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Fertilization increases sensitivity of canopy stomatal conductance and transpiration to throughfall reduction in an 8-year-old loblolly pine plantation

Stan M. Bartkowiak[a], Lisa J. Samuelson[a,*], Mary Anne McGuire[b], Robert O. Teskey[b]

[a] School of Forestry & Wildlife Sciences, Auburn University, Auburn, AL 36849, USA
[b] Warnell School of Forestry and Natural Resources, University of Georgia, Athens, GA 30602, USA

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ABSTRACT

Loblolly pine (*Pinus taeda* L.) is the most important plantation species in the southeastern United States and therefore reductions in productivity associated with climate change may have significant economic impacts. To better understand the potential impact of drought on loblolly pine productivity, we studied the combined effects of reduced water availability and soil fertility on transpiration and canopy stomatal conductance (G_S) over one year in an 8-year-old loblolly pine plantation by applying a throughfall treatment (ambient versus an approximate 30% reduction in throughfall) and a fertilization treatment (no fertilization versus one-time fertilization with N, P, K and micronutrients). We hypothesized that stomatal behavior would regulate water loss under a throughfall reduction treatment and the response would be greater under fertilization, due to an increase in leaf area index. Significant interactions between treatments indicated lower average monthly transpiration per unit ground area (E_G) and per unit leaf area (E_L), lower whole-plant hydraulic conductance, and lower average monthly midday G_S in response to throughfall reduction only in the fertilized treatment, most likely due to increases in the leaf-to-sapwood area ratio in addition to isohydric regulation of water loss. In the throughfall reduction treatment but not the ambient throughfall treatment, reference G_S (at vapor pressure deficit = 1 kPa, G_{Sref}) was significantly related to soil relative extractable water (REW) to a 0.6 m soil depth, and sensitivity of G_{Sref} to REW was greater when combined with fertilization. These results indicate that the influence of drought on canopy-level processes of loblolly pine will be greater with fertilization.

1. Introduction

The southeastern United States (U.S.) comprises 40% of the nation's timber land, and loblolly pine (*Pinus taeda* L.) plantations represent approximately 50% of the standing pine volume in the region (Wear and Greis, 2012; Oswalt et al., 2014). Climate change-related reductions in water availability (Marion et al., 2014) may affect the productivity of forests in the Southeast (Johnsen et al., 2014) and subsequently impact timber supplies and forest ecosystem services. Climate projections for the southeastern U.S. indicate that the frequency of extreme precipitation events may increase, and that evapotranspiration (ET) and the duration and intensity of summertime droughts may also increase in proportion to the rate of warming (Dai, 2011; Kunkel et al., 2012; IPCC, 2013). There is clearly a potential for projected changes in global and regional climate to impact the hydrologic cycle of forested ecosystems, of which ET is a major component (Cao et al., 2006), and ET is closely related to ecosystem productivity (Law et al., 2002). Forest canopy transpiration on a ground area basis (E_G) accounts for approximately 42–72% of forest ET in the southeastern U.S. ecoregion (Lawrence et al., 2007; Oishi et al., 2008; Schlesinger and Jasechko, 2014), and E_G is linked to gross primary productivity through stomatal regulation of water vapor and carbon dioxide fluxes (Kim et al., 2014).

The majority of research exploring the impact of water availability on stand water use in loblolly pine plantations has been in the context of irrigation treatment or relatively short-term natural drought (Pataki et al., 1998; Ewers et al., 2000; Albaugh et al., 2004). As an example, studies of E_G and growth of loblolly pine on experimental sites with similar annual precipitation and potential evapotranspiration (PET) and conducted when annual precipitation was close to the long-term average have shown little effect of irrigation in a younger stand (Samuelson et al., 2008b) but a

* Corresponding author.
E-mail address: samuelj@auburn.edu (L.J. Samuelson).

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positive effect in an older stand with higher basal area and higher leaf area (Samuelson and Stokes, 2006). In a case when annual precipitation was 36% lower than the long-term average, irrigation nearly doubled annual E_G in an 11-year-old loblolly pine plantation (Gonzalez-Benecke and Martin, 2010). Short-term drought has been shown to reduce leaf and canopy stomatal conductance (G_S) and carbon assimilation in loblolly pine (Ellsworth, 2000; Domec et al., 2009), but the influence of increased drought duration, intensity and frequency on canopy-level processes and forest productivity is not well understood (Johnsen et al., 2014). Sensitivity of radial growth to precipitation even under moderate temperatures has been documented (Samuelson et al., 2013).

Over the period of 2000–2004 approximately 570,000 ha yr^{-1} of pine plantations were fertilized in the southeastern U.S., an increase of 600% relative to annual rates before 1991 (Albaugh et al., 2007). Fertilization of loblolly pine plantations can greatly increase productivity before canopy closure by increasing leaf area index (LAI) (Fox et al., 2007). However, when combined with drought, higher LAI may not result in the expected growth increases, because plant strategies to reduce water loss and avoid hydraulic failure may also limit carbon assimilation (Domec and Johnson, 2012; Goldstein et al., 2013). Fertilization has been shown to reduce carbon allocation to fine root growth and induce changes in root xylem anatomy that reduce the risk of root embolism during drought, but these changes may decrease root and whole-plant hydraulic conductance (Ewers et al., 2000). Severe drought may negate the positive effect of fertilization on leaf area production (Tang et al., 2004).

