

Drought tolerance of a *Pinus palustris* plantation

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ABSTRACT

Longleaf pine (*Pinus palustris* Mill.) forests are thought to be drought tolerant and if so, planting longleaf pine presents a forest management strategy for climate change adaptation in the southeastern United States (U.S.). To better understand how longleaf pine copes with drought, leaf water relations, sap flow, canopy stomatal conductance (G_s), and growth were studied over three growing seasons in response to ambient throughfall (ambient treatment) versus an approximate 40% reduction in throughfall (drought treatment) in a 13-year-old plantation. An exceptional drought occurred the first year of the study and decreased mean predawn (Ψ_{pd}) and midday (Ψ_{MD}) leaf water potential to -2.9 MPa and -3.6 MPa, respectively, and decreased average monthly midday G_s to near zero for at least one month in both treatments. Stomatal closure occurred at a Ψ_{MD} of -3.0 MPa in both treatments. Leaf water potentials and transpiration recovered quickly following significant rain events that terminated the drought and mortality was similar among years and treatments (2.8%). Longleaf pine responded to drought treatment with greater stomatal control of plant water loss rather than adjustments in leaf area, the sapwood to leaf area ratio, or leaf water potential at the turgor loss point (Ψ_{TLP}). Annual transpiration per unit leaf area was reduced 16% by drought treatment, but greater stomatal control of water loss in response to drought treatment was associated with decreases in growth efficiency and volume, and no improvement in water use efficiency.

1. Introduction

Climate projections for the southeastern U.S. indicate that with increasing temperatures, evapotranspiration and the duration and intensity of summertime droughts may increase in proportion to the rate of warming (Dai, 2011; Kunkel et al., 2013; IPCC, 2013; Williams et al., 2017). More intense summer droughts and heavy rainfall events have been observed in the southeastern U.S. during recent decades (Wang et al., 2010), and some forests in the region are exposed to increasing water deficits during the growing season (Clark et al., 2016a). Periodic drought is expected even in areas projected to become wetter, and shorter droughts will become more lethal under warmer conditions (Allen et al., 2015). The combined effects of increased vapor pressure deficits and reduced precipitation increase the magnitude of drought, which can affect tree growth and mortality rates (Williams et al., 2013; Anderegg et al., 2015).

Tree mortality related to drought has been documented in forests worldwide (Allen et al., 2010) and in southeastern U.S. forests (Klos et al., 2009). Multi-year declines in tree growth following severe drought preceded tree death across a range of sites in the southeastern U.S. (Berdanier and Clark, 2016). Some pines in the southeastern U.S.

rank high in sensitivity to summer drought (Klos et al., 2009; Bracho et al., 2012; Clark et al., 2014), although drought-related mortality may be lagged (Klockow et al., 2018). Longleaf pine (*Pinus palustris* Mill.) is believed to be more drought tolerant than other southern pines (e.g. *Pinus taeda* L. and *Pinus elliottii* Engelm. var. *elliottii*). This assumption is based on hydraulic traits of longleaf pine (high sapwood and root to leaf area ratios, high root hydraulic conductivity, and deep, wide-spreading root systems) (Gonzalez-Benecke et al., 2010; Samuelson et al., 2012, 2017), low tree water use (Gonzalez-Benecke et al., 2011), and dominance of longleaf pine on xeric sands and clay ridges (Mitchell et al., 2014). Longleaf pine forests are typically low-density stands that are repeatedly disturbed by prescribed fire, and as such, their stand structure and management may confer resistant to stressors such as drought (van Mantgem et al., 2016; Bottero et al., 2017). In addition, impacts of low-intensity fire, such as loss of foliage and fine roots and damage to the hydraulic system, are similar to those from drought disturbance (Michaletz, 2018). Starr et al. (2016) observed reductions in gross photosynthetic rates of longleaf pine ecosystems during repeated natural drought episodes over a seven-year period that did not increase mortality, suggesting drought resilience in this species. Because of longleaf pine's tolerance of disturbance and potential for long-term

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carbon sequestration, there is increased interest in the restoration of these forests (Johnsen et al., 2009; Samuelson et al., 2017). Planting tree species more tolerant of drought and natural disturbance is a possible adaptation strategy that forest landowners in the southeastern U.S. could employ to adapt to climate change (Susaeta et al., 2014; Clark et al., 2016b). However, precipitation manipulation experiments in forests are rare and critical to understanding forest ecosystem response to future precipitation extremes (Asbjornsen et al., 2018).

To understand the potential impacts of reduced precipitation on growth of longleaf pine and the mechanisms by which longleaf pine copes with drought, we examined drought tolerance strategies in response to an approximate 40% reduction in throughfall (drought treatment) over three growing seasons in a 13-year-old plantation. Drought tolerance was defined following Moran et al. (2017) as the ability to survive and maintain growth during water shortages and involves strategies for avoidance and resistance to drought exposure. We hypothesized that longleaf pine would tolerate water stress imposed by drought treatment primarily by decreasing leaf area and increasing the sapwood to leaf area ratio ($A_S:A_L$), as reported for another southern conifer loblolly pine (*Pinus taeda* L.) in response to 30% throughfall exclusion (Samuelson et al., 2018) as well as other pines in response to drier climates (DeLucia et al., 2000). We expected that drought treatment would have less effect on stomatal control of plant water loss, based on results from loblolly pine (Samuelson et al., 2018), and leaf water potential (Ψ_L) at the turgor loss point (Ψ_{TLP}) (Lenz et al., 2006).

2. Materials and methods

2.1. Site description

The experiment was located in a longleaf pine plantation in Marion County, GA (32.55278°, -84.47694°) on land owned by Georgia Department of Natural Resources. The area is in the Sand Hills Ecoregion and characterized by Entisol sands (Griffith et al., 2002). The experimental site is comprised of Lakeland Series soils, which are very deep, excessively drained, rapid to very rapidly permeable, and with < 5% slope. Soils to a 1 m depth are greater than 90% sand with less than 5% silt or clay. Average bulk density of soils is 1.5 g cm⁻³ and field capacity is 7.1%. The site is located on top of a ridge at 210 m elevation. The 30-year average (1986–2015) daily maximum and minimum temperature for Americus, GA (approximately 60 km from site) is 24.6 °C and 11.5 °C, respectively, and average annual precipitation is 1226 mm (<http://www.ncdc.noaa.gov/cdo-web>, accessed March 2016). Based on data from a well located 92 km away at an elevation of 145 m in the same Southeastern Coastal Plain aquifer system (31.76917°, -84.79528°), the depth to the water table likely exceeds 40 m (<https://groundwaterwatch.usgs.gov>, accessed January 29, 2018).

