



Fertilization intensifies drought stress: Water use and stomatal conductance of *Pinus taeda* in a midrotation fertilization and throughfall reduction experiment [☆]



Eric J. Ward ^{a,*}, Jean-Christophe Domec ^{a,b}, Marshall A. Laviner ^c, Thomas R. Fox ^c, Ge Sun ^d, Steve McNulty ^{d,e}, John King ^a, Asko Noormets ^a

^a Department of Forestry and Environmental Resources, North Carolina State University, 920 Main Campus Drive, Suite 300, Raleigh, NC 27606, USA

^b Bordeaux Sciences-Agro, University of Bordeaux, Gradignan Cedex, France

^c Department of Forest Resources and Environmental Conservation, Virginia Polytechnic Institute and State University, 310 West Campus Drive, Blacksburg, VA 24061, USA

^d Eastern Forest Environmental Threat Assessment Center, United States Forest Service, 920 Main Campus Drive, Suite 300, Raleigh, NC 27606, USA

^e South East Regional Climate Hub, United States Department of Agriculture, 920 Main Campus Drive, Suite 300, Raleigh, NC 27606, USA

ARTICLE INFO

Article history:

Received 22 December 2014

Received in revised form 1 April 2015

Accepted 10 April 2015

Available online 7 May 2015

Keywords:

Fertilization
Drought
Gas exchange
Loblolly pine
Sap flux
Transpiration

ABSTRACT

While mid-rotation fertilization increases productivity in many southern pine forests, it remains unclear what impact such management may have on stand water use. We examined the impact of nutrient and water availability on stem volume, leaf area, transpiration per unit ground area (E_C) and canopy conductance per unit leaf area (G_S) of a pine plantation during its 8th and 9th growing seasons. Treatments consisted of a factorial combination of throughfall reduction (30% reduction in throughfall versus ambient) and fertilization (a complete suite of essential nutrients) beginning in April 2012. Overall, our results indicate that despite unusually high rainfall in the study period and a lack of leaf area index (LAI) response, both E_C and G_S decreased in response to fertilization and throughfall reduction. Fertilization increased stem volume increment 21% in 2013. Treatment differences were greatest in the growing season of 2013, when E_C was on average 19%, 13% and 29% lower in the throughfall reduction (D), fertilization (F) and combined treatment (FD) than the control (C), respectively. The responses of G_S to volumetric soil water content (VWC) indicate that lower E_C in F was associated with a decrease relative to C in G_S at high VWC . Decreases of G_S in D relative to C were associated with lower VWC , but little change in the response of G_S to VWC . Decreases observed in FD resulted from a combination of these two factors. The pattern of G_S responses in the different treatments suggests that structural or physiological changes underlie this fertilization response, possibly in fine root area or hydraulic conductivity. In the short term, this led to large increases in the water use efficiency of stem production, which could suggest greater resiliency to minor water stress. However, impacts on long-term sensitivity to drought remain a concern, as the E_C reduction triggered by the fertilization treatment was of comparable magnitude to the 30% throughfall exclusion treatment and the greatest reductions were found in the combined treatment.

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1. Introduction

It has been long been suggested that site fertility is the primary limitation to leaf area development in loblolly pine (*Pinus taeda* L.) stands of the southeastern U.S. and this, in turn, limits stand productivity (Vose and Allen, 1988). Although it is recognized that site water availability plays a secondary role in these limitations, site fertility is thought to be a greater limitation to leaf area index (LAI ,

m^2 projected leaf area m^{-2} ground area), growth efficiency and stand production on most sites, even on excessively drained soils (Albaugh et al., 2004; Fox et al., 2007). In a review of fertilization practices and potential effects in southern pine forests, Fox et al. (2007) concluded that stands with LAI less than 3.5 do not fully utilize available solar radiation and may thus benefit from fertilizer application. Early in stand development, nutrient availability is usually adequate for stand growth. Nutrient demand is relatively low and there is an initial pulse of available nutrients, especially N, associated with harvesting, site preparation and planting disturbances. Over the last 25 years, mid-rotation fertilization of managed pine forests has become an increasingly common practice in this region. About 570,000 ha of pine forests were fertilized each year from 2000

[☆] This article is part of a special issue entitled "Carbon, water and nutrient cycling in managed forests".

* Corresponding author. Tel.: +1 919 452 6652.

E-mail address: ejward3@ncsu.edu (E.J. Ward).

to 2004, compared to less than 81,000 ha y^{-1} before 1991 (Albaugh et al., 2004). While more than 95% of fertilization in 1969 was within 2 years of stand establishment, about 75% of fertilization occurred in stands older than 2 years from 2000 to 2004.

Forests in the southeastern U.S. are predicted to experience more variable precipitation in the future, including increased precipitation intensity during El Niño events (Meehl et al., 2007), and a moderate decrease in water availability (precipitation minus evapotranspiration (ET)), although considerable uncertainty in and disagreement between projections remain (Seager et al., 2009). While it seems clear that mid-rotation fertilization increases productivity in many pine forests of the southeastern U.S., there is a need to understand the effects of widespread fertilization in the face of periodic or persistent droughts in this region. Recent analyses suggest that many forests shift carbon allocation from fine roots to woody tissues (stem and coarse roots) when nutrient availability increases (Högberg et al., 2003; Treseder et al., 2007; Janssens et al., 2010; Chen et al., 2013). It has been suggested that such structural changes in faster-growing, unstressed stands make them more vulnerable than chronically stressed stands to drought-induced diebacks in future climates with more variable precipitation regimes (McNulty et al., 2014).

Furthermore, the water use of managed forests is of importance in the context of other uses of water on the landscape. Past studies have demonstrated that carbon and water cycles are closely coupled in terrestrial ecosystems (Gholz et al., 1990; Law et al., 2002; Sun et al., 2011b), linking increased forest productivity to increased forest ET and reduction of water yield in forest watersheds. ET is the largest water output in forests and is closely related to LAI (Sun et al., 2011a). Increasing LAI and productivity of fertilized pine forests could thus lead to a concomitant increase in water use, in terms of transpiration per unit ground area (E_C), unless its regulation changes proportionally, through decreased canopy conductance per unit leaf area (G_S) and increased water use efficiency.

In the Carolina Sand Hills, where soils are excessively drained, after seven years of fertilization with a suite of macro- and micronutrients, a 15-year old loblolly pine stand decreased G_S at high soil moisture by 50%, in proportion to a doubling of LAI . Plots that received irrigation in addition to fertilization did not experience this reduction, despite having even higher LAI than fertilized plots (Ewers et al., 1999). Later empirical and modeling work suggested that this was linked to lower root area and less conductive (but more drought resistant) root xylem in fertilized plots without irrigation (Ewers et al., 2000). In contrast, fertilization of a loblolly pine stand in the Sand Hills for 4 years following establishment increased G_S 43% while increasing LAI 24%, leading to a near doubling of stand water use, while irrigation had no effect on either G_S or stand water use (Samuelson et al., 2008b).

