PHYSIOLOGICAL AND PHENOLOGICAL RESPONSES TO EXPERIMENTAL THROUGHFALL REDUCTION AND PARAMETERIZATION OF THE 3-PG MODEL FOR MODELING LONG-TERM RESPONSES TO CLIMATE CHANGE IN LONGLEAF PINE FORESTS

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Physiological and Phenological Responses to Experimental Throughfall Reduction and Parameterization of the 3-PG Model for Modeling Long-Term Responses to Climate Change in Longleaf Pine Forests

by

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A dissertation submitted to the Graduate Faculty of
Auburn University
in partial fulfillment of the
requirements for the Degree of
Doctor of Philosophy

Auburn, Alabama
December 11, 2021

Keywords: *Pinus palustris*, drought responses, physiological responses, phenological responses, 3-PG model, forest modeling

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Abstract

Ongoing changes in earth's climate are having profound effects on forest ecosystems in many regions. Longleaf pine (*Pinus palustris* Mill.) is considered one of the most drought-resistant pines in the southeastern U.S. and could serve as a suitable long-term carbon sink and important species for adapting southern forests to climate change. However, questions remain about the sensitivity of longleaf pine to reduced water availability over prolonged periods. For this reason, understanding and forecasting how longleaf pine forests will respond to projected changes in precipitation is necessary for managing these forests in the face of climate change. Here, we studied how three years of reduced rainfall – imposed by a 40% experimental throughfall reduction – impacted leaf- and canopy-scale physiology, shoot and foliage development patterns, and canopy-scale leaf area and litterfall dynamics in established longleaf pine trees. Although among the most drought-resistant pine species in the southeastern U.S., we still expected that a 40% reduction in throughfall would result in significant changes in tree physiology and phenology, as well as canopy dynamics. However, we found that throughfall reduction resulted in rather small reductions in leaf- and canopy-scale function. We also found that reductions in throughfall had small effects on shoot and needle phenology and growth, as well as on leaf area index and litterfall dynamics. Our results show quite clearly that longleaf pine trees and established forests may be relatively resistant to reductions in total rainfall and reduced water availability. If reductions in water availability persist over the long term, more drought-resistant species such as longleaf could be favored over less drought-resistant species. To test this assumption, we also carried out the first parameterization of the 3-PG process-based model for planted longleaf pine stands. The 3-PG model uses a combination of climate, stand, and physiological parameters for performing predictions, and represents a practical tool for forecasting forest carbon sequestration potential, establishing better management strategies, and assessing the impact of projected climate changes on forests. We used a large and geographically extensive long-term dataset across the species' range to estimate important parameters for the model. The model was tested against data from stands of varying climate and soil characteristics that were distributed across the southeastern United States. Although some factors need further attention as new datasets become available, the parameters reported here allowed 3-PG to produce accurate estimates, with predictions showing good correspondence with observations of most stand growth and development variables. The use of the 3-PG model for longleaf pine stands can help improve the predictability of longleaf pine forest productivity and describe growth and physiological dynamics of this species across a wide range of ages, stand, and climate characteristics.

Acknowledgments

This research would not have been accomplished without the considerable assistance from many collaborators, committee members, co-workers, friends, and family. I would like to thank my former major advisor, Dr. Lisa Samuelson, for believing in me, giving me the opportunity, and supporting and guiding me during the development of this project. I also would like to thank my major advisor and committee chair, Dr. Michael Aspinwall, for the support, guidance, encouragement, and for teaching me so much in such a short period. I also appreciate the other members of my research committee, Dr. Carlos Gonzalez-Benecke, Dr. Nancy Loewenstein, Dr. Edward Loewenstein, and Dr. Scott Enebak, for their guidance, advice, and interest in my development as a research scientist. I am also grateful to Michael Ramirez and Jake Blackstock for their help with research and fieldwork and support throughout grad school. A special thanks to Tom Stokes for the endless patience and support. I also would like to thank my friends from Brazil and my Auburn friends that were essential during this journey. Lastly, but foremost, I would like to thank my parents, Rosi and Anderson Mendonça, who I would never be able to have done anything without. Your support and unconditional love made this to be possible.

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List of Abbreviations

^{13}C	Stable isotope carbon
AGB	Above-ground biomass
BA	Basal area
C	Carbon
CanCover	Canopy cover
CO_2	Carbon dioxide
DBH	Diameter at breast height
DOY	Day of the year
$\Delta\Psi$	Difference between predawn and midday leaf water potentials
E	Plant transpiration
FB	US Army at Fort Benning, GA
FR	Fertility rating
GC	Growth cessation
GD	Growth duration
GHG	Greenhouse gases
GLD	Ground-line diameter
GPP	Gross primary production
GR	Growth rate
g_s	Leaf-level stomatal conductance
Gs	Canopy-level stomatal conductance
GS	Growth start

G_{Smax}	Maximum canopy-level stomatal conductance
HEF	Harrison Experimental Forest
Ht	Height
IPCC	Intergovernmental Panel on Climate Change
iWUE	Intrinsic water use efficiency
J_v	Sap flux density
K	Whole-tree hydraulic conducatnce
LAI	Leaf area index
LMA	Leaf dry mass per unit area
MSE	Mean square error
N	Nitrogen
N_{area}	Leaf nitrogen per unit area
NPP	Net primary production
NWF	National Wildlife Federation
PAR	Photosynthetically active radiation
pF	Proportion of foliage biomass to total tree biomass
pFS	Proportion of foliage biomass to stem biomass
P_{net}	Net photosynthesis
pS	Proportion of stem biomass to total tree biomass
QMD	Quadratic mean diameter
REW	Relative soil extractable water
RMSE	Root mean square error
SG	Wood basic specific gravity

SI	Site index
SNA	Specific needle area
SSPSSS	Southwide Southern Pine Seed Source Study
TNC	The Nature Conservancy
TR_0	Ambient throughfall treatment
TR_{40}	40% throughfall reduction treatment
V_{ib}	Volume inside the bark
V_{ob}	Volume outside the bark
VPD	Vapor pressure deficit between plant leaves and the atmosphere
V_{ratio}	Volume ratio between volume inside and outside the bark
W_F	Foliage biomass
W_R	Root biomass
W_S	Stem biomass
Ψ	Water potential
Ψ_{close}	Midday leaf water potential at stomatal closure
Ψ_{MD}	Midday leaf water potential
Ψ_{PD}	Predawn leaf water potential
Ψ_{tlp}	Leaf water potential at turgor loss point
$\delta^{13}C$	Isotopic carbon composition
θ	Volumetric soil moisture

CHAPTER I

CLIMATE CHANGE AND THE USE OF LONGLEAF PINE FORESTS AS A MITIGATION TOOL: AN INTRODUCTION

Introduction

Climate Change and Forests

Anthropogenic activities have altered global climate conditions (IPCC 2014, Tian et al. 2020). The intensified accumulation of carbon dioxide (CO_2) and other greenhouse gases (GHG) in the atmosphere as a result of human activities is directly related to global climate variability, altering temperature and precipitation regimes (Allen et al. 2010, Kunkel et al. 2013, IPCC 2014). The southeastern U.S. is projected to experience increases in temperature and more frequent and severe climate events, such as heatwaves, over the next century (IPCC 2014). Along with these temperature changes, changes in precipitation patterns, with the occurrence of more extreme precipitation events, as well as more frequent, and extended drought periods, are also predicted to occur in the coming years (Kunkel et al. 2013, IPCC 2014, Melillo et al. 2014). Since the 1970s, every decade has been the warmest on record (Konrad et al., 2013). Likewise, increased variability in interannual precipitation patterns with more intense summer droughts has occurred in the last several decades (Wang et al., 2010). The percentage of summer days without rain has increased from approximately 35-45% in the last few decades (Wang et al., 2010).

Changes in climate have the potential to affect and alter forest ecosystem dynamics, generating considerable modifications in forest function, composition, and distribution

(Marques et al. 2007, Sugden et al. 2008, Allen et al. 2010). Decreased water availability can be a strong driver of changes in the structure of vegetation and plant physiological responses and leads to reduced forest net primary production (NPP) (Allen et al. 2010, Will et al. 2013). Increases in drought occurrence, duration, and severity may amplify forest change and impact terrestrial environments (Choat et al. 2012, Bottero et al. 2016). Warmer temperatures can aggravate the effects of reduced water availability, increasing the vapor pressure deficit between plant leaves and the atmosphere (VPD). This increase in VPD can increase tree water loss rates (i.e., transpiration), consequently increasing the risk of hydraulic failure during drought. Furthermore, the effect of drought on trees is cumulative, with the vulnerability to mortality increasing during subsequent droughts (Berdanier and Clark 2015). Hence, tree water stress is expected to increase with elevated temperatures and reduced soil water availability, which can ultimately lead to declines in forest growth and tree survival (Breshears et al. 2013, Will et al. 2013, Allen et al. 2015). Decreased soil water availability may favor more drought-tolerant species and alter successional pathways. In this context, understanding the effects and forecasting how forest ecosystems respond to drought is necessary for managing ecosystems in the face of climate change (Sugden et al. 2008, Allen et al. 2010).

Longleaf Pine Forests: Importance and Resistance to a Changing Climate

Longleaf pine (*Pinus palustris* Mill.) forests were once among the most extensive ecosystems in the southern U.S., occurring on a wide variety of sites (Landers et al. 1995, Jose et al. 2007). Longleaf pine ecosystems support high plant biodiversity levels in the mid- and understory while also providing habitat to several endangered wildlife species (Jose et al. 2007). Across the South region of the U.S., longleaf pine forests are also recognized for producing high-quality timber, sustainable wood products, and providing important ecosystem services (e.g., long-term above and belowground carbon storage) (Outcalt 2000, NWF 2009). Historically, fire and moisture availability were the major factors controlling longleaf distribution within its natural range (Outcalt 2000). Historically, the disturbance tolerance (i.e., fire and low nutrient-water tolerance) (Landers et al. 1995), as well as the disease and insect tolerance, facilitated the successful establishment and dominance of this pioneer species across the southern U.S. (Outcalt 2000, Kara and Loewenstein 2015). However, over the last two centuries, logging for timber production, urban and agricultural development, and fire suppression have drastically reduced the occurrence of longleaf pine ecosystems (Outcalt 2000, USDA 2016). Remnant natural longleaf pine forests presently occur in small parts of the original range (Landers et al. 1995, Outcalt 2000, USDA 2016), and many studies have demonstrated that most of the remaining longleaf stands are currently aging without replacement (Brockway and Outcalt 2000, Dyson et al. 2012). For these reasons, longleaf pine ecosystems are considered one of the most threatened ecosystems in the U.S. (Jose et al. 2007).

In the past, efforts to restore longleaf pine were mostly unsuccessful due to difficulties with natural regeneration and the exclusion of fire as a management practice (Outcalt 2000). However, with improved planting and management techniques, the successful restoration of longleaf pine forests has become possible, and it is a conservation priority in the southeastern U.S. in recent years. Interest in the restoration of longleaf pine forests has increased not just because of their high natural biodiversity and the high value of timber and non-timber products (Johnsen et al. 2009, Outcalt 2000, Starr et al. 2016), but also because this species represents a potential improvement in the resilience and adaptability of southern forests to changing climate conditions (NWF 2009, Samuelson et al. 2014).

Longleaf pine may be more resistant to reduced water availability than the other southern conifers (Samuelson et al. 2019). In this species, structural acclimation to withstand drier conditions has been reported, such as increased biomass allocation to roots relative to shoots (Gonzalez-Benecke et al. 2010, Samuelson and Whitaker 2012). Additionally, physiological plasticity and survival capabilities under reduced water availability in longleaf pine were demonstrated by Starr et al. (2016), who observed that longleaf pine reduced photosynthetic activity during drought periods, with no increases in mortality, which may enhance ecosystem resilience. Similarly, Samuelson et al. (2012) showed that longleaf pine had less negative leaf water potential than loblolly pine *(Pinus taeda* L.) and slash pine (*Pinus elliottii* Engelm. var. *elliottii*) on the same site, suggesting adaptation to drier environments through mechanisms related to hydraulic changes. In this context, longleaf pine ecosystems may be an important tool for mitigating climate change, which increases the need for improving our knowledge and for understanding better how this species will respond to future changes in climate and potential reduced water availability.

The purpose of this dissertation research was to determine the impact of reduced water availability on several processes ranging from the leaf- to canopy-scale. Chapter II focuses on the impact of 40% throughfall reduction at the stand-level over three years on leaf- and tree-scale physiology. Chapter III focuses on the impact of 40% throughfall reduction on leaf and branch development and phenology, and canopy leaf area and litterfall dynamics. Chapter IV focuses on parameterizing the process-based forest model 3-PG for longleaf pine forests, utilizing an extensive network of sites and stands with trees ranging from saplings to 83 year old. The purpose of Chapter IV is to develop a modelling framework that can help characterize and predict longleaf pine productivity dynamics over space, time, and under novel climate conditions.

