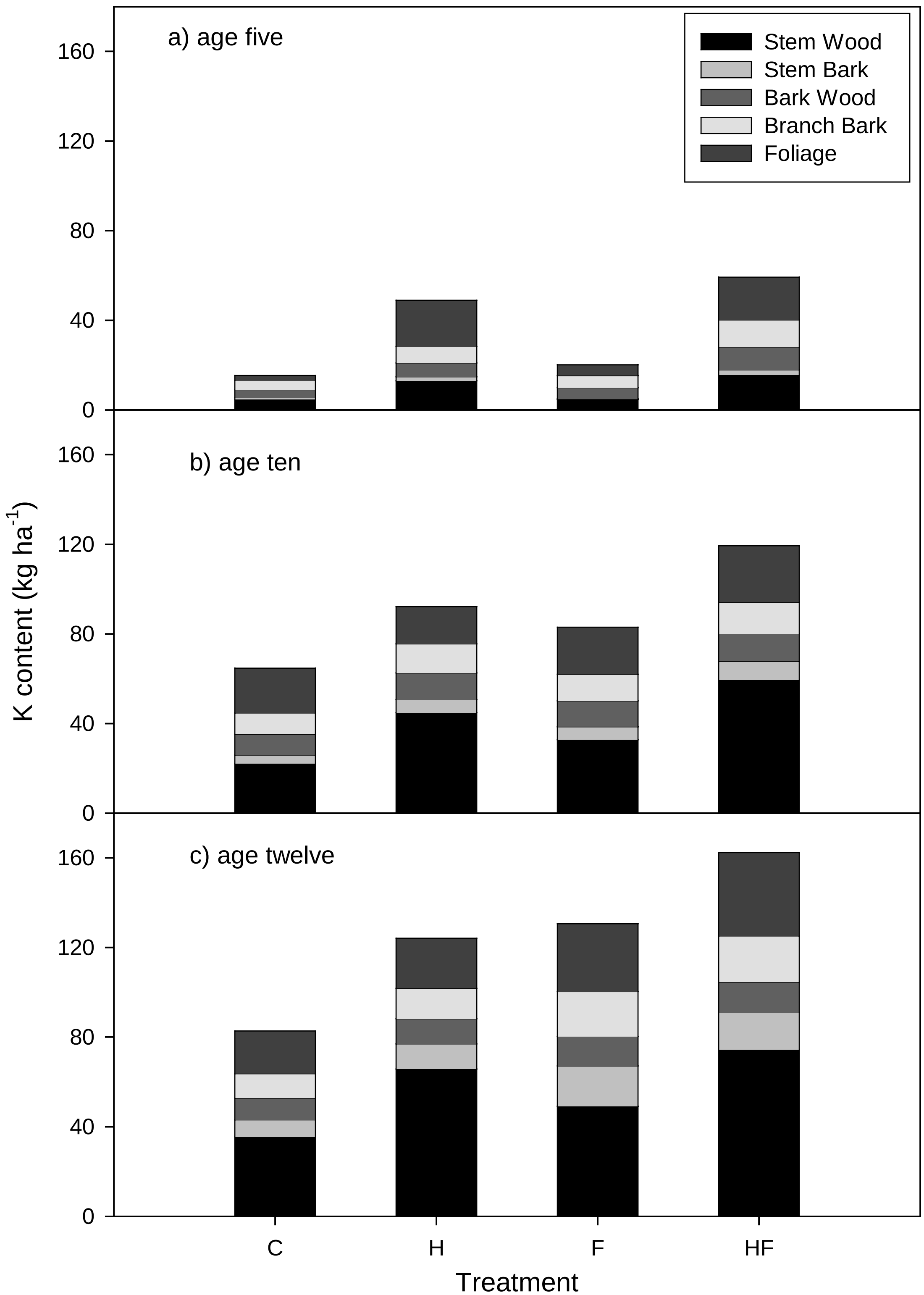

a) age six
b) age ten
c) age twelve
Stem Wood
Stem Bark
Branch Wood
Branch Bark
Foliage
N content (kg ha-1)
0
100
200
300
400
C
H
F
HF
Treatment

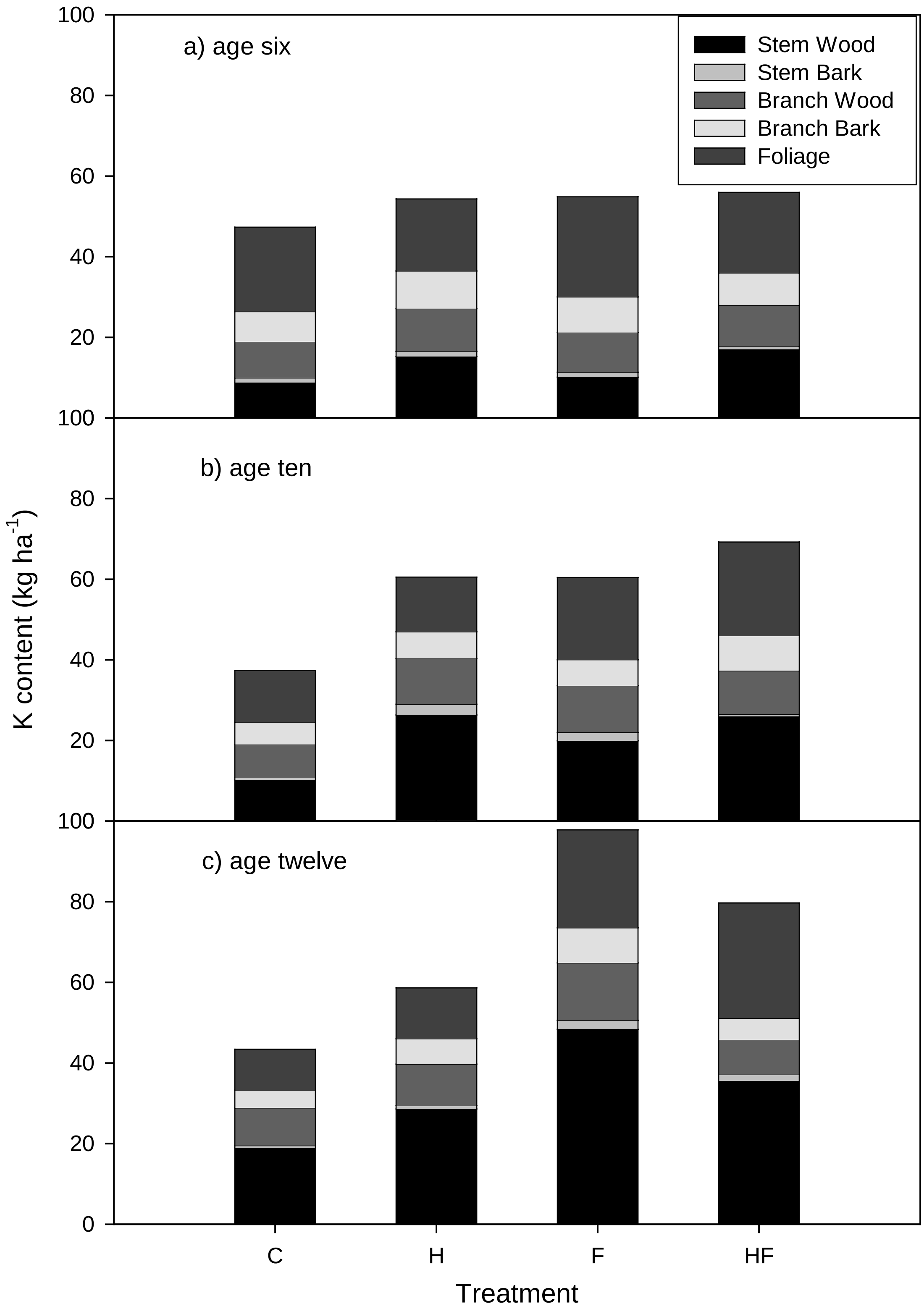
Figure 3-11: BF Grant, GA *Pinus taeda* above ground tree phosphorus (P) content by tree component for control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide x fertilizer (HF) treatments for stands established in 1995 (age five), 1990 (age ten) and 1988 (age twelve). Tree components stacked in each vertical bar graph from bottom to top: stem wood, stem bark, branch wood, branch bark and foliage.



a) age five
b) age ten
c) age twelve
Stem Wood
Stem Bark
Bark Wood
Branch Bark
Foliage
K content (kg ha^{-1})
0
40
80
120
160
C
H
F
HF
Treatment

Figure 3-12: Waycross, GA *Pinus taeda* above ground tree phosphorus (P) content by tree component for control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide x fertilizer (HF) treatments fro stands established in 1993 (age six), 1989 (age ten) and 1987 (age twelve). Tree components stacked in each vertical bar graph from bottom to top: stem wood, stem bark, branch wood, branch bark and foliage.

Note: branch wood concentrations from BF Grant were used for the calculation of branch wood content at Waycross.



100
80
60
40
20
a) age six
Stem Wood
Stem Bark
Branch Wood
Branch Bark
Foliage
100
80
60
40
20
b) age ten
100
80
60
40
20
0
c) age twelve
K content (kg ha-1)
C
H
F
HF
Treatment

Figure 3-13: BF Grant, GA *Pinus taeda* above ground tree potassium (K) content by tree component for control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide x fertilizer (HF) treatments for stands established in 1995 (age five), 1990 (age ten) and 1988 (age twelve) at the BF Grant site. Tree components stacked in each vertical bar graph from bottom to top: stem wood, stem bark, branch wood, branch bark and foliage.

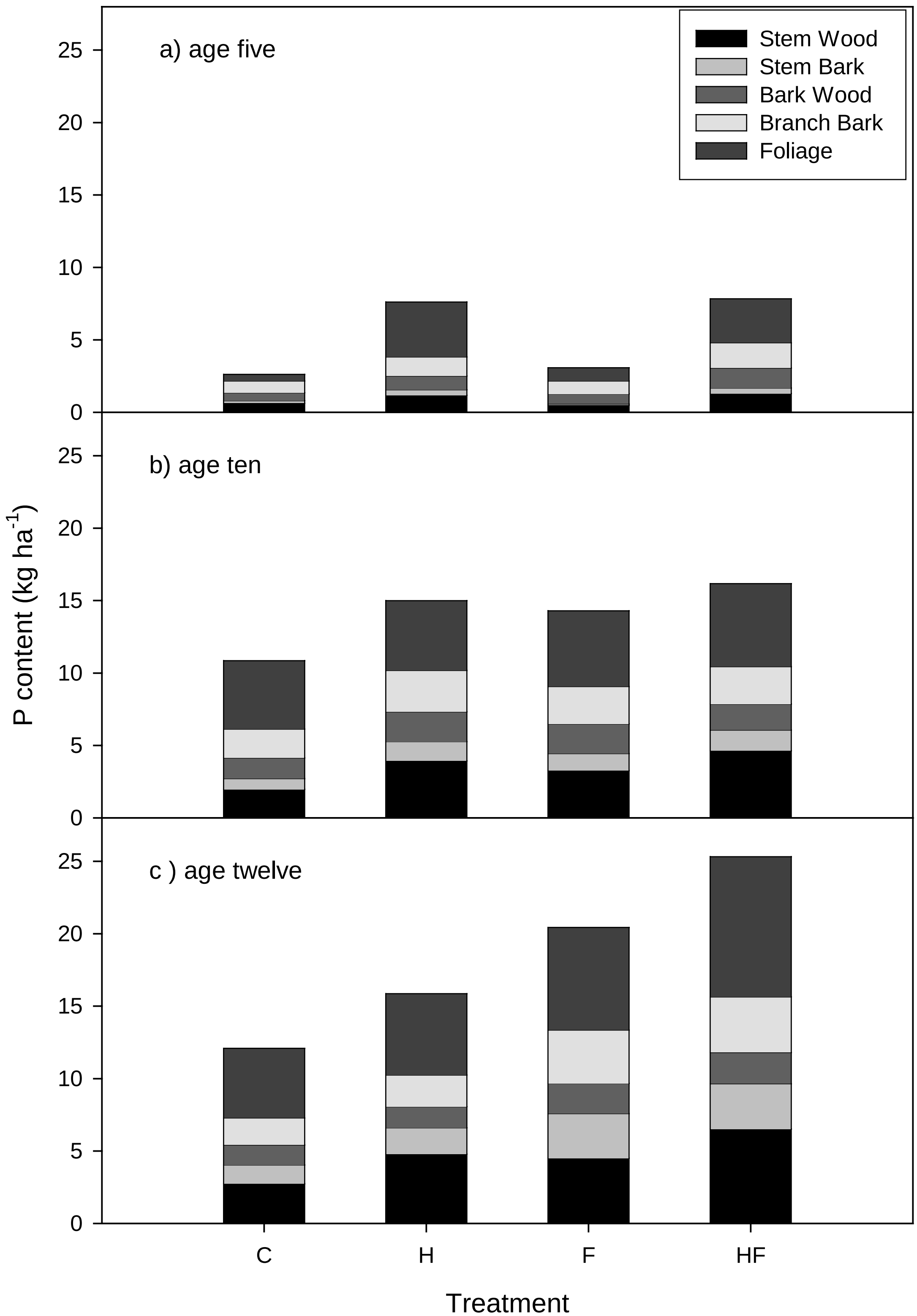
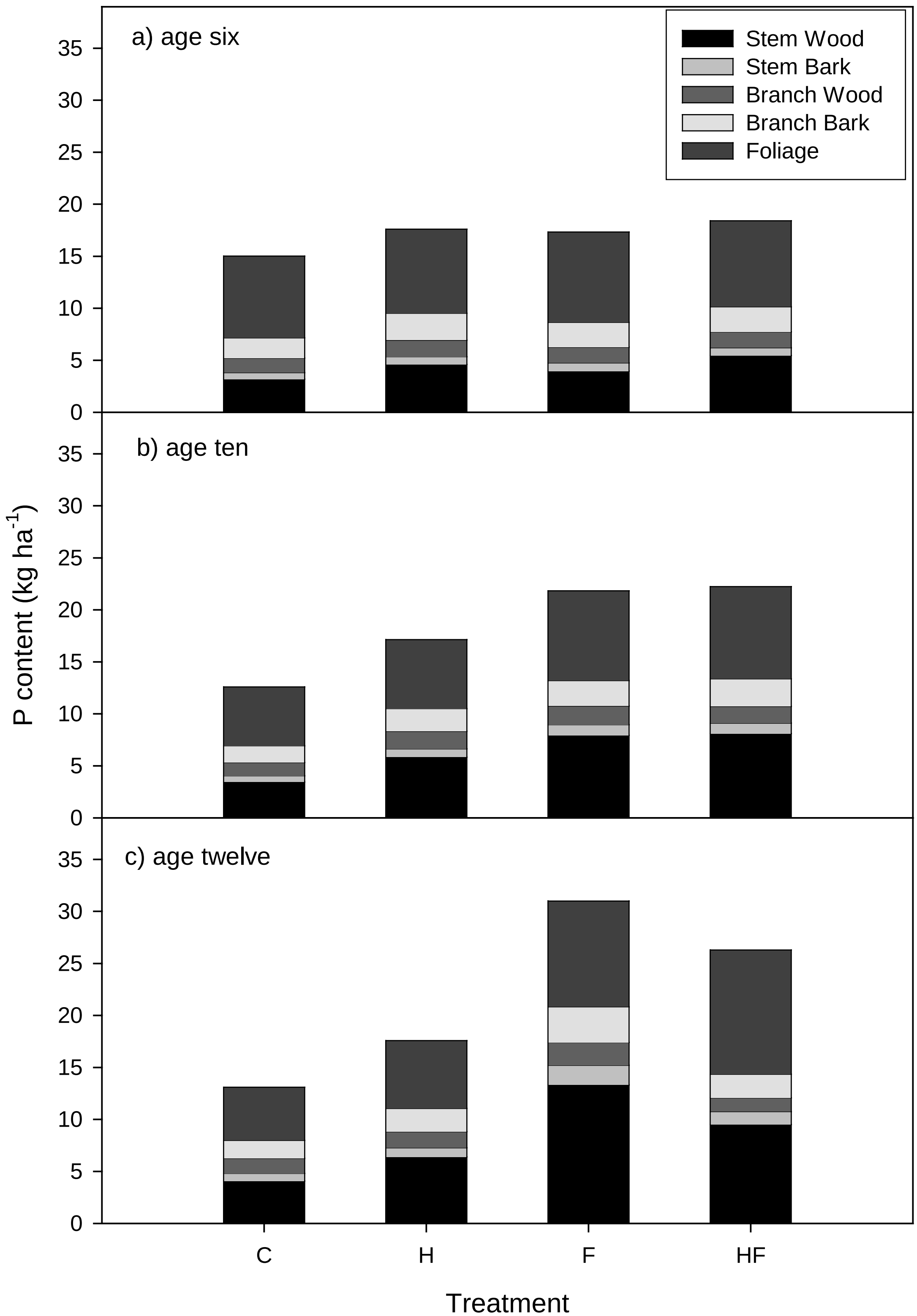

