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Two-year throughfall and fertilization effects on leaf physiology and growth of loblolly pine in the Georgia Piedmont

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ABSTRACT

Loblolly pine is the most extensively planted and productive commercial pine species in the southeastern United States, but future increases in drought frequency and intensity may affect plantation productivity. To better understand the potential impacts of reduced precipitation on loblolly pine productivity, the interactive effects of throughfall (ambient versus an approximate 30% reduction) and fertilization (no fertilization versus one time fertilization with 224 kg N ha^{-1}, 28 kg P ha^{-1}, 56 kg K ha^{-1}, and micronutrients) on growth, leaf area index (LAI), intercepted photosynthetically radiation (IPAR) and leaf-level physiology in a 7-year-old loblolly pine plantation were studied over two years. During a year with below average annual precipitation (831 mm), the throughfall reduction treatment decreased predawn leaf water potential, leaf gas exchange rates, needle elongation, basal area increment and stemwood production, and effects were independent of fertilization treatment. Leaf light-saturated net photosynthesis and stemwood production were on average 12% and 13% lower, respectively, in response to reduced throughfall treatment. During the following year with higher precipitation (1413 mm), reduced throughfall treatment decreased only leaf water potential. One-time fertilization had the largest impact on growth through increases in LAI, IPAR and total absorbed photosynthetically active radiation rather than changes in growth efficiency. Enhancement of growth by fertilization was independent of the reduced throughfall treatment in both years.

1. Introduction

Loblolly pine is the most extensively planted and productive commercial pine species in the southeastern United States. The high productivity of loblolly pine plantations is a result, in part, of increased use of fertilization (Fox et al., 2007). Over 6.5 million forested hectares were fertilized in the southeastern U.S. from 1969 to 2004 with the number of fertilized hectares doubling from 1991 to 1999, primarily in loblolly pine plantations (Albaugh et al., 2007). It is well established that fertilization, in particular N and P applications, on nutrient limited sites increases loblolly pine productivity by increasing photosynthesis in the short term (Gough et al., 2004; King et al., 2008) and leaf area over the long term (Will et al., 2005; Fox et al., 2007; Samuelson et al., 2008). Leaf area index (LAI) and intercepted photosynthetically active radiation (IPAR) are linearly related in young loblolly pine plantations and correlated with aboveground net productivity (Allen et al., 2005; Campoe et al., 2013). Across the range of loblolly pine, low nutrient availability is the main factor limiting LAI, but low precipitation combined with high evaporative demand may reduce the production and retention of foliage (Fox et al., 2007). In most cases, nutrient availability has been shown to have a greater effect on loblolly pine productivity than water availability (Jokela et al., 2004). However, higher LAI in response to fertilization may induce greater and faster soil water depletion (Linder et al., 1987), which could result in a reduction in leaf stomatal conductance (g_s) to limit canopy water loss (Ewers et al., 1999). This reduction in g_s may decrease photosynthesis and stemwood growth (Munger et al., 2003).

The majority of experimental research on the effects of water availability on loblolly pine productivity has been in response to water addition rather than precipitation reduction (Jokela et al., 2004; Samuelson et al., 2008), and in some studies increased water availability enhanced fertilizer effectiveness. For example, in a long-term productivity study of loblolly pine in southern Georgia, irrigation increased LAI and growth, but irrigation plus fertilization had the greatest effect (Samuelson et al., 2004, 2008). Fertilization with irrigation increased tree foliage mass more than fertilization

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alone in a 13-year-old loblolly pine plantation (Albaugh et al., 2006). In the same study, fertilization with irrigation had the largest effect on absorbed photosynthetically active radiation (APAR) and aboveground net primary production (Campoe et al., 2013). In contrast, no growth response to irrigation or enhancement of fertilizer effects by irrigation was reported for 4-year-old loblolly pine by Coyle et al. (2008). In a novel throughfall reduction study with 18-year-old loblolly pine, Tang et al. (2004) studied the interaction between fertilization and throughfall treatments. They observed reduced leaf net photosynthesis in response to throughfall exclusion treatment and an increase in tree foliage mass in response to fertilization but only in the ambient throughfall treatment and not in the throughfall reduction treatment. Thus, future increases in drought frequency and intensity in the southern U.S. (Karl et al., 2009; Seager et al., 2009) may affect the efficacy of fertilization and productivity of loblolly pine stands.

To better understand the potential impacts of reduced precipitation on loblolly pine productivity, we examined the interactive effects of throughfall reduction and fertilization treatment on growth and leaf-level physiology in a 7-year-old loblolly pine plantation over two years. The influence of fertilization treatments (none or fertilized) and throughfall reduction treatments (ambient or approximately a 30% reduction) on growth, LAI, IPAR, light-saturated net photosynthesis (P_{net}), g_s, leaf water potential (Ψ_L) and foliar $\delta^{13}C$ was measured. We hypothesized that (1) higher LAI in response to fertilizer would exacerbate soil water depletion in the throughfall reduction treatment and result in lower Ψ_L, g_s, and P_{net}, increased foliar water use efficiency, and reduced growth compared with the ambient throughfall treatment, and/or (2) that reduced soil water availability in the throughfall reduction treatment would diminish the enhancement of LAI by fertilizer. This project was conducted in conjunction with a large integrated network of research on loblolly pine productivity under changing climate known as PINEMAP (Pine Integrated Network: Education, Mitigation, Adaptation Project (www.pinemap.org)). Similar throughfall experiments were established in Florida, North Carolina and Oklahoma with the goal of adapting forest management practices to increase forest resilience and sustainability under future climate (Will et al., submitted for publication).