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CHAPTER II

EXPERIMENTAL THROUGHFALL REDUCTION CAUSES SMALL REDUCTIONS IN LEAF- AND CANOPY-SCALE PHYSIOLOGY IN A LONGLEAF PINE PLANTATION

Abstract

Longleaf pine (*Pinus palustris* Mill.) is considered one of the most drought-resistant pines in the southeastern U.S. and could serve as a suitable long-term carbon sink and important species for adapting southern forests to climate change. However, questions remain about the sensitivity of established longleaf pine to reduced water availability over more extended periods. In this study, we evaluated the effects of 40% throughfall reduction on leaf- and canopy-scale physiology in a 12-year-old longleaf pine plantation in Georgia, USA, over a period of three years (2017-2019). Averaged over time, throughfall reduction decreased volumetric soil water content but resulted in only small reductions in leaf-level stomatal conductance and net photosynthesis, and no changes in leaf-scale water use efficiency (instantaneous or isotopically determined). Reduced throughfall caused a similarly small reduction in maximum canopy-level stomatal conductance, but did not reduce whole-tree hydraulic conductance. Moreover, throughfall reduction had no effect on leaf- or canopy-scale stomatal sensitivity to vapor pressure deficit. Our results indicate that established longleaf pine trees were not strongly affected by throughfall reduction and may be relatively resistant to reductions in average rainfall. Less frequent rain and longer dry spells in the southeast US, especially during warmer months, might have stronger negative effects on tree function than changes in total annual rainfall alone.

1. Introduction

Global climate change is expected to alter the productivity, function, and persistence of many forests worldwide (Allen et al., 2010; Braatz, 2012; Tian et al., 2020). The southeastern United States (U.S.) is the "wood basket" of the nation. Since 1986, the region has produced more wood annually than any other region in the U.S. or country in the world (Wear and Greis, 2013). Average air temperatures in the region are expected to increase, coupled with increased atmospheric demand for water (i.e., vapor pressure deficit, VPD), greater evapotranspiration, and more intense and widely spaced precipitation events (IPCC, 2013; Melillio et al., 2014; Samuelson et al., 2019). These changes are expected to result in reduced soil moisture, increased drought severity, and a greater risk of drought impacts on trees and forests. Nonetheless, the impacts of drier conditions on forests in the southeastern U.S. remain unclear and may depend upon species, the relative reduction in water availability, and local site conditions. New studies are needed to improve our understanding of the impacts of reduced water availability on forest ecosystems in the region, which could inform approaches to adapt southern forests to climate change.

Water availability strongly influences tree growth and development, as well as leaf- and whole-tree physiology. Reduced soil water availability (i.e., drought) leads to reduced hydraulic conductance and water deficit in the leaf tissue, which usually leads to reduced rates of leaf-scale stomatal conductance (g_s) and net photosynthesis (P_{net}), and reduced rates of CO_2 and H_2O exchange at the canopy-scale (Allen et al., 2010; Choat et al., 2018; Mitchell et al., 2016; Starr et al., 2016). As drought persists, stomatal closure slows but does not stop the decline in leaf and xylem water potentials (Ψ) or hydraulic capacity (Creek et al., 2020). Prolonged or repeated drought periods can lead to widespread and irreversible xylem embolism, which can eventually lead to tree death (Choat et al., 2008; Creek et al., 2020; Hubbard et al., 2001; Vilagrosa et al., 2003). However, tree species exhibit a spectrum of water use strategies and drought sensitivity (or tolerance) (Klein, 2014). At one end of the spectrum, anisohydric species are relatively insensitive to reduced soil moisture and tolerate drought by maintaining stable g_s and transpiration (E) at a low Ψ. This strategy allows for continued C fixation at the risk of cavitation (Blackman et al., 2019; Hochberg et al., 2017; McDowell et al., 2008; Roman et al., 2015). Isohydric species, by contrast, show the opposite response to reduced soil moisture - decreased g_s and lower E and P_{net}, yet near homeostasis of leaf water potential and lower risk of cavitation in the short-term (Choat et al., 2018, 2008; Creek et al., 2020; Hubbard et al., 2001; Vilagrosa et al., 2003). Thus, during drought, isohydric species tend to avoid further reductions in leaf water potential by reducing leaf- and canopy-scale water use. In general, conifer species tend to be relatively isohydric while angiosperm species vary from strongly anisohydric to strongly isohydric (Blackman et al., 2019; Hubbard et al., 2001; Johnson et al., 2018; Klein, 2014; Mitchell et al., 2013). However, among and within conifer species, the degree of isohydry may vary (Hochberg et al., 2017) in part due to differences in habitat adaptation (Attia et al., 2015; Roman et al., 2015; Tardieu and Simonneau, 1998). Moreover, seedling responses to short-term drought conditions might not reflect tree responses to dry field conditions over longer time periods. Evaluating species responses to reduced soil moisture in the field over longer time periods is critical to determining their sensitivity to soil moisture, and potential consequences for forest growth and function.

Because stomatal regulation is an important determinant of drought resistance, tolerance or avoidance, and influences leaf- and canopy-scale H_2O and C fluxes, understanding leaf- and canopy-level responses to reduced water availability is essential to understanding drought impacts on trees and forests. Canopy conductance is a key regulator of ecosystem-scale E and is an important input parameter in models that predict H_2O fluxes over large spatial scales (Novick et al., 2009; Siqueira et al., 2006). Leaf-level g_s (often measured at the top of the canopy) is often different than G_s because radiation, temperature, and VPD conditions experienced by individual leaves generally differ from conditions integrated throughout the canopy (Leuning et al., 1995). Also, the physiology and responsiveness (i.e. sensitivity) of individual leaves may not reflect the physiology and responsiveness of the entire canopy. Moreover, combining g_s measurements with G_s estimates allows for testing whether stomatal sensitivity to VPD depends on the scale of observation (Wullschleger et al., 2002) or whether reductions in soil moisture increase or decrease g_s and G_s sensitivity to VPD. In general, factors (e.g., species differences, growth conditions) that lead to lower g_s at optimal VPD (i.e., ~1.5 kPa) also tend to result in reduced sensitivity to VPD (Oren et al. 1999). Recent studies also suggest that trees growing under long-term reductions in soil moisture show reduced stomatal sensitivity to VPD (Grossiord et al., 2018, 2017). However, changes in stomatal sensitivity to VPD resulting from reduced soil moisture may depend upon species, average precipitation for the location, and the severity of the soil moisture reduction. Studies across additional species and site conditions could provide further insight into drought impacts on stomatal sensitivity to VPD at both the leaf- and canopy-scales.

Understanding drought impacts on tree function and predicting potential drought risks is essential for informing adaptation strategies for increasing forest resilience to climate change. Some tree species may be more resistant or tolerant of stressful conditions than others and may be utilized to enhance forest health and prevent forest declines (Bolte et al., 2009). In the southeastern U.S., longleaf pine (*Pinus palustris* Mill.) is considered one of the most drought-resistant southern pines. This perception is partly based on the observation that, despite a broad geographic distribution, it often occurs on drier sites, including xeric sand hills and montane upland sites where water is limited, and related pine species (e.g., *Pinus taeda* L.) are less common or less productive. Compared to other species, longleaf pine has also demonstrated considerable resistance to drought through physiological and structural modifications that help reduce water use or demand (Gonzalez-Benecke et al., 2010; Samuelson et al., 2019; Starr et al., 2016). For example, a long-term study performed by Starr et al., (2016) demonstrated that longleaf pine trees avoided or resisted drought through phenological plasticity. Specifically, following drought exposure longleaf trees replaced older and less drought-resistant foliage with newer and more drought-resistant foliage, allowing for continued function during and after the stress period. Likewise, Samuelson et al., (2019) demonstrated that longleaf can increase sapwood to leaf area ratios, root to leaf area ratios, root hydraulic conductivity, and rooting distribution to help maintain water uptake and transport. Therefore, restoration of longleaf forests, or perhaps converting stands of less drought-resistant species to longleaf pine, could aid drought adaptation efforts. However, new studies, especially those carried out over longer time periods at both the leaf- and canopy-scales, are required to improve our fundamental understanding of physiological responses to drought in longleaf pine.

The objective of this study was to determine the impacts of throughfall reduction on longleaf pine leaf and canopy physiology, as well as leaf-and canopy-scale stomatal sensitivity to VPD. To accomplish this, we carried out a 3-year-long (2017 to 2019) experimental rainfall reduction experiment (40% throughfall reduction) in a young (12-14 yr. old) longleaf plantation in west Georgia, USA. This article builds upon the previous study by Samuelson et al. (2019), who examined the impacts of throughfall reduction on stand-level water use and productivity in longleaf pine at the same site. Each year, during the growing season (from May through September), we repeatedly measured (every 3-4 weeks) leaf-scale P_{net}, g_s, intrinsic water-use efficiency (iWUE, calculated as the ratio of P_{net} to g_s), as well as predawn and midday leaf water potential (Ψ_{PD} and Ψ_{MD}, respectively) in ambient throughfall and reduced throughfall plots. We also assessed potential changes in foliar nitrogen (N) and foliar ^{13}C isotopic composition [$\delta^{13}C$] (additional measure of intrinsic water-use efficiency) with throughfall reduction. In addition, we used continuous sap-flux measurements to estimate maximum daily canopy conductance (G_{Smax}) and whole-tree hydraulic conductance (K). We hypothesized that longleaf would employ a relatively conservative (i.e. isohydric) strategy and would reduce g_s with reduced throughfall (low soil moisture) to help maintain relatively constant leaf water midday potentials. Reduced g_s in reduced throughfall plots would lead to lower P_{net} but higher iWUE (measured both instantaneously and isotopically). Over time, reductions in g_s would be coupled with reduced G_{smax} and K. Because we expected that reduced throughfall would result in reduced g_s and G_{smax}, we hypothesized that stomatal sensitivity to VPD at the leaf- and canopy-scale would also decrease with throughfall reduction.

2. Materials and methods

2.1. Study site and experimental design

A complete description of the experimental site and experimental design was previously described in Samuelson et al. (2019). Here, we briefly describe the site and design. The study was established in an 11-year-old longleaf pine plantation in the Chattahoochee Fall Line Wildlife Management Area in Marion County, GA (32.5528˚ N, -84.776˚ W) in May 2016. Thirty-year mean (1981-2010) annual precipitation for Americus, GA (approximately 60 km from site) is 1245 mm, mean annual minimum and maximum air temperatures are 11.0 °C and 24.6 °C and mean annual temperature at the site is 17.8 °C (*https://www.ncdc.noaa.gov/cdo-web/datatools/normals*, accessed February 2021). The site elevation is 210 m. The site was planted in early 2005 at an approximate spacing of 2.6 m x 2.6 m (density ~1479 trees ha^{-1}). Soils at the site are in the Lakeland Series (2-5% slopes), which are Thermic, coated Typic Quartzipsamments, that consist of very deep, excessively drained, and rapid to very rapidly permeable soils.

The study utilized a randomized complete block design with three blocks (replicates), each containing two plots that were randomly assigned to one of two throughfall treatments: ambient throughfall (TR_0) or an approximate 40% reduction of throughfall (TR_{40}). Each treatment plot was 21 m x 31 m (0.07 ha) in dimension with a central 11 m x 21 m (0.02 ha) measurement plot. The size of the treatment plot was determined by excavating and measuring one root from three trees adjacent to the project site. Roots were found to extend an average of 4.5 m from the base of the tree. By extending the treatment 5 m in all directions around the measurement plot, trees in the measurement plot would not receive water from outside of the treatment. Plots within each block were surrounded by two rows of buffer trees. Blocks were selected based on pre-treatment estimates of stand basal area. Pretreatment means for basal area, density, DBH, and height across all plots were 18.2 m^2 ha^{-1}, 1029 trees ha^{-1}, 14.7 cm, and 9.5 m, respectively.

The 40% throughfall reduction was determined based on the 100-year mean annual precipitation for the area. The approximate 60% residual throughfall represented the 1st percentile of annual precipitation (i.e., 1- in 100-year drought event) for Americus, Georgia (802 mm). To limit throughfall by approximately 40% and reduce soil moisture, throughfall exclusion troughs spanning 1.54 m were installed between rows. The troughs were an average height of 1.3 m and were separated by a gap of 50 cm within a row. The throughfall exclusion tray frames were constructed from pressure-treated lumber and steel studded t-posts. Troughs were constructed out of 12 mil polyethylene sheeting (Polyscrim 12, Americover Inc., Escondido, CA). A total of 16 troughs were installed per plot and covered 40% of the ground area in each plot. Throughfall is intercepted by the troughs and collected in large, corrugated pipes that carry the water at least 20 m from the edge of plots.

2.2. Environmental data

A weather station was installed approximately 0.55 km from the site in a 0.65 ha clearing to measure wind-speed, precipitation, air temperature, and relative humidity (both temperature and relative humidity used in VPD determination) (6152 Vantage Pro 2 Wireless Weather Station, Davis Instruments, Vernon Hills, Illinois). Relative humidity and air temperature were also measured by three sensors (HOBO U23 Pro v2 Temperature/Relative Humidity

Logger, Onset Computer Corporation, Bourne, Massachusetts) under the canopy at approximately 2 m height at three locations in-between adjacent plots. Volumetric soil moisture (θ, cm^3 water cm^{-3} soil) was recorded every minute at 5 cm, 15 cm, 50 cm, and 100 cm depths in all plots, and the average recorded every 30 minutes with 10HS Large Soil Moisture Sensors (Decagon Devices, Inc., Pullman, WA, USA). A soil specific calibration was calculated following Starr and Paltineanu (2002). Soil moisture sensors were linked to data loggers (HOBO Micro Station Data Logger, Onset Computer Corp, Bourne, MA, USA). Sensors were located in the center of a plot in the middle of the row and spaced 60 cm apart. Thus, in the throughfall reduction plots, soil moisture sensors were located under troughs. As the TR_{40} covered 40% of plot area, the soil moisture used in 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.