Longleaf pine seedlings were planted in 2003 at an approximate spacing of 2.6 m × 2.6 m, resulting in an average planting density of 1479 trees ha⁻¹. The most recent prescribed burn occurred in January 2016, approximately five months before treatment initiation. Prior to the 2016 prescribed burn, the site experienced a wildfire in August 2009. Tropical storms passed over the site on September 11, 2017 (Irma) and October 11, 2018 (Michael). No mortality was observed following the prescribed burn or tropical storms.

2.2. Drought treatments

Ambient and drought treatment plots were 31 m × 21 m (0.065 ha) in size with an interior 21 m × 11 m (0.023 ha) measurement plot. Based on excavations of three lateral coarse roots originating from three different trees inside the measurement plot, lateral roots extended on average 4.5 m from a tree. Thus, roots of trees near the boundary of the measurement plot did not likely extend outside the treatment plot. A minimum distance of 17 m of untreated buffer was retained between

treatment plots. Each treatment plot contained an average of 72 trees and each measurement plot contained an average of 24 trees. Plots were grouped into three blocks based on similarities in basal area and the two treatments (ambient versus drought) were randomly assigned to plots within a block.

The drought treatment was implemented using throughfall exclusion troughs designed to remove approximately 40% of throughfall. Troughs were installed between rows to cover 40% of the treatment plot area in May 2016 when the plantation was 13 years of age. Based on the average annual precipitation (1255 mm) for Americus, GA over a hundred-year period beginning in 1915, 60% of average annual precipitation lies between the two driest years on record (674 and 802 mm, respectively). Annual throughfall for longleaf pine plantations of similar age and forest structure ranges from 80 to 88% of annual precipitation (Roth and Chang, 1981; Bryant et al., 2005). Two trough support structures measuring approximately 0.52 m wide with an average height of 1.0 m were fit between each row and spanned the entire length of the row. The two troughs were separated by a 0.46 m gap to minimize soil moisture banding. Clear U.V. stabilized polyethylene with embedded high strength cord (Polyscric 12, Americover Inc, Escondido, CA) was secured on top of each support structure. Troughs were sloped to drain water off the end of each trough into corrugated pipe that transported the water a minimum distance of 20 m from all plots. The amount of throughfall intercepted by troughs was not measured but visual observations during heavy rain events indicated no overflow out of troughs. Uniformity in slope across the site and the deep, excessively drained, sandy soil suggests that lateral flow was minimal.

2.3. Environmental monitoring

The Palmer Drought Severity Index (PDSI) was obtained for Georgia Climate Division 4 (<https://www1.ncdc.noaa.gov/pub/orders/CDODiv8050857640243.txt>, last accessed May 1, 2019). An onsite weather station (Davis Vantage Pro2, Davis Instruments Corp., Hayward, CA) was installed in an open field approximately 0.6 km from the study site and measured standard meteorological data. Photosynthetically active radiation (PAR) was measured at the weather station using a PAR sensor (S-LIA-M003, Onset Computer Corp., Bourne, MA). Within canopy relative humidity and temperature were measured at approximately 2 m height at three locations between plots (Hobo U23 External Temperature/Relative Humidity Data Logger, Onset Computer Corp., Bourne, MA) to calculate average vapor pressure deficit (D) following Buck (1981). All environmental data were measured every minute and the 30-minute averages were recorded.

Volumetric soil moisture sensors (10HS Soil Moisture Sensor, Meter Group, Inc., Pullman, WA) 10 cm in length were vertically inserted at 5, 15, and 50 cm depths in each plot in the center of a row near plot center and spaced approximately 60 cm apart. Soil moisture was measured every minute and 30-minute averages recorded. A soil specific calibration was calculated following methods described by Starr and Paltineanu (2002). A quadratic function fit to the calibration data indicated that the lowest soil moisture value obtainable was 2.26%. Relative extractable water content (REW) to a 25 cm depth (excluding the top 5 cm lacking sensors) was calculated for each plot following Granier et al. (2000). The minimum soil water content for each sensor was the minimum observed and the maximum was the maximum observed mean monthly water content (Meir et al., 2015). The maxima for drought plots were set to the values observed in the ambient plot in the same block. Since soil moisture in drought plots was measured under the troughs, which covered 40% of plot area, the soil moisture used in REW calculations was estimated as the sum of soil moisture under the trough weighted by 40% and soil moisture in the companion ambient plot weighted by 60%. We assumed that the ambient plot represented soil moisture in the uncovered area in the drought plot in the same block.