2. Materials and methods

2.1. Experimental design

The study was conducted in a loblolly pine plantation located in Taliaferro County, GA owned by Plum Creek Timber Company. The study site is located near Washington, GA at an elevation of 152 m and latitude 33°37′32.61″N and longitude 82°47′56.54″W. The 30-year average daily maximum and minimum temperature for Washington, GA is 22.7 °C and 10.1 °C, respectively, and average annual precipitation is 1109 mm (http://www.ncdc.noaa.gov/do-web/datasets/ANNUAL/locations/ZIP:30673/detail, accessed January 2014). The Palmer Drought Severity Index (PDSI) during the study was downloaded for Climate Division 3 in Georgia (http://www1.ncdc.noaa.gov/pub/data/cirs/drd964x.pdsi.txt/ accessed January 2014). Precipitation and temperature prior to November 2012 were for Washington, GA (http://www.ncdc.noaa.gov/do-web/datasets/ANNUAL/locations/ZIP:30673); thereafter, both were measured continuously on-site using a rain gauge tipping bucket (TR-5251, Texas Electronics Inc., Dallas, TX) and temperature sensor (CS500-L, Campbell Scientific, Logan, UT, USA), respectively.

Soil at the site comprised mostly the Lloyd series with only a small portion as the Cecil series. The Lloyd series is a fine, koalintic, thermic Rhodic Kanhapludult, while the Cecil series is a fine, kaolinitic, thermic Typic Kanhapludult (http://websoilsurvey.sc.egov.usda.gov). These soils are common on gently sloping to moderately steep uplands of the Piedmont and are generally well drained with medium to rapid runoff and moderate permeability. Averaged across samples collected from the 16 plots, pre-treatment soil pH, and C and N concentrations in the 0–10 cm depth were 4.84, 16.3 mg g^{-1}, and 0.82 mg g^{-1}, respectively (Will et al., submitted for publication).

The site was plowed and bedded in 2005 and before and following planting herbicide was applied for herbaceous weed control. Seedlings from an open-pollinated source were hand planted in February 2006 at a spacing of approximately 3 m × 2 m, which, depending on plot, resulted in densities ranging from 1233 to 1466 trees ha^{-1} (average density of 1383 trees ha^{-1} at age 6). At the time of study initiation and during this study the stands did reach canopy closure and all trees were dominant in the canopy. The study was designed as a 2 × 2 factorial with four blocks and two levels of throughfall treatment, ambient and an approximate 30% reduction, and two levels of fertilization treatment, none and fertilized. Each 0.10 ha treatment plot contained an average of 136 trees, a 0.03 ha measurement plot with 40 trees, and a 6.1 m buffer. Plots were grouped into blocks based on similarities in stand attributes (height and DBH) at age 6 before study initiation and proximity of plots to one another. To achieve a reduction in ambient throughfall, exclusion troughs were installed in May 2012 between tree rows to cover 30% of the ground area. In throughfall reduction treatment plots, support structures measuring approximately 1.8 m wide with an average height of 1.3 m (height varied with topography) were built from lumber to fit between each row and span the length of the row. Two collection troughs were constructed of lumber and covered with two layers of clear U.V. stabilized coextruded polyethylene with embedded high strength cord (Polyscrim 12, Americover Inc., Escondido, CA, USA) and secured on top of each support structure over its entire length. Troughs were separated by a 30.5 cm opening to minimize banding in soil moisture. The troughs transported water off the treatment plot into the buffer areas a minimum of 3 m beyond the treatment plots. It was assumed that covering 30% of the area of the plots would cause a substantial reduction in the total amount of precipitation entering the soil. However, this amount can vary from plot to plot and with treatments that affect leaf area and growth, so the effect of this treatment was determined by measuring soil moisture and predawn leaf water potentials (Ψ_L), as described in Section 2.4. While the predawn leaf Ψ_L measurements are the most accurate representation of plant-available soil water, the soil water content measurements, made in the upper 12 cm of soil, can provide an additional index of treatment effects.

The fertilization treatment consisted of 224 kg N ha^{-1}, 28 kg P ha^{-1}, 56 kg K ha^{-1}, and a micronutrient blend evenly broadcast by hand across each plot in March 2012. Nitrogen and P were applied as a mix of urea (432 kg ha^{-1}) and diammonium phosphate (140 kg ha^{-1}) and K was applied using potassium chloride. A granular micronutrient mix (Southeast Mix, Cameron Chemicals, Inc., Virginia Beach, VA, USA) was applied at a rate of 22.4 kg ha^{-1} and contained 6% sulfur, 5% boron, 2% copper, 6% manganese, and 5% zinc.

2.2. Growth

Stand inventories were conducted before treatment application in December 2011 (age 6) and following treatment initiation in December 2012 (age 7) and December 2013 (age 8). Stem (plus bark) oven-dried weight was calculated from DBH using an allometric equation developed for loblolly pine in southern Georgia at ages 5 and 6 across a range of irrigation and fertilization treatments (Samuelson et al., 2004). No influence of fertilization