THE SHORT-TERM EFFECTS OF FERTILIZATION ON LOBLOLLY PINE PHOTOSYNTHESIS AND BIOMASS

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Abstract—The physiological processes in loblolly pine leading to enhanced growth in response to fertilization have not been clearly established. We tracked net photosynthesis (P_n), height, basal diameter, and volume changes in loblolly pine seedlings in response to fertilization during the entire 2004 growing season. P_n measurements were conducted prior to fertilization and after fertilization in early May. The seedlings that received fertilization showed an increase in P_n rates above the controls for most of the growing season. Also, the fertilized seedlings had height, basal diameter, and volume increases of 10, 13, and 34 percent over the unfertilized seedlings. We conclude that fertilization led to an initial increase in P_n rates, which helped create extra photoassimilate to be used in building larger leaf areas, which in turn led to more above ground biomass.

INTRODUCTION

One common silvicultural management tool used to increase tree growth is forest fertilization. Nitrogen (N) and phosphorus (P) are typically considered particularly crucial elements in determining the productivity of forest species (Helms 1976). Fertilization is a practical method of enhancing the nutrient content of infertile soil types, such as sandy coastal plain soils. Loblolly pine stands in the South are often fertilized due to their positive biological and economic responses to nutrient applications (Colbert and Allen 1996, Jokela and Stearns-Smith 1993). The North Carolina State Forest Nutrition Cooperative (2000) noted that 75 percent of the planted lands in the region were planted in pine and almost 1.6 million acres of planted pine were fertilized in 1999.

Although fertilization often results in increased pine tree biomass, the physiological reasons for this rise in productivity are still unclear. Teskey and others (1987) state that specific leaf photosynthesis rate, respiration rate of foliage tissue, leaf area, and surface area of a tree are responsible for governing net carbon gains. Several studies have focused on gas exchange and leaf area in fertilized forests, but the results have been contradictory. Literature surveyed generally show that net photosynthesis favorably responds to N fertilization or increased foliar N concentrations over the long term. This is a logical relationship since N is a vital component in Rubisco and chlorophyll. Eight out of 12 journal articles surveyed reported an increase in net photosynthesis either all or partially due to the effects of N fertilization (Chandler and Dale 1995, Kellomaki and Wang 1997, Lavigne and others 2001, Murthy and others 1996, Murthy and others 1997, Roberntz and Stockfors 1998, Schoettle and Smith 1999, Strand 1997). The other four articles reported no significant difference or varying differences in net photosynthesis due to N fertilization (Gough and others 2004a, Schaberg and others 1997, Teskey and others 1994, Zhang and others 1997). For example, Murthy and others (1996) noted a significant difference in net photosynthesis (P_n) of young loblolly pine foliage due to fertilization. However, no increase in P_n was found in loblolly pines that had increased leaf N content and chlorophyll content in a study by Zhang and others (1997). Some studies have suggested that the primary reason productivity increases is due to increased leaf areas and stem wood in fertilized loblolly pine stands (Teskey and others 1987, Vose and Allen 1988).

Gough (2003) initially studied this topic on loblolly pine seedlings in a greenhouse environment. Gough planted these seedlings in a relatively infertile soil type from the North Carolina Sandhills region [sandy, siliceous, thermic Psammentric Hapludult (Wakulla series), USDA Forest Service, unpublished data]. He reported that following N fertilization, foliar N concentrations increased above the controls and remained elevated for approximately 50 days. Gough found that the N levels returned to control levels around 146 days after fertilization. Also, Gough reported light saturated photosynthesis (A_{sat}) levels that were statistically greater in the N fertilized loblolly pines than in the controls 6 days after the treatment application. A_{sat} levels remained high throughout most of the study but began to decrease towards control levels over the last 100 days. Furthermore, Gough noted that, 4 weeks after the initial increase in photosynthetic capacity, aboveground biomass in the seedlings was statistically higher in the fertilized loblolly pines. More specifically, the fertilized seedlings' ground diameters and heights were greater. Also, projected leaf areas at the end of the study were 36.5 percent greater in the fertilized seedlings. Hence, Gough hypothesized that increased N uptake into foliage led to an initial increase in photosynthetic capacity, which helped create extra photo-assimilate to be used in creating larger leaf areas. Afterwards, the seedling would have higher overall photosynthesis due to larger amounts of photosynthetic tissue and this would lead to increased above ground biomass. However, Gough (2003) noted that his findings in the greenhouse might not translate to a field setting. Hence, the objective of this study will be to clarify the physiological mechanisms involved in increasing loblolly pine biomass with an emphasis on leaf specific photosynthesis.