a) age five
b) age ten
c) age twelve
Stem Wood
Stem Bark
Bark Wood
Branch Bark
Foliage
P content (kg ha-1)
0
5
10
15
20
25
C
H
F
HF
Treatment

Figure 3-14: Waycross, GA *Pinus taeda* above ground tree potassium (K) content by tree component for control (C-no treatment), herbicide (H-complete interspecific competition control), fertilizer (F-annual N fertilization with periodic P and K fertilization) and herbicide x fertilizer (HF) treatments for stands established in 1993 (age six), 1989 (age ten) and 1987 (age twelve). Tree components stacked in each vertical bar graph from bottom to top: stem wood, stem bark, branch wood, branch bark and foliage.

Note: branch wood concentrations from BF Grant were used for the calculation of branch wood content at Waycross.


a) age six
b) age ten
c) age twelve
Stem Wood
Stem Bark
Branch Wood
Branch Bark
Foliage
0
5
10
15
20
25
30
35
P content (kg ha^{-1})
C
H
F
HF
Treatment

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CHAPTER FOUR:

SUMMARY AND CONCLUSIONS

Annual fertilizer applications caused a significant pulse of N in the litter leachate solution shortly after fertilization. The fertilized treatments had significantly less retention of nitrate and ammonium compared to the non-fertilized treatments. Fertilization had no impact on organic nitrogen content in litter leachate, however fertilizer doubled organic N in throughfall, which significantly increased the retention of organic nitrogen in the litter layer. The effect of fertilizer on N retention in the litter layer was sustained after the initial fertilizer pulse had passed through the litter layer. The decrease in retention of inorganic N in the litter layer was not due to a change in throughfall, but from a greater amount of inorganic N in litter leachate. The increased retention of organic N in the fertilized treatments was associated with a large retention of organic N was due to greater throughfall and no change in litter leachate. The large increase in throughfall DON associated with fertilization applications had not been reported in previous research. Competition control had no effect on the flux of nitrate or ammonium from the litter layer. The lower retention of organic nitrogen in the competition control treatments resulted from the lower amount of organic nitrogen leached from the canopy. The flux of inorganic N did vary seasonally. No significant age effect was found for any form of N. The fertilizer accelerated stand development with, deeper, more developed litter layers and increased N concentration in fresh litterfall.

The N fluxes indicate that mineralization occurred at a greater rate in the fertilized treatments likely due to better litter quality, better developed litter layer and the high amount of throughfall DON being available for microbe consumption. Although inorganic nitrogen content in the litter leachate increased for the fertilized treatments, the litter layer was still a net sink of N as microbes were still N limited. The amount of inorganic N leaving the litter layer in the litter leachate in the fertilized treatments (8 kg ha^{-1}) would be 14% of the annual tree uptake of 58 kg N ha^{-1} yr^{-1}. In contrast, the amount of inorganic N leaving the litter layer in the litter leachate from the non-fertilized treatments contributed 6% of the annual N uptake. The N flux from in the litter layer has changed in response to fertilizer inputs, although not enough to approach the amount of N that was applied annually. However, the total amount of inorganic N released from age fourteen to age 30 could be over 100 kg ha^{-1} which would have an important impact on N supply in plantation forests of the southeastern United States.

Above ground *P. taeda* NPK pools were affected by annual fertilization. The canopy dominated the above ground tree components nutrient pools with the majority of additional NPK taken up in association with the herbicide and fertilizer treatments ending up in the canopy. Fertilization reduced the majority of nutrients relative to N. This is a strong indication that the tree cannot readily change the rate of uptake of other nutrients to compensate for increased N supply in the canopy. The effects of age generally did not affect foliar NPK concentrations.

The current foliage in the upper canopy acted as a store of additional nutrients. The comparison of critical foliar NPK concentrations with foliar NPK concentrations and measures of efficiency from the different treatments in this study showed that traditional inferences from critical concentrations may be not correct because growth increased in proportion with increased nutrient concentration. Although NPK critical concentrations may correspond to leaf physiology, they did not correspond well with potential leaf area development and growth.

The information on nutrient release from the litter layer and changes in nutrient pools have given a partial picture on the nutrient dynamics of *P. taeda* under extreme treatments of annual fertilization and complete competition control. Measurements of above ground nutrient pools over the growing season would be needed to fully understand the effect of the nutrient pools and to see if the pools change the following dormant season. A large piece of the puzzle missing was nutrient content and concentration in the roots. It would be naïve to state that one fully understood nutrient dynamics under the treatments without discussing roots. For example, the roots of *P. taeda* can act as a large store of nutrients retranslocated from abscised needles. The research conducted has made an important step in our understanding of *P. taeda* nutrient dynamics, however further research is needed before a comprehensive understanding can be reached.

Fertilizer accelerated stand development with more N cycling from the litter layer, retranslocation and canopy storage in the P. taeda ecosystem. Despite the extreme treatments of compete competition control and fertilization, *P. taeda* stands remained N limited system and over 50% of applied N can be accounted in *P. taeda's* biomass. The amount and timing of the fertilization and competition control needs to be reviewed to boost uptake of other nutrients, including P and K, so growth is not limited by foliar N deficiencies. The concept of critical concentration had little meaning in explaining the treatment effects on nutrient concentration and measures of efficiency.

APPENDIX A: Estimated precipitation, throughfall and litter leachate volume (mm) for each collection at Waycross.

Collection 1 = 4/23/00 to 5/16/00, collection 2 = 5/21/00 to 6/13/00, collection 3 = 6/15/00 to 6/22/00, collection 4 = 6/27/00 to 7/18/00, collection 5 = 7/24/00 to 8/14/00, collection 6 = 8/29/00 to 9/19/00, collection 7 = 9/21/00 to 10/26/00, collection 8 = 11/13/00 to 12/8/00, collection 9 = 12/13/00 to 1/14/01, collection 10 = 1/16/01 to 2/9/01, collection 11 = 2/10/01 to 3/6/01, collection 12 = 3/12/01 to 4/3/01 and collection 13 = 4/15/01 to 5/9/01.

Collection Period	Precipitation mm	Throughfall mm	Litter Leachate mm
1	72	45	14
2	68	42	11
3	192	137	37
4	61	47	14
5	194	169	48
6	194	133	34
7	85	63	29
8	67	48	11
9	62	45	14
10	58	37	9
11	34	24	7
12	151	102	36
13	26	17	3
Total	**1264**	**909**	**267**

APPENDIX B

Nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) in the foliage, branch bark, branch wood, stem bark, stem wood and the above ground tree components biomass. For BF Grant, nutrients measured were boron (B), calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), molybdenum (Mo), nitrogen (N), phosphorus (P) and zinc (Zn) in stands established at 1988 (age 12), 1990 (age 10) and 1995 (age 5). For Waycross, nutrients measured were boron (B), calcium (Ca), copper (Cu), iron (Fe), potassium (K), magnesium (Mg), manganese (Mn), nitrogen (N) and phosphorus (P) in stands established at 1987 (age 12), 1989 (age 10) and 1993 (age 6). Molybdenum (Mo) was only measured for foliage at Waycross.

Tree samples were collected at BF Grant (GA) in January 2000 and at Waycross (GA) in December 1998 and January 1999.

Table I: BF Grant foliar nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide + fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

		Boron		Calcium	
Age		Content	Concentration x 10^{-3}	Content	Concentration
5	C	0.002 ± 0.0002	6.53 ± 0.19	0.67 ± 0.06	1.96 ± 0.05
	H	0.020 ± 0.0020	6.59 ± 0.39	5.34 ± 0.01	1.80 ± 0.07
	F	0.004 ± 0.0009	6.51 ± 1.27	1.56 ± 0.66	2.16 ± 0.07
	HF	0.027 ± 0.0020	10.45 ± 2.32	4.57 ± 0.05	1.73 ± 0.28
10	C	0.019 ± 0.0041	4.83 ± 1.08	8.37 ± 2.29	2.16 ± 0.31
	H	0.019 ± 0.0064	4.64 ± 1.25	8.22 ± 3.41	1.95 ± 0.32
	F	0.018 ± 0.0020	4.49 ± 0.62	6.19 ± 0.97	1.59 ± 0.27
	HF	0.028 ± 0.0079	6.10 ± 0.83	7.68 ± 1.41	1.80 ± 0.19
12	C	0.020 ± 0.0027	4.92 ± 0.68	7.16 ± 1.46	1.78 ± 0.26
	H	0.026 ± 0.0047	5.32 ± 1.04	8.66 ± 0.97	1.77 ± 0.18
	F	0.038 ± 0.0049	7.77 ± 0.70	8.70 ± 1.27	1.79 ± 0.20
	HF	0.047 ± 0.0089	7.25 ± 1.48	11.72 ± 1.20	1.82 ± 0.19

		Copper		Iron	
Age		Content	Concentration x 10^{-3}	Content	Concentration
5	C	0.001 ± 0.0002	3.28 ± 0.66	0.02 ± 0.005	0.071 ± 0.010
	H	0.011 ± 0.0026	3.87 ± 1.02	0.21 ± 0.016	0.070 ± 0.008
	F	0.002 ± 0.0006	2.53 ± 0.12	0.06 ± 0.023	0.078 ± 0.001
	HF	0.009 ± 0.0002	3.55 ± 0.59	0.18 ± 0.048	0.065 ± 0.008
10	C	0.007 ± 0.0010	1.85 ± 0.40	0.26 ± 0.061	0.067 ± 0.007
	H	0.011 ± 0.0046	2.58 ± 0.71	0.27 ± 0.068	0.065 ± 0.006
	F	0.011 ± 0.0050	2.53 ± 0.94	0.28 ± 0.031	0.073 ± 0.014
	HF	0.010 ± 0.0029	2.09 ± 0.30	0.31 ± 0.075	0.070 ± 0.005
12	C	0.008 ± 0.0014	1.89 ± 0.28	0.30 ± 0.064	0.074 ± 0.013
	H	0.010 ± 0.0013	2.05 ± 0.36	0.33 ± 0.048	0.067 ± 0.006
	F	0.018 ± 0.0057	3.57 ± 0.64	0.34 ± 0.062	0.069 ± 0.005
	HF	0.015 ± 0.0021	2.24 ± 0.19	0.45 ± 0.073	0.068 ± 0.005