2.3. Leaf physiology

Leaf gas-exchange was measured to determine the effects of throughfall reduction on leaf physiology. Measurements were made between 1000 to 1400 h on sunny days and conducted every 3-4 weeks during the growing season (May – September) in 2017, 2018, and 2019. Leaf gas-exchange was measured using a portable photosynthesis system fitted with a 2 x 3 cm cuvette and a red/blue LED light source (LICOR 6400XT, Licor Inc., Lincoln, NE, USA). Measured variables included net photosynthesis (P_{net}, μmol m^{-2} s^{-1}), stomatal conductance (g_s, mmol m^{-2} s^{-1}), and intrinsic water use efficiency (iWUE, μmol mol^{-1}), calculated as the ratio of P_{net} to g_s. One scaffolding unit (6 m tall) was installed in each plot to facilitate access to the upper canopy of at least three measurement trees per plot. For each tree and on each measurement date, two fascicles (3 needles per fascicle) from two branches were sampled. The order in which blocks and plots within blocks were sampled was randomized across and within measurement dates. Leaf samples were chosen at random from the upper third of the canopy of each tree, ensuring that foliage was fully exposed to sunlight and from the most recent fully developed flush. Light intensity within the leaf chamber was maintained at 1800 μmol m^{-2} s^{-1} photosynthetic photon flux density (PPFD). The flow rate was held constant at 500 μmol s^{-1}, and chamber reference [CO_2] was set at 410 μmol mol^{-1}. Water vapor inside the leaf chamber was not scrubbed so that RH inside the cuvette approximated ambient conditions. Temperature was not controlled and was allowed to fluctuate with ambient conditions. Leaf temperature and VPD inside the leaf chamber (T_{leaf} and VPD_{leaf}, respectively) during leaf gas-exchange measurements ranged from 13.1 to 45.3 °C and 0.84 to 7.81 kPa, respectively. Due to heating of the photosynthesis system by solar radiation (direct exposure to sunlight) and the proximity of the photosynthesis system to the metal scaffoldings, T_{leaf} and VPD_{leaf} were often a few units higher than the ambient air temperature and atmospheric VPD measured by the weather station. Nonetheless, gas-exchange measurements in both treatment plots were carried out across the same range of T_{leaf} and VPD_{leaf}, allowing for valid comparison of leaf gas-exchange over time between treatments. Measurements were made on detached needles. Detachment tests showed no effect of detachment within the first 5 minutes. Gas-exchange variables were recorded once P_{net} and g_s reached steady-state, typically within 2-5 minutes of sealing the needles in the cuvette. Total needle area (all-sided needle area) within the cuvette was calculated from measurement of fascicle diameter and needle length following Samuelson et al. (2012).

Following measurements, sampled leaves were dried at 70 °C for 48 hours and leaf dry mass per unit area (LMA, g m^{-2}) was calculated as the ratio of leaf dry mass to all-sided leaf area.

2.4. Leaf water potential

Predawn and midday measurements of leaf water potential (Ψ_{PD} and Ψ_{MD}, respectively) were made on the same trees as leaf gas-exchange measurements, every 3-4 weeks (measured on same dates as leaf gas-exchange), using a pressure chamber (1505D Pressure Chamber Instrument, PMS Instruments, Albany, WA, USA). Ψ_{PD} samples were collected before sunrise when it is assumed that water potential of the xylem and soil are in near equilibrium due to minimal transpiration. Ψ_{MD} samples were collected during the middle of the day (between 1100 to 1300 hours). Five fascicles were collected from each tree for both Ψ_{PD} and Ψ_{MD} measurements. Samples were collected from recently mature foliage in the upper canopy. Scaffolding was used to access foliage for Ψ_{PD} and Ψ_{MD} measurements. Once removed from the tree, samples were placed in sealed plastic bags containing damp paper and put into a cooler for approximately 30-120 minutes until measured. Importantly, Samuelson et al., (2019) reported average Ψ_{PD} and Ψ_{MD} values across both treatments for 2017 and 2018. We use the same Ψ_{PD} and Ψ_{MD} data from Samuelson et al., (2019), as well as Ψ_{PD} and Ψ_{MD} values from an additional year (2019), for calculating whole-tree hydraulic conductance (see below).

2.5. Sap flux and whole-tree hydraulic conductance

A sap flow system with 30 mm thermal dissipation probes (TDP-30, Dynamax, Inc., Houston, Texas) was used to determine tree sap flow in 4-5 trees per plot (30 trees total), representing the range in basal area distribution in each measurement plot (Čermák et al., 2004). Trees selected for sap flow measurements were also the same used for leaf gas exchange and water potential measurements and ranged in DBH from 14.0 to 19.3 cm at the start of the study. Thermal dissipation probes were used to monitor temperature differences between a heated probe and a reference probe (FLGS-TDP Sap Velocity System Model XM1000, Dynamax, Inc., Houston, Texas). Probes were installed on selected trees at DBH (approximately 1.37 m). The outer bark was removed to install the probes, which were placed in two small holes spaced 9 cm apart vertically in each tree. Reflective insulation was wrapped around the probes and the stem around the probes to minimize temperature gradients. The heat from the heated probe radiates outwards and warm the reference probe as water in the xylem flows. Probe temperatures were measured every minute and averaged every 30 minutes; 30-minute means were then recorded. To correct instances where the difference in maximum temperature was not attained at night, Baseliner (an open-source software for processing sap flow data) was used as described in Oishi et al. (2016). Sap flux density (J_v, mol m^{-2} s^{-1}) was calculated according to Granier (1987). For each measured tree, J_v was divided by the difference between the two water potential measures (Ψ_{PD} and Ψ_{MD}, here denoted as $\Delta\Psi$) to calculate whole-tree hydraulic conductance, K (mol m^{-2} s^{-1} MPa^{-1}).

2.6. Canopy conductance

Calculations of canopy conductance (G_s) followed Bartkowiak et al., (2015) – inverting the Penman-Monteith equation and assuming sap flow as transpiration. Values of G_s were calculated when VPD ≥ 0.75 kPa to reduce possible effects of instrument error (Ewers and Oren, 2000). Because VPD was below 0.75 kPa on many days during the winter months, monthly means were not calculated between November and February. Also, sap flow time series was shifted to maximize the correlation with VPD to account for a time lag in the response of transpiration to VPD, following Domec et al., (2009). Importantly, Samuelson et al., (2019) assessed the impacts of throughfall reduction on G_s in the same trees at the same site between 2016 and 2018. Here, we focus on examining the impacts of throughfall reduction on maximum daily G_s (G_{smax}) on the same dates (2017 – 2019) as leaf gas-exchange, water leaf potential, and K measurements, as well as the sensitivity of G_{smax} to VPD and the potential modifying effects of throughfall reduction. This allowed us to compare aspects of leaf- and canopy-scale function at common dates and conditions throughout the experiment.

2.7. Foliar $\delta^{13}C$, and carbon and nitrogen content

Foliar δ^{13}C (‰), as well as carbon concentration (%C) and nitrogen concentration (%N), were measured on foliage collected in October or November of 2017, 2018, and 2019. δ^{13}C provides a time-integrated measure of intrinsic water-use efficiency; higher (less negative) δ^{13}C values indicate higher intrinsic water use efficiency. The trees sampled were the same as those used for leaf gas-exchange and leaf water potential measurements. Five needles from two terminal shoots (one primary and one secondary) of two branches per tree were collected from three different trees in each of the six plots. In total, samples were collected from four different branches per tree. Oven-dried samples were finely ground and homogenized with a ball mill grinder (Spex 8000, SPEX SamplePrep LCC, Metuchme, NJ, USA). The ratio of ^{13}C:^{12}C (i.e., $\delta^{13}C$), and %C and %N were determined using a continuous flow mass spectrometer (Thermo Finnigan Plus XL, Thermo Fisher Scientific, Waltham, MA, USA). Leaf N per unit area (N_{area}, g N m^{-2}) was also calculated as the product of %N content and LMA (LMA measured on the same trees and on the same date as %N). $\delta^{13}C$, %C, %N, and N_{area} data were pooled by plot.

2.8. Data analysis

All statistical analyses were performed in SAS v9.3 (SAS Institute Inc. 2010, Cary, NC USA). All tests of statistical significance were conducted at α=0.05. Because 'plot' is the experimental unit, in most cases, we averaged data collected across measurement trees in each plot. A linear mixed model (PROC MIXED) was used to test the effects of measurement date (i.e. time), treatment (TR_0 versus TR_{40}), and date × treatment interactions on the leaf- and canopy-scale physiological variables. A linear mixed model was also used to test for treatment effects on non-repeated measurements (e.g. $\delta^{13}C$, %C, and %N). In both models, block was considered a random effect. When appropriate, data were log-transformed to fulfill assumptions of normality.

We examined stomatal sensitivity to VPD at the leaf- and canopy-scale, and the potential modifying effects of throughfall reduction, by assessing relationships between g_s and VPD_{leaf} and G_{smax} and VPD. Following Oren et al. (1999), the response of g_s and G_{smax} to increasing VPD was assessed using the linear function: g_s

(or G_{smax}) = $b_{ref} + -m \cdot ln(VPD)$, where m quantifies the sensitivity of g_s or G_{smax} to increasing VPD (mmol m^{-2} s^{-1} $ln(\text{kPa})^{-1}$), and b_{ref} is the reference g_s or G_{smax} at VPD =1 kPa. To assess g_s and G_{smax} responses to VPD across a similar range of VPD, we excluded g_s data measured at $VPD_{leaf} > 5$ kPa from our analysis, which is higher than maximum daily VPD. Also, because leaf-level measurements occurred every 3-4 weeks, resulting in fewer data points than G_{smax}, we were unable to use quantile regression and upper boundary analysis to examine the relationship between g_s and VPD_{leaf}. Analysis of covariance was used to test whether m or b_{ref} differed between throughfall treatments. In this analysis, VPD (or VPD_{leaf}) was a covariate and 'treatment' (TR_0, TR_{40}) was a factor. If treatment influenced the relationship between g_s and VPD, a significant interaction between treatment and VPD was observed, and different m estimates were fit for each treatment. If treatment and VPD were both significant, but the interaction between treatment and VPD were not, equations with different b_{ref} estimates for each treatment, but a common m estimate, were fit to the data. If only the covariate was significant, one equation with a common b_{ref} and m estimate was fit to data from both treatments.

3. Results

3.1. Environmental conditions

Under ambient conditions, annual precipitation at the site was 1234 mm in 2017, 1451 mm in 2018, and 1232 mm in 2019 (Figure 1a). Annual precipitation in 2017 and 2019 was slightly lower than the long-term (30-year) mean annual precipitation for the location (1245 mm). Total precipitation in 2018 was approximately 17% higher than the long-term mean for the location. Under 40% throughfall reduction, total precipitation was estimated to be 740 mm in 2017, 871 mm in 2018, and 739 mm in 2019. Precipitation during the growing season (May - September) varied over the years. Growing season precipitation was 549 mm in 2017, 678 mm in 2018, and 506 mm in 2019.

Mean daily average, maximum, and minimum temperatures were similar among years and averaged 18.3 °C, 24.9 °C, and 12.8 °C, respectively (Figure 1b). However, daily maximum temperatures in 2017 and 2019 were sometimes above the average daily maximum temperature for the study area. Daily maximum vapor pressure deficit (VPD_{max}) was similar among years and ranged from 0.03 to 4.65 kPa (Figure 1a).