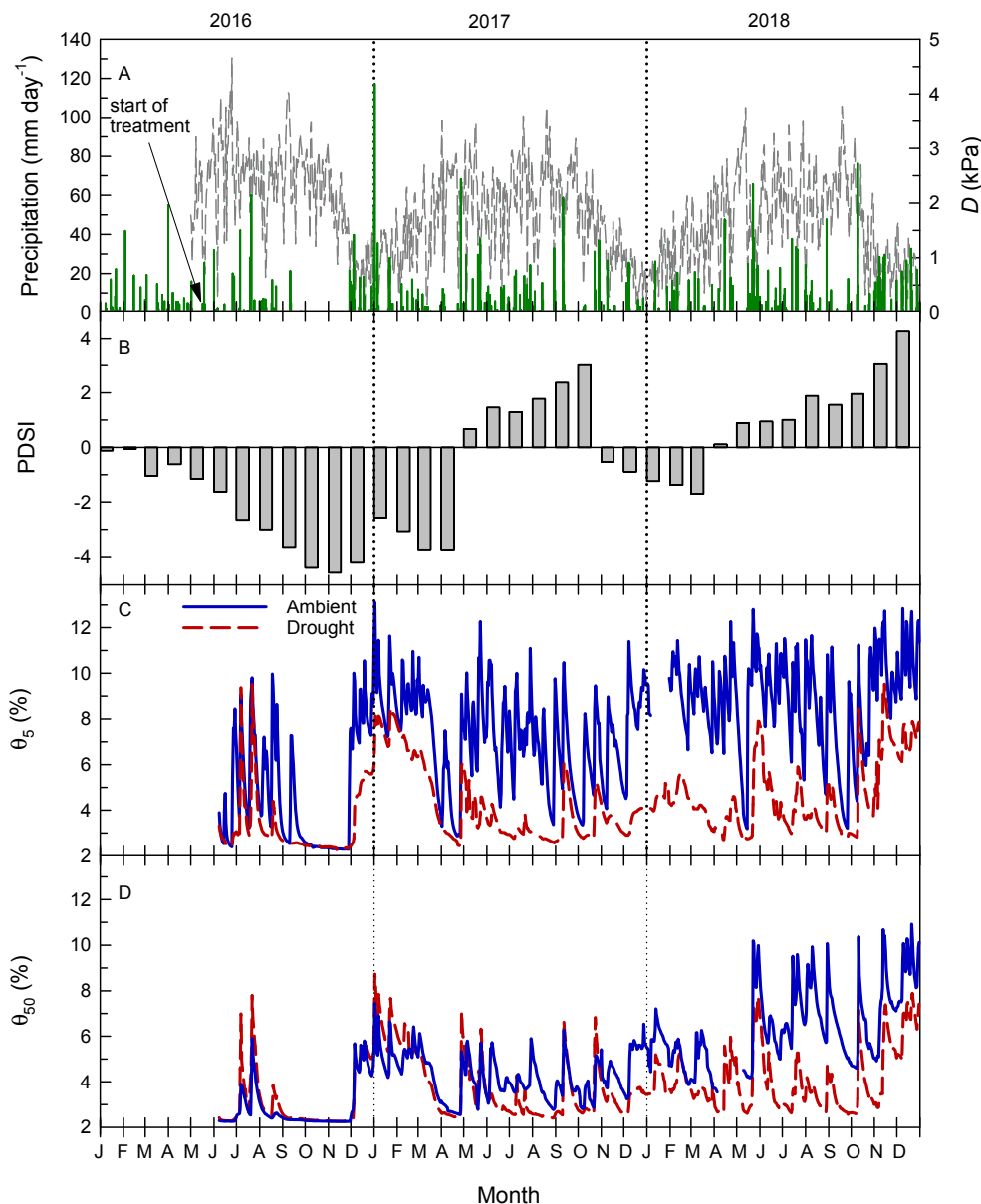


Fig. 1. Daily precipitation and daily maximum vapor pressure deficit (D) [A], the Palmer Drought Severity Index (PDSI) [B], and mean daily soil volumetric water content at 5 cm (θ_5) [C] and 50 (θ_{50}) cm [D] depth in a longleaf pine plantation in response to drought treatment. Soil moisture in the drought treatment was measured under throughfall exclusion troughs.

Table 1

Observed probability values for the effects of measurement date and drought treatment on predawn (Ψ_{PD}) and midday (Ψ_{MD}) leaf water potential, the leaf water potential at the turgor loss point (Ψ_{TLP}), monthly transpiration on a ground area (E_G) and leaf area (E_L) basis, and mean monthly midday canopy stomatal conductance (G_S) of a longleaf pine plantation.

Effect	Ψ_{PD}	Ψ_{MD}	Ψ_{TLP}	E_G	E_L	G_S
Date	< 0.001	< 0.001	0.428	< 0.001	< 0.001	< 0.001
Treatment	< 0.001	0.364	0.688	< 0.001	0.008	< 0.001
Date × treatment	0.515	0.943	0.815	< 0.001	0.016	0.009

2.4. Leaf water potential measurements

Leaf water potential was measured from June 2016 through September 2018 on sunny, clear days using a pressure chamber (1505D Pressure Chamber Instrument PMS Instruments, Albany, OR). Leaf samples were collected before sunrise to measure Ψ_{PD} , and between

1100 and 1300 h to measure midday leaf water potential (Ψ_{MD}). Due to morning frost, only Ψ_{MD} was measured January and March 2018. All samples were collected from sun-exposed branches from the upper third of the canopy. From June 2016 to February 2017, four samples from four sap flow trees per plot were collected for Ψ_{PD} and Ψ_{MD} measurements using a 4 m tall stepladder. In February 2017, one permanent access tower 6 m in height was installed in each plot to improve upper canopy access, after which five samples were collected from two to three sap flow trees per plot. Samples consisted of the most recent mature flush. Once removed from the tree, samples were placed in a sealable plastic bag containing a moist paper towel, placed in a cooler, and measured within two hours.

Pressure volume (P-V) curves were constructed on mature current-year foliage collected in August and September 2018 using the pressure-chamber technique and bench dehydration (Koide et al., 1989). One shoot was collected from the upper crown of one tree in each plot each sampling date. Shoots were collected at 1800 h, placed in black plastic bags with moist paper towels, transported to the laboratory in a cooler,

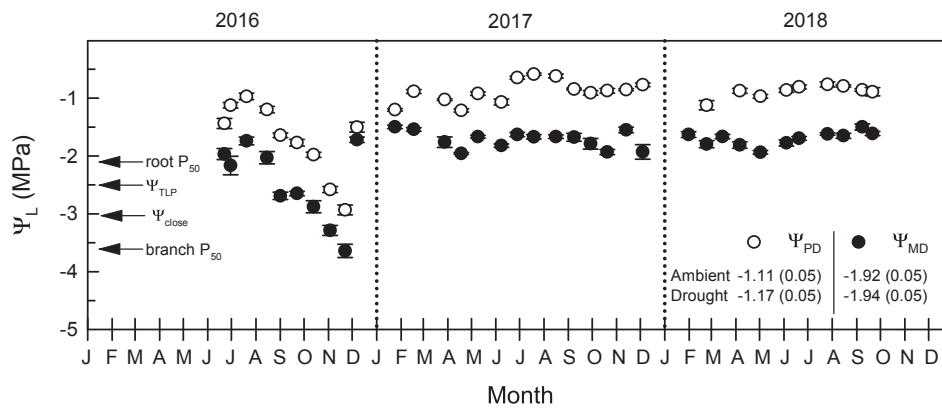


Fig. 2. Temporal patterns in mean (SEM) leaf water potential (Ψ_L) measured at predawn (Ψ_{PD}) and midday (Ψ_{MD}) in a longleaf pine plantation. Means (SEM) for the drought treatments are also shown. Arrows indicate the branch and root P_{50} (water potential at 50% loss of hydraulic conductivity), the leaf water potential at the turgor loss point (Ψ_{TLP}), and the Ψ_{MD} at stomatal closure (Ψ_{close}). Branch and root P_{50} values for longleaf pine are from Lodge et al. (2018).

re-cut in distilled water, and hydrated overnight for approximately nine hours. The P-V curves were constructed on two fascicles per shoot following Bartlett et al. (2012). Relationships between Ψ_L and fresh weight were examined for the presence of plateaus at high levels of leaf water potential (Parker and Pallardy, 1987), with none indicated. The Ψ_{TLP} was calculated following Bartlett et al. (2012).