Table I continued

		Potassium		Magnesium	
Age		Content	Concentration	Content	Concentration
5	C	2.14 ± 0.14	6.26 ± 0.02	0.48 ± 0.06	1.39 ± 0.07
	H	20.54 ± 1.47	6.94 ± 0.78	3.02 ± 0.31	1.02 ± 0.15
	F	4.87 ± 2.40	6.53 ± 0.76	0.85 ± 0.28	1.24 ± 0.11
	HF	19.06 ± 3.92	6.97 ± 0.40	2.75 ± 0.28	1.02 ± 0.05
10	C	19.98 ± 5.25	5.12 ± 0.81	4.77 ± 0.91	1.23 ± 0.08
	H	16.62 ± 2.69	4.20 ± 0.50	5.53 ± 1.87	1.32 ± 0.20
	F	20.92 ± 4.76	5.17 ± 0.76	4.50 ± 0.77	1.13 ± 0.12
	HF	25.17 ± 7.96	5.48 ± 0.75	5.23 ± 1.11	1.18 ± 0.04
12	C	19.03 ± 2.61	4.72 ± 0.60	5.01 ± 0.37	1.25 ± 0.09
	H	22.39 ± 0.95	4.55 ± 0.16	5.60 ± 0.20	1.14 ± 0.09
	F	30.30 ± 6.54	6.09 ± 0.77	5.16 ± 0.59	1.05 ± 0.05
	HF	37.19 ± 7.63	5.57 ± 0.46	7.49 ± 0.74	1.15 ± 0.09

		Manganese		Molybdenum	
Age		Content	Concentration	Content	Concentration x 10^{-3}
5	C	0.15 ± 0.04	0.43 ± 0.07	0.0002 ± 0.00000	0.48 ± 0.04
	H	0.97 ± 0.11	0.33 ± 0.05	0.0012 ± 0.00004	0.40 ± 0.00
	F	0.31 ± 0.17	0.41 ± 0.08	0.0003 ± 0.00021	0.38 ± 0.15
	HF	0.97 ± 0.03	0.36 ± 0.04	0.0015 ± 0.00025	0.55 ± 0.01
10	C	1.63 ± 0.27	0.42 ± 0.02	0.0013 ± 0.00072	0.32 ± 0.15
	H	1.83 ± 0.61	0.44 ± 0.08	0.0011 ± 0.00056	0.25 ± 0.10
	F	1.44 ± 0.37	0.36 ± 0.07	0.0015 ± 0.00107	0.35 ± 0.22
	HF	1.90 ± 0.31	0.44 ± 0.04	0.0020 ± 0.00117	0.43 ± 0.21
12	C	1.45 ± 0.25	0.36 ± 0.08	0.0014 ± 0.00019	0.34 ± 0.05
	H	2.15 ± 0.16	0.44 ± 0.01	0.0014 ± 0.00036	0.28 ± 0.06
	F	1.59 ± 0.18	0.33 ± 0.04	0.0012 ± 0.00036	0.25 ± 0.09
	HF	2.76 ± 0.23	0.43 ± 0.04	0.0021 ± 0.00094	0.30 ± 0.12

Table I continued

Age		Phosphorous Content			Phosphorous Concentration			Nitrogen Content			Nitrogen Concentration		
5	C	0.45	±	0.03	1.31	±	0.01	4.90	±	0.11	14.35	±	0.60
	H	3.78	±	0.18	1.27	±	0.01	46.94	±	3.94	15.77	±	0.67
	F	0.92	±	0.38	1.29	±	0.01	10.32	±	3.21	15.08	±	1.51
	HF	3.04	±	0.48	1.12	±	0.01	45.35	±	6.28	16.77	±	0.20
10	C	4.72	±	0.66	1.23	±	0.06	49.98	±	7.59	12.98	±	0.89
	H	4.82	±	0.88	1.20	±	0.04	52.85	±	10.06	13.14	±	0.64
	F	5.23	±	0.77	1.31	±	0.04	58.23	±	7.03	14.64	±	0.33
	HF	5.73	±	1.55	1.27	±	0.09	69.98	±	15.53	15.79	±	0.77
12	C	4.80	±	0.30	1.19	±	0.03	53.26	±	7.18	13.18	±	1.39
	H	5.63	±	0.18	1.15	±	0.08	63.97	±	4.43	13.09	±	1.50
	F	7.07	±	0.82	1.44	±	0.01	86.92	±	9.46	17.76	±	1.10
	HF	9.68	±	1.60	1.46	±	0.07	115.20	±	19.00	17.41	±	0.99

Age		Zinc Content			Zinc Concentration		
5	C	0.006	±	0.0003	0.017	±	0.0002
	H	0.051	±	0.0003	0.017	±	0.0008
	F	0.011	±	0.0049	0.016	±	0.0006
	HF	0.042	±	0.0032	0.016	±	0.0012
10	C	0.067	±	0.0104	0.017	±	0.0019
	H	0.078	±	0.0254	0.019	±	0.0024
	F	0.061	±	0.0047	0.016	±	0.0030
	HF	0.079	±	0.0214	0.018	±	0.0015
12	C	0.074	±	0.0071	0.018	±	0.0011
	H	0.087	±	0.0155	0.018	±	0.0043
	F	0.092	±	0.0057	0.019	±	0.0013
	HF	0.126	±	0.0092	0.019	±	0.0020

Table II: Waycross foliar nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

		Boron		Calcium	
Age		Content	Concentration x 10^{-3}	Content	Concentration
6	C	0.055 ± 0.021	11.35 ± 3.09	10.09 ± 1.52	2.13 ± 0.21
	H	0.048 ± 0.013	9.46 ± 2.83	9.60 ± 0.56	1.88 ± 0.03
	F	0.053 ± 0.015	9.81 ± 2.17	10.42 ± 1.40	1.96 ± 0.13
	HF	0.062 ± 0.023	11.14 ± 3.68	9.79 ± 1.17	1.79 ± 0.14
10	C	0.040 ± 0.011	9.64 ± 2.28	8.67 ± 2.00	2.10 ± 0.54
	H	0.056 ± 0.018	12.42 ± 3.76	8.50 ± 1.70	1.89 ± 0.40
	F	0.064 ± 0.030	10.77 ± 3.17	9.64 ± 0.68	1.81 ± 0.48
	HF	0.055 ± 0.016	9.24 ± 2.27	8.00 ± 2.26	1.39 ± 0.46
12	C	0.037 ± 0.011	10.12 ± 2.16	6.52 ± 1.68	1.86 ± 0.22
	H	0.042 ± 0.005	9.45 ± 1.76	8.73 ± 2.69	1.86 ± 0.40
	F	0.087 ± 0.025	11.84 ± 2.66	9.66 ± 1.56	1.53 ± 0.25
	HF	0.094 ± 0.025	12.31 ± 2.72	11.28 ± 1.84	1.51 ± 0.30

		Copper		Iron	
Age		Content	Concentration x 10^{-3}	Content	Concentration
6	C	0.0125 ± 0.0052	2.55 ± 0.82	0.309 ± 0.085	0.064 ± 0.013
	H	0.0125 ± 0.0005	2.45 ± 0.14	0.339 ± 0.073	0.067 ± 0.015
	F	0.0137 ± 0.0009	2.62 ± 0.32	0.357 ± 0.091	0.066 ± 0.012
	HF	0.0130 ± 0.0010	2.42 ± 0.34	0.361 ± 0.074	0.065 ± 0.009
10	C	0.0084 ± 0.0014	2.03 ± 0.39	0.277 ± 0.044	0.066 ± 0.009
	H	0.0121 ± 0.0039	2.70 ± 0.91	0.375 ± 0.007	0.083 ± 0.002
	F	0.0122 ± 0.0000	2.26 ± 0.45	0.419 ± 0.134	0.073 ± 0.009
	HF	0.0112 ± 0.0020	1.94 ± 0.45	0.465 ± 0.097	0.079 ± 0.013
12	C	0.0061 ± 0.0023	1.68 ± 0.51	0.263 ± 0.048	0.076 ± 0.003
	H	0.0062 ± 0.0017	1.37 ± 0.30	0.353 ± 0.039	0.078 ± 0.002
	F	0.0128 ± 0.0026	1.99 ± 0.33	0.478 ± 0.052	0.075 ± 0.006
	HF	0.0124 ± 0.0053	1.60 ± 0.67	0.590 ± 0.090	0.077 ± 0.009

Table II continued

Age		Potassium Content			Potassium Concentration			Magnesium Content			Magnesium Concentration		
6	C	20.93	±	6.52	4.31	±	0.94	6.79	±	0.75	1.44	±	0.06
	H	17.83	±	2.15	3.48	±	0.38	7.43	±	0.62	1.45	±	0.06
	F	24.83	±	2.42	4.70	±	0.35	6.59	±	0.69	1.24	±	0.05
	HF	20.03	±	1.36	3.68	±	0.08	6.32	±	0.71	1.16	±	0.09
10	C	12.83	±	2.18	3.10	±	0.61	6.02	±	0.82	1.45	±	0.24
	H	13.56	±	2.12	3.01	±	0.51	5.89	±	0.19	1.30	±	0.02
	F	20.43	±	1.79	3.73	±	0.42	7.09	±	0.81	1.29	±	0.11
	HF	23.21	±	0.12	3.97	±	0.18	6.58	±	0.27	1.13	±	0.10
12	C	10.11	±	2.59	2.87	±	0.42	5.32	±	1.03	1.55	±	0.22
	H	12.65	±	1.42	2.79	±	0.08	7.37	±	1.28	1.62	±	0.16
	F	24.32	±	4.65	3.79	±	0.52	8.86	±	0.50	1.40	±	0.03
	HF	28.62	±	4.98	3.75	±	0.50	9.90	±	0.35	1.32	±	0.11

Age		Manganese Content			Manganese Concentration			Molybdenum Content			Molybdenum Concentration $\times 10^{-3}$		
6	C	1.45	±	0.29	0.31	±	0.07	0.0025	±	0.0011	0.52	±	0.21
	H	1.27	±	0.32	0.25	±	0.06	0.0022	±	0.0008	0.43	±	0.15
	F	1.44	±	0.35	0.28	±	0.09	0.0017	±	0.0007	0.34	±	0.14
	HF	1.26	±	0.45	0.24	±	0.10	0.0017	±	0.0005	0.32	±	0.09
10	C	0.90	±	0.58	0.22	±	0.14	0.0019	±	0.0008	0.45	±	0.21
	H	1.62	±	1.23	0.36	±	0.28	0.0031	±	0.0015	0.69	±	0.35
	F	1.27	±	0.94	0.27	±	0.22	0.0021	±	0.0015	0.45	±	0.36
	HF	1.15	±	0.91	0.20	±	0.17	0.0022	±	0.0010	0.39	±	0.20
12	C	0.90	±	0.56	0.27	±	0.16	0.0011	±	0.0006	0.29	±	0.13
	H	1.17	±	0.64	0.24	±	0.11	0.0011	±	0.0007	0.24	±	0.15
	F	1.29	±	0.80	0.21	±	0.13	0.0013	±	0.0007	0.21	±	0.11
	HF	1.58	±	1.06	0.22	±	0.15	0.0015	±	0.0012	0.19	±	0.14

Table II continued

Age		Nitrogen Content			Nitrogen Concentration			Phosphorus Content			Phosphorus Concentration		
6	C	67.79	±	12.75	14.18	±	1.18	7.85	±	1.58	1.64	±	0.18
	H	71.01	±	5.48	13.91	±	1.00	8.07	±	0.27	1.58	±	0.06
	F	83.20	±	11.03	15.62	±	0.90	8.69	±	1.29	1.63	±	0.11
	HF	76.14	±	6.03	13.98	±	0.44	8.26	±	0.91	1.51	±	0.06
10	C	52.92	±	0.10	12.74	±	0.38	5.66	±	1.06	1.37	±	0.29
	H	61.18	±	3.99	13.56	±	1.05	6.62	±	2.26	1.47	±	0.52
	F	80.34	±	14.42	14.38	±	0.26	8.63	±	1.23	1.56	±	0.09
	HF	92.41	±	1.22	15.79	±	0.58	8.87	±	0.08	1.52	±	0.06
12	C	45.20	±	10.90	12.74	±	0.57	5.11	±	1.70	1.45	±	0.28
	H	58.49	±	7.54	12.86	±	0.30	6.54	±	1.78	1.41	±	0.25
	F	106.69	±	7.48	16.79	±	0.40	10.17	±	0.78	1.60	±	0.01
	HF	130.38	±	14.32	17.17	±	1.07	11.95	±	1.06	1.58	±	0.08

Table III: BF Grant branch bark nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

		Boron		Calcium	
Age		Content	Concentration x 10^{-3}	Content	Concentration
5	C	0.015 ± 0.0049	10.42 ± 1.67	5.67 ± 1.53	3.93 ± 0.42
	H	0.026 ± 0.0021	8.43 ± 0.08	9.29 ± 0.43	3.03 ± 0.07
	F	0.016 ± 0.0030	8.48 ± 0.28	7.44 ± 2.38	3.95 ± 0.67
	HF	0.042 ± 0.0081	9.16 ± 0.17	14.32 ± 3.95	3.08 ± 0.21
10	C	0.029 ± 0.0066	7.01 ± 0.50	15.68 ± 2.66	3.96 ± 0.56
	H	0.045 ± 0.0063	6.79 ± 0.46	24.37 ± 1.73	3.68 ± 0.24
	F	0.037 ± 0.0025	6.69 ± 0.67	14.37 ± 0.83	2.58 ± 0.14
	HF	0.042 ± 0.0065	7.10 ± 0.83	16.35 ± 1.22	2.76 ± 0.26
12	C	0.028 ± 0.0028	6.92 ± 0.30	13.61 ± 1.45	3.34 ± 0.36
	H	0.036 ± 0.0065	7.01 ± 0.16	16.28 ± 2.95	3.13 ± 0.21
	F	0.051 ± 0.0101	7.60 ± 0.39	17.43 ± 2.74	2.65 ± 0.22
	HF	0.056 ± 0.0050	7.92 ± 0.45	19.09 ± 1.42	2.72 ± 0.25