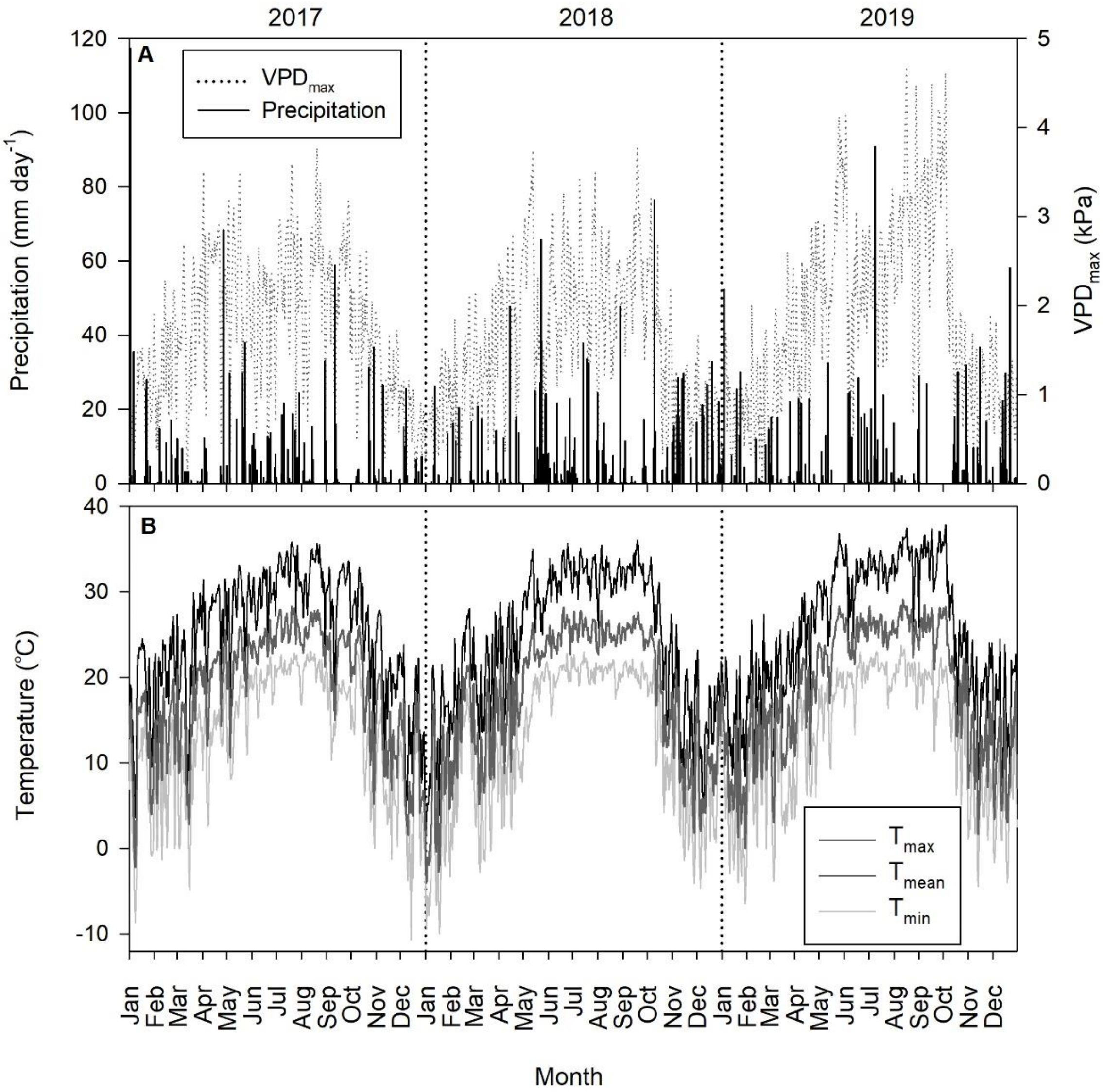

Figure 1. (A) Daily rainfall (bars) and daily maximum vapor pressure (VPD$_{max}$, dotted line), and (B) daily maximum, mean, and minimum temperature (T$_{max}$, T$_{mean}$, and T$_{min}$, respectively) in a longleaf pine plantation in Marion County, Georgia, USA.

3.2. Soil Moisture

In both treatments, volumetric soil moisture was frequently lower at deeper positions within the soil profile (Figure 2). Daily mean volumetric soil moisture in the throughfall reduction treatment was often lower than in the ambient treatment (Figure 2). As soil depth increased, the difference in volumetric soil moisture between TR_{40} and TR_0 treatments generally decreased (Figure 2). Over time, volumetric soil moisture at 5, 15, 50, and 100 cm depths were on average 47, 41, 32, and 34% lower, respectively, in the TR_{40} plots compared with the TR_0 plots (Figure 2). Among years, monthly mean volumetric soil moisture at 5 cm depth varied between 7.3% and 8.8% in the TR_0 treatment and between 4.1% and 4.6% in the TR_{40} treatment. At 50 cm depth monthly mean volumetric soil moisture varied between 4.3% and 6.5% in the TR_0 treatment and between 3.8% and 4.5% in the TR_{40} treatment.

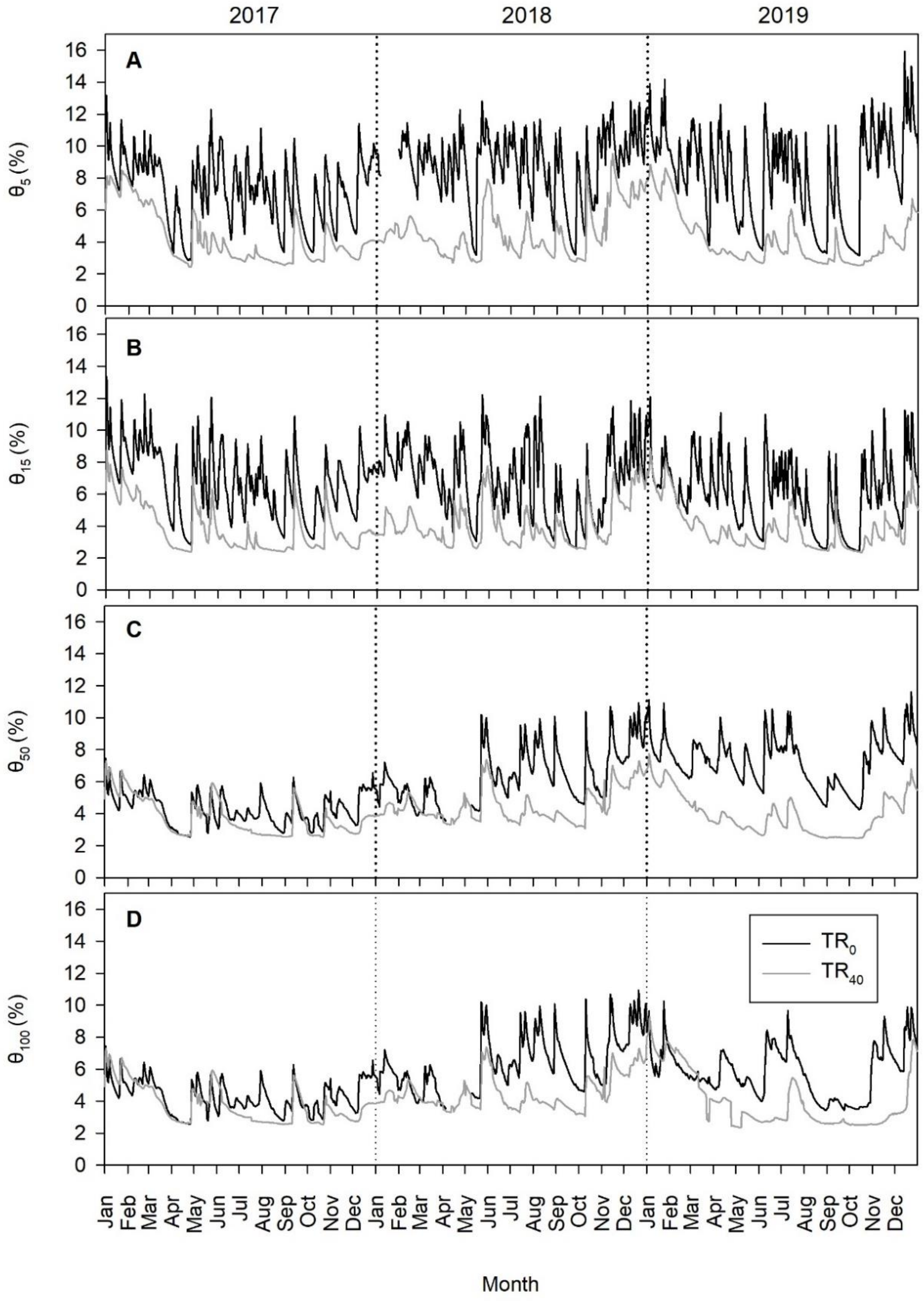

Figure 2. Mean daily soil volumetric water content at 5 cm (θ_5) [A], 15 cm (θ_{15}) [B], 50 cm (θ_{50}) [C], and 100 cm (θ_{100}) [D] depth in a longleaf pine plantation under an experimental throughfall reduction treatment (TR_{40}) and ambient throughfall treatment (TR_0). Soil volumetric water content in the TR_{40} was measured under throughfall exclusion trays.

3.3. Leaf-level gas-exchange responses

Averaged over time, throughfall reduction reduced g_s by 21%, from 49.8 to 39.5 mmol m^{-2} s^{-1} (Table 1, Figure 3). Throughfall reduction caused a small reduction in P_{net} (-13%); this effect was marginally significant (Table 1, Figure 3). In general, both treatments showed reduced g_s and P_{net} during drier periods (Figure 3). For instance, during a 20-day period between May and June of 2019 soil moisture was as low as 4%, and values of g_s and P_{net} were much lower compared to relatively wet periods (Figure 3).

In general, iWUE increased during dry periods when g_s was low and decreased during wet periods when g_s was relatively high. However, averaged over time, iWUE was similar between treatments (Table 1, Figure 3). Foliar $\delta^{13}C$ (time-integrated estimate of water use efficiency) differed among years (Table 1) and was -30.9 ± 0.3, -29.3 ± 0.3, and -27.9 ± 0.3 ‰ in 2017, 2018, and 2019, respectively. However, $\delta^{13}C$ did not differ between treatments (Table 1). We conclude that throughfall reduction caused small reductions in leaf gas-exchange but did not change leaf-scale water use efficiency.

Foliar %C was similar across years but %N, and N_{area} varied among measurement years (Table 1). %N averaged 1.3 ± 0.04, 1.1 ± 0.04, and 0.9 ± 0.04 % in 2017, 2018, and 2019, respectively. N_{area} averaged 1.07 ± 0.05, 0.87 ± 0.05, and 0.84 ± 0.05 g N m^{-2} in 2017, 2018, and 2019, respectively. Although LMA varied among measurement dates (Table 1, Figure 3), and %N and N_{area} varied among years, all three traits and %C were similar between treatments (Table 1). No date × treatments interactions were detected for any trait (Table 1).

Table 1. Analysis of variance results for the effects of measurement date (D), throughfall treatment (T), and their interaction on leaf- and canopy-scale physiological traits in longleaf pine trees growing in a plantation in Georgia, Unites States. Numerator and denominator degrees of freedom (*d.f.*) and probability values (*p*-values) are provided for each factor. Mean (± standard error) values for leaf gas-exchange, leaf water potential, whole-tree water flux traits, and leaf composition traits are shown for the ambient throughfall (TR_0) and reduced throughfall (TR_{40}) treatments.

Variable	Date		Treatment		Date × Treatment		TR_0	TR_{40}
	d.f.	*P > F*	*d.f.*	*P > F*	*d.f.*	*P > F*		
P_{net} (μmol m^{-2} s^{-1})	26,103	**<0.001**	1,4	0.063	26,103	0.677	3.97 (0.1)	3.45 (0.1)
g_s (mmol m^{-2} s^{-1})	26,103	**<0.001**	1,4	**0.047**	26,103	0.373	49.9 (2.6)	39.5 (2.6)
iWUE (μmol mol^{-1})	26,103	**<0.001**	1,4	0.223	26,103	0.486	92.0 (4.1)	100.4 (4.1)
Ψ_{PD} (MPa)	26,103	**<0.001**	1,4	0.157	26,103	0.095	-0.84 (0.02)	-0.89 (0.02)
Ψ_{MD} (MPa)	26,103	**<0.001**	1,4	0.174	26,103	0.983	-1.67 (0.03)	-1.74 (0.03)
$\Delta\Psi$ (MPa)	26,103	**<0.001**	1,4	0.600	26,103	0.741	0.82 (0.28)	0.85 (0.28)
K (mol m^{-2} s^{-1} MPa^{-1})	23,90	**<0.001**	1,4	0.235	23,90	0.076	2.18 (0.15)	1.88 (0.15)
G_{smax} (mmol m^{-2} s^{-1})	24,93	**<0.001**	1,4	**0.026**	24,93	0.277	69.9 (3.0)	56.3 (3.0)
LMA (g m^{-2})	26,103	**<0.001**	1,4	0.433	26,103	0.156	87.3 (1.9)	85.0 (1.9)
$\delta^{13}C$ (‰)	2,8	**<0.001**	1,4	0.291	2,8	0.521	-29.57 (0.23)	-29.19 (0.23)
%C (%)	2,8	0.454	1,4	0.749	2,8	0.473	53.9 (1.0)	54.4 (1.0)
N_{area} (g N m^{-2})	2,8	**0.002**	1,4	0.962	2,8	0.491	0.93 (0.05)	0.92 (0.05)
%N (%)	2,8	**<0.001**	1,4	0.436	2,8	0.869	1.10 (0.05)	1.17 (0.05)

Parameter descriptions: P_{net}, net photosynthesis; g_s, leaf-level stomatal conductance; iWUE, intrinsic water use efficiency; Ψ_{PD}, predawn leaf water potential; Ψ_{MD} midday leaf water potentials; $\Delta\Psi$, the difference between predawn and midday leaf water potentials; K, whole-tree hydraulic conductance; G_{Smax}, maximum canopy-level stomatal conductance; LMA, leaf specific mass per unit area; $\delta^{13}C$, foliar ^{13}C isotopic composition; %C, leaf carbon content; N_{area}, leaf nitrogen per unit area; and %N leaf nitrogen content. Average Ψ_{PD} and Ψ_{MD} used in this analysis were partially (2017-2018) provided by Samuelson et al., (2019).