2.5. Sap flow measurements

Four sample trees in each plot representing the range in basal area distribution in each measurement plot were selected in July 2016 for sap flow measurements following the selection method of Čermák et al. (2004). Trees selected for sap flow measurements ranged in DBH from 14.0 to 19.3 cm at the start of the study. Thermal dissipation probes with a 30 mm integrated length (TDP-30, Dynamax Inc., Houston, TX) were connected to a sap velocity system (FLGS-TDP-XM1000, Dynamax, Inc., Houston, TX). To install the probes, the outer bark was removed and two small holes spaced 9 cm apart vertically were drilled into the sapwood approximately 1.3 m above ground level at a northern aspect. Probes and the stem around probes were wrapped with reflective insulation (Reflectix Inc., Markleville, IN) to reduce thermal gradients. Probe temperatures were measured every 1 min and the 30-minute means were recorded.

Sap flux density (J_s , $g\ m^{-2}\ s^{-1}$) was calculated following Granier (1985):

$$J_s = 119 \times ((\Delta T_{max} - \Delta T) / \Delta T)^{1.231}$$

where ΔT is the temperature differences between the heated and reference (unheated) probe and ΔT_{max} is the ΔT at zero flow. The open-source Baseline program (Baseline, Duke University, Oishi et al., 2016) was used to establish a zero-flow reference value with user-defined parameters set at $D < 0.2$ kPa for at least two consecutive hours a night. Sap flow was calculated as the product of J_s (summed by 30 min) and individual tree sapwood area (Granier, 1987) measured monthly near each probe. To determine sapwood area, the relationship between diameter outside bark (DOB) and diameter inside bark (DIB) ($DIB = 0.953 * DOB - 2.17$; $R^2 = 0.93$) at DBH was determined in June 2016 on four trees per plot using a bark thickness gauge (Haglof Barktax Bark Gauge, Haglof Inc., Madison, MS). Given the young age of the stand, all wood was assumed sapwood. Variation in J_s across the radial profile was examined from February 2017 through July 2017 in one additional tree in each plot (DBH ranged from 17.9 to 20.5 cm). Radial variation was measured at two depths (0–30 mm and 30–60 mm) on the same tree using two pairs of probes. The 30 mm depth was monitored throughout the remainder of the study, thus providing five sap flow tree replicates per plot beginning February 2017. Linear regressions were fit between J_s at the 0–30 mm depth and J_s at the 30–60 mm depth by day (Lu et al., 2000) to determine the correction factor for depths deeper than 30 mm. A mean daily slope was then determined for each tree by averaging across all days. Slopes did not

differ between treatments so an average correction factor of 0.55 was used to calculate J_s for the deeper depths.

Transpiration on a ground area basis (E_G) was calculated by multiplying mean sap flow per plot area by the ratio of plot sapwood area to the mean sapwood area of sap flow sample trees (Čermák et al., 2004). The ratio was determined from annual inventories. To convert E_G to a leaf area basis (E_L), E_G was divided by leaf area index (LAI).

Single tree gaps in J_s due to sensor malfunction were filled using linear relationships with another tree in the same plot. The tree with the highest correlation for a minimum period of seven days before or after the gap served as the reference tree. Plot-level data gaps occurred 14 days in 2016, 2 days in 2017, and 32 days in 2018. These gaps were filled by regressing the daily sum of E_G against environmental variables such as average daily soil moisture, D or the daily sum of PAR for a minimum of seven days before or after the gap.

2.6. Canopy stomatal conductance calculation

Canopy stomatal conductance was calculated following Bartkowiak et al. (2015) by inverting the Penman-Monteith equation and assuming sap flow as transpiration. We assumed that the atmosphere and canopy are well coupled in the open canopy of longleaf pine. To reduce effects of instrument error, G_s was calculated when $D \geq 0.75$ kPa, which is within the 0.6–1.0 kPa range recommended by Ewers and Oren (2000). To account for any time lag with transpiration, the sap flow time series was shifted to maximize correlation with D (Domec et al., 2009). Correlations between J_s and D were examined by month and treatment, and the sap flow time series was lagged up to two hours. The majority of months did not require a lag or the lag was 30 min. Mean midday G_s was calculated as the average of G_s from 1100 to 1500 h. Due to $D < 0.75$ kPa on many days within winter months, monthly means were not calculated for November through February. The October 2018 tropical storm resulted in power outages in some plots, and since G_s was not gap filled, means for that month were not calculated.

2.7. LAI and growth measurements

Leaf area index was measured optically approximately every three weeks along three fixed 5 m long diagonal transects in each plot using a plant canopy analyzer (LAI-2200C, Li-Cor Inc., Lincoln, NE). Each transect was divided evenly into five measurement points. A second analyzer positioned in a 0.65 ha clearing 500 m from the study recorded above-canopy measurements. Data were averaged by transect and then by plot. All measurements were made in diffuse light conditions at either dawn or dusk.

Inventories were conducted before treatment initiation (February 2016), and in December of 2016, 2017 and 2018. Measurements included DBH and total tree height. Stem volume outside-bark was calculated following Gonzalez-Benecke et al. (2014). Stem, branch and leaf biomass were predicted using allometric equations developed for