		Copper		Iron	
Age		Content	Concentration x 10^{-3}	Content	Concentration
5	C	0.004 ± 0.0002	2.98 ± 0.35	0.11 ± 0.003	0.082 ± 0.012
	H	0.010 ± 0.0010	3.20 ± 0.11	0.30 ± 0.014	0.097 ± 0.002
	F	0.005 ± 0.0006	2.66 ± 0.07	0.15 ± 0.021	0.080 ± 0.001
	HF	0.016 ± 0.0082	3.30 ± 1.10	0.38 ± 0.052	0.084 ± 0.007
10	C	0.010 ± 0.0056	2.38 ± 0.69	0.30 ± 0.087	0.073 ± 0.006
	H	0.016 ± 0.0024	2.47 ± 0.68	0.57 ± 0.084	0.086 ± 0.010
	F	0.014 ± 0.0060	2.52 ± 1.15	0.44 ± 0.066	0.079 ± 0.014
	HF	0.012 ± 0.0024	1.97 ± 0.35	0.43 ± 0.061	0.072 ± 0.006
12	C	0.015 ± 0.0063	3.89 ± 1.73	0.33 ± 0.048	0.080 ± 0.009
	H	0.014 ± 0.0059	2.52 ± 0.64	0.45 ± 0.084	0.087 ± 0.010
	F	0.020 ± 0.0041	3.30 ± 1.29	0.50 ± 0.123	0.074 ± 0.008
	HF	0.017 ± 0.0022	2.38 ± 0.32	0.53 ± 0.104	0.073 ± 0.010

Table III continued

Age		Potassium Content			Potassium Concentration			Magnesium Content			Magnesium Concentration		
5	C	4.22	±	0.89	2.96	±	0.13	1.81	±	0.43	1.26	±	0.09
	H	7.43	±	1.00	2.41	±	0.16	3.31	±	0.11	1.09	±	0.11
	F	5.36	±	1.37	2.88	±	0.29	2.05	±	0.44	1.11	±	0.07
	HF	12.24	±	0.06	2.80	±	0.61	4.69	±	0.15	1.07	±	0.19
10	C	9.52	±	1.66	2.40	±	0.30	4.44	±	0.82	1.11	±	0.07
	H	12.97	±	2.62	1.94	±	0.26	7.07	±	0.40	1.07	±	0.09
	F	11.88	±	1.95	2.13	±	0.35	5.73	±	0.53	1.03	±	0.12
	HF	14.09	±	2.09	2.36	±	0.32	6.20	±	0.45	1.04	±	0.02
12	C	10.92	±	1.99	2.64	±	0.32	4.48	±	0.63	1.09	±	0.12
	H	13.51	±	3.85	2.52	±	0.25	5.32	±	1.15	1.02	±	0.13
	F	20.06	±	3.59	3.03	±	0.20	6.74	±	1.27	1.02	±	0.09
	HF	20.63	±	4.59	2.84	±	0.26	7.78	±	1.16	1.09	±	0.07

Age		Manganese Content			Manganese Concentration			Molybdenum Content			Molybdenum Concentration x 10^{-3}		
5	C	0.35	±	0.12	0.24	±	0.04	0.0011	±	0.0003	0.84	±	0.32
	H	0.53	±	0.06	0.17	±	0.03	0.0021	±	0.0007	0.66	±	0.20
	F	0.37	±	0.09	0.20	±	0.02	0.0009	±	0.0000	0.49	±	0.09
	HF	0.85	±	0.12	0.19	±	0.01	0.0043	±	0.0031	0.84	±	0.51
10	C	0.86	±	0.20	0.21	±	0.02	0.0009	±	0.0004	0.24	±	0.11
	H	1.39	±	0.06	0.21	±	0.03	0.0026	±	0.0008	0.39	±	0.10
	F	0.99	±	0.04	0.18	±	0.01	0.0010	±	0.0007	0.19	±	0.12
	HF	1.34	±	0.28	0.22	±	0.03	0.0019	±	0.0011	0.32	±	0.19
12	C	0.76	±	0.09	0.19	±	0.02	0.0023	±	0.0007	0.56	±	0.17
	H	1.18	±	0.26	0.23	±	0.03	0.0030	±	0.0012	0.56	±	0.14
	F	1.17	±	0.21	0.18	±	0.01	0.0037	±	0.0011	0.59	±	0.22
	HF	1.53	±	0.29	0.21	±	0.02	0.0042	±	0.0007	0.59	±	0.09

Table III continued

Age		Nitrogen Content			Nitrogen Concentration			Phosphorous Content			Phosphorous Concentration		
5	C	8.13	±	0.87	5.79	±	0.36	0.81	±	0.15	0.57	±	0.01
	H	16.03	±	2.81	5.19	±	0.55	1.33	±	0.18	0.43	±	0.03
	F	9.99	±	1.06	5.49	±	0.29	0.89	±	0.16	0.49	±	0.01
	HF	24.80	±	4.20	5.47	±	0.24	1.75	±	0.38	0.38	±	0.00
10	C	19.96	±	5.49	4.85	±	0.32	1.99	±	0.50	0.49	±	0.03
	H	30.17	±	4.26	4.50	±	0.21	2.85	±	0.36	0.43	±	0.02
	F	30.75	±	2.68	5.49	±	0.28	2.59	±	0.13	0.47	±	0.03
	HF	31.76	±	2.67	5.34	±	0.34	2.58	±	0.23	0.43	±	0.04
12	C	19.95	±	1.89	4.87	±	0.24	1.88	±	0.18	0.46	±	0.02
	H	23.88	±	5.67	4.52	±	0.41	2.18	±	0.43	0.42	±	0.01
	F	39.77	±	5.72	6.04	±	0.22	3.69	±	0.45	0.56	±	0.04
	HF	40.06	±	5.53	5.63	±	0.35	3.84	±	0.45	0.54	±	0.02

Age		Zinc Content			Zinc Concentration		
5	C	0.032	±	0.001	0.023	±	0.003
	H	0.052	±	0.008	0.017	±	0.001
	F	0.030	±	0.003	0.017	±	0.001
	HF	0.057	±	0.007	0.013	±	0.001
10	C	0.056	±	0.014	0.014	±	0.001
	H	0.090	±	0.015	0.013	±	0.001
	F	0.066	±	0.004	0.012	±	0.001
	HF	0.074	±	0.007	0.013	±	0.001
12	C	0.061	±	0.003	0.015	±	0.001
	H	0.074	±	0.012	0.014	±	0.001
	F	0.089	±	0.010	0.014	±	0.001
	HF	0.094	±	0.009	0.013	±	0.001

Table IV: Waycross branch bark nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

		Boron		Calcium	
Age		Content	Concentration x 10^{-3}	Content	Concentration
6	C	0.038 ± 0.005	10.73 ± 0.64	11.88 ± 0.59	3.38 ± 0.38
	H	0.050 ± 0.005	10.48 ± 2.27	17.44 ± 0.94	3.67 ± 0.35
	F	0.045 ± 0.017	10.91 ± 0.52	12.85 ± 3.31	3.24 ± 0.31
	HF	0.046 ± 0.011	10.02 ± 1.73	14.27 ± 1.31	3.11 ± 0.29
10	C	0.032 ± 0.002	9.92 ± 6.68	10.61 ± 0.03	3.30 ± 0.34
	H	0.050 ± 0.008	9.98 ± 1.37	17.69 ± 1.37	3.56 ± 0.22
	F	0.032 ± 0.016	7.00 ± 0.30	11.08 ± 1.80	2.41 ± 0.27
	HF	0.040 ± 0.005	8.58 ± 2.99	12.22 ± 0.16	2.56 ± 0.54
12	C	0.053 ± 0.033	13.70 ± 7.44	12.80 ± 2.99	3.46 ± 0.45
	H	0.039 ± 0.008	8.30 ± 0.50	12.84 ± 1.94	2.76 ± 0.27
	F	0.050 ± 0.012	9.96 ± 2.33	13.48 ± 3.11	2.34 ± 0.48
	HF	0.030 ± 0.013	7.94 ± 2.18	9.22 ± 2.59	2.65 ± 0.33

		Copper		Iron	
Age		Content	Concentration x 10^{-3}	Content	Concentration
6	C	0.009 ± 0.003	2.77 ± 1.54	0.22 ± 0.07	0.059 ± 0.004
	H	0.011 ± 0.003	2.23 ± 1.39	0.26 ± 0.03	0.055 ± 0.005
	F	0.009 ± 0.002	2.65 ± 1.35	0.21 ± 0.06	0.053 ± 0.012
	HF	0.012 ± 0.005	2.73 ± 1.27	0.26 ± 0.04	0.057 ± 0.006
10	C	0.008 ± 0.005	2.59 ± 1.46	0.16 ± 0.02	0.049 ± 0.006
	H	0.013 ± 0.007	2.81 ± 1.56	0.27 ± 0.06	0.053 ± 0.003
	F	0.013 ± 0.013	2.81 ± 1.54	0.26 ± 0.04	0.057 ± 0.011
	HF	0.012 ± 0.009	2.85 ± 1.40	0.27 ± 0.06	0.055 ± 0.004
12	C	0.009 ± 0.006	2.46 ± 1.36	0.22 ± 0.04	0.059 ± 0.005
	H	0.011 ± 0.006	2.21 ± 1.43	0.26 ± 0.02	0.056 ± 0.003
	F	0.012 ± 0.009	2.07 ± 1.22	0.35 ± 0.05	0.061 ± 0.002
	HF	0.005 ± 0.004	1.97 ± 1.20	0.26 ± 0.10	0.064 ± 0.005

Table IV continued

Age		Potassium Content			Potassium Concentration			Magnesium Content			Magnesium Concentration		
6	C	7.49	±	1.67	2.11	±	0.38	4.28	±	0.60	1.20	±	0.09
	H	9.37	±	1.78	1.95	±	0.36	5.93	±	0.91	1.24	±	0.13
	F	8.83	±	1.14	2.33	±	0.18	4.15	±	0.62	1.09	±	0.12
	HF	7.95	±	0.38	1.74	±	0.15	5.03	±	0.56	1.11	±	0.18
10	C	5.55	±	0.18	1.73	±	0.05	4.08	±	0.14	1.27	±	0.17
	H	6.69	±	0.37	1.35	±	0.21	6.48	±	1.02	1.29	±	0.19
	F	6.43	±	2.96	1.40	±	0.42	5.76	±	0.45	1.25	±	0.16
	HF	8.77	±	0.07	1.84	±	0.39	5.42	±	0.17	1.13	±	0.17
12	C	4.44	±	1.84	1.21	±	0.42	5.15	±	1.29	1.39	±	0.18
	H	6.30	±	1.41	1.35	±	0.23	6.61	±	0.70	1.44	±	0.17
	F	8.69	±	2.02	1.53	±	0.31	8.49	±	1.29	1.50	±	0.24
	HF	5.29	±	2.02	1.42	±	0.28	5.54	±	2.03	1.45	±	0.14

Age		Manganese Content			Manganese Concentration			Nitrogen Content			Nitrogen Concentration		
6	C	0.61	±	0.11	0.17	±	0.09	18.07	±	2.98	5.02	±	0.27
	H	0.77	±	0.13	0.16	±	0.07	24.25	±	1.85	5.09	±	0.19
	F	0.56	±	0.04	0.16	±	0.05	21.27	±	4.73	5.43	±	0.13
	HF	0.82	±	0.32	0.18	±	0.08	23.12	±	0.71	5.06	±	0.04
10	C	0.43	±	0.20	0.14	±	0.11	16.01	±	1.71	4.91	±	0.20
	H	0.98	±	0.56	0.22	±	0.08	23.42	±	4.78	4.61	±	0.23
	F	0.73	±	0.54	0.16	±	0.07	23.99	±	0.24	5.20	±	0.23
	HF	0.73	±	0.42	0.16	±	0.06	26.84	±	4.58	5.51	±	0.22
12	C	0.60	±	0.36	0.17	±	0.09	18.01	±	3.87	4.80	±	0.23
	H	0.64	±	0.29	0.14	±	0.08	22.74	±	1.83	4.95	±	0.36
	F	0.86	±	0.48	0.15	±	0.09	34.05	±	3.69	6.02	±	0.52
	HF	0.46	±	0.29	0.15	±	0.07	24.16	±	9.45	6.01	±	0.55

Table IV continued

Age		Phosphorous					
		Content			Concentration		
6	C	1.95	±	0.24	0.55	±	0.07
	H	2.60	±	0.26	0.54	±	0.03
	F	2.38	±	0.52	0.61	±	0.01
	HF	2.42	±	0.11	0.53	±	0.06
10	C	1.62	±	0.24	0.51	±	0.07
	H	2.18	±	0.14	0.45	±	0.07
	F	2.46	±	0.20	0.53	±	0.08
	HF	2.64	±	0.31	0.55	±	0.06
12	C	1.73	±	0.45	0.46	±	0.07
	H	2.23	±	0.35	0.48	±	0.07
	F	3.42	±	0.48	0.60	±	0.08
	HF	2.29	±	0.91	0.58	±	0.05

