EFFECTS OF FERTILIZATION AND THREE YEARS OF THROUGHFALL REDUCTION ON LEAF PHYSIOLOGY OF LOBLOLLY PINE

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Abstract—Climate models project decreased soil water availability in the southeastern United States, which may impact loblolly pine (*Pinus taeda* L.) productivity. In conjunction with an interdisciplinary project known as PINEMAP, the objective of this study was to investigate the interactive effects of fertilization and a 30 percent reduction in throughfall on physiological characteristics that affect forest productivity. Stand growth, leaf area index (LAI) and leaf physiology were monitored over three years of treatment. Only the most recent preliminary results are presented here for June 2014. The study is a factorial combination of throughfall reduction (30 percent versus ambient) and fertilization (fertilized versus non-fertilized) treatments in a now 9-year-old loblolly pine plantation located in Georgia. No interactive effects of treatment were significant for any variable. Fertilization increased basal area by 19 percent, basal area increment by 27 percent, and peak LAI by 29 percent. Throughfall reduction reduced peak LAI by 17 percent. Fertilization decreased stomatal conductance, likely in response to higher LAI and increased water use combined with low ambient precipitation. These results indicate fertilization can increase growth and LAI but increased LAI may lead to short-term leaf physiological sensitivity to drought.

INTRODUCTION

Climate projections for the southeastern United States (U.S.) indicate that over the next century there is likely to be increases in annual temperatures along with increased frequency and intensity of extreme precipitation events (Kunkle and others 2012). Higher levels of evapotranspiration, due to a warmer atmosphere, along with decreases in soil moisture, resulting from increased precipitation runoff, will ultimately lead to increased drought severity (IPCC 2013, Kunkle and others 2012).

Historically, water availability was considered to be the dominant factor limiting forest productivity (Gholz and others 1990). However, more recent studies have identified nutrient availability as having a greater impact on forest productivity (Jokela and others 2004). The majority of available research has been focused on the effects of nutrient addition with irrigation. These studies have found that the greatest increase in productivity is realized when nutrients are supplied while water is not limiting, due to an additive effect (Albaugh and others 1998, Samuelson and Stokes 2006). It has been well established that increased nutrient availability, especially on nutrient poor sites, can increase loblolly pine productivity. Increasing nutrient and water availability can increase height, diameter, and volume as well as total leaf area (Wear and Greis 2012). However, low water availability coupled with increased evapotranspiration may reduce productivity because of decreased retention of foliage or reductions in leaf-level gas exchange (Allen and others 2005, Fox and others 2007). Increased drought intensity and frequency could decrease the efficacy of fertilization and therefore the productivity of loblolly pine.

Due to the importance of loblolly pine as an economic species and in order to investigate the effects of climate variability on loblolly pine productivity, the Pine Integrated Network: Education, Mitigation, and Adaptation Project (PINEMAP) was established. PINEMAP's goal is to enable southern pine landowners to better manage forests under a variable climate. As a part of PINEMAP's efforts, the objective of this study was to explore the interactive effects of reduced precipitation, achieved by throughfall reduction, and fertilization on physiological factors that affect the productivity of loblolly pine. We hypothesized that increased leaf area in response to fertilization will increase the sensitivity of leaf-level gas exchange to drought imposed by throughfall reduction. Preliminary results are presented from the most recent year (2014) of an ongoing three-year analysis.

METHODS

Experimental Design

This study was conducted on a 44.5 ha loblolly pine plantation located in Taliaferro county, GA (33° 37' 35.77"N, 82° 47' 53.48"W). The 30-year average annual precipitation is 1109 mm with average daily

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maximum temperatures of 22.7 °C and minimums of 10.1 °C (NOAA National Centers for Environmental Information, Asheville, NC, Annual Summaries, Station ID COOP: 099157, http://www.ncdc.noaa.gov accessed February 2015). The Palmer Drought Severity Index was downloaded for GA Climate Division 3 (http://www7.ncdc.noaa.gov/CDO/CDODivisionalSelect.jsp# accessed February 2015). Precipitation data was collected continuously with an onsite weather station and a local nearby weather station when needed (NOAA National Centers for Environmental Information, Asheville, NC, Daily Summaries, Station ID COOP: 099157, http://www.ncdc.noaa.gov accessed February 2015). The study was designed as a 2x2 factorial combination of throughfall reduction (approximate 30 percent reduction versus ambient) and fertilization (N, P, K, and micro nutrient fertilization versus non-fertilized) replicated with four blocks. Throughfall reduction was achieved by the use of throughfall exclusion trays which covered approximately 30 percent of the ground area. The fertilization treatment was applied once in March 2012. Each treatment plot measured 0.10 ha and contained approximately 136 trees. Further details on the experimental site and treatments were provided by Samuelson and others (2014).