The objective of this study was to examine the main and interactive effects of throughfall treatment (ambient versus an approximate 30% reduction in throughfall) and fertilization treatment (no fertilization versus one-time fertilization) on stand-level transpiration, canopy stomatal conductance (G_S) and whole-plant hydraulic conductance in an 8-year-old loblolly pine plantation located in Georgia. Loblolly pine has been shown to be isohydric (i.e. stomatal responsiveness to reduced water availability) (Domec et al., 2009). We tested the hypothesis that stomatal behavior would regulate water loss under a throughfall reduction treatment and the response would be greater with fertilization, due to increases in LAI and the leaf-to-sapwood area ratio (A_L:A_S) (Samuelson and Stokes, 2006). Concurrent work on this study reported increases in LAI from fertilization the two growing seasons following treatment initiation and decreases in leaf-level net photosynthesis and stomatal conductance in response to throughfall reduction treatment during a drier but not wetter than average year (Samuelson et al., 2014). During both years, no significant interactive influence of throughfall and fertilization treatments on leaf-level physiology was detected. However, leaf-level measurements are discrete and dependent upon individual leaf physiology, canopy position, and irradiance (Norman, 1980; Baldocchi and Amthor, 2001). The continuous sap flux measurements made in this study may better capture treatment effects at broader spatial and temporal scales.

2. Materials and methods

2.1. Study site and experimental design

This experiment was part of the PINEMAP project (www.pinea-map.org) designed to better understand the effects of drought on loblolly pine productivity and one of four throughfall experiments installed across the range of loblolly pine (Will et al., 2015). The study was installed on land owned by Plum Creek Timber Company, Inc. located in the Georgia Piedmont physiographic region (33°37′35″N, 82°47′54″W) in Taliaferro County, Georgia. The 30-year average daily maximum/minimum temperature and annual precipitation measured in Washington, Georgia are 22.7 °C/10.1 °C and 1109 mm, respectively (1983–2012; NOAA National Weather Service Cooperative Observer Program (COOP): 099157 – http://www.ncdc.noaa.gov/cdo-web/datasets/ANNUAL/locations/ZIP:30673/detail accessed June 2015).

The study site and experimental design were previously described in more detail by Samuelson et al. (2014). The site is comprised of three similar soils from the Catula-Cecil (CcB2 and CcD2) and Lloyd (LdB2) series (USDA soil classification – http://www.nrcs.usda.gov/wps/portal/nrcs/detailfull/soils/home/ accessed June 2013). The dominant LdB2 complex is a fine, kaolinitic, thermic Rhodic Kandiudult. The remaining CcB2 and CcD2 complexes are fine, kaolinitic, thermic Typic Kandhapludults, which can be more acidic. All soils are well drained with medium to rapid runoff and moderate permeability. The previous loblolly pine stand was clear cut in 2005. The site was hand planted with bare root seedlings in 2006 on a 3 m by 2 m spacing (1544 trees ha^{-1}). Seedlings were from an open-pollinated, genetically improved, second generation seed source.

The experimental design was a randomized complete block design replicated four times with throughfall and fertilization treatments arranged as a 2 × 2 full factorial. The treatment plots were 0.10 ha (34.1 m × 28.0 m) and included a central 0.03 ha (21.3 m × 14.0 m) measurement plot containing approximately 40 trees. Fertilization treatments included no fertilization and a standard, operational fertilization treatment (224 kg N ha^{-1}, 28 kg P ha^{-1} P, 56 kg K ha^{-1}) hand broadcast around trees in March 2012. Nitrogen and P were applied as urea and diammonium phosphate (DAP), and K was applied as potassium chloride. A micronutrient blend that consisted of S – 6%, B – 5%, Cu – 2%, Mn – 6%, and Zn – 5% by weight (Southeast Mix, Cameron Chemicals, Inc., Portsmouth, Virginia) was also applied. Throughfall manipulation treatments began May 2012 and included an ambient throughfall control and an approximate 30% reduction in throughfall, which corresponds to the driest projections for the region (Christensen et al., 2007). In order to reduce throughfall, exclusion trays covering 30% of total plot area were installed between each row of trees to divert throughfall from the treatment plots. A supporting structure was built to a height of 1.3 m and a width of 1.5 m. Two throughfall exclusion trays were constructed on top of the supporting structure and separated by a 30.5 cm opening to minimize microclimate effects and soil moisture banding. The trays were covered with flexible 12 mil (0.3 mm) extrusion laminate with two layers of U.V. stabilized coextruded polyethylene and high strength cord grid (Poly Scrim 12, Global Plastic Sheeting, Vista, California). The amount of water being moved off the plots by the exclusion trays was not measured; therefore, the actual reduction in throughfall is unknown. Predawn leaf water potential was decreased by throughfall reduction treatment in 2012 and 2013 and indicates an effect of throughfall treatment on soil water availability (Samuelson et al., 2014). In addition, soil moisture in the 0–12 cm soil layer was measured periodically in all four exclusion studies and was reduced on average from 18% to 29% in 2013 (Will et al., 2015).

A cellular networked weather station consisting of a data logger (CR1000, Campbell Scientific, Inc., Logan, Utah) and cellular modem, located in an open area in the center of the site, collected continuous meteorological data over the study period beginning in January 2013, including: precipitation (TR-525I Rain Gauge Tipping Bucket, Texas Electronics Inc., Dallas, Texas), photosynthetic active radiation (PQS 1 PAR Quantum Sensor; Kipp & Zonen USA Inc., Bohemia, New York), temperature and relative humidity (CS500-L, Campbell Scientific, Logan, Utah), and volumetric water content (VWC) in the top 12 cm of soil using wireless time domain reflectometry probes (Wireless Soil Water Reflectometer, CWS655, Campbell Scientific, Logan, Utah).