Table V: BF Grant branch wood nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

Age		Boron Content	Boron Concentration x 10^{-3}	Calcium Content	Calcium Concentration
5	C	0.008 ± 0.0001	2.96 ± 0.52	3.56 ± 0.39	1.35 ± 0.08
	H	0.019 ± 0.0028	3.11 ± 0.24	7.01 ± 1.00	1.17 ± 0.09
	F	0.011 ± 0.0012	3.18 ± 0.23	5.03 ± 1.49	1.41 ± 0.17
	HF	0.026 ± 0.0041	2.99 ± 0.18	10.66 ± 4.06	1.15 ± 0.21
10	C	0.018 ± 0.0042	2.43 ± 0.35	10.06 ± 2.02	1.35 ± 0.25
	H	0.028 ± 0.0030	2.46 ± 0.31	16.27 ± 1.40	1.46 ± 0.30
	F	0.024 ± 0.0057	2.35 ± 0.51	11.70 ± 1.52	1.14 ± 0.14
	HF	0.027 ± 0.0070	2.31 ± 0.42	12.55 ± 0.79	1.11 ± 0.10
12	C	0.023 ± 0.0028	2.91 ± 0.17	8.99 ± 0.77	1.16 ± 0.15
	H	0.023 ± 0.0047	2.44 ± 0.36	10.11 ± 1.74	1.07 ± 0.14
	F	0.030 ± 0.0055	2.80 ± 0.42	11.37 ± 1.67	1.06 ± 0.15
	HF	0.033 ± 0.0054	2.82 ± 0.09	11.68 ± 1.01	1.03 ± 0.16

Age		Copper Content	Copper Concentration x 10^{-3}	Iron Content	Iron Concentration
5	C	0.005 ± 0.0004	1.87 ± 0.46	0.21 ± 0.03	0.085 ± 0.026
	H	0.012 ± 0.0033	1.90 ± 0.42	0.50 ± 0.04	0.083 ± 0.001
	F	0.007 ± 0.0012	2.03 ± 0.04	0.41 ± 0.11	0.126 ± 0.053
	HF	0.025 ± 0.0026	3.05 ± 0.94	0.86 ± 0.50	0.088 ± 0.037
10	C	0.011 ± 0.0035	1.38 ± 0.14	0.80 ± 0.22	0.103 ± 0.008
	H	0.016 ± 0.0017	1.41 ± 0.20	1.35 ± 0.54	0.127 ± 0.062
	F	0.017 ± 0.0009	1.61 ± 0.05	0.90 ± 0.15	0.087 ± 0.014
	HF	0.018 ± 0.0015	1.60 ± 0.08	1.03 ± 0.16	0.090 ± 0.008
12	C	0.011 ± 0.0009	1.42 ± 0.09	0.74 ± 0.12	0.094 ± 0.012
	H	0.013 ± 0.0018	1.38 ± 0.06	0.93 ± 0.20	0.097 ± 0.009
	F	0.018 ± 0.0020	1.64 ± 0.06	0.93 ± 0.17	0.091 ± 0.030
	HF	0.018 ± 0.0020	1.57 ± 0.11	0.78 ± 0.13	0.067 ± 0.007

Table V continued

Age		Potassium Content			Potassium Concentration			Magnesium Content			Magnesium Concentration		
5	C	3.51	±	0.77	1.31	±	0.07	1.23	±	0.20	0.461	±	0.003
	H	6.22	±	0.94	1.04	±	0.08	2.58	±	0.15	0.432	±	0.005
	F	4.99	±	1.31	1.41	±	0.12	1.62	±	0.25	0.467	±	0.013
	HF	10.03	±	1.74	1.14	±	0.05	3.96	±	0.92	0.443	±	0.009
10	C	9.23	±	2.28	1.21	±	0.13	3.58	±	0.83	0.465	±	0.009
	H	11.87	±	2.57	1.01	±	0.07	5.48	±	0.35	0.485	±	0.057
	F	11.63	±	0.21	1.13	±	0.05	4.79	±	0.37	0.465	±	0.025
	HF	12.25	±	1.26	1.08	±	0.03	5.27	±	0.50	0.464	±	0.022
12	C	9.68	±	1.60	1.23	±	0.12	3.65	±	0.25	0.468	±	0.011
	H	11.26	±	2.31	1.17	±	0.05	4.07	±	0.65	0.428	±	0.022
	F	13.18	±	1.93	1.21	±	0.10	4.70	±	0.48	0.436	±	0.031
	HF	13.53	±	2.38	1.15	±	0.05	5.38	±	0.74	0.463	±	0.040

Age		Manganese Content			Manganese Concentration			Molybdenum Content			Molybdenum Concentration x 10^{-3}		
5	C	0.43	±	0.15	0.16	±	0.03	0.0005	±	0.0005	0.21	±	0.21
	H	0.66	±	0.06	0.11	±	0.02	0.0013	±	0.0008	0.20	±	0.12
	F	0.50	±	0.15	0.14	±	0.02	0.0006	±	0.0002	0.19	±	0.08
	HF	1.09	±	0.27	0.12	±	0.00	0.0011	±	0.0000	0.13	±	0.02
10	C	1.11	±	0.25	0.14	±	0.01	0.0004	±	0.0006	0.06	±	0.08
	H	1.58	±	0.16	0.14	±	0.03	0.0007	±	0.0010	0.07	±	0.10
	F	1.34	±	0.12	0.13	±	0.01	0.0017	±	0.0020	0.16	±	0.19
	HF	1.71	±	0.35	0.15	±	0.02	0.0010	±	0.0014	0.08	±	0.11
12	C	0.95	±	0.10	0.12	±	0.01	0.0013	±	0.0009	0.16	±	0.11
	H	1.30	±	0.27	0.14	±	0.01	0.0012	±	0.0007	0.13	±	0.08
	F	1.29	±	0.19	0.12	±	0.01	0.0012	±	0.0011	0.10	±	0.08
	HF	1.63	±	0.31	0.14	±	0.01	0.0014	±	0.0007	0.11	±	0.05

Table V continued

Age		Nitrogen Content			Nitrogen Concentration			Phosphorous Content			Phosphorous Concentration		
5	C	9.22	±	3.23	3.36	±	0.65	0.55	±	0.09	0.208	±	0.000
	H	21.28	±	2.28	3.61	±	0.64	0.95	±	0.24	0.157	±	0.029
	F	14.95	±	6.52	4.07	±	1.12	0.69	±	0.16	0.197	±	0.009
	HF	36.04	±	0.95	4.21	±	0.79	1.38	±	0.47	0.151	±	0.021
10	C	25.72	±	3.49	3.48	±	0.48	1.42	±	0.36	0.185	±	0.019
	H	40.41	±	8.28	3.51	±	0.47	2.05	±	0.25	0.179	±	0.020
	F	42.32	±	3.61	4.12	±	0.32	2.04	±	0.06	0.198	±	0.005
	HF	40.35	±	8.33	3.52	±	0.54	1.80	±	0.06	0.159	±	0.007
12	C	28.37	±	6.62	3.59	±	0.67	1.37	±	0.19	0.175	±	0.019
	H	29.94	±	8.81	3.11	±	0.66	1.46	±	0.19	0.155	±	0.011
	F	44.92	±	11.16	4.03	±	0.53	2.08	±	0.13	0.196	±	0.027
	HF	44.23	±	13.92	3.67	±	0.77	2.15	±	0.19	0.187	±	0.023

Age		Zinc Content			Zinc Concentration		
5	C	0.023	±	0.002	0.0090	±	0.0023
	H	0.039	±	0.011	0.0065	±	0.0014
	F	0.023	±	0.001	0.0069	±	0.0009
	HF	0.046	±	0.010	0.0051	±	0.0001
10	C	0.040	±	0.009	0.0053	±	0.0003
	H	0.063	±	0.014	0.0053	±	0.0004
	F	0.051	±	0.005	0.0049	±	0.0004
	HF	0.045	±	0.004	0.0040	±	0.0003
12	C	0.040	±	0.002	0.0052	±	0.0003
	H	0.041	±	0.005	0.0044	±	0.0004
	F	0.044	±	0.004	0.0041	±	0.0006
	HF	0.044	±	0.003	0.0039	±	0.0005

Table VI: Waycross branch wood nutrient content (kg ha^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: the mean only.

Note: No branch wood concentrations measured for Waycross, therefore assumed that the concentrations would be the same as BF Grant branch wood. If there was no treatment effect for a particular nutrient at BF Grant, then the mean concentration was used across treatments and age. If there was a treatment (or interaction effect) effect for a particular nutrient at BF Grant, the concentrations used were the values of the treatments.

Table VI continued

Age		Boron				Calcium			
		Content			Concentration x 10^{-3}	Content			Concentration
6	C	0.020	±	0.003	n.a.	8.73	±	1.11	n.a.
	H	0.026	±	0.002	n.a.	11.62	±	0.75	n.a.
	F	0.022	±	0.005	n.a.	9.58	±	2.13	n.a.
	HF	0.025	±	0.001	n.a.	11.17	±	0.46	n.a.
10	C	0.018	±	0.002	n.a.	7.97	±	0.98	n.a.
	H	0.028	±	0.005	n.a.	12.36	±	2.27	n.a.
	F	0.025	±	0.000	n.a.	11.26	±	0.10	n.a.
	HF	0.027	±	0.003	n.a.	11.82	±	1.45	n.a.
12	C	0.021	±	0.004	n.a.	9.07	±	1.72	n.a.
	H	0.025	±	0.002	n.a.	11.24	±	0.96	n.a.
	F	0.031	±	0.004	n.a.	13.86	±	1.77	n.a.
	HF	0.021	±	0.007	n.a.	9.48	±	3.27	n.a.

Age		Copper				Iron			
		Content				Content			
6	C	0.016	±	0.002	n.a.	0.69	±	0.09	n.a.
	H	0.021	±	0.001	n.a.	0.92	±	0.06	n.a.
	F	0.018	±	0.004	n.a.	0.76	±	0.17	n.a.
	HF	0.021	±	0.001	n.a.	0.88	±	0.04	n.a.
10	C	0.010	±	0.001	n.a.	0.63	±	0.08	n.a.
	H	0.015	±	0.003	n.a.	0.98	±	0.18	n.a.
	F	0.014	±	0.000	n.a.	0.89	±	0.01	n.a.
	HF	0.014	±	0.002	n.a.	0.94	±	0.11	n.a.
12	C	0.012	±	0.001	n.a.	0.72	±	0.14	n.a.
	H	0.014	±	0.001	n.a.	0.89	±	0.08	n.a.
	F	0.017	±	0.002	n.a.	1.10	±	0.14	n.a.
	HF	0.012	±	0.004	n.a.	0.75	±	0.26	n.a.

Table VI continued

Age		Potassium				Magnesium			
		Content			Concentration	Content			Concentration
6	C	9.00	±	1.15	n.a.	3.31	±	0.42	n.a.
	H	10.59	±	0.69	n.a.	4.41	±	0.29	n.a.
	F	9.87	±	2.20	n.a.	3.63	±	0.81	n.a.
	HF	10.18	±	0.42	n.a.	4.23	±	0.17	n.a.
10	C	8.22	±	1.01	n.a.	3.02	±	0.37	n.a.
	H	11.26	±	2.07	n.a.	4.68	±	0.86	n.a.
	F	11.60	±	0.11	n.a.	4.27	±	0.04	n.a.
	HF	10.78	±	1.32	n.a.	4.48	±	0.55	n.a.
12	C	9.35	±	1.77	n.a.	3.44	±	0.65	n.a.
	H	10.25	±	0.87	n.a.	4.26	±	0.36	n.a.
	F	14.28	±	1.82	n.a.	5.25	±	0.67	n.a.
	HF	8.64	±	2.98	n.a.	3.59	±	1.24	n.a.

Age		Manganese				Nitrogen			
		Content			Concentration	Content			Concentration
6	C	1.08	±	0.14	n.a.	24.94	±	3.18	n.a.
	H	1.12	±	0.07	n.a.	33.20	±	2.15	n.a.
	F	1.18	±	0.26	n.a.	31.21	±	6.95	n.a.
	HF	1.08	±	0.04	n.a.	36.41	±	1.49	n.a.
10	C	0.91	±	0.11	n.a.	22.78	±	2.81	n.a.
	H	1.49	±	0.27	n.a.	35.30	±	6.48	n.a.
	F	1.28	±	0.01	n.a.	36.70	±	0.33	n.a.
	HF	1.43	±	0.17	n.a.	38.54	±	4.72	n.a.
12	C	0.91	±	0.17	n.a.	25.91	±	4.91	n.a.
	H	1.28	±	0.11	n.a.	32.12	±	2.74	n.a.
	F	1.39	±	0.18	n.a.	45.17	±	5.77	n.a.
	HF	1.08	±	0.37	n.a.	30.91	±	10.66	n.a.

Table VI continued

Age		Phosphorous Content	Phosphorous Concentration
6	C	1.39 ± 0.18	n.a.
	H	1.59 ± 0.10	n.a.
	F	1.52 ± 0.34	n.a.
	HF	1.53 ± 0.06	n.a.
10	C	1.27 ± 0.16	n.a.
	H	1.69 ± 0.31	n.a.
	F	1.79 ± 0.02	n.a.
	HF	1.62 ± 0.20	n.a.
12	C	1.44 ± 0.27	n.a.
	H	1.54 ± 0.13	n.a.
	F	2.20 ± 0.28	n.a.
	HF	1.30 ± 0.45	n.a.