METHODS AND MATERIALS

Study Site

The study site was located in Patrick County, VA (36° 40' N, 80° 10' W) at the Reynolds Homestead Forestry Research Center. The site was in the upper Piedmont province, where

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the topography consists of gently rolling hills. The elevation varies between 300 and 350 m above sea level. The site was located in the temperate climate zone with warm, humid summers and cool, moist winters. The average minimum temperature is -1.4°C, and the average maximum is 29.2°C. Precipitation is evenly distributed throughout the seasons and averages 1.3 m/year.

The soils consist of the Lloyd clay loam, Louisa loam, and Hiwassee loam series and are well-drained, deep Ultisols originating from granite, schist, and gneiss parent material. The site has been heavily farmed for two centuries, which has resulted in a loss of essentially all of the old A horizon. Instead there is a reduced profile, with a surface Ap horizon and clayey B horizons mixed in below.

The study site consisted of 8 square plots of 25 different loblolly pine clones that were planted May 19, 2003. The site preparations included a treatment of Roundup®, ripping, and shallow cultivation in the planting rows. The clones were evenly spaced 2.4 m apart in rows consisting of five clones that were randomly selected. All rows were evenly spaced 3.0 m apart, and the clones were numbered in a serpentine pattern from 1 to 25 starting in the lower left hand corner of the plot. There was also a row of buffer seedlings surrounding and separating the eight study plots. Thus, the total size of each plot was approximately 338.2 m^2. The clones were provided by the Forest Biology Research Cooperative (FBRC) (University of Florida, Gainesville, FL). The parents were selected from the Atlantic Coast and Florida provenances that are bred by the Loblolly Pine Lower Gulf Elite Population. The study plots were mowed and weeded periodically during the growing seasons in order to reduce competition and confounding factors. Oust® (Dupont Corp.) and Roundup® (Monsanto Co.) herbicides were also used to clear out competition from the seedling rows. No other environmental variables were controlled during the experiment in order to allow the seedlings to experience typical field grown conditions.

Pre-fertilization Measurements

Prior to application of the fertilizer treatment, growth measurements including height and basal diameter were collected on all 200 seedlings. Seedling growth was monitored periodically during the growing season by tracking the changes in the variables above. Also, any dead or dying seedlings were noted and excluded from the study. Out of the 25 loblolly pine clones, 8 were chosen for intensive physiological and growth measurements.

In order to establish the short-term effects of fertilization on loblolly pine physiology, measurements were taken twice, one in late April and one in early May, to establish a base of comparison for subsequent measurements after treatment application in May. Net photosynthesis and a foliar C and N analysis were conducted on one new, fully expanded needle fascicle per clone. The data collected the previous time governed how often each measurement was taken. On days when all measurements were taken, a total of 192 samples were recorded.

Net photosynthesis measurements under saturating light conditions (A_{sat}) were conducted using a LiCor 6400 Portable Photosynthesis System (LiCor Inc., Lincoln, Nebraska). A_{sat} was measured on a fascicle of needles immediately after detachment from the seedling. Photosynthesis was recorded 3 times per fascicle over a period of 10 seconds, and the mean of the three samples was used for subsequent data analysis. Thus, 64 mean A_{sat} values were used for data analysis. All chamber conditions remained at ambient for this study with the exception of photosynthetically active radiation (PAR; 1,600 µmol m^{-2} s^{-1}) and [CO_2] (360 µmol mol^{-1}). Hence, the data collected was reflective of the environmental conditions experienced by the field-grown seedlings. After A_{sat} measurements, each removed fascicle diameter was measured using digital calipers, and then the fascicles were enclosed in an envelope. The following equation was used to calculate A_{sat} on a per leaf area basis given the information collected (Ginn and others 1991):

$$LA_l = (n*l*d) + (\pi*d*l) \qquad (1)$$

where

n = number of needles per fascicle,

d = fascicle diameter, and

l = needle length.

The A_{sat} fascicles were stored and used to obtain foliar C and N concentrations. All needles were oven-dried and ground up prior to C and N analysis.

Nutrient Addition and Post-fertilization Measurements

Within each of the 4 blocks, 1 plot was randomly chosen for fertilization. The other half of the block were the unfertilized control plots. Two types of fertilizer were applied to achieve a fertilization level of 112 kg of elemental N/ha (100 pounds per acre N). The fertilizer application consisted of 224 kg/ha (200 pounds per acre) of diammonium phosphate (DAP) and 184 kg/ha (164.5 pounds per acre) of ammonium nitrate. Hence, the DAP supplied 47.5 kg/ha (42.4 pounds per acre) N and 23.2 kg/ha (20.7 pounds per acre) P while the ammonium nitrate supplied the other 64.5 kg/ha (57.6 pounds per acre) N. The fertilizer was spread by hand using a banded application technique, over the 4 randomly selected fertilization treatment plots on May 6, 2004.