As illustrated by these differing results within the same physiographic region, the effect of fertilization on stand water use of loblolly pine depends on the interacting factors of site water availability and the timing of fertilization in stand development, to which trees may respond dynamically, by temporarily adjusting G_S , or developmentally through structural changes that affect hydraulic supply of the foliage. As water must pass from the soil to stomatal cavities through roots, trunk, branches and leaves, the hydraulic conductivity and sapwood to LAI ratio of these organs may limit G_S , as may increases in path length that accompany height growth (Whitehead et al., 1984; Whitehead, 1998; McDowell et al., 2002). Thus, while an increase in LAI may be expected to follow fertilization, water use may not increase proportionally if the hydraulic supply of leaves (e.g. fine root area and conductivity) does not increase to the same degree. This, in turn, depends on whether LAI increases observed with fertilization of loblolly pine are the primarily the result of increased growth or a shift in carbon allocation.

Leaf area responses to fertilization may take four or more years to fully develop in a mid-rotation stand (Albaugh et al., 1998), as may shifts in basal-area to peak LAI ratios (Albaugh et al., 2004). Initial increases in photosynthetic rates following fertilization (Murthy et al., 1996; Maier et al., 2008) may decrease with time (Gough et al., 2004). Therefore, the response of E_C and G_S in the first one or two growing seasons following fertilization of a mid-rotation stand may be dependent on the relative timing of photosynthetic and LAI responses and differ considerably from those of later years. As water use is an integrated response of the root-to-leaf transport system and may be monitored with less labor and disturbance than belowground carbon dynamics, E_C and G_S responses may also give early indications of shifts in physiology that occur with fertilization. In loblolly pine stands, metrics such as height, sapwood-to-leaf-area and root-to-leaf-area ratios have been linked to changes in stomatal responses in many studies (e.g. Ewers et al., 2000; Samuelson and Stokes, 2006; Samuelson et al., 2008b; Ward et al., 2013).

Given the extensive practice of mid-rotation fertilization of loblolly pine plantations, the USDA NIFA-funded Pine Integrated Network: Education, Mitigation and Adaptation Project (PINEMAP; www.pinemap.org) installed experiments to evaluate the interaction of water availability and mid-rotation fertilization at 4 locations in VA, GA, FL and OK (Will et al., in review), in stands ranging from 4 to 9 years since establishment. Treatments consisted of a factorial combination of throughfall reduction (30% reduction in throughfall versus ambient) and fertilization (a complete suite of essential nutrients) beginning in 2012. Here we report on the effects of these treatments on the E_C and G_S of stands at the VA site for the first two years of study, employing measurements of LAI and stem growth, as well as from a network of environmental and sap flux sensors. At this site near the northern extreme of the native range of *P. taeda* in the Piedmont physiographic region, we tested the hypotheses that fertilization would increase stem volume increment and decrease G_S over the first two growing seasons, consistent with a shift in allocation away from fine roots toward woody tissues. We expected some increase in LAI with fertilization by the end of this period, resulting in less effect on E_C than G_S . We also hypothesized that throughfall reduction would decrease E_C and G_S , as well as stem volume increment, consistent with a greater G_S limitation of photosynthesis.

2. Materials and methods

2.1. Site description

The study site is located in the Appomattox-Buckingham State Forest in Buckingham County, VA (37°27'37"N, 78°39'50"W). It is an upland site with 0–15% slopes in the Piedmont physiographic region. The soil is a well-drained, fine, mixed, subactive, mesic Typic Hapludult of the Littlejoe soil series, characterized as a silt loam overlying a silty clay loam subsoil. Soil carbon and nitrogen were estimated as 3.74 and 0.13 mg g^{-1} in the top 10 cm of mineral soil (Will et al., in review). Mean annual precipitation is 1120 mm with mean annual temperature of 13.6 °C. Minimum January daily temperature averages -4.4 °C and maximum August daily temperature averages 30.6 °C. The site was planted in 2003 with 1200 seedlings per ha from a seed orchard mix appropriate to the region. In February 2011, trees were 8.79 m tall on average with a mean DBH of 145 mm and natural mortality had reduced stand density to approximately 789 trees per ha. Before establishment of treatments in April 2012, all competing vegetation was eliminated by manual clearing and a broadcast spray below the canopy with imazapyr, metsulfuron methyl, and

glyphosate. Targeted application of glyphosate was used as needed to control competing vegetation.

The fertilization treatment was representative of operational applications to loblolly pine plantations and consisted of 224 kg N ha⁻¹, 27 kg P ha⁻¹, 52 kg K ha⁻¹ and 1.12 kg ha⁻¹ of a micronutrient mix containing 6% sulfur, 5% boron, 2% copper, 6% manganese, and 5% zinc. The throughfall reduction treatment consists of covering approximately 30% of the ground area with troughs to capture and funnel throughfall from the plots. Paired troughs, each 0.6 m wide, with a 0.4 m gap between them to reduce soil moisture banding, were covered with clear 12 mil, UV stabilized polyethylene. Water was funneled a minimum of 3 m from each plot, with care taken to route water away and downslope from adjacent plots. Treatments were applied in a randomized complete block design with 4 blocks, with a square treatment plot 32.9 m on a side (0.356 ha) and an internal measurement plot 20.7 m on a side (0.141 ha). This resulted in four treatment combinations: control (C), throughfall reduction (D), fertilization (F) and the combined treatment (FD).

2.2. Biometric measurements and interpolation

The height, diameter at breast height (DBH, mm), crown length and crown width of all trees in measurement plots were recorded in annual winter surveys. Dendrometer bands were installed on all trees with sap flux sensors (5 per plot) and read biweekly from May through September. To generate daily estimates of sapwood area for scaling sap flux measurements, sapwood areas (m²) were calculated for all measurement dates using an allometric relationship (Gonzalez-Benecke and Martin, 2010): $\ln(As) = 2.185 \ln(DBH) - 15.347$. We used a single relationship for all treatments to account for bark in scaling sapwood area as *P. taeda* does not typically develop heartwood at this age, a fact confirmed from trees harvested outside the measurement plots. We assumed plot sapwood area index (SAI; m² sapwood m⁻² ground area) followed the same relative pattern of growth as the treatment average sapwood area of trees with dendrometer bands, linearly interpolating the biweekly measurements. Total stem volume estimates inside bark were made from annual DBH and height surveys after Sherrill et al. (2011).

Leaf area index (LAI) was estimated from the transmission of diffuse solar radiation with one of two Plant Canopy Analyzer models (LI-COR, Lincoln, NE USA) on February 14, 2012 (LAI-2000 model), February 20, 2013 (LAI-2200 model), September 4–5, 2013 (LAI-2200 model) and April 2, 2014 (LAI-2200 model), roughly corresponding to times of minimum and maximum leaf area of *P. taeda* in this area. Measurements employed a 15° view cap and the analyzer's lowest angle of view (68°) was masked in post-processing of data, to limit the sensor view angle to the treatment plot canopy. Phenology derived from published leaf area data from a *P. taeda* stand (Duke FACE site) about 160 km from our study site, in the same physiographic region (McCarthy et al., 2007; Ward et al., 2013) was used as a proxy for the phenology of our study site (see Supplemental Information), allowing us to interpolate daily values for LAI of each treatment.