Table VII: BF Grant stem bark nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

		Boron		Calcium	
Age		Content	Concentration x 10^{-3}	Content	Concentration
5	C	0.005 ± 0.002	4.48 ± 0.15	5.93 ± 2.58	5.49 ± 0.03
	H	0.012 ± 0.001	4.46 ± 0.07	12.48 ± 5.85	4.35 ± 1.82
	F	0.004 ± 0.000	4.60 ± 0.53	2.29 ± 0.39	2.64 ± 0.06
	HF	0.014 ± 0.001	4.63 ± 0.07	9.33 ± 2.42	3.10 ± 0.89
10	C	0.018 ± 0.001	3.68 ± 0.33	9.83 ± 1.39	1.99 ± 0.22
	H	0.034 ± 0.004	3.50 ± 0.12	15.05 ± 0.92	1.55 ± 0.11
	F	0.024 ± 0.002	3.74 ± 0.51	11.05 ± 0.82	1.70 ± 0.19
	HF	0.039 ± 0.006	3.75 ± 0.56	16.34 ± 4.63	1.56 ± 0.40
12	C	0.033 ± 0.003	3.72 ± 0.33	16.12 ± 2.20	1.84 ± 0.26
	H	0.045 ± 0.006	3.51 ± 0.17	29.10 ± 9.75	2.18 ± 0.55
	F	0.055 ± 0.006	5.15 ± 0.08	17.24 ± 3.05	1.60 ± 0.13
	HF	0.063 ± 0.007	4.06 ± 0.26	23.54 ± 3.73	1.52 ± 0.23

		Copper		Iron	
Age		Content	Concentration x 10^{-3}	Content	Concentration
5	C	0.008 ± 0.003	7.40 ± 0.36	0.067 ± 0.035	0.059 ± 0.007
	H	0.018 ± 0.008	6.43 ± 2.29	0.120 ± 0.027	0.043 ± 0.007
	F	0.003 ± 0.001	3.88 ± 0.20	0.045 ± 0.006	0.052 ± 0.001
	HF	0.015 ± 0.003	4.84 ± 1.08	0.103 ± 0.006	0.034 ± 0.003
10	C	0.011 ± 0.002	2.27 ± 0.24	0.182 ± 0.076	0.036 ± 0.012
	H	0.018 ± 0.003	1.85 ± 0.13	0.244 ± 0.037	0.025 ± 0.003
	F	0.015 ± 0.002	2.26 ± 0.17	0.183 ± 0.034	0.029 ± 0.008
	HF	0.022 ± 0.003	2.11 ± 0.24	0.277 ± 0.025	0.027 ± 0.001
12	C	0.020 ± 0.002	2.30 ± 0.31	0.217 ± 0.015	0.025 ± 0.002
	H	0.037 ± 0.011	2.80 ± 0.63	0.358 ± 0.023	0.028 ± 0.002
	F	0.027 ± 0.001	2.54 ± 0.16	0.258 ± 0.047	0.024 ± 0.004
	HF	0.039 ± 0.003	2.54 ± 0.20	0.377 ± 0.065	0.025 ± 0.006

Table VII continued

Age		Potassium						Magnesium					
		Content			Concentration			Content			Concentration		
5	C	0.75	±	0.25	0.73	±	0.09	0.33	±	0.15	0.30	±	0.01
	H	1.78	±	1.01	0.62	±	0.32	0.58	±	0.21	0.20	±	0.06
	F	0.33	±	0.09	0.38	±	0.05	0.13	±	0.02	0.15	±	0.00
	HF	2.40	±	0.84	0.80	±	0.30	0.59	±	0.09	0.20	±	0.03
10	C	3.95	±	0.33	0.81	±	0.07	1.21	±	0.14	0.25	±	0.02
	H	5.96	±	1.37	0.60	±	0.09	2.12	±	0.23	0.22	±	0.02
	F	5.74	±	1.27	0.87	±	0.16	1.98	±	0.36	0.30	±	0.05
	HF	8.28	±	1.05	0.80	±	0.06	2.72	±	0.42	0.26	±	0.04
12	C	7.65	±	0.95	0.88	±	0.13	2.43	±	0.26	0.28	±	0.04
	H	11.23	±	3.15	0.85	±	0.16	3.63	±	1.04	0.28	±	0.06
	F	17.96	±	2.25	1.68	±	0.09	5.37	±	0.90	0.50	±	0.03
	HF	16.59	±	1.75	1.08	±	0.16	5.28	±	0.58	0.34	±	0.03

Age		Manganese						Molybdenum					
		Content			Concentration			Content			Concentration x 10^{-3}		
5	C	0.06	±	0.04	0.048	±	0.016	0.0002	±	0.0001	0.23	±	0.03
	H	0.08	±	0.01	0.027	±	0.003	0.0005	±	0.0004	0.16	±	0.12
	F	0.03	±	0.01	0.033	±	0.002	0.0001	±	0.0001	0.16	±	0.08
	HF	0.09	±	0.01	0.030	±	0.004	0.0006	±	0.0002	0.20	±	0.06
10	C	0.19	±	0.02	0.038	±	0.001	0.0007	±	0.0006	0.14	±	0.11
	H	0.41	±	0.04	0.041	±	0.001	0.0027	±	0.0019	0.25	±	0.16
	F	0.23	±	0.02	0.035	±	0.002	0.0021	±	0.0006	0.30	±	0.06
	HF	0.43	±	0.02	0.042	±	0.003	0.0020	±	0.0004	0.19	±	0.03
12	C	0.38	±	0.08	0.044	±	0.010	0.0021	±	0.0002	0.24	±	0.04
	H	0.68	±	0.10	0.052	±	0.002	0.0040	±	0.0002	0.32	±	0.03
	F	0.67	±	0.14	0.062	±	0.008	0.0026	±	0.0015	0.26	±	0.16
	HF	0.78	±	0.08	0.052	±	0.009	0.0037	±	0.0015	0.25	±	0.12

Table VII continued

Age		Nitrogen						Phosphorus					
		Content			Concentration			Content			Concentration		
5	C	3.59	±	2.41	2.90	±	0.95	0.17	±	0.07	0.16	±	0.01
	H	9.10	±	0.64	3.26	±	0.03	0.38	±	0.17	0.13	±	0.05
	F	2.86	±	0.50	3.30	±	0.08	0.09	±	0.01	0.11	±	0.01
	HF	8.23	±	1.19	2.70	±	0.31	0.38	±	0.09	0.12	±	0.03
10	C	14.15	±	3.62	2.80	±	0.52	0.74	±	0.05	0.15	±	0.01
	H	27.57	±	7.33	2.75	±	0.60	1.33	±	0.20	0.14	±	0.01
	F	29.97	±	3.76	4.65	±	0.89	1.18	±	0.15	0.18	±	0.01
	HF	29.94	±	6.18	2.89	±	0.54	1.43	±	0.25	0.14	±	0.02
12	C	32.32	±	9.46	3.68	±	1.06	1.30	±	0.19	0.15	±	0.02
	H	42.17	±	9.52	3.24	±	0.42	1.81	±	0.44	0.14	±	0.02
	F	54.66	±	12.14	5.04	±	0.73	3.08	±	0.51	0.29	±	0.03
	HF	65.63	±	17.23	4.19	±	0.81	3.13	±	0.22	0.20	±	0.01

Age		Zinc					
		Content			Concentration		
5	C	0.006	±	0.003	0.0055	±	0.0000
	H	0.014	±	0.005	0.0048	±	0.0015
	F	0.003	±	0.000	0.0035	±	0.0000
	HF	0.016	±	0.001	0.0051	±	0.0005
10	C	0.016	±	0.002	0.0032	±	0.0002
	H	0.033	±	0.006	0.0034	±	0.0005
	F	0.021	±	0.001	0.0031	±	0.0002
	HF	0.031	±	0.004	0.0030	±	0.0004
12	C	0.030	±	0.003	0.0035	±	0.0003
	H	0.055	±	0.013	0.0042	±	0.0007
	F	0.068	±	0.020	0.0063	±	0.0014
	HF	0.063	±	0.010	0.0040	±	0.0003

Table VIII: Waycross stem bark nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

		Boron		Calcium	
Age		Content	Concentration x 10^{-3}	Content	Concentration
6	C	0.017 ± 0.006	2.99 ± 0.79	4.82 ± 0.62	0.99 ± 0.13
	H	0.020 ± 0.002	2.47 ± 1.04	10.95 ± 2.03	1.36 ± 0.16
	F	0.015 ± 0.003	2.51 ± 0.43	5.95 ± 0.67	1.01 ± 0.33
	HF	0.019 ± 0.004	2.45 ± 0.62	7.82 ± 1.02	1.01 ± 0.19
10	C	0.009 ± 0.008	1.14 ± 1.22	10.67 ± 0.58	1.27 ± 0.29
	H	0.047 ± 0.026	3.19 ± 1.13	20.37 ± 5.89	1.41 ± 0.13
	F	0.042 ± 0.012	3.49 ± 0.78	15.76 ± 2.38	1.33 ± 0.39
	HF	0.016 ± 0.016	1.05 ± 0.76	16.94 ± 0.17	1.03 ± 0.22
12	C	0.027 ± 0.011	2.47 ± 0.94	16.68 ± 3.25	1.62 ± 0.24
	H	0.031 ± 0.014	2.04 ± 0.73	21.77 ± 3.37	1.45 ± 0.17
	F	0.041 ± 0.016	2.81 ± 0.99	19.40 ± 3.73	1.09 ± 0.15
	HF	0.048 ± 0.014	2.65 ± 0.73	24.49 ± 4.02	1.38 ± 0.24

		Copper		Iron	
Age		Content	Concentration x 10^{-3}	Content	Concentration
6	C	0.009 ± 0.002	1.78 ± 0.50	0.104 ± 0.042	0.018 ± 0.003
	H	0.014 ± 0.005	1.76 ± 0.38	0.171 ± 0.016	0.022 ± 0.004
	F	0.012 ± 0.001	2.01 ± 0.34	0.111 ± 0.013	0.019 ± 0.003
	HF	0.015 ± 0.002	1.93 ± 0.21	0.171 ± 0.060	0.022 ± 0.007
10	C	0.015 ± 0.004	1.83 ± 0.40	0.191 ± 0.057	0.022 ± 0.012
	H	0.035 ± 0.008	2.47 ± 0.45	0.305 ± 0.018	0.022 ± 0.014
	F	0.029 ± 0.001	2.47 ± 0.45	0.211 ± 0.050	0.018 ± 0.002
	HF	0.028 ± 0.006	1.71 ± 0.16	0.359 ± 0.103	0.021 ± 0.002
12	C	0.023 ± 0.007	2.10 ± 0.29	0.392 ± 0.211	0.037 ± 0.015
	H	0.030 ± 0.006	2.02 ± 0.36	0.360 ± 0.060	0.024 ± 0.013
	F	0.036 ± 0.007	2.03 ± 0.30	0.760 ± 0.324	0.044 ± 0.002
	HF	0.039 ± 0.005	2.16 ± 0.19	0.320 ± 0.033	0.018 ± 0.017

Table VIII continued

Age		Potassium Content			Potassium Concentration			Magnesium Content			Magnesium Concentration		
6	C	1.04	±	0.60	0.17	±	0.07	0.61	±	0.25	0.11	±	0.04
	H	1.24	±	0.84	0.14	±	0.12	0.68	±	0.25	0.08	±	0.04
	F	1.22	±	0.66	0.22	±	0.05	0.76	±	0.28	0.13	±	0.02
	HF	0.83	±	0.47	0.10	±	0.05	0.63	±	0.11	0.08	±	0.02
10	C	0.55	±	0.55	0.07	±	0.06	0.84	±	0.14	0.10	±	0.03
	H	2.70	±	0.39	0.19	±	0.04	1.73	±	0.60	0.12	±	0.07
	F	2.08	±	0.40	0.18	±	0.05	1.68	±	0.25	0.14	±	0.02
	HF	0.47	±	0.47	0.03	±	0.04	1.06	±	0.10	0.06	±	0.01
12	C	0.59	±	0.33	0.07	±	0.04	1.30	±	0.57	0.12	±	0.03
	H	0.84	±	0.48	0.06	±	0.04	1.50	±	0.13	0.10	±	0.06
	F	2.22	±	1.14	0.13	±	0.05	3.59	±	1.12	0.20	±	0.02
	HF	1.58	±	0.99	0.09	±	0.05	2.40	±	0.45	0.13	±	0.05

Age		Manganese Content			Manganese Concentration			Nitrogen Content			Nitrogen Concentration		
6	C	0.06	±	0.02	0.010	±	0.005	19.28	±	6.79	3.43	±	0.30
	H	0.07	±	0.00	0.009	±	0.003	25.79	±	2.93	3.20	±	0.19
	F	0.06	±	0.01	0.010	±	0.004	21.79	±	2.17	3.62	±	0.19
	HF	0.06	±	0.02	0.008	±	0.002	24.90	±	0.88	3.23	±	0.28
10	C	0.07	±	0.02	0.009	±	0.006	25.44	±	2.27	3.01	±	0.16
	H	0.18	±	0.08	0.014	±	0.009	42.27	±	6.79	2.96	±	0.30
	F	0.15	±	0.08	0.013	±	0.005	36.48	±	1.54	3.09	±	0.23
	HF	0.14	±	0.06	0.009	±	0.002	49.50	±	6.60	2.98	±	0.24
12	C	0.15	±	0.08	0.014	±	0.005	33.34	±	9.17	3.09	±	0.10
	H	0.17	±	0.05	0.011	±	0.009	48.99	±	7.78	3.25	±	0.41
	F	0.34	±	0.20	0.019	±	0.008	61.13	±	9.36	3.47	±	0.23
	HF	0.28	±	0.13	0.016	±	0.007	59.81	±	6.31	3.29	±	0.25