Post-fertilization measurements were conducted immediately following a soaking rain within a week after application. Measurements were conducted in the exact same fashion as the pre-fertilization measurements. Initially, measurements were conducted twice a week so that the short term physiological changes in foliar C and N concentrations and A_{sat} were not missed. However, measurements were taken at less frequent intervals later in the growing season as measurements began to stabilize.

Statistical Analysis

The study was conducted using a completely randomized block design with a split plot. A fertilized plot and a control plot made up each of 4 main blocks. The split plot consisted of the 8 different loblolly pine clones. The analysis was conducted using the PROC GLM procedure in SAS (SAS Institute, Cary, NC). Individual ANOVAs by date were used to determine significance between the fertilized and unfertilized clones at $\alpha = 0.05$. Multiple linear regression analysis in SAS was used to determine any significant environmental effects on A_{sat}.

RESULTS AND DISCUSSION

Although not always statistically significant, fertilization increased leaf specific photosynthesis on most dates sampled (fig. 1). Shortly after fertilization, there was some variation in P_n rates, but the fertilized seedlings had significantly higher rates ($p<0.05$) on the May 25 and June 16 sampling dates. Subsequent measurements in late July showed the fertilized seedling P_n rates rose above the unfertilized rates and remained there through the final December sampling date. Net photosynthesis rates between the fertilized and unfertilized clones differed significantly ($p \le 0.1$) on three other sampling dates (fig. 1).

These findings are in agreement with a greenhouse study of loblolly pine seedlings conducted by Gough and others (2004b). He reported statistically greater light saturated photosynthesis (A_{sat}) rates in the N-fertilized loblolly pines 6 days after the treatment application. A_{sat} levels in controls ranged from 1.5 μmol/m²/s to 4 μmol/m²/s, while fertilized foliage levels ranged from 1.5 μmol/m²/s to 6 μmol/m²/s and were almost always higher than the control levels. A_{sat} levels remained high throughout most of the study but began to decrease towards control levels over the last 100 days. Despite these similarities, our study showed trends that were slightly muted in comparison to Gough's findings. One possible explanation for less-pronounced differences in P_n after fertilization could be due to the soil base fertility. Our study was in the Piedmont of Virginia on an old field site with a heavy clay subsoil that may have had a higher base soil fertility. Hence, the addition of N fertilizer may not have dramatically increased the N content of the soil as it would have in Gough's very sandy, infertile, Wakulla series soil type.

Fertilization also increased all of the biomass characteristics sampled during the study. The fertilized seedlings' mean height and basal diameter growth were 10 and 13 percent > the unfertilized seedlings by December (figs. 2 and 3). Mean volume growth was 34 percent greater in the fertilized seedlings by the last sampling date as well (fig. 4). Hence, the biomass differences between treatments support claims that an increase in P_n lead to a larger C pool to be used in creating larger leaf areas (Gough and others 2004b). Then these larger leaf areas contribute to improved growth and productivity due to increases in stemwood (Teskey and others 1987, Vose and Allen 1988).

Gough and others (2004b) found similar increases in basal diameters and heights about 4 weeks after the initial increase in A_{sat}. He found significant differences in his biomass characteristics whereas our values were only approaching significance ($p=0.118$ basal diameter, $p=0.286$ height, and $p=0.145$ volume) by the end of December when growth ceased. Also, projected leaf areas at the end of Gough's study were 36.5 percent greater in the fertilized seedlings. Albaugh and others (1998) recorded height, volume, and diameter changes between loblolly pines during a fertilization study at the Southeast Tree Research and Education Site (SETRES) in the North Carolina sandhills region. The results showed the fertilized pines had increases in diameter (30 percent), height (23 percent), volume (81 percent), and basal area (68 percent) over the controls (Albaugh and others 1998).