2.3. Sap flux and environmental sensor network

In each plot, a sample of 5 trees representative of the DBH distribution of the plot were equipped with thermal dissipation probes (TDPs) built in our lab after the design of Granier (1985) and installed at 0–20 mm depth in the xylem of the north-northwest side of the trunk at breast height. The sensor signal was converted to sap flux density (J_s , g m⁻² s⁻¹) according to Granier (1987), accounting for the effects of non-zero night-time fluxes on the signal baseline (Oishi et al., 2008). Multiple studies

have shown that there was minimal to no significant difference in azimuthal J_s within trees for this species (Schäfer et al., 2002; Ford et al., 2005; Domec et al., 2010), probably due to the homogeneity of pine trunks. Over 22 months of study, we replaced 99 sensors due to breakages. Some sensor locations experienced multiple breaks, giving a mean sensor longevity of 12 months when averaged by location. Of approximately 2.53 million possible half-hourly observations over the study period, we accepted 1.79 million (71%) after accounting for sensor breakage, power interruptions, datalogger failures and acceptable zero-flow calibrations.

Micrometeorological sensors were mounted atop a triangular tower at the center of the first treatment block. These included a tipping bucket for precipitation (TE525 Campbell Scientific, Inc., Logan, UT), a photosynthetically active radiation (PAR, $\mu\text{mol m}^{-2} \text{s}^{-1}$) quantum sensor (LI-190, LI-COR, Inc., Lincoln, NE), and a relative humidity and air temperature (T_A , °C) sensor (HMP45 probe, Campbell Scientific). Relative humidity was converted to vapor pressure deficit (VPD, kPa) based on T_A after Campbell and Norman (1998).

Volumetric soil water content (VWC, m³ water m⁻³ soil) was monitored with time domain reflectometer (TDR) sensors (CWS655 soil water reflectometer, Campbell Scientific, Logan, UT) from 0 to -120 mm soil depth. In C and F measurement plots, we deployed one TDR sensor, while in D and FD plots we placed one TDR sensor beneath a trough and another in the open area between troughs within the central measurement area of the plot, randomizing the location within these areas. All analyses used throughfall treatment averages of VWC, filling all gaps in individual sensor time series by linear regression to limit the effect of uneven sampling on the treatment mean (see Supplemental Information). The treatment averages for D and FD plots were calculated by weighting measurements from below and between the troughs proportional to their areal coverage, (30% and 70%, respectively).

2.4. Canopy transpiration and stomatal conductance

Granier-style sap flux sensors offer an efficient method to monitor continuously water use by forests. However, there are some limitations to their use. First, the growth of the trees invariably results sensor breakage over long-term use, creating gaps in data. Secondly, replacement sensors cannot be placed in the same location, resulting in shifts in signal magnitude that are products of the data collection procedure, rather than changes in the system being observed. Finally, there is a mismatch between the scale of the observations (small cross-sectional areas of sapwood) and the processes of most interest (canopy scale transpiration and canopy-averaged stomatal conductance), which cannot be directly measured in a natural forest. These factors make it desirable to employ a hierarchical inferential model in analysis of such data (Clark et al., 2011) to quantify uncertainties at both the data (i.e. individual sensor) and process (i.e. canopy) level.

To assess the treatment effects on stand water use, we employed the State-space Canopy Conductance (StaCC) Model, a hierarchical Bayesian model of canopy averaged stomatal conductance (G_s , mmol m⁻² leaf area s⁻¹) from inference on J_s of individual sensors (Ward et al., 2013; Bell et al., in press). This approach has been shown to be efficient at dealing with missing data from individual sensors and predicting latent states of interest (Clark et al., 2011), such as G_s and canopy-averaged transpiration per unit ground area (E_c , mm s⁻¹), and provides a rigorous way of combining a basic understanding of stomatal responses with observations of J_s (Ewers, 2013).

In brief, the StaCC model combines a random effects data model for individual sensors with a process model for G_s based on multiplicative model responses to VWC, VPD and PAR, similar to those of

Jarvis (1976), such that the response of steady-state canopy conductance (G_{SS}) is described as:

$$G_{SS} = G_{SRef} f_{VPD} f_{VWC} f_{PAR}, \quad (1)$$

where $f_{VPD} = (1 - \lambda \ln(VPD))$ and both f_{VWC} and f_{PAR} vary positively from 0 to 1, making G_{SRef} an index of G_S at high PAR, high VWC and 1 kPa VPD (Oren et al., 1999). The dynamic response of G_S is based on that of the previous time step, such that:

$$G_{S(t)} = G_{S(t-dt)} + (G_{SS(t)} - G_{S(t-dt)}) \left(1 - \exp\left(\frac{-dt}{\tau}\right) \right), \quad (2)$$

where dt is 30 min. The stomatal time constant (τ) has been shown to range from 15 to 50 min for responses to changes in leaf irradiance in *P. taeda* (Whitehead and Teskey, 1995). We used a value of $\tau = 20$ min and $dt = 30$ min for all model runs, i.e. $(1 - \exp(\frac{-dt}{\tau})) = 0.777$. To capture seasonal and developmental shifts in the regulation of G_S , we ran the model separately for 20,000 iterations for each treatment in each of 4 model periods: growing season 2012 (June–September), dormant season 2012 (October 2012–March 2013), growing season 2013 (April–September) and dormant season 2013 (October 2013–March 2014). More model details are given in Ward et al. (2013), including functions for f_{VWC} and f_{PAR} , while a full model description and sensitivity analyses are given in Bell (2011) and Bell et al. (in press).

Given the relatively small stature of the trees and similarity in tree size between treatments, we ignored time lags associated with hydraulic capacitance within the stem and canopy of the trees. As we only monitored sap flux in the outer 20 mm of sapwood, the sapwood area of all plots was multiplied by 0.88 to account for decreasing sapwood conductivity in older xylem. This effective sapwood area was calculated as the ratio of mean sap flux in the outer 20 mm to that of all sapwood from the Duke FACE stand at age 18 (Ward et al., 2013), which is the youngest age at which measurements to 60 mm were analyzed. These assumptions may affect the absolute values of G_{SRef} , but are unlikely to affect the relative responses f_{VPD} , f_{VWC} and f_{PAR} , nor the treatment comparisons that are the focus of this study.

2.5. Statistical analyses

Statistical analyses were performed in R (R Core Team, 2014). To evaluate the effects of the treatments on plot mean tree height, population density, quadratic mean dbh, sapwood area and leaf area index, we used the *Anova* function in the *car* package (Fox and Weisberg, 2010) to conduct a repeated measures ANOVA with measurement date as an intra-subject design factor and using fixed effects for block, fertilization, throughfall reduction, and the interaction of the two treatments. We used backward selection to evaluate treatment fixed effects, first removing the interaction term if not significant, then the main term for each effect. Block effects were kept in all models, as were terms with significant interactions with measurement date. Reported *p*-values are for Type II MANOVA using the Pillai's Trace test statistic.

Treatment differences for time series of E_L and G_S were evaluated with normal parametric bootstraps of the posterior monthly sums of E_L and monthly daytime means of G_S for each treatment. Normal parametric bootstraps were also used to evaluate the effect of treatments on stem volume increment, annual E_C sums and their ratio (WUE_{Vol}) for 2013, using standard errors of volume increment, sums of posterior distribution standard deviation for E_C and the fractional sum of these error estimates for WUE_{Vol} . We adopted this conservatively large estimate of error in WUE_{Vol} as volume increment and E_C are both scaled by DBH and are not strictly independent of one another (Taylor, 1997).