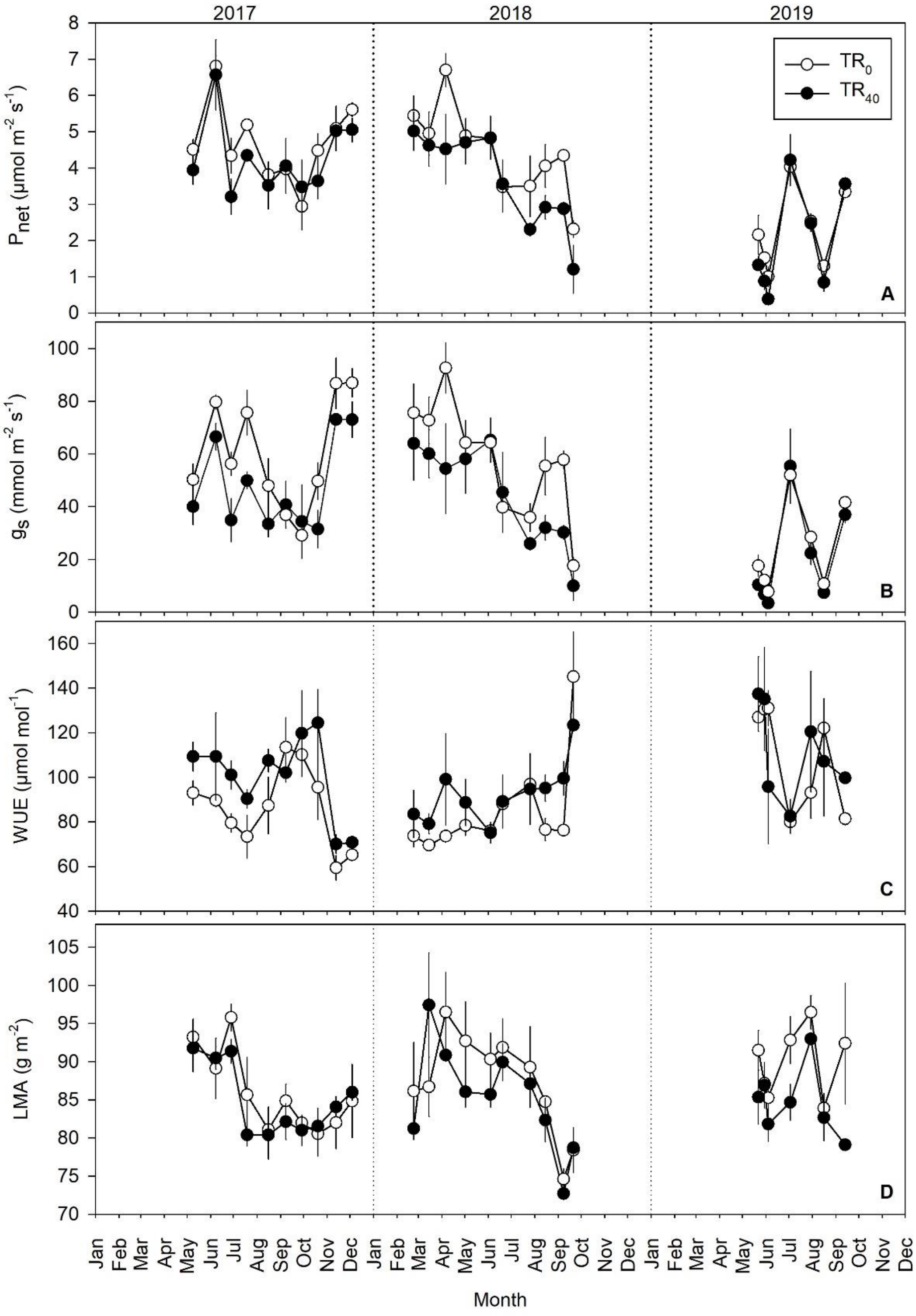

Figure 3. Mean (± standard error) values of net photosynthesis (P_{net}) [A], stomatal conductance (g_s) [B], intrinsic water use efficiency (iWUE) [C], and leaf dry mass per unit area (LMA) [D] in ambient throughfall (TR_0) and 40% throughfall reduction (TR_{40}) treatments in a longleaf pine plantation.

3.4. Leaf water potential

Ψ_{PD} and Ψ_{MD} varied across sampling dates but did not differ between treatments (Table 1, Figure 4). Over time and across treatments, average Ψ_{PD} and Ψ_{MD} was -0.87 ±0.02 MPa and -1.71 ±0.03 MPa, respectively (Table 1, Figure 4). In both treatments, Ψ_{PD} and Ψ_{MD} were lower during periods of low soil moisture. The differences between Ψ_{PD} and Ψ_{MD} measurements (Ψ_{PD}-Ψ_{MD}, here referred as $\Delta\Psi$) were also analyzed. These differences represent the proportional change in leaf water potentials between periods of minimal transpiration (predawn) and periods of high transpiration (midday). Overall, throughfall reduction had no effect on $\Delta\Psi$ (Table 1). No date × treatments interactions were detected for any leaf water potential variable (Table 1).

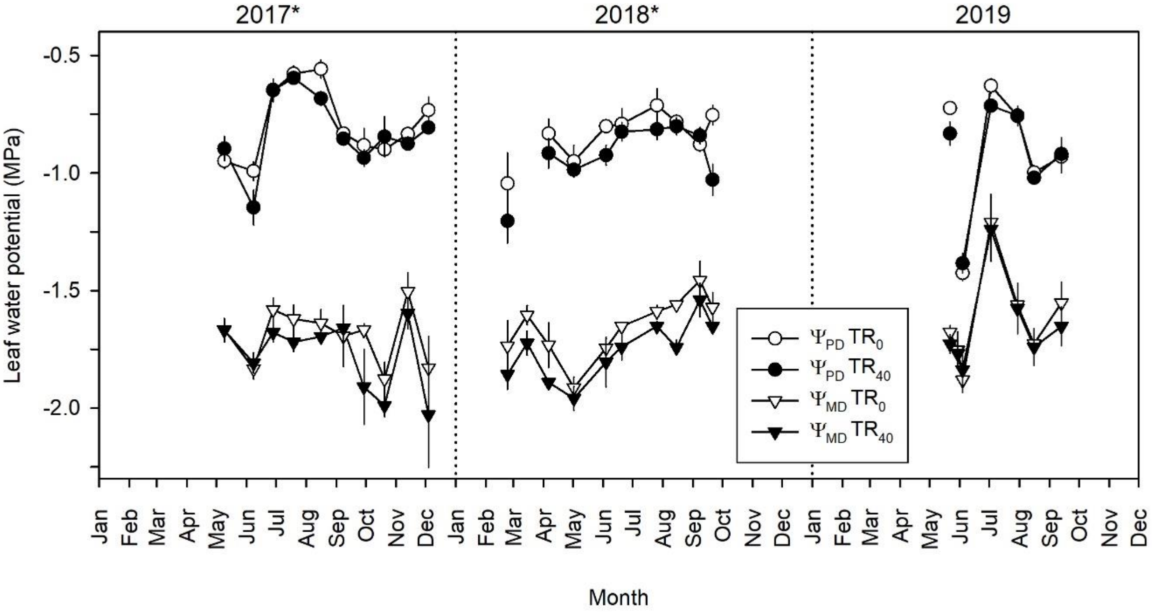

Figure 4. Mean (± standard error) values for predawn leaf water potential (Ψ_{PD}) and midday leaf water potential (Ψ_{MD}) in ambient throughfall (TR_0) and 40% throughfall reduction (TR_{40}) treatments in a longleaf pine plantation. *Data from 2017 and 2018 were previously reported in Samuelson et al. (2019).

3.5. Whole-tree hydraulic conductance and canopy conductance

Whole-tree hydraulic conductance (K) showed a marginally significant date × treatment interaction (Table 1, Figure 5). Throughfall reduction decreased K at only two time points during the study period: June of 2018 (p=0.003) and September of 2018 (p=0.002) (Figure 5). Across both treatments, K was generally higher during warmer periods than colder periods and declined as soil moisture declined.

We determined the effects of the throughfall exclusion on G_{smax} measured on the same days as leaf gas-exchange, water potential, and K measurements. Over the study period (2017-2019), throughfall reduction significantly reduced G_{smax} from 69.9 to 56.3 mmol m^{-2} s^{-1}; a reduction of 20% (Table 1, Figure 5). No date × treatment interaction was detected for G_{smax}.

As expected, g_s and G_{smax} both declined as VPD increased. The relationship between g_s and VPD_{leaf} (R^2=0.22, Figure 6a) was weaker than the relationship between G_{smax} and VPD (R^2=0.40, Figure 6a). Reference conductance at 1 kPa (i.e., b_{ref}) and stomatal sensitivity to VPD (m) were both higher at the canopy-scale (G_{smax}) than at the leaf-scale (g_s) (Figures 6a and 6b). Importantly, throughfall reduction did not influence leaf- or canopy-scale responses to VPD. In other words, g_s and G_{smax} both declined with increasing VPD and did so consistently across treatments (p=0.46 and p=0.54 for treatment differences in g_s and G_s responses to changing VPD, respectively).

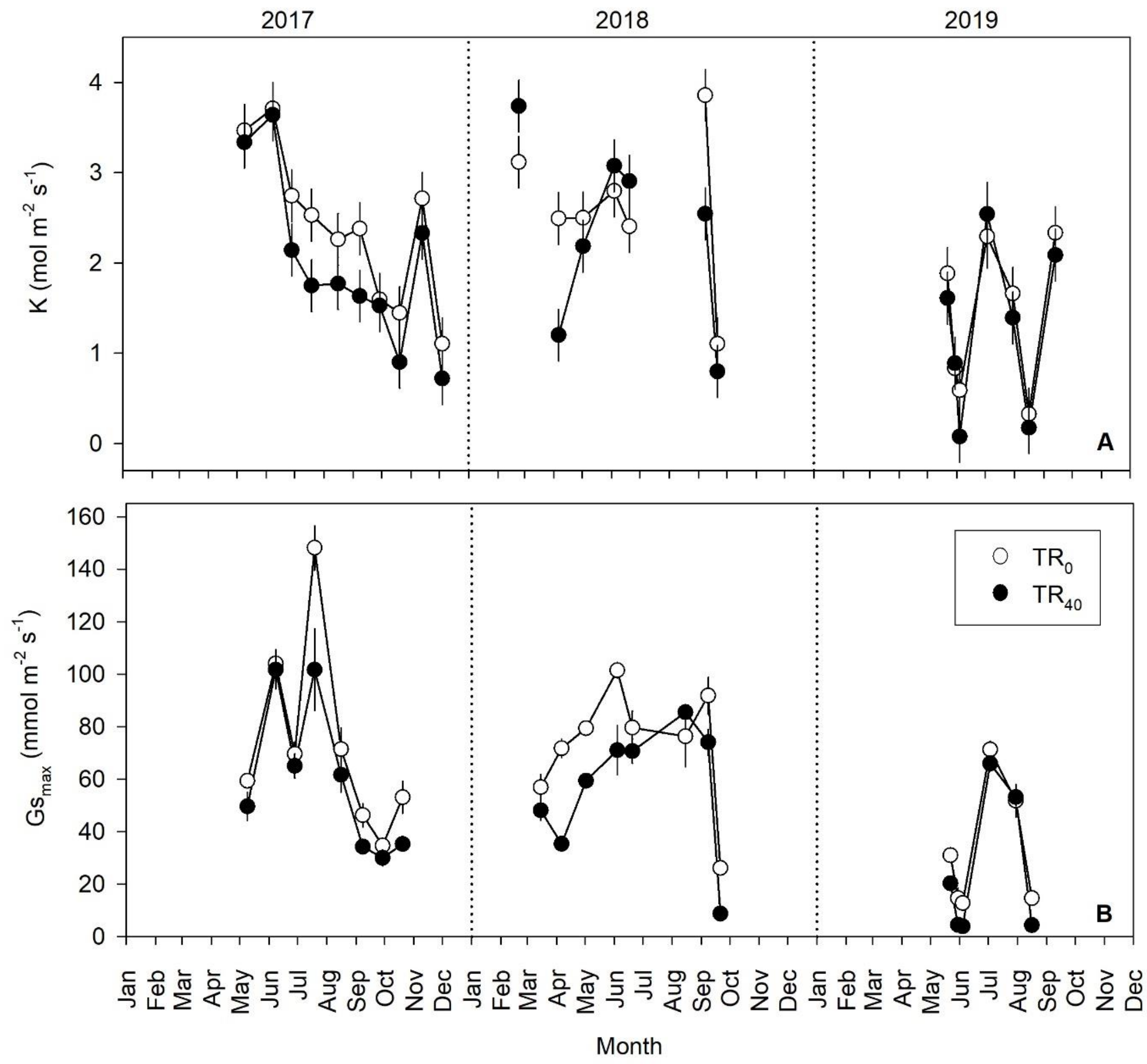

Figure 5. Mean (± standard error) values for maximum canopy-level stomatal conductance (G_{Smax}) across the same dates as the leaf water potential measurements [A] and whole-tree hydraulic conductance (K) [B] in ambient throughfall (TR_0) and 40% throughfall reduction (TR_{40}) treatments in a longleaf pine plantation.

