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

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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.



## 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

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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