3. Results

The effect of throughfall reduction on estimated volumetric soil water content (VWC) varied with time and season (Fig. 1). At the time of sensor installation (June 2012; 2 months after treatment initiation), we estimated that VWC in throughfall displacement treatment (D) was approximately 0.06 (as a fraction of total soil volume) lower than in the control treatment (C). Over the first model period (June to September 2012, see Methods), this difference remained at this level, with a markedly greater difference after seasonal soil moisture recharge in September. In the following dormant season (October–March), when soil moisture is typically high, this difference was 0.12, while in the 2013 growing season (April–September) it was 0.11 and 0.08 in the following dormant season. The range of observed VWC values in all treatments was 0.05–0.45. Taking this as a proxy of extractable water, we calculated an average 25% reduction in plant available water in the throughfall reduction treatment from October 2012 to March 2014. Water stress in loblolly pine typically sets in around 30–40% of total plant available water (Gonzalez-Benecke and Martin, 2010), so we may expect a water stress threshold of 0.17–0.21 VWC. The combined treatment (FD) had an intermediate VWC values, with a 15% reduction in plant available water relative to the control over this period. Annual precipitation in 2013 (1224 mm yr^{-1}) was 9% higher than the 30-year mean (1120 mm yr^{-1}) in the area. This can be seen in the high VWC that persisted through August of this year. Additionally, while maximum VPD observed in 2012 was 5.77 kPa, in 2013 it was only 3.68 kPa (Fig. 1), indicating much less atmospheric demand for water vapor and thus, water use by trees.

The treatments imposed on randomly selected blocks of the 8-yr old stand did not differ ($p > 0.100$ for all treatment effects) in leaf area index (LAI, Fig. 2), population density, quadratic mean DBH or plot sapwood area before the initiation of treatments (Table 1). There was a weak trend ($p = 0.075$) toward shorter trees in the D treatment in 2011 before treatment initiation (~ 20 cm). Conducting the repeated measures ANOVA across years, we detected an effect of throughfall reduction ($p = 0.038$), but no interaction with measurement year, suggesting that this weak trend persisted through the study period. There was an interactive effect of fertilization and year on quadratic mean DBH ($p = 0.002$), indicating slightly faster growth in this treatment. We detected a similar interactive effect of fertilization and year on plot sapwood area ($p < 0.001$), which reflects the combined effects of growth and mortality to produce higher sapwood area in fertilized plots over the study period (Table 1).

Although the difference of LAI between treatment means was up to 0.5, the relative rankings of treatments by the leaf area index (LAI) were different on the four measurement dates (Fig. 2). Repeated-measures ANOVA failed to detect an interaction of fertilization and throughfall reduction effects ($p = 0.378$) or an effect of fertilization ($p = 0.825$) on LAI. We did detect a weak trend of higher LAI in the throughfall reduction treatment ($p = 0.067$). We detected no interactions with measurement date of any of these effects ($p > 0.100$ for all). A clear trend of increasing LAI existed in all plots over the measurement period (Fig. 2), indicating that canopy development is still underway in these stands.

We detected an 8% higher monthly mean sap flux density in 0–20 mm sapwood depth (J_s , g m^{-2} sapwood area s^{-1}) for the fertilized treatment (F) relative to the control (C) in June 2012 (Fig. 3), whereas we detected a relative decrease in most of the 2013 growing season (with the exception of September). We also detected decreases in the throughfall reduction (D) and combined (FD) treatments for the growing season of 2013 (April–September). During this period, we estimated a 21%, 15% and 32% decrease relative to C in D, F and FD, respectively. Similar to J_s , canopy

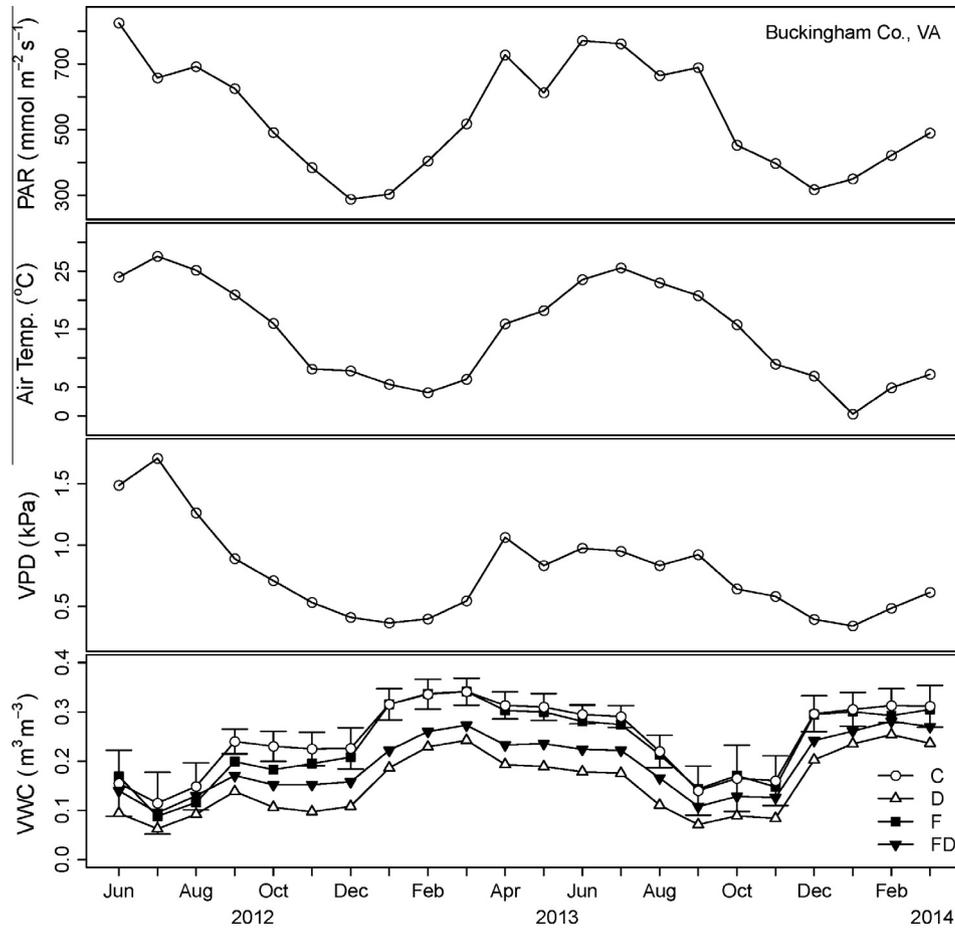


Fig. 1. Mean monthly daytime photosynthetically active radiation (PAR), air temperature, daytime vapor pressure deficit (VPD) and volumetric water content of soil (WVC) for the study period. Treatment abbreviations: C – control, F – fertilization, D – throughfall reduction, FD – fertilization and throughfall reduction. Bars representing one standard deviation across sensors are given only for C treatment to maintain clarity.