Table VIII continued

Age		Phosphorus Content			Phosphorus Concentration		
6	C	0.63	±	0.30	0.11	±	0.02
	H	0.74	±	0.12	0.09	±	0.03
	F	0.80	±	0.13	0.14	±	0.01
	HF	0.73	±	0.08	0.09	±	0.01
10	C	0.59	±	0.13	0.07	±	0.01
	H	0.79	±	0.11	0.06	±	0.03
	F	1.02	±	0.22	0.09	±	0.03
	HF	1.00	±	0.11	0.06	±	0.02
12	C	0.74	±	0.32	0.07	±	0.02
	H	0.87	±	0.17	0.06	±	0.03
	F	1.89	±	0.62	0.11	±	0.01
	HF	1.25	±	0.16	0.07	±	0.03

Table IX: BF Grant stem wood nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

		Boron		Calcium	
Age		Content	Concentration x 10^{-3}	Content	Concentration
5	C	0.012 ± 0.0057	2.75 ± 0.24	3.16 ± 1.45	0.77 ± 0.03
	H	0.031 ± 0.0020	2.35 ± 0.08	8.93 ± 1.10	0.67 ± 0.06
	F	0.009 ± 0.0015	2.73 ± 0.08	2.64 ± 0.66	0.76 ± 0.04
	HF	0.039 ± 0.0039	2.61 ± 0.03	10.00 ± 0.18	0.68 ± 0.05
10	C	0.047 ± 0.0031	1.85 ± 0.19	17.95 ± 1.03	0.70 ± 0.02
	H	0.125 ± 0.0333	2.11 ± 0.25	40.25 ± 7.48	0.69 ± 0.05
	F	0.075 ± 0.0130	1.86 ± 0.06	27.54 ± 4.83	0.69 ± 0.04
	HF	0.147 ± 0.0200	2.01 ± 0.23	50.26 ± 4.52	0.69 ± 0.02
12	C	0.085 ± 0.0030	1.75 ± 0.15	29.92 ± 2.31	0.61 ± 0.04
	H	0.163 ± 0.0280	1.91 ± 0.25	55.04 ± 5.78	0.65 ± 0.04
	F	0.133 ± 0.0142	1.80 ± 0.17	47.61 ± 3.21	0.65 ± 0.01
	HF	0.182 ± 0.0256	1.73 ± 0.34	72.82 ± 8.15	0.67 ± 0.02

		Copper		Iron	
Age		Content	Concentration x 10^{-3}	Content	Concentration
5	C	0.007 ± 0.002	1.80 ± 0.39	0.30 ± 0.16	0.069 ± 0.011
	H	0.024 ± 0.006	1.78 ± 0.39	0.66 ± 0.07	0.050 ± 0.007
	F	0.007 ± 0.000	1.98 ± 0.24	0.28 ± 0.12	0.076 ± 0.021
	HF	0.041 ± 0.016	2.72 ± 0.83	0.72 ± 0.00	0.049 ± 0.005
10	C	0.047 ± 0.025	1.93 ± 1.15	1.41 ± 0.38	0.055 ± 0.016
	H	0.083 ± 0.024	1.46 ± 0.43	2.82 ± 0.45	0.049 ± 0.006
	F	0.059 ± 0.030	1.42 ± 0.57	2.26 ± 0.96	0.054 ± 0.017
	HF	0.079 ± 0.011	1.08 ± 0.17	4.13 ± 1.37	0.057 ± 0.021
12	C	0.053 ± 0.005	1.08 ± 0.12	1.91 ± 0.08	0.039 ± 0.002
	H	0.162 ± 0.086	1.90 ± 1.01	3.95 ± 0.46	0.047 ± 0.006
	F	0.099 ± 0.041	1.31 ± 0.47	3.15 ± 0.46	0.043 ± 0.005
	HF	0.201 ± 0.070	1.86 ± 0.58	5.17 ± 0.55	0.048 ± 0.004

Table IX continued

Age		Potassium Content			Potassium Concentration			Magnesium Content			Magnesium Concentration		
5	C	4.76	±	1.99	1.18	±	0.02	1.63	±	0.82	0.39	±	0.04
	H	12.99	±	2.31	0.98	±	0.15	4.38	±	0.13	0.33	±	0.00
	F	4.61	±	0.80	1.34	±	0.03	1.28	±	0.28	0.37	±	0.01
	HF	15.49	±	0.17	1.05	±	0.08	4.78	±	0.26	0.32	±	0.01
10	C	22.04	±	2.87	0.86	±	0.08	7.54	±	0.69	0.29	±	0.01
	H	44.79	±	11.83	0.75	±	0.09	18.32	±	2.68	0.32	±	0.01
	F	32.79	±	5.46	0.82	±	0.03	13.22	±	2.20	0.33	±	0.01
	HF	59.54	±	7.61	0.81	±	0.08	23.85	±	2.34	0.33	±	0.02
12	C	35.46	±	3.60	0.72	±	0.07	14.16	±	0.92	0.29	±	0.01
	H	65.76	±	10.01	0.77	±	0.08	25.35	±	0.18	0.30	±	0.01
	F	49.16	±	1.94	0.67	±	0.03	21.18	±	1.93	0.29	±	0.02
	HF	74.43	±	6.61	0.69	±	0.04	32.30	±	3.69	0.30	±	0.02

Age		Manganese Content			Manganese Concentration			Molybdenum Content			Molybdenum Concentration $x 10^{-3}$		
5	C	0.52	±	0.31	0.12	±	0.03	0.0003	±	0.0003	0.13	±	0.13
	H	1.20	±	0.10	0.09	±	0.01	0.0014	±	0.0003	0.10	±	0.03
	F	0.31	±	0.12	0.09	±	0.02	0.0010	±	0.0001	0.28	±	0.02
	HF	1.49	±	0.24	0.10	±	0.01	0.0039	±	0.0001	0.26	±	0.03
10	C	2.55	±	0.37	0.10	±	0.01	0.0024	±	0.0011	0.09	±	0.04
	H	5.75	±	1.02	0.10	±	0.01	0.0091	±	0.0047	0.15	±	0.07
	F	3.81	±	0.98	0.09	±	0.01	0.0036	±	0.0038	0.08	±	0.08
	HF	8.51	±	1.77	0.12	±	0.02	0.0139	±	0.0127	0.21	±	0.20
12	C	4.34	±	0.38	0.09	±	0.01	0.0071	±	0.0032	0.15	±	0.06
	H	9.78	±	0.77	0.12	±	0.01	0.0174	±	0.0086	0.20	±	0.10
	F	8.48	±	1.50	0.11	±	0.02	0.0071	±	0.0032	0.10	±	0.04
	HF	12.97	±	3.06	0.12	±	0.02	0.0096	±	0.0075	0.10	±	0.08

Table IX continued

Age		Nitrogen Content			Nitrogen Concentration			Phosphorus Content			Phosphorus Concentration		
5	C	2.70	±	2.70	1.17	±	1.17	0.63	±	0.30	0.15	±	0.008
	H	12.25	±	12.25	0.90	±	0.90	1.17	±	0.33	0.09	±	0.022
	F	3.11	±	3.11	1.12	±	1.12	0.49	±	0.03	0.14	±	0.019
	HF	17.83	±	17.83	1.32	±	1.32	1.29	±	0.03	0.09	±	0.006
10	C	17.46	±	17.30	0.71	±	0.68	1.98	±	0.33	0.08	±	0.009
	H	47.41	±	41.07	0.89	±	0.73	3.94	±	1.06	0.07	±	0.010
	F	8.08	±	9.90	0.27	±	0.33	3.26	±	0.61	0.08	±	0.008
	HF	27.52	±	23.82	0.42	±	0.37	4.63	±	1.17	0.06	±	0.011
12	C	51.86	±	42.37	1.08	±	0.89	2.74	±	0.29	0.06	±	0.006
	H	62.22	±	62.61	0.69	±	0.69	4.79	±	1.25	0.06	±	0.012
	F	92.51	±	75.69	1.26	±	1.04	4.51	±	0.33	0.06	±	0.008
	HF	89.31	±	74.29	0.94	±	0.84	6.52	±	0.70	0.06	±	0.005

Age		Zinc Content			Zinc Concentration		
5	C	0.020	±	0.011	0.004	±	0.001
	H	0.039	±	0.001	0.003	±	0.000
	F	0.013	±	0.004	0.004	±	0.000
	HF	0.029	±	0.016	0.002	±	0.001
10	C	0.062	±	0.005	0.002	±	0.000
	H	0.147	±	0.037	0.002	±	0.000
	F	0.106	±	0.024	0.003	±	0.000
	HF	0.132	±	0.021	0.002	±	0.000
12	C	0.131	±	0.031	0.003	±	0.001
	H	0.219	±	0.018	0.003	±	0.000
	F	0.139	±	0.022	0.002	±	0.000
	HF	0.223	±	0.053	0.002	±	0.000

Table X: Waycross stem wood nutrient content (kg ha^{-1}) and concentration (g kg^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

		Boron		Calcium	
Age		Content	Concentration x 10^{-3}	Content	Concentration
6	C	0.039 ± 0.010	1.30 ± 0.21	21.00 ± 4.23	0.69 ± 0.03
	H	0.059 ± 0.011	1.16 ± 0.26	33.73 ± 4.48	0.67 ± 0.07
	F	0.050 ± 0.009	1.41 ± 0.19	25.75 ± 8.01	0.68 ± 0.04
	HF	0.073 ± 0.010	1.46 ± 0.17	35.67 ± 9.03	0.70 ± 0.15
10	C	0.085 ± 0.005	1.41 ± 0.07	36.88 ± 4.58	0.61 ± 0.01
	H	0.119 ± 0.010	1.24 ± 0.29	52.89 ± 2.74	0.55 ± 0.02
	F	0.087 ± 0.065	0.94 ± 0.18	54.83 ± 2.99	0.55 ± 0.08
	HF	0.174 ± 0.024	1.50 ± 0.46	67.20 ± 7.61	0.56 ± 0.16
12	C	0.069 ± 0.041	0.86 ± 0.36	44.63 ± 14.78	0.56 ± 0.04
	H	0.119 ± 0.031	1.03 ± 0.23	63.29 ± 8.80	0.56 ± 0.04
	F	0.255 ± 0.021	1.47 ± 0.38	99.64 ± 11.34	0.56 ± 0.05
	HF	0.192 ± 0.092	1.30 ± 0.41	87.42 ± 9.57	0.58 ± 0.06

		Copper		Iron	
Age		Content	Concentration x 10^{-3}	Content	Concentration
6	C	0.06 ± 0.03	2.00 ± 0.28	1.51 ± 0.90	0.05 ± 0.04
	H	0.08 ± 0.01	1.69 ± 0.73	1.24 ± 1.11	0.02 ± 0.04
	F	0.08 ± 0.02	2.26 ± 0.97	1.65 ± 1.00	0.06 ± 0.01
	HF	0.13 ± 0.05	2.63 ± 0.96	1.96 ± 1.23	0.04 ± 0.03
10	C	0.12 ± 0.05	1.92 ± 0.62	3.36 ± 1.82	0.06 ± 0.03
	H	0.08 ± 0.08	0.99 ± 0.65	5.13 ± 4.32	0.06 ± 0.03
	F	0.06 ± 0.03	0.55 ± 1.13	3.14 ± 1.56	0.03 ± 0.03
	HF	0.30 ± 0.16	2.31 ± 1.11	5.34 ± 3.88	0.05 ± 0.04
12	C	0.12 ± 0.04	1.60 ± 0.54	2.74 ± 1.48	0.04 ± 0.02
	H	0.21 ± 0.06	1.85 ± 0.53	7.53 ± 5.40	0.06 ± 0.04
	F	0.27 ± 0.13	1.49 ± 1.02	8.07 ± 5.24	0.05 ± 0.03
	HF	0.26 ± 0.14	1.68 ± 0.64	7.21 ± 4.41	0.05 ± 0.04

Table X continued

Age		Potassium Content			Potassium Concentration			Magnesium Content			Magnesium Concentration		
6	C	8.86	±	3.64	0.30	±	0.13	9.51	±	1.69	0.32	±	0.04
	H	15.27	±	5.68	0.30	±	0.10	15.64	±	2.53	0.31	±	0.02
	F	10.12	±	2.00	0.32	±	0.10	11.32	±	3.16	0.30	±	0.01
	HF	16.97	±	5.04	0.34	±	0.10	16.23	±	2.58	0.32	±	0.04
10	C	10.24	±	2.52	0.18	±	0.08	18.34	±	3.51	0.30	±	0.03
	H	26.30	±	2.68	0.28	±	0.03	28.92	±	10.20	0.29	±	0.03
	F	19.90	±	11.51	0.21	±	0.05	31.36	±	4.40	0.31	±	0.02
	HF	26.00	±	2.44	0.22	±	0.11	38.54	±	9.90	0.31	±	0.04
12	C	18.89	±	9.89	0.24	±	0.09	22.51	±	6.37	0.28	±	0.03
	H	28.60	±	6.83	0.25	±	0.04	36.36	±	4.31	0.32	±	0.04
	F	48.33	±	17.59	0.27	±	0.07	56.52	±	10.78	0.31	±	0.03
	HF	35.55	±	9.93	0.24	±	0.11	49.39	±	10.27	0.32	±	0.04