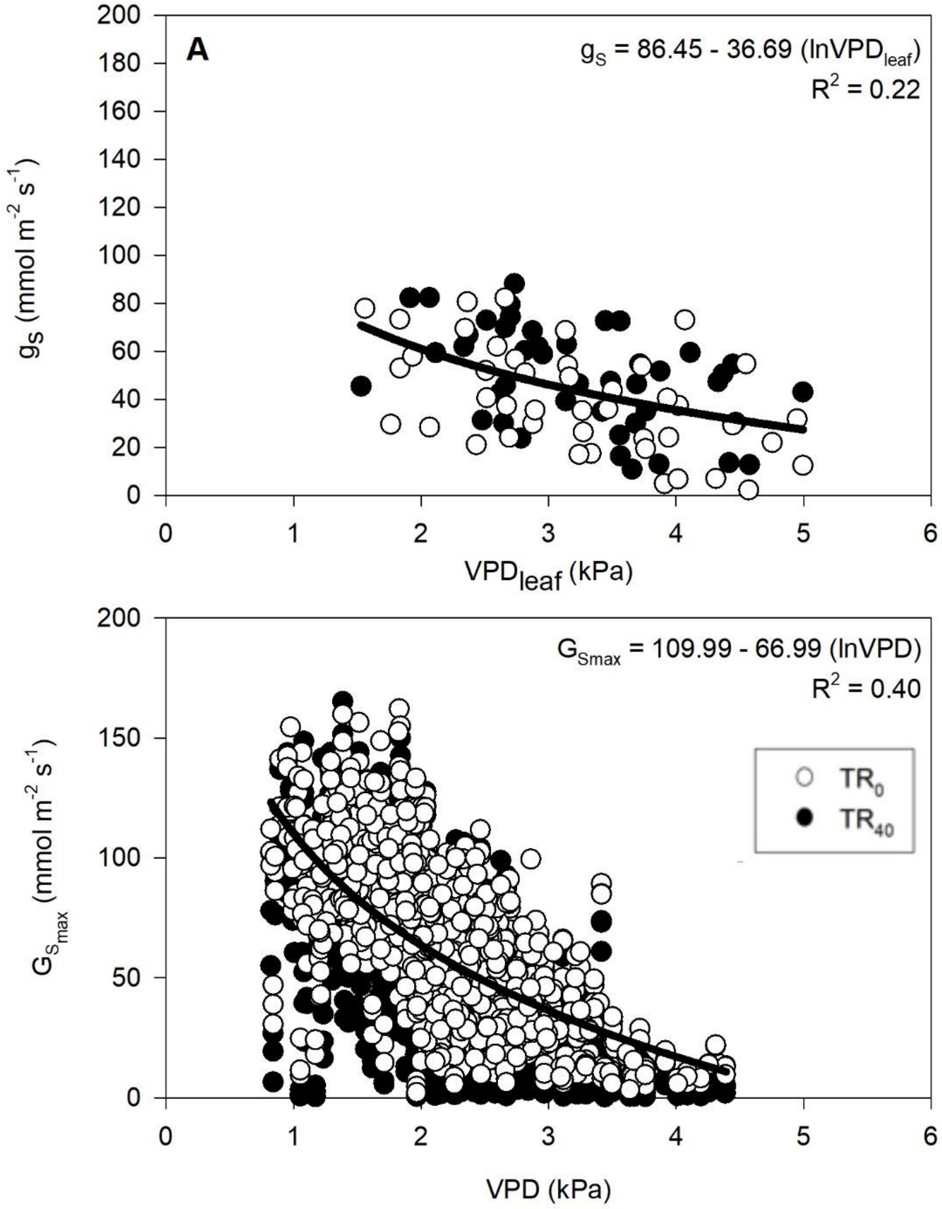

Figure 6. [A] The responses of leaf-level stomatal conductance (g_s) to the leaf chamber vapor pressure deficit (VPD$_{leaf}$), and [B] the response of maximum daily canopy-level stomatal conductance (G_{Smax}) to vapor pressure deficit (VPD) in longleaf pine trees growing under ambient throughfall (TR$_0$) and 40% throughfall reduction (TR$_{40}$) treatments.

4. Discussion

Here, we determined the effects of 40% throughfall reduction on leaf- and canopy-scale physiology in a 12- to 14-year-old longleaf pine plantation over a three-year period. We hypothesized that longleaf pine would respond to throughfall reduction by reducing g_s to maintain relatively constant Ψ_{MD}. Reduced g_s, in turn, would result in lower P_{net} but higher iWUE. We also expected that reduced leaf- and canopy-scale conductance with throughfall reduction would result in reduced stomatal sensitivity to VPD. Over three years, we found that 40% throughfall reduction decreased volumetric soil water content but resulted in relatively small reductions in g_s and P_{net} and did not change instantaneous or isotopically determined leaf-scale water use efficiency. Reduced throughfall also caused as small reduction in K and G_{smax}. Importantly, throughfall reduction had no effect on leaf- or canopy-scale stomatal sensitivity to VPD. The results of this experiment show that, even on a sandy, well-drained site, established longleaf pine trees may be relatively resistant to a 40% reduction in annual rainfall.

Averaged over time, 40% throughfall reduction resulted in lower soil moisture and a small decrease in g_s. Reduced g_s was expected and is a typical response to soil water deficit, particularly in tree species that are generally considered to be more isohydric (Clark et al., 2012; Domec et al., 2009; Fuchs and Livingston, 1996; Hubbard et al., 2001). Reductions in g_s were coupled with small reductions in P_{net}. Realized P_{net} is determined by physical (e.g., stomatal resistance to CO_2 diffusion) and biochemical limitations (e.g., mesophyll conductance and Rubisco carboxylation, Andersson and Backlund, 2008; Flexas et al., 2004; Parry et al., 2002). Although we did not carry out photosynthetic CO_2-response measurements to determine the biochemical capacity of photosynthesis, we hypothesize that stomatal rather than biochemical limitations were largely responsible for the small reductions in P_{net} under throughfall reduction. We expect this given that the reduction in g_s with throughfall reduction was somewhat small, suggesting a weak drought effect on leaf physiology (Flexas and Medrano, 2002). We also found that leaf N, on both a percent (mass) basis (%N) and leaf area basis (N_{area}), was not affected by throughfall reduction. Foliar N serves as a measure of the total enzyme (photosynthetic, respiratory) content of the foliage and often scales positively with the maximum capacity for Rubisco carboxylation (i.e., V_{cmax}, Atkin et al., 2015; Diaz-Espejo et al., 2007; Medlyn et al., 2002). If throughfall reduction did alter photosynthetic biochemistry, we might expect differences in leaf N between treatments (Lal et al., 1996; Parry et al., 2002; Pelloux et al., 2001). Previous studies have found that drought effects on photosynthetic biochemistry are complex. Droughts that are modest or short in duration typically have little effect on mesophyll conductance or photosynthetic biochemistry (Flexas and Medrano, 2002), and reduced g_s is considered the primary limitation to net CO_2 uptake and plant production. However, more severe and long-lasting droughts can significantly reduce mesophyll conductance and lead to down-regulation of photosynthetic capacity (Diaz-Espejo et al., 2007; Drake et al., 2016; Flexas et al., 2004; Flexas and Medrano, 2002). Taken together, it is likely that stomatal limitation was the primary limitation of P_{net} under 40% throughfall reduction, although further investigations would help determine whether photosynthetic capacity was affected.

Despite small reductions in g_s and a trend for reductions in P_{net}, iWUE was not increased under the throughfall reduction treatment as we expected. Likewise, the 40% throughfall reduction and subsequent reductions in g_s and P_{net} were not strong enough to change foliar $\delta^{13}C$, suggesting no increase in time-integrated foliar iWUE. Under marked reductions in g_s, increased foliar $\delta^{13}C$ is usually expected for trees under water stress, indicating higher iWUE (Castillo et al., 2018; Helle and Schleser, 2004; Shestakova et al., 2017). These results reinforce our conclusion that throughfall reduction had little effect on leaf-scale physiology of longleaf pine trees in this study.

Reduced Ψ usually has varied effects on g_s and leaf water loss, depending on the species and the frequency or intensity of the stress. Samuelson et al., (2019) found exceptionally low Ψ_{PD} and Ψ_{MD} values in the same longleaf pine trees (average lows of -2.9 and -3.6 MPa for Ψ_{PD} and Ψ_{MD}, respectively) during an extreme drought event during late summer to early autumn 2016. During that event, which lasted 77 days with very little to no rain, trees in both treatments were equally stressed and ceased transpiration at the canopy-scale. However, in our study, regardless of the changes in g_s under the reduced throughfall treatment, changes in Ψ did not occur as hypothesized. Overall, trees in the throughfall treatment were able to maintain relatively stable Ψ_{PD} over time. Studies with other southern pines, including longleaf pine, have shown that Ψ_{PD} levels must be strongly reduced during drought to impact leaf-level physiology. For example, in loblolly pine, Tang et al., (2004) showed that P_{net}, g_s, and transpiration declined sharply when Ψ_{PD} fell below -0.8 MPa. Domec et al., (2009) also showed that Ψ_{PD} declines steadily in loblolly pine when relative extractable water (REW) drops below 40-50%. In comparison, Samuelson et al., (2019) found that Ψ_{PD} declines at a lower REW level (~20%) in longleaf pine, indicating greater drought tolerance. During our study period there were many instances when REW dropped below 20% (volumetric water content ≤ ~4%), but these declines were likely too brief to cause severe reductions in Ψ_{PD} and leaf physiology. Samuelson et al., (2019) also found that Ψ_{MD} at stomatal closure (Ψ_{close}) and the turgor loss point (Ψ_{tlp}), both indicators of drought resistance (Bartlett et al., 2012; Martin-StPaul et al., 2017), were as low as -2.9 and -3.0 MPa, respectively, in longleaf pine. These threshold Ψ_{MD} values were never surpassed in our study, which might explain the relatively small effect of throughfall reduction on g_s. Similar to previous studies, substantial variation in K was observed over time in both treatments in response to changes in soil moisture (Addington et al., 2004; Oren et al., 2001). Yet, overall, throughfall reduction had little effect on K, suggesting that the 40% throughfall reduction treatment was not strong enough to severely impact tree hydraulic integrity during the study period.

The small reductions in g_s and in P_{net} were apparently not sufficient to impact growth either. In the same study, Samuelson et al., (2019) showed that three years of throughfall reduction had little effect on individual tree diameter, height, forest productivity (e.g., above-ground net primary production), or tree mortality. However, the effect of small reductions in tree function may be slowly accumulating. Samuelson et al., (2019) reported that stand volume was reduced by 21% by the 40% throughfall reduction treatment, although ANPP was generally unaffected. Samuelson et al. (2019) also reported no differences in peak leaf area index (LAI) between treatments (average peak ranged between 2.6-3.2 m^2 m^{-2}). Relatively low LAI compared to other southern pines at the same age (Domec et al., 2009) may partly explain the small effects of throughfall reduction on the physiology of longleaf pine trees in this study. It is possible that larger and more persistent reductions in precipitation are required to significantly reduce longleaf productivity, even on sandy well-drained sites.

During the time period for our study, precipitation was relatively similar among years and relatively frequent within years. The maximum period observed with no rain was 20 days, and the average interval between rain events was five days. Our results and those of Samuelson et al., (2019) suggest that relatively large reductions in total annual precipitation are unlikely to have strong negative impacts on established longleaf pine forests, even on xeric sites, unless reductions in average rainfall also coincide with long dry spells (Engelbrecht et al., 2017; Phillips et al., 2016). Future experimental work might consider treatments that alter rainfall timing and frequency, in addition to rainfall amount.

In comparison to our results with longleaf pine, studies with loblolly pine have shown stronger reductions in tree function and growth with a smaller reduction (-30%) in throughfall (Maggard et al., 2016; Samuelson et al., 2018; Tang et al., 2004). Moreover, the study sites with loblolly pine were more poorly drained, and soil moisture was generally higher than in our study (Gonzalez-Benecke et al., 2011b; A. O. Maggard et al., 2016; Samuelson et al., 2018; Tang et al., 2004). The different sensitivity of longleaf and loblolly pine to reduced precipitation fits with the general view that longleaf is better adapted to low soil moisture conditions. Even so, previous work provides mixed support for this view. For example, in a similar study with longleaf growing on a xeric sandhills site, Addington et al., (2004) found that g_s was reduced by 53% during ~2-month drought ($\theta < \sim 2\%$) compared to a recovery period. Their results indicate that longleaf pine can be sensitive to prolonged periods of reduced soil moisture, especially on xeric sites. A drought of this severity was not observed in our study. Also, longleaf growing on xeric sites may tolerate drier conditions through adjustments in whole-tree biomass partitioning or hydraulic architecture. For example, Addington et al., (2006) found that longleaf pine trees on xeric sites can show equal or greater g_s compared to trees growing on mesic sites, which may reflect adjustments in hydraulic architecture.

Previous studies with longleaf pine have demonstrated reductions in g_s and G_s with increasing VPD (Addington et al., 2006, 2004; Gonzalez-Benecke et al., 2011a; Samuelson et al., 2019; Samuelson and Whitaker, 2012). We determined whether throughfall reduction changes how g_s and G_{smax} respond to increasing VPD; a question that, to our knowledge, has not been tested. Previous work in other species indicates that reductions in G_s at a reference VPD of 1 kPa with reduced precipitation coincide with reductions in stomatal sensitivity to VPD (Grossiord et al., 2018; 2017), calculated based on Oren et al. (1999). Thus, we expected that any decline in g_s and G_{smax} with throughfall reduction would be coupled with decreased stomatal sensitivity to VPD at the leaf- and canopy-scale. However, we found no treatment differences in stomatal sensitivity to VPD, at the leaf- or canopy-scale. In other words, trees growing under a 40% reduction responded similarly to increasing VPD as trees growing under ambient, high rainfall conditions. We argue that the reduction in g_s and G_{smax} with throughfall reduction was rather small over time, and not strong enough to cause changes in stomatal sensitivity to VPD. This result highlights the potential importance of species differences, site conditions, and the severity of drought when considering tree responses to increasing VPD. We note that another study that examined stomatal sensitivity to VPD in longleaf pine found that canopy-scale b_{ref} and m were lower than leaf-scale b_{ref} and m (Addington et al., 2004). In other words, leaf-scale g_s is higher and more sensitive to VPD than G_s. We observed the opposite; canopy-scale b_{ref} and m were higher than leaf-scale values. Several factors could explain the differences between studies including different chamber conditions for leaf-scale measurements, or the use of G_{smax} instead of G_s, and differences in tree age and stand conditions.