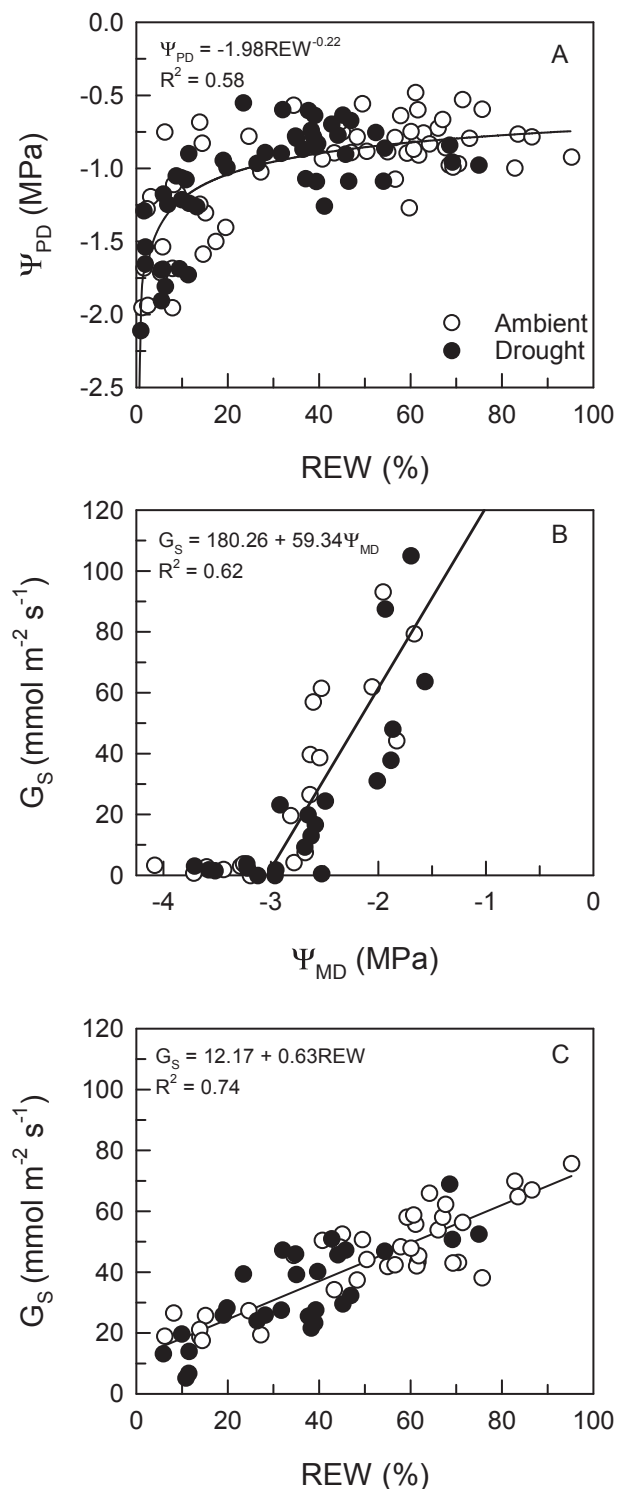


Fig. 3. The responses of predawn leaf water potential (Ψ_{PD}) to relative extractable water content (REW) from 5 to 25 cm depth over three growing seasons (April–October) [A], maximum daily canopy stomatal conductance (G_S) to midday leaf water potential (Ψ_{MD}) in 2016 [B], and mean midday G_S to REW over the 2017 and 2018 growing seasons [C] in a longleaf pine plantation.

longleaf pine (Samuelson et al., 2017) to calculate plot-level above-ground net primary productivity (ANPP). Growth efficiency was calculated as the ratio of the ANPP to peak LAI, and water use efficiency (WUE) was determined by the ratio of ANPP to the annual sum of E_G .

2.8. Statistical analysis

The plot was considered the experimental unit. Repeated measures analysis of variance (Proc Mixed, SAS Inc., Cary, NC) was used to test for main and interaction effects of treatment and time. Selection of the covariance structure was based on visual assessment of residuals and minimizing the Akaike Information Criterion. Main and interactive treatment effects were considered significant at $\alpha \leq 0.05$. Means were separated using Tukey's paired comparison procedure. When an interaction was significant, the SLICE option of Proc Mixed was used for means separation. Data were log transformed when necessary to achieve normality. Linear and nonlinear regression analyses were used to examine relationships between G_S , Ψ_{MD} and REW. Treatment differences in slopes and intercepts of linear regressions were tested using analysis of covariance (Draper and Smith, 2014).

3. Results

3.1. Climate and soil moisture

An exceptional drought occurred in the southeastern U.S. during the fall of 2016 and peaked in October–November 2016 (Williams et al., 2017). The drought developed rapidly because of low precipitation and record high temperatures (Williams et al., 2017). The PDSI indicated severe to extreme drought conditions from August through December of 2016 (Fig. 1). During the drought, no or negligible precipitation fell on the study site for 77 days and daily maximum D in October and November was higher than observed the following years (Fig. 1). During that period, soil moisture at both depths and in both treatments remained at the minimum for at least two months (Fig. 1). Rainfall resumed in early December and rapidly increased soil moisture at both depths in both treatments. The PDSI indicated mild drought or no drought conditions beginning May 2017 and by the end of 2018 conditions were classified as extremely moist. Annual precipitation at the site was 860 mm in 2016 compared to 1234 mm in 2017 and 1451 mm in 2018. Annual potential evapotranspiration calculated using the Penman-Monteith method (Monteith and Unsworth, 1990) and data from the on-site weather station totaled 2838 mm in 2017 and 1332 mm in 2018.

In general, soil moisture was lower at 50 cm than at 5 cm depth (Fig. 1). At both depths and mainly following the 2016 drought, mean daily soil moisture in the drought treatment (measured under throughfall exclusion troughs) was often lower than in the ambient treatment. Averaged across months, monthly mean soil moisture at 5 cm depth was 6.6% in the ambient treatment versus 3.7% in the drought treatment. At 50 cm depth, the average was 4.2% in the ambient treatment and 3.4% in the drought treatment.

3.2. Leaf water potential

Predawn and midday Ψ_L varied with date of measurement (Table 1, Fig. 2). During the drought of 2016, Ψ_{PD} declined to an average of -2.9 MPa and Ψ_{MD} declined to an average low of -3.6 MPa. A small but significant effect of drought treatment on Ψ_{PD} was observed, with Ψ_{PD} decreasing from an average of -1.1 MPa in the ambient treatment to -1.2 MPa in response to drought treatment. No treatment effects on Ψ_{MD} were observed. When growing season (April through October) Ψ_{PD} data were pooled across years, a threshold response of Ψ_{PD} to REW was observed, with increased sensitivity of Ψ_{PD} to REW below 20% (Fig. 3). The Ψ_{TLP} was unaffected by measurement date or treatment (Table 1) and was on average -2.5 (± 0.1 SEM) MPa.

3.3. Transpiration

Treatment effects on monthly E_G and E_L varied with month (Table 1, Fig. 4). In 2016, drought treatment decreased monthly E_G from July