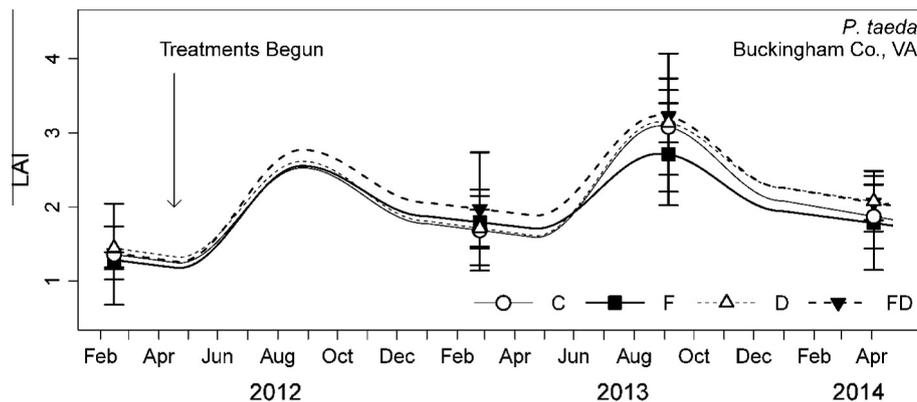


Fig. 2. Leaf area index (LAI) as estimated from diffuse radiation transmission (points) and approximated at the daily time step (lines) using these measurements with a fixed annual pattern (see Supplemental Information) for March 2012 to September 2013. Treatment abbreviations: C – control, F – fertilization, D – throughfall reduction, FD – fertilization and throughfall reduction.

transpiration per unit ground area (E_c) was 9% higher in F than in C for June 2012 (Fig. 4). For the remaining 21 months of study, total E_c was lower in F and the throughfall reduction treatment (D) than in C in 7 and 9 months, respectively, and lower in the combined treatment (FD) than C in 17 months. Treatment differences were greatest in the growing season of 2013, when mean monthly E_c was on 19%, 13% and 29% lower than C in D, F and FD, respectively.

Our estimates of stomatal control at the leaf level exhibited a similar pattern (Fig. 5), with decreased monthly daytime canopy-

averaged stomatal conductance (G_s , $\text{mmol m}^{-2} \text{leaf area s}^{-1}$) relative to C detected from March to May 2013 in F, April to November 2013 in D and August 2012 to November 2013 in FD. Again, treatment differences were greatest in the growing season of 2013, when mean G_s was on average 21%, 10% and 36% lower than C in D, F and FD, respectively. As a percentage of the total, uncertainties associated with E_c and G_s estimates increased in the dormant season, making it more difficult to detect differences (bottom panels of Figs. 3 and 4).

Table 1

Mean (and standard deviation, $n = 4$) stand structural metrics at the end of each growing season. Treatment abbreviations: C – control, F – fertilization, D – throughfall reduction, FD – fertilization and throughfall reduction.

		Height (m)	Tree density (ha^{-1})	Quadratic mean DBH (mm)	Sapwood area ($\text{m}^2 \text{ha}^{-1}$)
2011	C	8.9 (0.2)	739 (40)	150 (6)	9.1 (0.4)
	F	8.9 (0.2)	815 (57)	144 (5)	9.2 (0.6)
	D	8.6 (0.1)	809 (81)	145 (3)	9.2 (0.6)
	FD	8.8 (0.2)	797 (81)	147 (5)	9.3 (0.5)
2012	C	9.7 (<0.1)	739 (40)	165 (7)	11.2 (0.6)
	F	9.7 (0.4)	797 (64)	160 (6)	11.3 (0.9)
	D	9.4 (0.2)	809 (81)	159 (4)	11.4 (0.6)
	FD	9.5 (0.2)	791 (78)	163 (5)	11.6 (0.4)
2013	C	10.7 (0.4)	722 (33)	182 (7)	13.5 (0.7)
	F	10.6 (0.1)	797 (64)	179 (7)	14.4 (0.8)
	D	10.3 (0.1)	809 (81)	175 (4)	13.9 (0.7)
	FD	10.5 (0.2)	785 (77)	183 (6)	15.0 (0.7)

When we looked at the model estimates for the responses of G_S to vapor pressure deficit (VPD) at two different values of VWC (Fig. 6), the regulation underlying the temporal patterns of E_C and G_S was evident. At high VWC (0.3), F exhibited 24% lower E_C and 18% lower G_S than C across the VPD range, while at low VWC (0.1) the F treatment had higher E_C and G_S at low VPD values. At this low VWC value, estimated E_C and G_S were 10% and 19% higher, respectively, in F than C, averaged over the range of VPD observed in the growing season (Fig. 6). This translates to the pattern of reductions in E_C and G_S in F observed only in the early months of the growing season, when soil moisture was high (Figs. 4 and 5). If diffuse radiation measurements indicating lower LAI in F than C during this season (Fig. 2) were erroneous, these early season decreases in G_S would be even greater, as $StACC$ does not incorporate uncertainties in LAI .

In a similar manner, throughfall reduction did not cause large shifts in E_C or G_S within each fertilization treatment, at either 0.1 or 0.3 VWC (Fig. 6). However, the D and FD treatments experienced high VWC for much less time compared to the F or C treatments (Fig. 1). Thus, there was a persistent decrease in mean G_S of D and FD relative to C throughout the growing season of 2013 (Fig. 5), which can be largely ascribed to changes in VWC rather than patterns of stomatal response to VWC or VPD .

Fertilization had a strong effect on stem volume increment in 2013, with 21% and 26% greater increments in F and FD than C,

respectively (Fig. 7). If these increments are divided by annual transpiration estimates to obtain an index of the water use efficiency of stem volume production (WUE_{Vol}), the combined effect of transpiration reductions and stem volume increment increases result in a 39% and 75% increase in WUE_{Vol} in F and FD, respectively, compared to C. The D treatment showed a negligible (4%) increase in stem volume increment, but combined with reductions in annual E_C , this resulted in a 26% increase in WUE_{Vol} compared to C.

4. Discussion

We made several predictions of the changes we would observe with fertilization and throughfall reduction, based on previous studies of this species and global analyses of forest carbon allocation (Chen et al., 2013). Consistent with our hypotheses, we observed that fertilization decreased canopy-averaged stomatal conductance (G_S ; Fig. 6) and increased stem volume increment 21% in 2013 (Fig. 7). Contrary to our expectations, fertilization did not increase leaf area index (LAI ; Fig. 2) and we found decreases in canopy transpiration per unit ground area (E_C ; Fig. 5). Throughfall reduction decreased both E_C and G_S as expected, but also led to a negligible (4%) increase in 2013 stem volume increment, contrary to our hypothesis that decreased G_S would limit photosynthesis and thus stem growth.

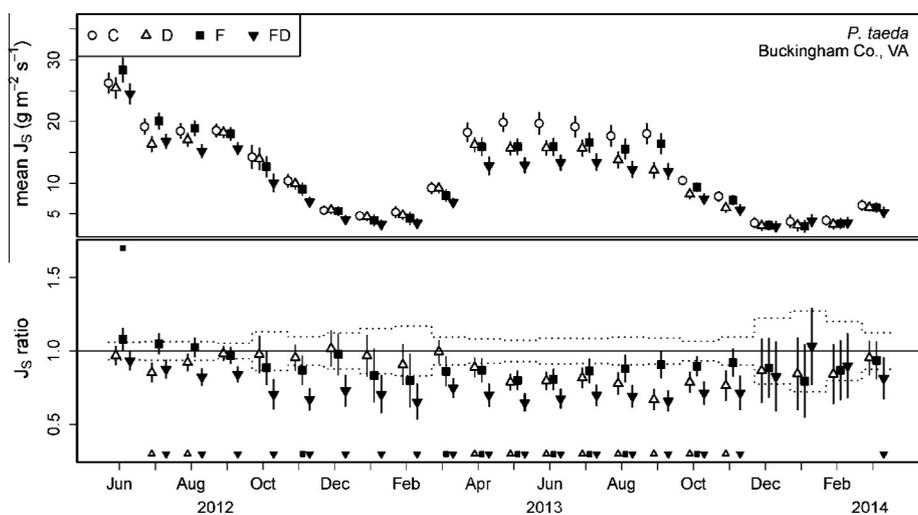


Fig. 3. Estimated mean monthly sap flux density from 0 to 20 mm sapwood depth (J_s , g per unit sapwood area) in each treatment (top) and the ratio of the J_s in each treatment to the control value (bottom), where a 95% credible interval of the control is indicated by the dotted line and by error bars for treatment values. Small symbols at the top and bottom of the panel represent treatments where monthly value was different from the control with 95% confidence using a normal parametric bootstrap of model posterior values. Treatment abbreviations: C – control, F – fertilization, D – throughfall reduction, FD – fertilization and throughfall reduction. Monthly values are staggered for clarity.