Growth and LAI

A year-end stand inventory was conducted in November 2014 at a stand age of 9 years. Leaf area index (LAI) was measured at peak LAI in August 2014 using a pair of LAI-2000 plant canopy analyzers (LI-COR Inc., Lincoln, NE).

Leaf Physiology

Light-saturated leaf-level photosynthesis (P_{net}), stomatal conductance (g_s), and predawn leaf water potentials (Ψ_L) were measured approximately monthly from March 2014 to October 2014. Only June 2014 data are presented. Gas exchange measurements were performed using a LI-6400 portable photosynthesis system (LI-COR Inc., Lincoln, NE) and water potentials were measured using a pressure chamber (PMS Instrument Corp., Albany, OR). Shoots were collected from fully exposed sun foliage from the upper third of three randomly selected trees within each plot. Predawn water potentials were measured on the same three trees selected for gas exchange measurements.

Statistical Analysis

The measurement order of blocks and plots within blocks was random. Data were averaged by block, and plot. All variables were analyzed with a two way analysis of variance (ANOVA) using the GLM procedure in SAS 9.3. Treatment effects were considered significant at $\alpha \leq 0.05$.

RESULTS AND DISCUSSION

In 2014, annual precipitation was 988 mm, which was lower than the 30-year average of 1109 mm resulting in a dryer than normal year (fig. 1). The PDSI indicated drought conditions for the entirety of the year (fig. 1). June, for the purpose of this report, served as a representative month to demonstrate treatment effects on leaf-level physiology. Conditions in June were dry with only a total of 50 mm of rainfall where the 30-year average for this month is 113 mm (fig. 1). The PDSI for June indicated “mild drought” conditions with mild drought being defined as PDSI values between -1.00 and -1.99 (fig. 1).

There were no interactive effects of fertilization and throughfall reduction treatments detected for any growth or physiological variable. In 2014, fertilization had a significant impact on growth while throughfall reduction had no effect on growth. Basal area and basal area increment both were increased by fertilization by 19 and 27 percent respectively (data not shown). Fertilization increased peak LAI from 2.8 $m^2 m^{-2}$ to 3.7 $m^2 m^{-2}$ (table 1). Increased growth from fertilization was likely a direct result of increased LAI (table 1). Albaugh and others (1998) determined that increased LAI from fertilization was the primary driver behind increased growth in 8 year-old loblolly pine. Because LAI represents photosynthetic surface area, LAI and growth are tightly coupled in stands before canopy closure (Allen and others 2005, Campoe and others 2013, Samuelson and others 2004, Wang and Jarvis 1990).

In addition to fertilization, a main effect of throughfall treatment on LAI was also observed. Peak LAI was reduced by 17 percent in response to throughfall reduction treatment (table 1). Needle expansion has been shown to be sensitive to water availability in conifers (Raison and others 1992). Lower predawn Ψ_L with throughfall reduction treatment (table 2) likely reduced leaf turgor pressure, which in turn retarded needle development and elongation. However, there was no significant effect of the throughfall treatment on g_s or P_{net} despite lower predawn Ψ_L in response to throughfall reduction (table 2). Lack of a throughfall treatment effect on leaf gas exchange may be because of increased water availability per unit leaf area in response to a smaller crown.

The increase in LAI with fertilization observed in this study was irrespective of water availability, as has been reported by other studies with loblolly pine when the observed drought condition was not severe (Jokela and others 2004, Samuelson and others 2004, 2014). In contrast, an interactive effect of drought and fertilization was significant in a throughfall treatment study by Tang and others (2004); 100 percent throughfall exclusion during a severe drought negated the positive effect of