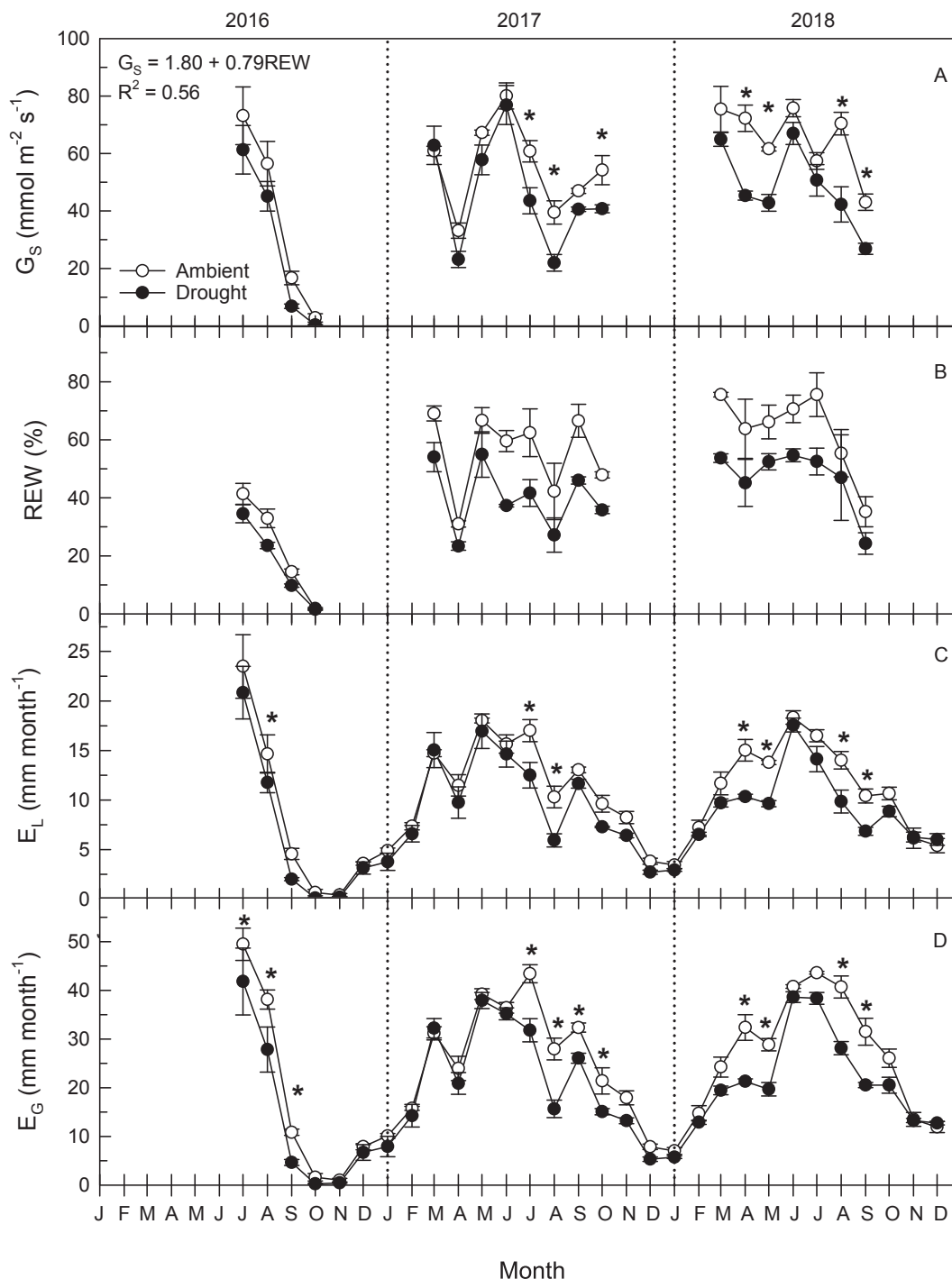


Fig. 4. Mean (SEM) monthly midday canopy stomatal conductance (G_s) [A], monthly relative extractable water content (REW) from 5 to 25 cm depth [B], and monthly sums of transpiration on a leaf area (E_L) [C] and ground area (E_G) [D] basis in a longleaf pine plantation in response to drought treatment. Asterisk (*) indicates a significant treatment difference. The linear relationship between G_s and REW is shown in [A].

through September, but when expressed per unit LAI, E_L decreased in response to drought treatment only in August 2016. Monthly E_G and E_L declined to near zero in both treatments in October and November of 2016. The following years, E_G and E_L were reduced by drought treatment mainly during growing season months.

Decreases in monthly E_G and E_L in response to drought treatment were sufficient to reduce annual E_G and E_L (Table 2); annual E_G decreased 19%, from 311 to 253 mm yr^{-1} , and annual E_L decreased 16%, from 133 to 111 mm yr^{-1} , in response to drought treatment. Annual E_G and E_L were similar between years.

3.4. Canopy stomatal conductance

The significant interaction between date and treatment (Table 1) indicated that drought treatment decreased mean monthly midday G_s seven months in 2017–2018 but had no significant effect on G_s in 2016 (Fig. 4). Decreases in mean monthly midday G_s in response to drought treatment ranged from 28 to 48%. Mean monthly midday G_s was linearly related to REW with REW explaining 56% of the monthly variation in G_s (Fig. 4). No treatment differences in the intercepts ($p = 0.320$) or slopes ($p = 0.358$) of the regressions were observed.

Table 2

Influence of year and drought treatment on mean (SEM) annual transpiration on a ground area (E_G) and leaf area (E_L) basis, the sapwood to leaf area ratio ($A_S:A_L$), growth efficiency and water use efficiency (WUE) of a longleaf pine plantation. Different lowercase letters indicate differences among years when the year effect is significant.

	E_G (mm yr ⁻¹)	E_L (mm yr ⁻¹)	$A_S:A_L$ (cm ² m ⁻²)	Growth efficiency (Mg ha ⁻¹ LAI ⁻¹)	WUE (kg ha ⁻¹ mm H ₂ O ⁻¹)
<i>Year</i>					
2016	– ^a	– ^a	4.9 (1.1) ab	3.0 (0.8)	– ^a
2017	282 (12)	124 (6)	5.2 (0.8) a	3.5 (0.3)	33.5 (2.5)
2018	283 (16)	121 (7)	4.6 (0.9) b	2.8 (0.3)	31.7 (3.4)
<i>Treatment</i>					
Ambient	311 (8)	133 (4)	5.1 (0.9)	3.7 (0.2)	32.7 (2.9)
Drought	253 (4)	111 (4)	4.7 (0.7)	2.5 (0.4)	32.5 (3.2)
<i>P > F</i>					
Year	0.763	0.429	0.001	0.084	0.647
Treatment	0.004	0.005	0.079	0.040	0.965
Year × treatment	0.326	0.698	0.804	0.883	0.894

^a Transpiration was not measured the entire year.

Mean monthly G_S declined to near zero in both treatments in October 2016.

To determine Ψ_L at stomatal closure (Ψ_{close}), relationships between daily maximum G_S and Ψ_{MD} during the 2016 drought were explored. Daily maximum G_S was linearly related to Ψ_{MD} , and Ψ_{MD} explained 62% of the variation in G_S (Fig. 3). No effect of treatment on the intercepts ($p = 0.310$) or slopes ($p = 0.541$) of the linear regressions was observed and Ψ_{close} was -3.0 MPa.