5. Conclusion

Here, we studied how three years of reduced rainfall amount (throughfall reduction) impacted leaf- and canopy-scale physiology of relatively large, established longleaf pine trees. Although longleaf is considered to be among the most drought resistant tree species in the southeastern U.S., we still expected significant changes in leaf- and canopy-scale physiology. Instead, we found that a 40% reduction in rainfall resulted in small reductions in leaf- and canopy-scale function. Previous findings from the same experiment showed that stress conditions only occur during long dry spells with little or no rainfall. Therefore, changes in rainfall frequency (or dry spell duration), especially during warmer seasons, could potentially have larger impacts on tree function than changes in total annual rainfall. Although logistically challenging, future experiments that alter multiple aspects of rainfall timing, frequency, or amount would help advance our understanding of drought resistance and resilience in longleaf pine.

Acknowledgements

Support for this work was provided by USDA National Institute of Food and Agriculture McIntire Stennis Program (Award 1018413), the Intergovernmental Support Agreement between the U.S. Army – through the Natural Resources Branch at Fort Benning – and Auburn University (Award BENNING-IGSA-16-00), the Auburn University Intramural Grants Program (Award 180286), and the Alabama Agricultural Experiment Station – Agriculture Research Enhancement & Seed Funding Program (Award 1025522). The authors thank Jake Blackstock for assistance with experiment installation and data collection, Dr. George Matusick for assistance with project funding, site selection and maintenance, the Georgia Department of Natural Resources for permitting site access and housing, and The Nature Conservancy (grant no. 2282-1) for assisting with site maintenance, housing, and funds for the sap flow equipment.

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CHAPTER III

EXPERIMENTAL THROUGHFALL REDUCTION HAS LITTLE EFFECT ON SHOOT AND NEEDLE PHENOLOGY AND DEVELOPMENT PATTERNS OR LEAF AREA DYNAMICS IN A YOUNG LONGLEAF PINE PLANTATION

Abstract

Reduced precipitation and, consequently, low soil moisture are known to limit tree growth and function. However, the impacts of reduced rainfall on shoot and foliage phenology and development in some species, as well as canopy-scale leaf area dynamics and litterfall, remain unclear. Longleaf pine is considered one of the most drought-resistant forest species in the southeastern U.S. and could serve as a pathway to increase drought resistance of forests in the region. Still, reduced precipitation and low soil moisture impacts on longleaf canopy phenology and growth are not well understood. Over three years (2017-2019), we determined the effects of 40% throughfall reduction (TR_{40}) (relative to ambient throughfall treatment, TR_0) on shoot and foliage phenology and growth in a young (12-14 yr. old) longleaf pine (*Pinus palustris* Mill.) plantation. Each year, we repeatedly measured shoot and needle lengths on primary and secondary branch axes of multiple trees in each treatment plot. We fit growth curves for each tree and branch axis to estimate shoot and needle growth rate, growth start and cessation dates, growth duration (growth start - growth cessation), and final shoot and needle lengths. At the plot level, we documented temporal patterns of leaf area index (LAI) and litterfall to determine whether branch-scale phenological and growth responses to reduced water availability corresponded with temporal changes in LAI and litterfall. We observed significant and consistent differences in shoot and needle elongation patterns between primary and secondary branches. Timing of needle development varied among years and was generally later each successive year. However, shoot elongation patterns were relatively consistent across years. Although soil moisture was lower under throughfall reduction, shoot and needle growth patterns were not affected. LAI and litterfall patterns were also not affected by throughfall reduction. Our results indicate that reductions in rainfall amount (without changes in rainfall frequency or timing) may have little impact on shoot and needle phenology, canopy development, and litter production in established longleaf plantations, with implications for stand-scale resource use and nutrient cycling.

1. Introduction

Climate is warming, and precipitation patterns are changing in many parts of the world (Melillo et al. 2014, IPCC 2014, Carter et al. 2018). In the southeastern US, warmer temperatures and more frequent and intense summer dry spells (Dai, 2011; Williams et al., 2013) will likely result in increased atmospheric demand and evapotranspiration (McNulty et al. 2013). Population growth and greater water demand are also straining water resources in the region (Brantley et al., 2018). About 15 million hectares of pine plantations currently exist in the southeast US, a region that produces more wood annually than any other region in the U.S. or country in the world (Butler and Wear, 2013; Wear and Greis, 2013). Greater water demand and reduced water availability could negatively impact forest productivity and sustainability in the region (Allen et al., 2015; Bonan, 2008; Breshears et al., 2013; Piao et al., 2019; Will et al., 2013). However, there are still considerable uncertainties about the potential impacts of reduced water availability on forest productivity in the southeastern U.S. and underlying processes.

Temporal patterns of shoot and foliage development, or phenology, are known to be important determinants of leaf area development and turnover as well as canopy-scale carbon (C) and H_2O fluxes (Adams et al., 2015; Lieth, 1974; Piao et al., 2019). Over space and time, tree phenology is strongly determined by day length and temperature (Basler and Körner, 2014; Menzel et al., 2006; Vitasse et al., 2010; Way and Montgomery, 2015), and, in some systems or species, precipitation (Ogaya and Penuelas, 2004; Peñuelas et al., 2004). Notably, many studies have provided clear evidence that climate warming is altering tree phenology. Climate warming at the local scale is advancing dates for bud break, affecting shoot elongation and leaf development, and flowering time for many temperate tree species (Adams et al., 2015; Menzel, 2000; Menzel et al., 2006; Miller-Rushing and Primack, 2008; Peñuelas et al., 2002; Primack et al., 2009). As a result, climate warming generally lengthens the growing season and increases growing season C uptake and forest productivity (Boisvenue and Running, 2006; Kunkel et al., 2013; Peñuelas et al., 2002; Rennenberg et al., 2006). However, climate warming impacts on tree phenology and forest function could be intensified by co-occurring increases in vapor pressure deficit (VPD; (Adams et al., 2015; Peterson and Peterson, 2001; Williams et al., 2013). Once leaves are fully formed, increased VPD can drive increased tree water use in some species – which could intensify the effects of reduced water availability. In other species, increased VPD may induce stomatal closure and lower transpiration, simultaneously reducing C uptake and C available for tree growth, respiration, and defense (Grossiord et al., 2017; McDowell et al., 2019). High VPD conditions also tend to co-occur with drought conditions, further diminishing the potential positive effects of warming on tree performance (Adams et al., 2015; Overpeck and Udall, 2010; Williams et al., 2013).

While the effects of climate warming on tree phenology are increasingly understood, tree phenological responses to reduced rainfall and resulting impacts on canopy leaf area development are not well understood for many species and forest types. This knowledge gap limits our quantitative and predictive understanding of drought impacts on forests. In relatively arid regions, there is evidence that lower water availability caused by reduced precipitation can reduce the amount or rate of leaf development, contributing to reductions in tree growth and ecosystem productivity (Adams et al., 2015; Limousin et al., 2012; Massonnet et al., 2021; Ogaya and Penuelas, 2004). The impacts of reduced precipitation on tree phenology in more mesic regions remains unclear, although a recent study with *Fagus sylvatica* showed that prolonged drought can delay bud burst and advance leaf senescence – effectively shortening the growing growth season (Massonnet et al., 2021). The impacts of reduced water availability on tree phenology may depend upon the magnitude of the water deficiency, species differences, and other local edaphic conditions (Breshears et al., 2005; Engelbrecht et al., 2017, 2007; Johnson et al., 2018). Reduced foliage growth and elongation, decreased branching rate, and delayed leaf development have been reported in some rainfall exclusion experiments with forest trees (Borghetti et al., 1998; Girard et al., 2012, 2011; Limousin et al., 2012; Ogaya and Penuelas, 2004; Peñuelas et al., 2004). The negative effect of reduced precipitation on leaf development and area not only results in lower light interception and canopy-scale C fixation, but also lower transpiration. Lower transpiration at the leaf and canopy scale reduces the demand and consumption of water, which can temporarily improve tree drought resistance (Choat et al., 2018; López et al., 2021; Wang et al., 2009). More experimental field-based studies, carried over multiple years with different species growing in different climates, are urgently needed to better understand the impacts of reduced precipitation on tree phenology.

Changes in leaf phenology in response to reduced water availability may coincide with changes in leaf morphology, structure, biochemistry, or longevity (Adams et al., 2015; Escudero and Mediavilla, 2003; Gebauer et al., 2015; Limousin et al., 2012; Ogaya and Penuelas, 2004; Sheffield et al., 2003). For instance, delayed leaf emergence under reduced water availability was associated with reduced leaf and shoot growth (i.e., shorter or smaller needles and buds) in pine species in the southern U.S. (Adams et al., 2015; Grossiord et al., 2017; Limousin et al., 2012; Ogaya and Penuelas, 2004; Sheffield et al., 2003). Reduced leaf growth and development were likely caused by leaf turgor reductions rather than reductions in C fixation or C availability (Fatichi et al., 2014; Körner, 2003; Woodruff et al., 2004). Reduced water availability leads to negative pressure in the xylem and lower turgor pressure, which reduces the rate of cell division and expansion in the meristems (Hale and Orcutt, 1987; Woodruff et al., 2004). Thus, water limitations within plants are initially responsible for limiting growth more than C limitations, which can intensify as drought persists or intensifies. However, there are still uncertainties about the impacts of reduced water availability on branch and foliage phenology and development and whether reductions in water availability vary within the tree canopy (e.g., among branches axes). New studies that address these uncertainties could provide further information regarding coordinated changes in shoot and leaf phenology and growth, as well as spatial variation within tree canopies.

Longleaf pine (*Pinus palustris* Mill.) is an ecologically important timber species with a broad distribution in the southeastern United States. This species occurs across a wide range of sites, including sand hills and uplands, where low water availability is relatively common (Brockway et al., 2007; Landers et al., 1995; Oswalt et al., 2012) and other southern pines are less common or less productive. For this reason, longleaf pine is considered to be more resistant to reduced water availability than the other southern pine species (Samuelson et al., 2019, 2014). Greater drought resistance in longleaf pine could result from lower leaf area and water use (i.e., lower transpiration) and higher stomatal sensitivity to soil moisture (Brantley et al. 2018, Ford et al., 2008; Gonzalez-Benecke et al., 2011; Whelan et al., 2015). Increased resistance to reduced water availability could also be partly explained by physiological, phenological, and morphological adjustments that increase access to water or reduce water use (Addington et al., 2006, 2004; Gonzalez-Benecke et al., 2010; Samuelson et al., 2019; Sheffield et al., 2003; Starr et al., 2016; Whelan et al., 2015; Wright et al., 2013). For example, in a long-term study, Starr et al. (2016) demonstrated that longleaf pine trees avoided or resisted drought through phenological plasticity, such as the annual replacement of older drought-exposed needles with new needles that were drought-adapted, allowing for continued C uptake during and after the stress period. Likewise, Sheffield et al. (2003) found that mature longleaf pine trees on a xeric site showed reduced shoot elongation, delayed needle growth initiation, and lower needle growth rates than trees on a mesic site. However, Addington et al. (2006) found that mature longleaf pine trees on mesic and xeric sites maintained similar physiological activity and maintained comparable growth rates. Additional studies that determine the impacts of reduced precipitation on shoot and needle phenology and patterns of needle production will provide further insight into the potential impacts of reduced water availability on longleaf phenology and productivity. Also, longleaf pine litterfall patterns have not been investigated in detail under experimental throughfall exclusion and reduced water availability. Thus, it is still not clear how reduced water availability influences canopy turnover in longleaf forests. Potential changes in the timing or amount of litterfall could have important implications for nutrient cycling.

The purpose of this study was to determine the effects of reduced water availability on longleaf shoot and foliage phenology and development, as well as stand-scale leaf area dynamics and litterfall. To accomplish this, we carried out a throughfall manipulation experiment in a young (12-14 yr. old) longleaf pine plantation in Georgia, USA, for three years (2017 to 2019). The experiment included two treatments: ambient throughfall (TR_0)

and 40% throughfall reduction (TR_{40}). We repeatedly measured (biweekly measurements) shoot and needle lengths on primary and secondary branch axes (branch orders) of multiple trees in both treatments between late winter (February/March) and late autumn (October/November) to assess shoot and needle elongation and phenology. We also measured leaf area index (LAI) and litterfall (foliar and non-foliar litterfall) each month of the experiment to assess seasonal dynamics in leaf area development and turnover. We addressed the following questions: (1) Does reduced soil moisture caused by throughfall reduction alter patterns of shoot and needle development in longleaf pine, and if so, are the effects consistent across years and across different branch axes (i.e., primary versus secondary branch axes)?, and (2) Does reduced water availability caused by throughfall reduction change seasonal dynamics of leaf area development and turnover, and do changes in leaf area dynamics mirror changes in needle phenology and growth? We hypothesized that throughfall reduction would delay needle and shoot elongation, shorten the period of shoot and needle growth, reduce total shoot and needle lengths, and reduce LAI.