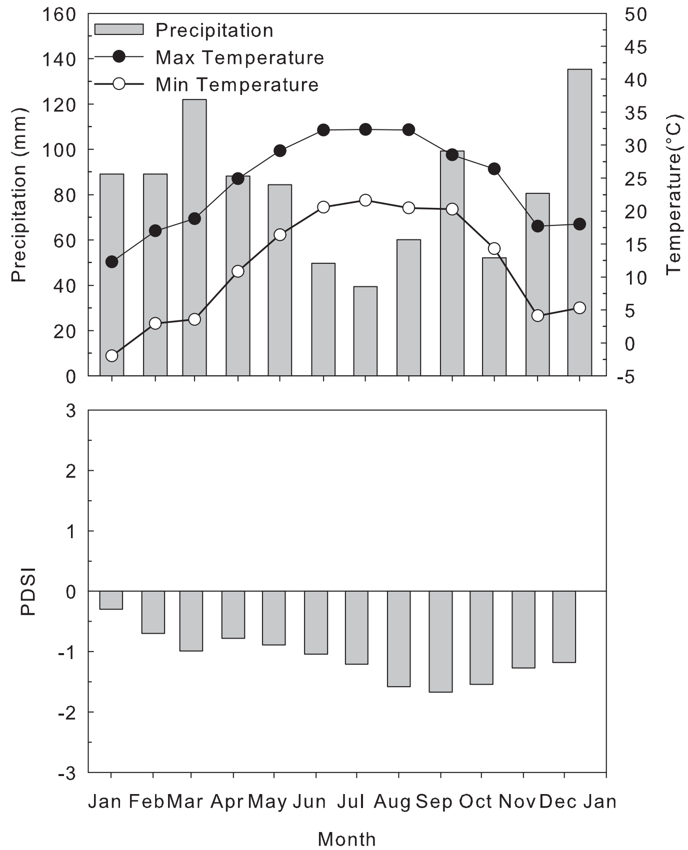

Figure 1—Monthly total precipitation, mean minimum and maximum daily temperature, and the Palmer Drought Severity Index for 2014.

Table 1—Mean (SE) responses and observed probabilities for the effects of throughfall (TR_0: ambient throughfall, TR_{30}: approximate 30% reduction) and fertilization ($Fert_0$: no fertilization $Fert_+$: one-time fertilization in March 2012) on peak LAI measured in August 2014. Bold values indicate significance at α ≤ 0.05

Treatment	Peak LAI (m^2 m^{-2})
TR_0	3.6 (0.2)
TR_{30}	3.0 (0.2)
$Fert_0$	2.8 (0.2)
$Fert_+$	3.7 (0.2)
P > F	
TR	**0.008**
Fert	**0.031**
TR x Fert	0.748

Table 2—Mean (SE) responses and observed probability values for the effects of throughfall (TR_0: ambient throughfall, TR_{30}: approximate 30% reduction) and fertilization ($Fert_0$: no fertilization $Fert_+$: one-time fertilization in March 2012) on light-saturated stomatal conductance (g_s), light-saturated leaf-level net photosynthesis (P_{net}) and predawn leaf water potential (Ψ_L) for June 2014. Bold values indicate significance at α ≤ 0.05

Treatment	g_s (mmol m^{-2} s^{-1})	P_{net} (μmol m^{-2} s^{-1})	Predawn Ψ_L (MPa)
TR_0	42.9 (6.5)	3.6 (0.3)	-0.72 (0.03)
TR_{30}	32.4 (3.1)	3.3 (0.2)	-0.83 (0.03)
$Fert_0$	45.4 (6.2)	3.8 (0.3)	-0.73 (0.04)
$Fert_+$	29.9 (2.2)	3.1 (0.2)	-0.82 (0.04)
P > F			
TR	0.126	0.361	**0.009**
Fert	**0.034**	0.062	**0.033**
TR x Fert	0.124	0.168	0.776

fertilization on leaf area production. In June 2014, the fertilization treatment reduced g_s from 45.4 mmol m^{-2} s^{-1} to 29.9 mmol m^{-2} s^{-1} (table 2), and predawn Ψ_L also decreased with fertilization (table 2). Therefore, higher LAI from fertilization and greater canopy water use induced some degree of water stress. Because of the nature of isohydric tree species such as loblolly pine, stomata close early in response to drought to reduce water loss and limit the decline in Ψ_L (Domec and Johnson 2012, Goldstein and others 2013).

In summary, fertilization had a positive effect on growth and LAI that was independent of throughfall treatment, but fertilization reduced g_s and predawn Ψ_L. In contrast, throughfall reduction did not affect leaf-level gas exchange and there was no reduction in growth in response to throughfall reduction despite a reduction in peak LAI and lower predawn Ψ_L. However, growth may decline in response to reduced LAI in subsequent years. Future analyses will include investigation of cumulative treatment effects over the three-year study, which will likely reveal more about the underlying mechanisms important to understanding the interaction between climate and growth in loblolly pine.