During the wetter 2017 and 2018 years with less variation in Ψ_{MD} , a strong linear relationship between mean midday G_S and REW, but not Ψ_{MD} , was observed (Fig. 3). Intercepts ($p = 0.201$) and slopes ($p = 0.324$) of the linear regressions were not different between treatments.

3.5. Growth

Peak LAI occurred in August or September of each year, and fall leaf senescence began in September and continued through winter (data not shown). Peak LAI was highest in 2018 ($3.2 \text{ m}^2 \text{ m}^{-2}$) and similar between 2016 and 2017 (average $2.6 \text{ m}^2 \text{ m}^{-2}$) (Table 3). Treatment had no significant effect on peak LAI. A trend ($p = 0.079$) for lower $A_S:A_L$ in response to drought treatment was noted (Table 2).

Height, DBH, basal area and volume increased with age (Table 3). Drought treatment had no significant effect on height, DBH, basal area, or ANPP, but volume was reduced 21%, from 97.6 to $77.4 \text{ m}^3 \text{ ha}^{-1}$. Drought treatment decreased growth efficiency by 32%, but had no significant effect on WUE (Table 2). WUE was similar between years and averaged $32.6 \text{ kg ha}^{-1} \text{ mm H}_2\text{O}^{-1}$. Mortality was also similar among years and treatments, and was on average 2.8% (Table 3).

Table 3

Influence of year and drought treatment on mean (SEM) tree and stand growth in a longleaf pine plantation. Different lowercase letters indicate differences among years when the year effect is significant.

	Height (m)	DBH (cm)	Basal area (m ² ha ⁻¹)	Volume (m ³ ha ⁻¹)	Mortality (%)	ANPP ^a (Mg ha ⁻¹ yr ⁻¹)	LAI ^b (m ² m ⁻²)
<i>Year</i>							
2016	10.3 (0.1) c	15.4 (0.3) c	19.2 (0.9) c	72.6 (4.2) c	3.3 (2.5)	7.9 (2.2)	2.6 (0.1) b
2017	10.9 (0.2) b	16.1 (0.3) b	20.6 (0.8) b	85.8 (5.4) b	2.3 (1.6)	9.4 (0.7)	2.7 (0.1) b
2018	11.7 (0.3) a	16.7 (0.3) a	21.8 (0.9) a	104.1 (7.4) a	2.9 (0.9)	9.0 (1.1)	3.2 (0.1) a
<i>Treatment</i>							
Ambient	11.2 (0.3)	16.2 (0.4)	21.5 (0.9)	97.6 (6.2)	1.9 (1.1)	10.5 (0.8)	2.9 (0.1)
Drought	10.7 (0.2)	16.0 (0.2)	19.5 (0.4)	77.4 (4.5)	3.8 (1.6)	7.0 (1.2)	2.8 (0.1)
<i>P > F</i>							
Year	< 0.001	< 0.001	< 0.001	< 0.001	0.913	0.553	< 0.001
Treatment	0.113	0.380	0.143	0.019	0.383	0.105	0.806
Year × treatment	0.562	0.176	0.972	0.786	0.270	0.230	0.829

^a Aboveground net primary productivity (ANPP).

^b Peak leaf area index (LAI).

Ψ_{close} in longleaf pine. Maximum daily G_s declined linearly with decreasing Ψ_{MD} until reaching Ψ_{close} (-3.0 MPa) in October 2016, and monthly E_L and mean monthly midday G_s in October were near zero. Following stomatal closure, Ψ_L continued to decline, possibly because of residual transpiration from cuticular water loss (Brodribb, 2017), incomplete stomatal closure (Brodribb, 2017), or loss of hydraulic functionality.

The Ψ_{TLP} of longleaf pine was lower than the average -2.2 MPa reported for *Pinus* by Bartlett et al. (2016), suggesting that longleaf pine ranks as a more drought tolerant pine (Bartlett et al., 2012). The Ψ_{TLP} measured in one season can characterize species' drought tolerance, but Ψ_{TLP} is plastic under drought and may have been lower during the drought due to osmotic adjustment (Bartlett et al., 2014). If the average 0.4 MPa reduction in Ψ_{TLP} observed for temperate conifers during drought (Bartlett et al., 2014) applies to longleaf pine, the adjusted Ψ_{TLP} of -2.9 MPa was similar to Ψ_{close} . Near the end of the drought, Ψ_{MD} dropped below the adjusted Ψ_{TLP} and wilting was observed in some trees.

Assuming equilibrium among tissues at predawn and Ψ_{PD} represents tissue Ψ , we suggest that Ψ did not fall below the branch P_{50} of -3.6 MPa reported for longleaf pine by Lodge et al. (2018). Mean Ψ_{PD} did decrease below the root P_{50} of -2.1 MPa but not the root P_{88} (-3.4 MPa) reported for longleaf pine (Lodge et al., 2018). Recovery of Ψ_L in mid-December following significant rain events that terminated the drought suggests rapid amelioration of drought-induced losses in root or soil hydraulic conductivity. In pines, embolism is initially localized in the repairable root xylem, and reversal of root embolism and new root growth can occur rapidly following rain events (West et al., 2007; Domec et al., 2009). Mean monthly E_L in December (3.4 mm month $^{-1}$) following the drought also appeared to recover based on the mean December sum the following year (3.3 mm month $^{-1}$).

4.2. Mortality following exceptional drought

In semiarid conifer forests of the southwestern U.S., Ψ_L was correlated with mechanisms of mortality, and trees died when Ψ_L fell below thresholds that resulted in prolonged stomatal closure (McDowell et al., 2016). Nonlethal loss of G_s during drought could be a precursor for multiyear morbidity, as low G_s can affect carbon balance and vigor following drought (Berdanier and Clark, 2016). Although mean monthly midday G_s was near zero in October (though stomata could be open to some degree in early morning) and likely so in November based on E_L , mortality did not vary with year or drought treatment and mortality was low, on average 2.8%. Kannenberg et al. (2019) reported a lack of drought legacy effects on radial growth of longleaf pine, which they attributed to wood anatomy and drought timing. Autumn needle drop during the drought may have extended the duration of stomatal opening by increasing $A_s:A_L$. In addition, longleaf pine has large reserves of stored carbohydrates in coarse roots that buffer the impact of chronic disturbance from fire (Aubrey and Teskey, 2018), or in this case possibly drought.