Age		Manganese Content			Manganese Concentration			Nitrogen Content			Nitrogen Concentration		
6	C	1.31	±	0.45	0.04	±	0.04	24.38	±	5.23	0.82	±	0.31
	H	1.47	±	0.15	0.03	±	0.02	61.00	±	8.55	1.21	±	0.29
	F	1.08	±	0.14	0.03	±	0.02	43.35	±	12.97	1.15	±	0.20
	HF	2.21	±	1.01	0.04	±	0.02	50.84	±	15.01	1.01	±	0.42
10	C	1.38	±	0.41	0.02	±	0.04	15.98	±	8.67	0.25	±	0.26
	H	6.64	±	4.50	0.08	±	0.03	52.89	±	37.95	0.49	±	0.25
	F	4.06	±	2.83	0.04	±	0.02	55.53	±	34.98	0.59	±	0.18
	HF	4.90	±	3.55	0.05	±	0.02	75.56	±	27.61	0.60	±	0.21
12	C	3.02	±	2.33	0.04	±	0.02	48.72	±	37.27	0.49	±	0.30
	H	4.40	±	1.74	0.04	±	0.02	53.74	±	52.59	0.45	±	0.39
	F	8.90	±	5.29	0.05	±	0.02	166.99	±	33.09	0.93	±	0.19
	HF	5.86	±	2.91	0.04	±	0.03	147.17	±	33.73	0.95	±	0.33

Table X continued

Age		Phosphorus					
		Content			Concentration		
6	C	3.19	±	0.91	0.10	±	0.02
	H	4.60	±	0.82	0.09	±	0.02
	F	3.95	±	1.26	0.10	±	0.02
	HF	5.47	±	1.64	0.11	±	0.03
10	C	3.46	±	0.06	0.06	±	0.01
	H	5.85	±	0.32	0.06	±	0.01
	F	7.94	±	0.14	0.08	±	0.03
	HF	8.11	±	2.08	0.07	±	0.03
12	C	4.08	±	1.21	0.05	±	0.00
	H	6.41	±	0.81	0.06	±	0.01
	F	13.32	±	3.54	0.07	±	0.00
	HF	9.51	±	1.62	0.06	±	0.01

Table XI: BF Grant total above ground tree components nutrient content (kg ha^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

Age	Trt	Boron			Calcium			Copper		
5	C	0.04	±	0.01	18.99	±	6.02	0.024	±	0.004
	H	0.11	±	0.01	43.06	±	8.39	0.075	±	0.015
	F	0.04	±	0.01	18.96	±	5.57	0.024	±	0.004
	HF	0.15	±	0.01	48.88	±	10.31	0.107	±	0.007
10	C	0.13	±	0.02	61.89	±	5.27	0.087	±	0.021
	H	0.25	±	0.04	104.15	±	8.96	0.144	±	0.025
	F	0.18	±	0.02	70.85	±	4.44	0.115	±	0.033
	HF	0.28	±	0.03	103.19	±	9.62	0.140	±	0.015
12	C	0.19	±	0.01	75.81	±	3.32	0.107	±	0.006
	H	0.29	±	0.02	119.19	±	17.40	0.236	±	0.103
	F	0.31	±	0.03	102.35	±	6.99	0.182	±	0.046
	HF	0.38	±	0.02	138.85	±	10.49	0.290	±	0.071

Age	Trt	Iron			Potassium			Magnesium		
5	C	0.72	±	0.18	15.38	±	4.04	5.47	±	1.66
	H	1.78	±	0.01	48.96	±	3.79	13.87	±	0.07
	F	0.93	±	0.07	20.17	±	5.97	5.94	±	1.27
	HF	2.24	±	0.51	59.23	±	1.57	16.78	±	0.62
10	C	2.95	±	0.47	64.72	±	8.55	21.53	±	1.90
	H	5.26	±	0.43	92.21	±	18.70	38.52	±	2.65
	F	4.06	±	0.85	82.96	±	12.81	30.23	±	2.59
	HF	6.18	±	1.28	119.33	±	18.57	43.26	±	3.53
12	C	3.49	±	0.20	82.74	±	3.85	29.73	±	0.99
	H	6.02	±	0.47	124.16	±	13.56	43.98	±	2.05
	F	5.18	±	0.56	130.66	±	9.49	43.14	±	3.41
	HF	7.30	±	0.77	162.38	±	20.61	58.23	±	5.86

Table XI continued

Age	Trt	Manganese			Molybdenum			Nitrogen		
5	C	1.51	±	0.65	0.002	±	0.001	28.54	±	3.92
	H	3.43	±	0.32	0.006	±	0.002	105.61	±	17.36
	F	1.52	±	0.53	0.003	±	0.000	41.23	±	8.17
	HF	4.49	±	0.12	0.011	±	0.003	132.25	±	15.51
10	C	6.34	±	0.84	0.006	±	0.002	127.28	±	25.50
	H	10.96	±	0.72	0.016	±	0.004	198.41	±	35.30
	F	7.80	±	1.40	0.010	±	0.007	169.35	±	12.47
	HF	13.90	±	2.48	0.021	±	0.014	199.54	±	18.17
12	C	7.87	±	0.64	0.014	±	0.003	185.76	±	47.21
	H	15.09	±	1.24	0.027	±	0.009	222.18	±	64.63
	F	13.21	±	1.96	0.016	±	0.005	318.79	±	70.76
	HF	19.67	±	3.88	0.021	±	0.006	354.42	±	56.46

Age	Trt	Phosphorus			Zinc		
5	C	2.62	±	0.64	0.09	±	0.01
	H	7.61	±	1.09	0.19	±	0.02
	F	3.09	±	0.74	0.08	±	0.01
	HF	7.84	±	0.42	0.19	±	0.00
10	C	10.85	±	1.17	0.24	±	0.03
	H	15.00	±	2.11	0.41	±	0.06
	F	14.31	±	1.45	0.30	±	0.02
	HF	16.16	±	2.94	0.36	±	0.04
12	C	12.09	±	0.22	0.34	±	0.03
	H	15.86	±	1.41	0.48	±	0.03
	F	20.43	±	0.63	0.43	±	0.03
	HF	25.32	±	2.71	0.55	±	0.06

Table XII: Waycross total above ground tree components nutrient content (kg ha^{-1}) by age and treatment. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples. Content and concentration values given are: mean ± one standard error.

Age	Trt	Boron			Calcium			Copper		
5	C	0.17	±	0.04	56.52	±	6.48	0.11	±	0.04
	H	0.20	±	0.02	83.35	±	6.11	0.14	±	0.02
	F	0.19	±	0.04	64.55	±	13.67	0.13	±	0.02
	HF	0.23	±	0.04	78.72	±	11.46	0.20	±	0.05
10	C	0.18	±	0.01	74.80	±	2.95	0.16	±	0.04
	H	0.30	±	0.07	111.80	±	10.56	0.16	±	0.08
	F	0.25	±	0.04	102.57	±	2.99	0.13	±	0.02
	HF	0.31	±	0.03	116.18	±	6.79	0.37	±	0.15
12	C	0.21	±	0.08	89.69	±	23.67	0.17	±	0.04
	H	0.26	±	0.06	117.87	±	16.08	0.28	±	0.06
	F	0.47	±	0.05	156.04	±	18.03	0.35	±	0.13
	HF	0.39	±	0.11	141.89	±	10.71	0.33	±	0.15

Age	Trt	Iron			Potassium			Magnesium		
5	C	2.83	±	0.71	47.31	±	11.26	24.50	±	3.15
	H	2.93	±	1.13	54.30	±	10.63	34.09	±	3.94
	F	3.09	±	0.70	54.87	±	2.81	26.44	±	4.90
	HF	3.64	±	1.06	55.96	±	4.73	32.45	±	3.20
10	C	4.62	±	1.62	37.39	±	4.41	32.30	±	2.77
	H	7.05	±	4.07	60.50	±	1.98	47.72	±	12.86
	F	4.92	±	1.33	60.44	±	12.17	50.16	±	4.55
	HF	7.36	±	3.50	69.22	±	3.34	56.07	±	10.44
12	C	4.33	±	1.68	43.37	±	15.05	37.72	±	9.37
	H	9.39	±	5.49	58.64	±	10.55	56.11	±	3.54
	F	10.75	±	5.40	97.85	±	21.33	82.72	±	10.48
	HF	9.13	±	4.15	79.67	±	12.47	70.82	±	11.81

Table XII continued

Age	Trt	Manganese			Nitrogen			Phosphorus		
5	C	4.50	±	0.78	154.46	±	22.49	15.01	±	3.01
	H	4.70	±	0.53	215.25	±	19.31	17.61	±	1.30
	F	4.32	±	0.15	200.83	±	36.49	17.34	±	3.28
	HF	5.44	±	1.65	211.42	±	22.30	18.40	±	2.19
10	C	3.69	±	1.09	133.13	±	15.37	12.60	±	1.33
	H	10.91	±	6.10	215.06	±	52.02	17.13	±	1.87
	F	7.49	±	4.38	233.04	±	18.44	21.85	±	0.97
	HF	8.34	±	4.78	282.84	±	44.73	22.23	±	2.78
12	C	5.57	±	3.36	171.19	±	63.37	13.09	±	3.76
	H	7.66	±	2.74	216.08	±	51.19	17.58	±	2.79
	F	12.77	±	6.56	414.03	±	47.35	31.00	±	3.43
	HF	9.26	±	4.09	392.43	±	57.50	26.31	±	3.58

Table XIII: Biomass (kg ha^{-1}) of the various parts of the above ground tree components by age and treatment for the BF Grant and Waycross sites. Treatments comprise of the control (C), herbicide (H), fertilizer (F) and herbicide x fertilizer (HF) treatments. For treatments at all ages n=2. Each experimental unit comprises six subsamples.

BF Grant

			Branch		Stem		
		Foliage	Bark	Wood	Bark	Wood	Total
Age	Treatment	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}
5	C	342	1419	2660	1081	4050	9552
	H	2972	3067	5972	2794	13231	28036
	F	713	1833	3495	863	3451	10355
	HF	2709	4576	8910	3035	14791	34020
10	C	3858	4052	7661	4951	25594	46117
	H	4058	6674	11609	9801	57994	90137
	F	3979	5583	10276	6596	40055	66489
	HF	4432	5957	11354	10314	73254	105310
12	C	4033	4089	7815	8789	49101	73828
	H	4936	5223	9559	12901	84696	117316
	F	4920	6609	10910	10677	73810	106926
	HF	6582	7145	11722	15541	108251	149241

Waycross

			Branch		Stem		
		Foliage	Bark	Wood	Bark	Wood	Total
Age	Treatment	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}	kg ha^{-1}
6	C	4728	3577	7262	5559	30233	51358
	H	5110	4761	9667	8134	50740	78412
	F	5296	3924	7966	6046	37082	60314
	HF	5447	4577	9293	7765	50250	77331
10	C	4156	3267	6632	8448	60418	82921
	H	4517	5063	10280	14186	97306	131353
	F	5606	4613	9367	11797	101798	133181
	HF	5863	4845	9836	16562	122090	159196
12	C	3520	3716	7545	10685	78934	104401
	H	4535	4606	9352	15015	113393	146901
	F	6360	5678	11529	17575	177807	218949
	HF	7559	3885	7889	18155	153758	191247

APPENDIX C: The type and amount of fertilizer applied to the fertilizer (F) and herbicide x fertilizer (HF) treatments for Powerline and Monitor sites at BF Grant and the total amount of nitrogen (N), phosphorus (P) and potassium (K) added for each year. Estimated by Dr Daniel Markewitz, University of Georgia, Athens, GA, USA.

	Type and amount of fertilizer applied					Amount of nutrient added		
Stand Age	DAP kg ha^{-1}	KCL kg ha^{-1}	NH_4NO_3 kg ha^{-1}	TSP kg ha^{-1}	Rainbow kg ha^{-1}	N kg ha^{-1}	P kg ha^{-1}	K kg ha^{-1}
1	280.15	112.06	56.03			78	59	58
2	280.15	112.06	56.03			78	59	58
3			168.09			59		
4			168.09			59		
5			168.09			59		
6			168.09			59		
7			168.09			59		
8			168.09			59		
9			168.09			59		
10			168.09			59		
11			336.18	140.075		118	36	
12			168.09		560.3	92	179	45
13			336.18			118		
Total						955	333	161

Fertilizer key:

DAP: Diammonium phosphate
KCL: Potassium chloride
NH_4NO_3: Ammonium nitrate
TSP: Triple super phosphate
Rainbow: Super rainbow

APPENDIX D: The type and amount of fertilizer applied to the fertilizer (F) and herbicide x fertilizer (HF) treatments for the Wet and Dry sites at Waycross and the total amount of nitrogen (N), phosphorus (P) and potassium (K) added for each year. Estimated by Dr Daniel Markewitz, University of Georgia, Athens, GA, USA.

	Type and amount of fertilizer applied					Amount of nutrient added		
Stand Age	DAP kg ha^{-1}	KCL kg ha^{-1}	NH_4NO_3 kg ha^{-1}	TSP kg ha^{-1}	Rainbow kg ha^{-1}	N kg ha^{-1}	P kg ha^{-1}	K kg ha^{-1}
1	280.15	112.06	56.03			78	59	58
2	280.15	112.06	56.03			78	59	58
3			168.09			59		
4			168.09			59		
5			168.09			59		
6			168.09			59		
7			168.09			59		
8			168.09			59		
9			168.09			59		
10			168.09			59		
11			336.18	140.075		118	36	
12			336.18			118		
13			168.09		560.3	92	179	45
Total						955	333	161

Fertilizer key:

DAP: Diammonium phosphate
KCL: Potassium chloride
NH_4NO_3: Ammonium nitrate
TSP: Triple super phosphate
Rainbow: Super rainbow