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LITERATURE CITED

Albaugh, T.J.; Allen, H.L.; Dougherty, M.P. [and others]. 1998. Leaf area and above-ground responses of loblolly pine to nutrient and water additions. Forest Science. 44(2): 317-328.

Allen, C.B.; Will, R.E.; McGarvey, R.C.; Coyle, D.R.; Coleman, M.D. 2005. The effect of water and nutrient availability on radiation use efficiency and gas exchange in fertigated stands of sweetgum and sycamore. Tree Physiology. 35(2): 191-200.

Campoe, O.C.; Stape, J.L.; Albaugh, T.J. [and others]. 2013. Fertilization and irrigation effects on tree level aboveground net primary production light interception and light use efficiency in a loblolly pine plantation. Forest Ecology and Management. 288: 43-48.

Domec, J.C.; Johnson, D.M. 2012. Does homeostasis or disturbance of homeostasis in minimum leaf water potential explain the isohydric versus anisohydric behavior of *Vitis nifiera* L. cultivars? Tree Physiology. 32(3): 245-248.

Fox, T.R.; Allen, H.L.; Albaugh, T.J. [and others]. 2007. Tree nutrition and forest fertilization of pine plantations in the southern United States. Southern Journal of Applied Forestry. 31(1): 5-11.

Gholz, H.L.; Ewel, K.C.; Teskey, R.O. 1990. Water and forest productivity. Forest Ecology and Management. 30: 1-18.

Goldstein, G.; Bucci, S.J.; Scholz, F.G. 2013. Why do trees adjust water relations and hydraulic architecture in response to nutrient availability? Tree Physiology. 33: 238-240.

IPCC. 2013 Climate Change 2013: the physical science basis. Contributions of working group I to the fifth assessment report of the intergovernmental panel on climate change. In: Stocker, T.F.; Qin, D.; Plattner, G.-K. [and others], eds. New York: Cambridge University Press. 1535 p.

Jokela, E.J.; Dougherty, P.M.; Martin, T.A. 2004. Production dynamics of intensively managed loblolly pine stands in the southern United States: A synthesis of seven long-term experiments. Forest Ecology and Management. 192: 117-130.

Kunkel, K.E.; Stevens, L.E.; Stevens, S.E. [and others]. 2012. Climate of the Southeast U.S. In: Regional climate trends and scenarios for the U.S. national climate assessment. NOAA Technical Report NESDIS 142-2. Washington, DC. U.S. Department of Commerce, National Oceanic and Atmospheric Administration. 98 p.

Raison, R.J.; Myers, B.J.; Benson, M.L. 1992. Dynamics of *Pinus radiata* foliage in relation to water and nitrogen stress: I. Needle production and properties. Forest Ecology and Management. 52: 139-158.

Samuelson, L.J.; Stokes, T.A. 2006. Transpiration and canopy stomatal conductance of five-year-old loblolly pine in response to intensive management. Forest Science. 52: 313-323.

Samuelson, L.J.; Johnsen, K.; Stokes, T.A. 2004. Production, allocation and stemwood growth efficiency of *Pinus taeda* L. stands in response to 6 years of intensive management. Forest Ecology and Management. 192: 59-70.

Samuelson, L.J.; Pell, C.J.; Stokes, T.A. [and others]. 2014. Two-year throughfall and fertilization effects on leaf physiology and growth of loblolly pine in the Georgia Piedmont. Forest Ecology and Management. 330: 29-37.

Tang, Z.; Sword-Sayer, M.A.; Chambers, J.L.; Barnett, J.P. 2004. Interactive effects of fertilization and throughfall exclusion on the physiological responses and whole-tree carbon uptake of mature loblolly pine. Canadian Journal of Botany. 82: 850-861.

Wang, Y.P.; Jarvis, P.G. 1990. Influence of crown structural properties and PAR absorption, photosynthesis, and transpiration in Sitka spruce: application of a model (MAESTRO). Tree Physiology. 7: 297-316.

Wear, D.N.; Greis, J.G. 2012. The southern forest futures project: summary report. Gen. Tech. Rep. SRS-GTR-168. Asheville, NC: U.S. Department of Agriculture Forest Service, Southern Research Station. 54 pp.