4.3. Effects of drought treatment on hydraulic architecture and G_s control of transpiration

Average annual E_G in the ambient treatment was 311 mm yr $^{-1}$ and comparable to the 340 mm yr $^{-1}$ reported for natural and older longleaf pine stands on mesic sites with lower LAI (1.7 m 2 m $^{-2}$) and basal area (15 m 2 ha $^{-1}$) (Ford et al., 2008). Annual E_L was lower than the 293 mm reported for loblolly pine stands of similar age, LAI and basal area (Bartkowiak et al., 2015), perhaps because of unusually high annual precipitation in the loblolly pine study and subsequently higher G_s in loblolly pine. For example, Bartkowiak et al. (2015) reported average monthly midday G_s ranging from 100 to 125 mmol m $^{-2}$ s $^{-1}$ compared to the maximum of 80 mmol m $^{-2}$ s $^{-1}$ we observed for longleaf pine.

Direct comparisons of leaf-level stomatal conductance between the two species do not indicate lower conductance in longleaf pine (Samuelson et al., 2012), and the longer needle lengths of longleaf pine have been associated with somewhat higher leaf gas exchange rates compared to loblolly pine (Wang et al., 2019).

A shift away from foliage production that increases $A_s:A_L$ or ratio of absorbing root area relative to leaf area under dry conditions is a common adjustment to drought in pines over a period of months to years, with stomatal regulation a more short-term response (Magnani et al., 2002). We hypothesized that longleaf pine would avoid drought mainly by adjusting hydraulic architecture, as observed for a loblolly pine plantation in response to 30% throughfall exclusion (Samuelson et al., 2018). More specifically, five years of 30% throughfall exclusion decreased peak LAI and increased $A_s:A_L$ of loblolly pine with only a small decrease (12%) in leaf-level stomatal conductance and no effects on growth efficiency. Stand age and structure of the loblolly pine plantation was similar to the longleaf plantation although the longleaf pine site was more xeric. Mean $A_s:A_L$ of loblolly pine was 4.9 cm 2 m $^{-2}$ in ambient throughfall versus 5.5 cm 2 m $^{-2}$ with throughfall exclusion and similar to the range of 4.6 – 5.2 cm 2 m $^{-2}$ in $A_s:A_L$ of longleaf pine. In contrast to loblolly pine, longleaf pine controlled plant water loss by reducing G_s rather than adjusting aboveground hydraulic architecture in response to drought treatment. Strong sensitivity of G_s to REW in longleaf pine the two years following exceptional drought combined with lower soil moisture on 40% of plot area likely accounts for lower G_s some months in response to drought treatment. Gonzalez-Benecke et al. (2011) also reported sensitivity of G_s of mature longleaf pine trees to REW. Reductions in G_s would also compensate for lower $A_s:A_L$ and lower Ψ_{PD} in response to drought treatment, since G_s can offset changes in $A_s:A_L$ in order to maintain the water potential gradient from soil to leaf (Whitehead et al., 1984).

It is possible that the drought treatment, rather than imposing chronic moderate water stress, exposed trees to intermittent short-term perturbations that were of insufficient duration or magnitude to induce structural change. Alternatively, maintenance of leaf area may be a strategy to maximize carbon fixation during well-watered periods. Wright et al. (2013) reported maintenance of leaf area during drought in longleaf pine trees growing on a xeric site but not on a mesic site, and leaf-level stomatal conductance was lower in xeric than mesic trees. Strong regulation of water loss through stomatal closure on drier sites rather than hydraulic or morphological adjustments was also reported for *Pinus ponderosa* Dougl. ex Laws (Anderegg and Hillerislamers, 2016). On the other hand, height of longleaf pine was on average 0.5 m less, though not significantly so, in drought plots, which may reflect an adjustment in hydraulic architecture to maintain canopy leaf area and thus whole-tree carbon assimilation when soil moisture or D is not limiting. Addington et al. (2006) reported higher leaf area per tree and lower $A_s:A_L$ in longleaf trees on a xeric compared to mesic site, but tree height was lower on the xeric site. They attributed similar maximum G_s between sites to less height and a high root-to-leaf area ratio at the xeric site.

4.4. Effects of drought treatment on stand growth

Although drought treatment had no significant effect on DBH, height, basal area, ANPP, and mortality over three growing seasons, volume was reduced 21%. Volume incorporates water stress effects on height and basal area and is thus a better indicator of response to drought than either variable alone (Rais et al., 2014). The drought treatment effect on volume was perhaps a result of decreases in leaf-level photosynthesis or increased allocation to root growth, suggested by the decrease in growth efficiency, or direct effects of reduced soil water availability on cell turgor and expansion (Raison et al., 1992). Similarly, volume growth of loblolly pine was sensitive to 30% throughfall exclusion in long-term experiments in Oklahoma and Georgia, but in contrast to our results LAI was reduced and growth

efficiency was unaffected by throughfall exclusion (Maggard et al., 2017; Bracho et al., 2018; Samuelson et al., 2018). Despite greater stomatal control of plant water loss, the drought treatment did not increase WUE. This was unexpected since higher WUE was observed in xeric versus mesic site longleaf pine (Ford et al., 2008) and in other pines in response to drought (Forner et al., 2018). Although the treatment effect on ANPP was not significant, ANPP was 20% lower in the drought treatment when averaged over 2017 and 2018, which would offset the average 19% reduction in annual E_G in response to drought treatment.

Assuming 40% removal, the drought treatment would have received 740 mm yr⁻¹ in 2017, an annual amount that lies between the two driest years in the 100-year record. In 2018, the drought plots received 871 mm yr⁻¹, which is still well below the 100-year average of 1255 mm yr⁻¹. It is therefore surprising that treatment effects on growth were not severe. While passive removal of throughfall can simulate extreme dry years, the number, length and seasonality of dry periods may be more important in influencing ecosystem function than the annual amount (Knapp et al., 2017). It is also possible that xeric longleaf pine ecosystems require longer treatment duration to detect thresholds in ecological responses (Asbjornsen et al., 2018). In addition, chronic exposure to mild drought can increase resistance to more severe drought (Backhaus et al., 2014).

5. Conclusions

Lloret et al. (2012) argue that vegetation stability under extreme climatic events is more frequent than assumed. Low mortality of longleaf pine under drought treatment the two years following exceptional drought supports this position. Longleaf pine tolerated the drought by reducing and then almost completely ceasing transpiration for two months. Rapid recovery in Ψ_L and transpiration occurred when significant rainfall events ended the drought. Longleaf pine avoided milder drought stress induced by the throughfall exclusion also by stomatal control of plant water loss, rather than hypothesized adjustments in LAI and $A_S:A_L$. Results from this precipitation manipulation experiment combined with an exceptional drought event indicate that drought tolerance in longleaf pine is facilitated by avoidance of embolism through stomatal control of plant water loss and possibly fast reversal of embolism in roots following extreme drought.

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