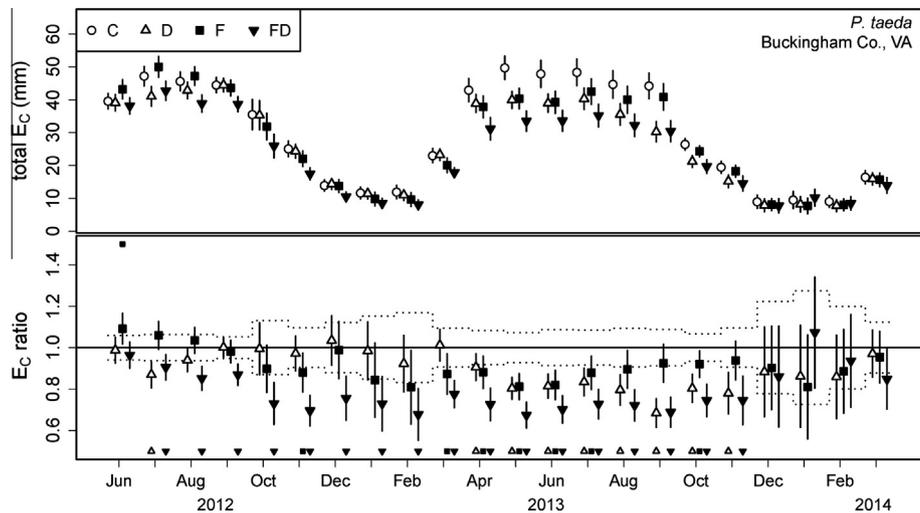


Fig. 4. Estimated monthly canopy transpiration (E_c , mm per unit ground area) in each treatment (top) and the ratio of the E_c in each treatment to the control value (bottom), where a 95% credible interval of the control is indicated by the dotted line and by error bars for treatment values. Small symbols at the top and bottom of the panel represent treatments where monthly value was different from the control with 95% confidence using a normal parametric bootstrap of model posterior values. Treatment abbreviations: C – control, F – fertilization, D – throughfall reduction, FD – fertilization and throughfall reduction. Monthly values are staggered for clarity.

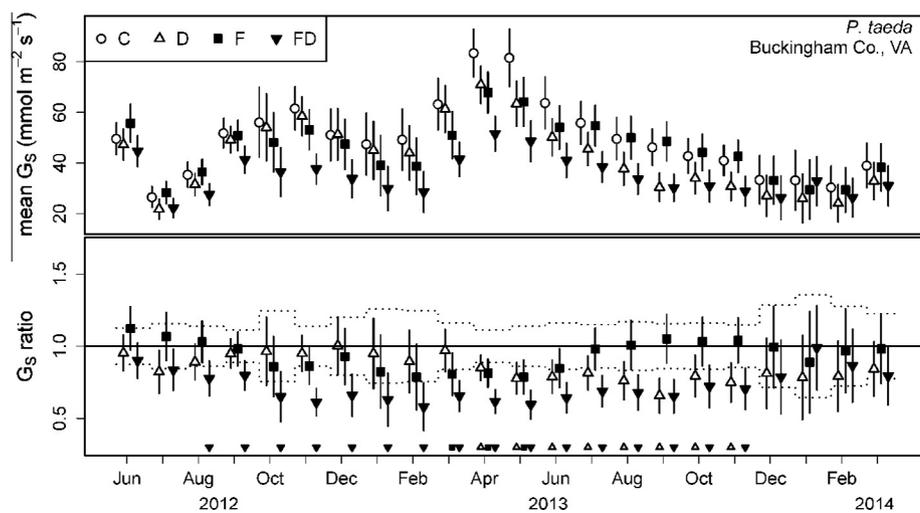


Fig. 5. Estimated monthly daytime canopy-averaged stomatal conductance (G_s , $\text{mmol m}^{-2} \text{ leaf area s}^{-1}$) in each treatment (top) and the ratio of the G_s in each treatment to the control value (bottom), where a 95% credible interval of the control is indicated by the dotted line and by error bars for treatment values. Small symbols at the top and bottom of the panel represent treatments where the monthly value was different from the control with 95% confidence using a normal parametric bootstrap of model posterior values. Treatment abbreviations: C – control, F – fertilization, D – throughfall reduction, FD – fertilization and throughfall reduction. Monthly values are staggered for clarity.

These results contribute to a body of research showing that loblolly pine stands may experience structural or physiological changes beyond a simple increase in LAI that have important implications to water use (and thus water yield) and canopy gas exchange (and thus photosynthesis and productivity) as they approach canopy closure under different resource availabilities (King et al., 1999; Ewers et al., 2000; Munger et al., 2003; Samuelson et al., 2004; Samuelson and Stokes, 2006; Samuelson et al., 2008a,b; Tyree et al., 2009). While further research is required to fully understand the underlying physiological mechanisms of these treatment responses, there are several conclusions we may draw based on the patterns of growth and water use observed.

4.1. Treatment effects on leaf area and stem growth

We found that neither throughfall reduction nor fertilization had a detectable effect on LAI in the first two growing seasons.

Literature reports of fertilization effects on LAI or leaf biomass of *P. taeda* have been mixed with regard to interactions with stand age, ranging from increasing with age (Will et al., 2002), to consistent across years (Albaugh and Allen, 1999; Samuelson et al., 2004, 2008a,b) to decreasing with age (Jokela and Martin, 2000). We hypothesize that this variability in observed responses is not due merely to the size, type and number of fertilizer applications, but also variability in nutrient status of the stands at the time of application. In most soils of the Southeastern U.S., nutrients, especially N, become limiting around the age of crown closure, typically around 10 years after establishment, depending on site conditions and stand density (Fox et al., 2007). This conclusion is drawn from many years of empirical research that has shown greater leaf biomass responses to fertilization in loblolly pine stands 10–12 years old than those 5–7 years old in the Sand Hills of NC (King et al., 1999; Retzlaff et al., 2001), as well as the Piedmont and Lower Coastal Plain of Georgia (Will et al., 2002).