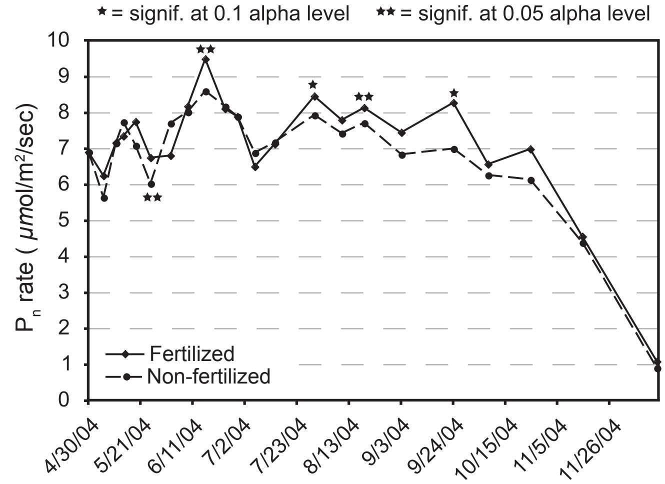

Figure 1—Loblolly pine mean net photosynthesis rates by treatment in a 2-year-old plantation located on the Virginia Piedmont (Patrick Co., VA).

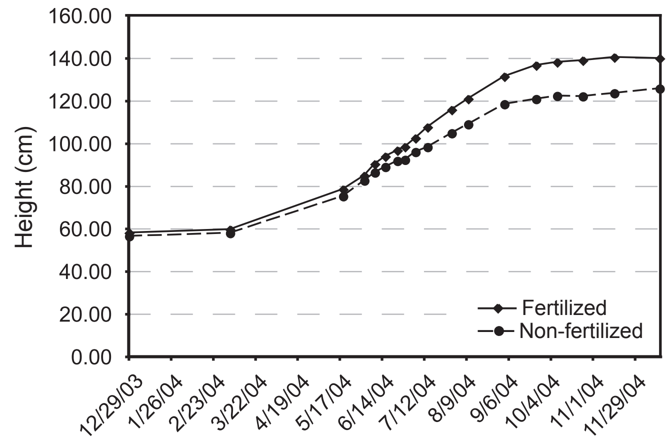

Figure 2—Loblolly pine mean height growth by treatment in a 2-year-old plantation located on the Virginia Piedmont (Patrick Co., VA).

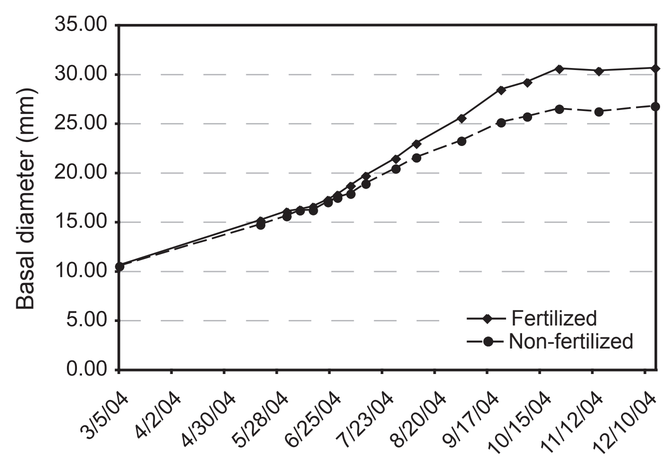

Figure 3—Loblolly pine mean basal diameter growth by treatment in a 2-year-old plantation located on the Virginia Piedmont (Patrick Co., VA).

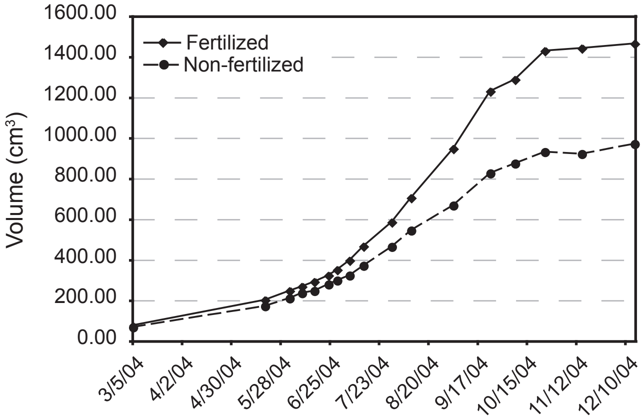

Figure 4—Loblolly pine mean volume growth by treatment (calculated from height and basal diameter data) in a 2-year-old plantation located on the Virginia Piedmont (Patrick Co., VA).

CONCLUSIONS

Our data support Gough's (2003) hypothesis as it relates to fertilized field grown loblolly pines although the effects were not as pronounced. The short term response of the loblolly pines to fertilization involved increasing P_n. This increase caused a larger build up of photoassimilates, which could be used in constructing larger leaf areas. Hence, the fertilized seedlings were able to build larger leaf areas making more tissue available to capture PAR. Due to these differences, the fertilized seedlings were able to increase basal diameter, height, and volume growth over the course of the growing season.

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