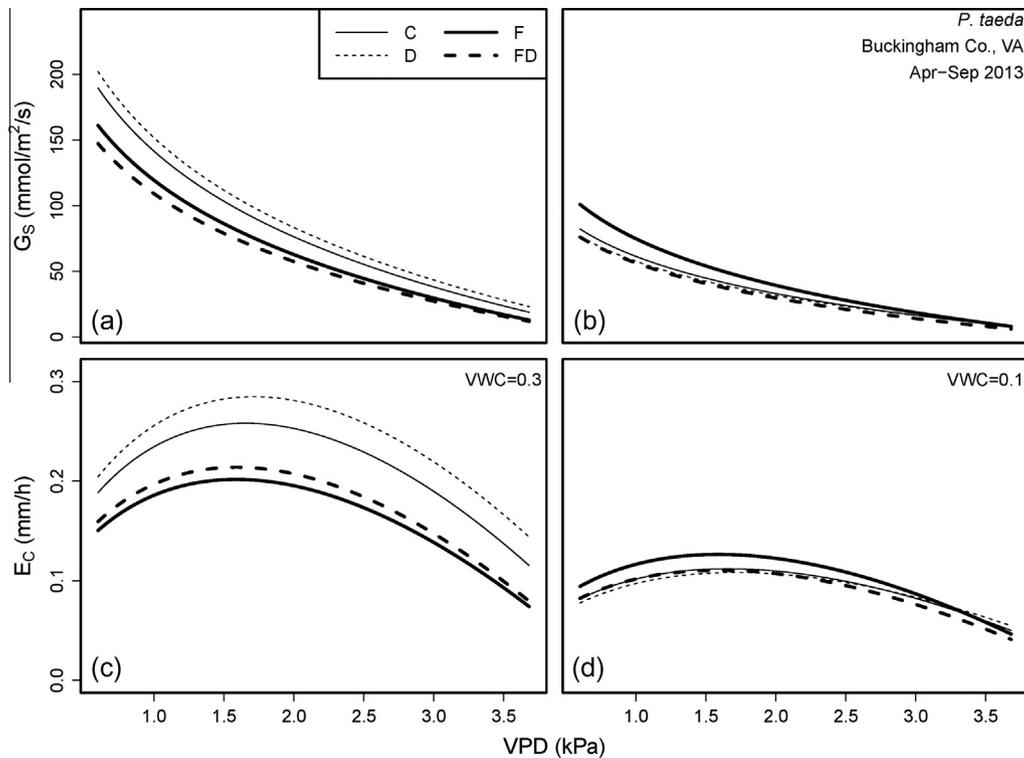


Fig. 6. Mean responses of canopy transpiration per unit ground area (E_c) and canopy-averaged stomatal conductance per unit leaf area (G_s) to vapor pressure deficit (VPD) at two different volumetric water contents of the soil (VWC), under saturating light conditions, as inferred from posterior process parameters for the 2013 growing season. E_c values assume mean leaf area index for the model period. Treatment abbreviations: C – control, F – fertilization, D – throughfall reduction, FD – fertilization and throughfall reduction.

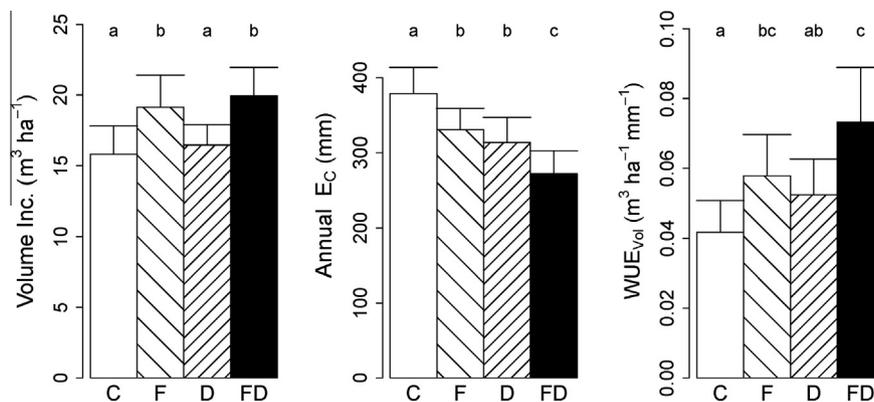


Fig. 7. Stem volume increment, annual transpiration per unit ground area (E_c) and water use efficiency of stem volume production (WUE_{Vol}) for each treatment in 2013. Error bars represent standard error of treatment means for stem volume increment ($n = 4$), standard deviation for posterior distributions of E_c in each treatment, and the fractional sum of these error estimates for WUE_{Vol} . Lowercase letters above each bar represents different groups at 95% confidence as determined using a normal parametric bootstrap. Treatment abbreviations: C – control, F – fertilization, D – throughfall reduction, FD – fertilization and throughfall reduction.

The increase of LAI over time in all plots of this study (Fig. 2) indicates that these stands have not yet reached canopy closure. While a limited amount of mortality has occurred in some treatments (Table 1) and suggests that a self-thinning density is being approached, it is unclear if this is a trend related to treatments or simply a stochastic, localized process. Peak LAI of *P. taeda* stands may be as high as 5, with productivity increasing until an LAI of ~ 3.5 (Vose and Allen, 1988) and possibly higher with intensive management (Fox et al., 2007). Accordingly, this stand is only now entering the phase at which demand for nutrients typically exceeds supply, so we may find a different pattern of treatment effects on LAI , as well as E_c and G_s , emerging in the following years. We have already seen an increase in stem volume production with

fertilization (Fig. 7), suggesting shifts in biomass production or allocation already underway in this stand.

This suggests that, while increased LAI is an important factor in the fertilization response of this species, it is not necessarily the first or most important such change in tree physiology. These results are consistent with studies that show the effects of fertilization on LAI (Albaugh et al., 1998), LAI to basal area ratios (Albaugh et al., 2004), and photosynthesis (Gough et al., 2004) continue to change over multiple years. In the first year after fertilization, nitrogen content has been shown to increase in both previous and current-year cohorts of leaves with only the latter exhibiting increases in photosynthetic capacity (Maier et al., 2008), suggesting that older leaves may serve as a temporary reservoir for later

use in *LAI* expansion. Stem to root biomass ratios vary by site and age in this species (Albaugh et al., 2006), suggesting that allocation responses to fertilization would as well. This is illustrated by the contrast of our results with the large (36%) increase in *LAI* with fertilization in a concurrent study with the same treatments in the Georgia Piedmont (Samuelson et al., 2014).

4.2. Fertilization effects on transpiration and stomatal conductance

Despite the lack of an increase in *LAI* in fertilized (F) plots relative to the control (C), we detected a decrease in stomatal conductance (G_s) in March–May 2013 (Fig. 5), leading to lower canopy transpiration (E_c) values in F than C in 7 of the study months (Fig. 4). The response functions to *VPD* fit by the StaCC model (Fig. 6) indicate a large decrease in both G_s and E_c with fertilization at high *VWC*, with no effect (or a slight increase) at low volumetric soil moisture (*VWC*). Thus, the observed decreases in mean J_s , G_s and E_c (Figs. 3–5) may be ascribed to changes in stomatal regulation. In the absence of large *LAI* (Fig. 2) or stem sapwood area (Table 1) changes, this shift in stomatal responses cannot be ascribed simply to changes in sapwood to leaf area ratios, suggesting that other structural or physiological changes underlie differences in G_s and E_c associated with fertilization in these stands.

These changes could involve shifts in either hydraulic system structure or conductivity. Hydraulic characteristics in *Pinus* species tend to respond to drought stress in tandem (Martinez-Vilalta et al., 2004), so it is likely that multiple such changes occurred in response to fertilization of this stand. While leaf conductivity in this species does respond to resource availability (Domec et al., 2009a), roots are thought to contribute the majority to total tree resistance, even under high water availabilities, and exhibit larger decreases in conductivity under dry conditions (Domec et al., 2009b). It is most plausible, therefore, that the largest changes occurred in the root area or hydraulic conductivity. Both of these factors were linked to decreased G_s in fertilized stands of *P. taeda* in an excessively drained soil (Ewers et al., 2000). Nutrient-mediated decreases in fine root area are a highly plausible mechanism supported by recent analyses of nutrient effects on carbon allocation (Högberg et al., 2003; Treseder et al., 2007; Janssens et al., 2010; Chen et al., 2013). While multiple studies of *P. taeda* have shown that fertilization increases, rather than decreases, coarse root biomass (King et al., 1999; Maier and Kress, 2000; Retzlaff et al., 2001; Samuelson et al., 2004), few have reported increased fine root biomass. Root distribution in the soil volume could also play a role in such responses. Samuelson et al. (2008a) showed that, although fertilized plots in a 10-year old coastal plain site had greater coarse root biomass, unfertilized plots had more extensive, albeit lower density root systems.

4.3. Throughfall reduction effects on transpiration and stomatal conductance

Throughfall reduction (D) decreased both G_s and E_c during the 2013 growing season, while the combined (FD) treatment created the largest and most consistent decreases. The effect of throughfall reduction on response functions fit by StaCC (Fig. 6) was small at both high and low *VWC*. Thus, the decreases in J_s , G_s and E_c observed in D (Figs. 3–5) cannot be ascribed to a change in the response of stomata, but rather to a decrease in *VWC* itself. The responses of G_s to *VPD* and *VWC* in the FD treatment (Fig. 6) are similar to those of F, indicating that the consistent decreases observed in this treatment result from a decreased G_s and E_c at high *VWC* due to fertilization, combined with a decreased *VWC* from throughfall reduction. September 2013 has the largest decreases in J_s and E_c found in D and FD from the control, when *VWC* reached in annual minimum (Figs. 3 and 4). This suggests that

in a drier year, we may have observed greater effect of this treatment.

The similarity of stomatal conductance functions with and without throughfall reduction at both fertilization levels lends credibility for the use of *VWC* at shallow depths (0–12 cm) in this analysis, insofar as it appears the effect of throughfall reduction can be explained mostly by this covariate alone. This is not to say that our representation of *VWC* could not be improved upon, as water below 12 cm is likely available to these trees. Furthermore, the decreases in modeled E_c at high values of *VPD* are not likely a realistic parameterization of stomatal behavior at the leaf level. While some porometric estimates of leaf level stomatal regulation exhibit decreasing transpiration at very high *VPD*, it is more commonly observed that transpiration asymptotically approaches a constant value (Sandford and Jarvis, 1986; Monteith, 1995; Oren et al., 1999). However, decreases in J_s and scaled transpiration with increasing *VPD* has been noted in other studies (e.g. Pataki et al., 2000), but this may be a product of correlation of high *VPD* with low *VWC* or the depletion of water in the rhizosphere that is not reflected in the *VWC* of bulk soil (Katul et al., 1997; Pataki et al., 1998).

4.4. Fertilization and drought risk

There is reason to believe that response of stomata to short-term water stress is indicative of mortality risk from prolonged, severe droughts in *Pinus* species. It has been hypothesized that drought-induced mortality in isohydric species such as *P. taeda* is not the product of hydraulic failure from cavitation itself, but rather the long-term stomatal closure necessary to avoid it (McDowell et al., 2008). This has shown to often be the case in *Pinus edulis* (Plaut et al., 2012), although hydraulic failure can occur under severe drought in some individuals (Sevanto et al., 2014). Mitchell et al. (2013) have also demonstrated this mechanism in drought-induced mortality of *Pinus radiata*, contrasting it with that of *Eucalyptus* species that maintained high rates of gas exchange at lower water potentials and were more likely to die from hydraulic failure. Thus, fertilization may not have the same implications for drought mortality risk in other species, especially ones that exhibit less isohydric stomatal regulation. For example, in a similar study of K fertilization and throughfall displacement in a *Eucalyptus grandis* plantation (Battie-Laclau et al., 2014), increased stomatal closure during drought periods was linked to depletion of soil water reserves from increased leaf area and transpiration under preceding unstressed conditions. Likewise, N fertilization was found to decrease predawn water potentials in *Eucalyptus globulus* plantations in south-western Australia due to increased leaf area and transpiration (White et al., 2009).

In the current study, the observed greater stomatal response to fertilization at high rather than at low soil water content (Fig. 6) suggests an increase in cavitation resistance as well as a decrease in root area or hydraulic conductivity. Furthermore, when *VWC* was at its annual minimum in September 2013, J_s and E_c in the F treatment were very similar to those in C, as were those in FD to those in D (Figs. 3 and 4). This raises the question of whether fertilization increased or decreased drought sensitivity of the resulting stands. Ewers et al. (2000) found lower root area and less conductive, but more drought resistant, root xylem with fertilization of *P. taeda* in the Carolina Sand Hills, where water availability is low due to excessive drainage. These researchers further concluded, based on results of a hydraulic model, that safety margins from hydraulic failure were minimal in fertilized stands and reductions of root area had made them more vulnerable to drought-induced mortality. It has been suggested more broadly that such structural changes in fast-growing, unstressed stands make them more vulnerable to drought-induced diebacks than

slower-growing, chronically-stressed stands, especially in future climates with more variable precipitation regimes (McNulty et al., 2014). Further research into the mechanisms behind the trends observed here is necessary.

4.5. Conclusions, limitations and future studies

Our study suggests rapid allocation and/or physiological responses to fertilization in *P. taeda* that, even during a wet period of only two growing seasons, exhibited a marked decline in E_C , as well as an increase in stem volume production, despite no major differences in *LAI*. In the short term, this led to large increases in the water use efficiency of stem production (WUE_{Vol} , Fig. 7), which could suggest greater resiliency of wood production to minor water stress. However, impacts on long-term sensitivity to drought remain a concern, as the E_C reduction triggered by the fertilization treatment was of comparable magnitude to the 30% throughfall exclusion treatment and the greatest reductions were found in the combined treatment. The pattern of G_S responses in the different treatments (Fig. 5) suggests that structural or physiological changes underlie this fertilization response. If so, fertilization-induced increases in *LAI* in future growing seasons may result in even greater divergence in G_S responses.

There are, however, limitations to the data and analyses we present here. Given that *P. taeda* maintains needles for up to two years, we were not able to make estimates of *LAI* based on litter collection for this time period. While most of the sapwood area in these trees predates the treatment, additional sap flux measurements deeper in the sapwood must be taken to evaluate if our assumption that radial variability in sap flux is similar across treatments holds. Measurements of root area distribution with depth are not only important for evaluating the appropriate characterization of soil moisture available to the trees, but also for improving our mechanistic understanding the developmental responses of root area, cavitation resistance and conductivity to management and environmental conditions. Future studies such as these will be critical for predicting forest responses to droughts under different management scenarios.

Acknowledgements

The Pine Integrated Network: Education, Mitigation, and Adaptation project (PINEMAP) is a Coordinated Agricultural Project funded by the USDA National Institute of Food and Agriculture, Award #2011-68002-30185.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.04.009>.

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