2. Material and Methods

2.1. Study site description and experimental design

The complete description of the experimental site and experimental design was previously described in Samuelson et al. (2019) and Mendonça et al. (*submitted*). Here, we briefly describe the site and design. The study was established in a longleaf pine plantation in the Chattahoochee Fall Line Wildlife Management Area in Marion County, GA (32.5528˚ N, -84.776˚ W) in May 2016. The site is owned by the Georgia Department of Natural Resources and managed by The Nature Conservancy. Thirty-year mean (1981-2010) annual precipitation for Americus, GA (approximately 60 km from site) is 1245 mm. Tropical storms passed over the site on September 11, 2017 (Irma), October 11, 2018 (Michael), and September 4, 2019 (Dorian). Mean annual minimum and maximum air temperatures are 11.0 °C and 24.6 °C, respectively. Mean annual temperature is 17.8 °C (https://www.ncdc.noaa.gov/cdo-web/datatools/normals, accessed February 2021). The site elevation is 210 m. The site was planted at the beginning of 2005 at an approximate spacing of 2.6 m x 2.6 m (1479 trees ha^{-1}). Soils at the site are in the Lakeland Series (2-5% slopes), which are Thermic, coated Typic Quartzipsamments, that consist of very deep, excessively drained, and rapid to very rapidly permeable soils (Soil Survey Staff 2016).

Six 21 m x 31 m (0.07 ha) treatment plots were established at the site. Plots were surrounded by two rows of buffer trees. In the center of each treatment plot, we established an 11 m x 21 m (0.02 ha) measurement plot. Half of the treatment plots (n=3) were randomly assigned to an ambient throughfall (TR_0) treatment. The other half of the treatment plots (n=3) were assigned to an approximate 40% throughfall reduction (TR_{40})

treatment. Pretreatment means for basal area, density, DBH, and height among all plots were 18.2 m^2 ha^{-1}, 1029 trees ha^{-1}, 14.7 cm, and 9.5 m, respectively. Blocks were selected based on pre-treatment estimates of stand basal area, which did not differ between TR_0 and TR_{40} plots prior to treatment initiation.

The 40% throughfall reduction was determined based on the 100-year mean annual precipitation for the area. The approximate 60% residual throughfall represented the 1st percentile of annual precipitation (i.e., 1 in 100-year drought event) for Americus, Georgia (802 mm). To limit throughfall by approximately 40%, and thereby reduce soil moisture, throughfall exclusion troughs spanning 1.54 m were installed between rows. The troughs are an average height of 1.3 m and separated by a gap of 50 cm within a row. The throughfall exclusion tray frames were constructed from pressure-treated lumber and steel studded t-posts. Troughs were constructed out of 12 mil polyethylene sheeting (Polyscrim 12, Americover Inc., Escondido, CA). A total of 16 troughs were installed per plot and covered 40% of the ground area in each plot. Throughfall is intercepted by the troughs and collected in large, corrugated pipes that carry the water at least 20 m from the edge of plots. Treatments were initiated 11 months before phenology measurements began in April 2017.

2.2. Environmental data

A weather station was installed approximately 0.55 km from the site in a 0.65 ha clearing to measure wind-speed, precipitation, air temperature, and relative humidity (both temperature and relative humidity used in VPD determination) (6152 Vantage Pro 2 Wireless Weather Station, Davis Instruments, Vernon Hills, Illinois). Relative humidity and air temperature were also measured by three sensors (HOBO U23 Pro v2 Temperature/Relative Humidity Logger, Onset Computer Corporation, Bourne, Massachusetts) under the canopy at approximately 2 m height at three locations in-between adjacent plots. Volumetric soil moisture (θ, %) was continuously monitored every minute at 5 cm, 15 cm, 50 cm, and 100 cm depths in all plots (10HS Large Soil Moisture Sensors – Decagon Devices, Inc., Pullman, WA, USA). Average θ was recorded every 30 minutes. A soil specific calibration was calculated following Starr and Paltineanu (2002). Soil moisture sensors were linked to data loggers (HOBO Micro Station Data Logger, Onset Computer Corp, Bourne, MA, USA). Sensors were located around the center of a plot and spaced 60 cm apart. Thus, in the throughfall reduction plots, soil moisture sensors were located under troughs. As the TR_{40} covered 40% of plot area, the soil moisture used in 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 soil moisture in the uncovered area in each of the TR_{40} plots was similar to that in the TR_0 plots in the same block.

2.3. Shoot and needle phenology

Shoot and needle phenological patterns were evaluated during the 2017, 2018, and 2019 growing seasons. Growing season length varied over the years but generally occurred between mid-February and late October. Biweekly measurements included total shoot length and needle length. One scaffolding unit (6 m tall) was installed in each measurement plot to help access the upper canopy of at least three measurement trees per plot. In each plot, two trees adjacent to the scaffolding were sampled. Two branches that were similar in size were selected on the two trees per plot. We conducted measurements on one primary and one secondary shoot axis of each branch, following Girard et al. (2012). Primary and secondary axes were defined as the main axis of the selected branch and the side branch subsidiary to its primary branch, respectively. Each branch and axis was tagged for the repeated shoot and needle elongation measurements, and the same branches were measured across the years. Shoot elongation measurements were carried out separately for each growth flush; in some cases, there were multiple growth flushes. Total shoot length was the sum of all flushes together. Needle elongation measurements were made on five needles in the first flush. A flexible tape was used to measure shoots, which were often curved. Digital calipers were used for fine-scale measurements of early needle elongation. A 50-cm ruler was used to measure needle lengths after needles exceed ~5 cm in length. In 2017, measurements began after shoot growth initiation (i.e., bud break), which prevented us from determining initial patterns of shoot elongation that year. In the following years (2018-2019), measurements started before bud break (mid-February). Hence, to guarantee the complete description of the patterns of shoot elongation, shoot growth curves were only established for 2018 and 2019. All three measurement years (2017-2019) were used to determine needle growth patterns since needle elongation began ~2 months after shoot growth initiation (see below). In all years, measurements were taken until shoot and needle growth ceased which was indicated by no change in shoot or needle lengths for several consecutive measurement dates.

2.4. Leaf area index (LAI)

Leaf area index (LAI, m^2 m^{-2}) was measured optically every three weeks in each measurement plot (LAI-2200C Plant Canopy Analyzer, LI-COR Inc., Lincoln, Nebraska). Below-canopy measurements were made in diffuse sunlight along three fixed 5m long diagonal transects in each plot. Each transect was divided evenly into five measurement points. A second sensor was placed in an open area (0.65 ha) adjacent to the site to record above-canopy measurements. The below-canopy measurements were paired to the above-ground (open sky) measurements using approximate measurement time by the software FV2200 v2.0 (provided by the manufacturer). Data were averaged by transect and then by treatment plot.

2.5. Litterfall patterns

Naturally abscised needles and small debris (i.e., non-foliar litterfall), such as small branches, bark, cones, and catkins, from the canopy were collected and recorded in each measurement plot every 3-4 weeks throughout the experiment. Litterfall was collected using traps composed of vinyl window screen stapled to 0.25 m^2 (0.5 m x 0.5 m) wood frames. Nine traps were placed in each plot. Locations were selected by randomly choosing a tree in the measurement plot, then assigning a location: within the row or between rows. Once assigned, the litter traps were randomly given a cardinal direction: north or south for traps in the rows, east or west for between the rows. Traps were then placed 1 m away from the base of the assigned tree in the randomly selected direction. In throughfall reduction plots, litter traps were placed on top of the throughfall reduction troughs. Litterfall samples were separated into needle and other small debris, dried to a constant mass, and weighed separately to quantify needlefall and other non-foliar debris.

2.6. Data Analyses

All statistical analyses were performed in SAS v9.3 (SAS Institute Inc. 2010). Individual needle and shoot elongation measurements were averaged by branch axis and tree. For each tree and branch axis, we plotted the relationship between needle length and day of the year (DOY) and shoot length and DOY. We considered several potential growth functions and found that a Gompertz (sigmoid) function adequately described these relationships. The function was written as:

Equation 1:

$$\text{Length}_{(\text{needle, shoot})} = \text{a} \times e^{-e^{\left(-\frac{DOY - c}{b}\right)}}$$

where parameter '*a*' is the estimated final length of the needle (mm) or shoot (cm), parameter '*b*' is the slope of the linear part of the growth curve and is an estimate of linear growth rate (GR, cm day^{-1}), and parameter '*c*' is the DOY when needle or shoot length reached the inflection point of the curve (~40% of the final length, Figure 3). The function in Equation 1 was fit using nonlinear least squared parameter estimation (PROC NLIN). This function provided an excellent fit to the needle and shoot length data with strong correlations between observed and predicted values (Figure 1). Using the parameter estimates for each tree and branch axis, we estimated several parameters that described stages of phenological development for needles and shoots (shown in Figure 2). The parameters were as follows:

growth start (GS, the day by which 3% of total needle or shoot growth had occurred), growth cessation (GC, the day by which 97% of total shoot or needle growth had occurred), and growth duration (GD, i.e., the number of days between GS and GC).

A linear mixed model (PROC MIXED) was performed to test the effects of year (2017, 2018, and 2019), branch axis (primary versus secondary axes), treatment (ambient throughfall versus 40% reduction throughfall), and respective interactions on the parameters (i.e., *a*, *b*, and *c*), GR, GS, GC, and GD. Because 'plot' is the experimental unit, in most cases, we averaged data collected across measurement trees in each plot. A linear mixed model (PROC MIXED) was used to test the effects of measurement date (i.e. time), treatment (ambient throughfall versus 40% reduction throughfall), and date × treatment on the patterns of LAI, needle fall, and non-foliar litterfall. All tests of statistical significance were conducted at $\alpha = 0.05$.

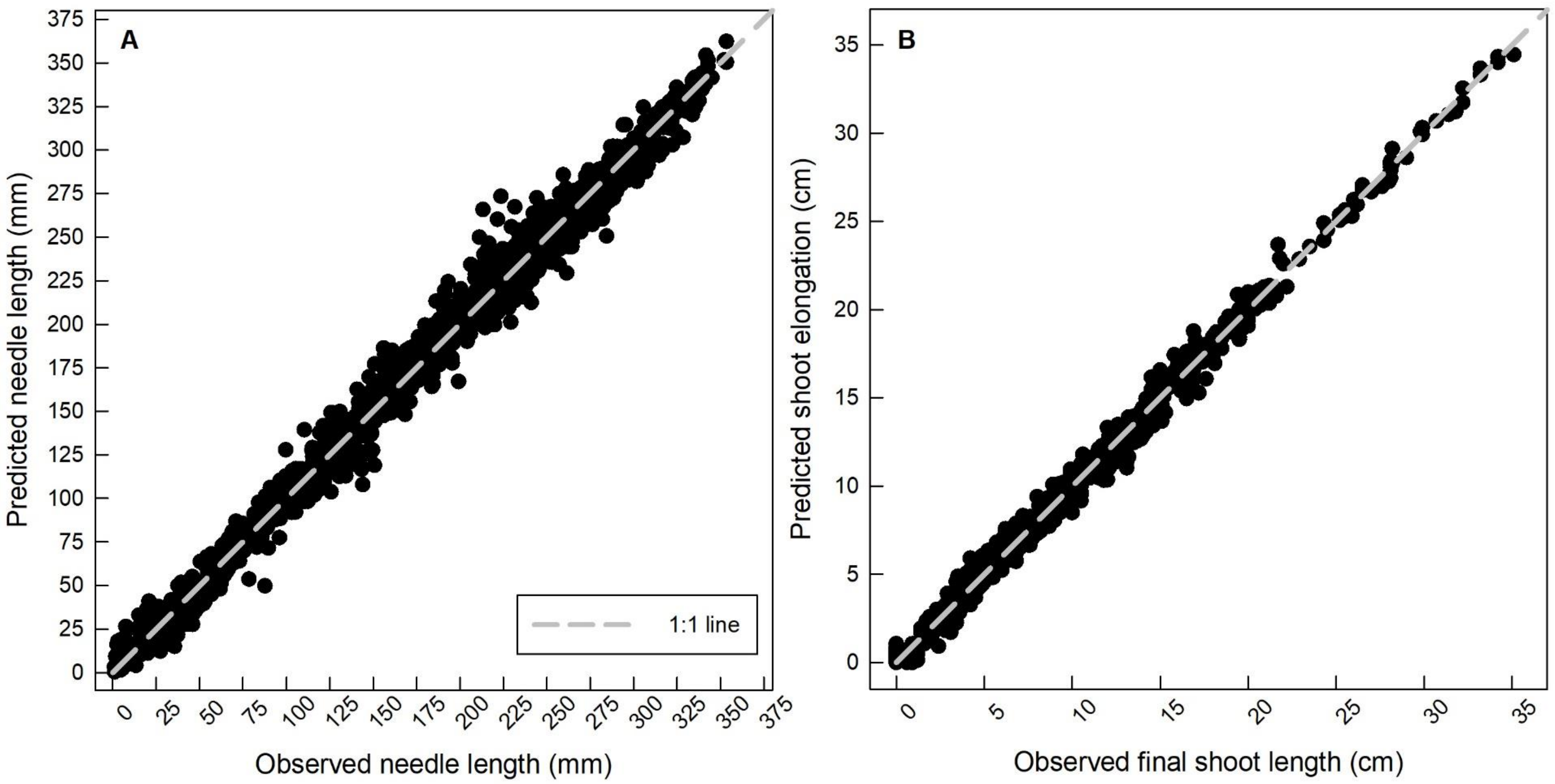

Figure 1. Observed versus predicted values of (A) needle length (mm) and (B) shoot length (cm). Predicted needle and shoot length values were determined using parameter estimates from the Gompertz sigmoidal function (Equation 1).

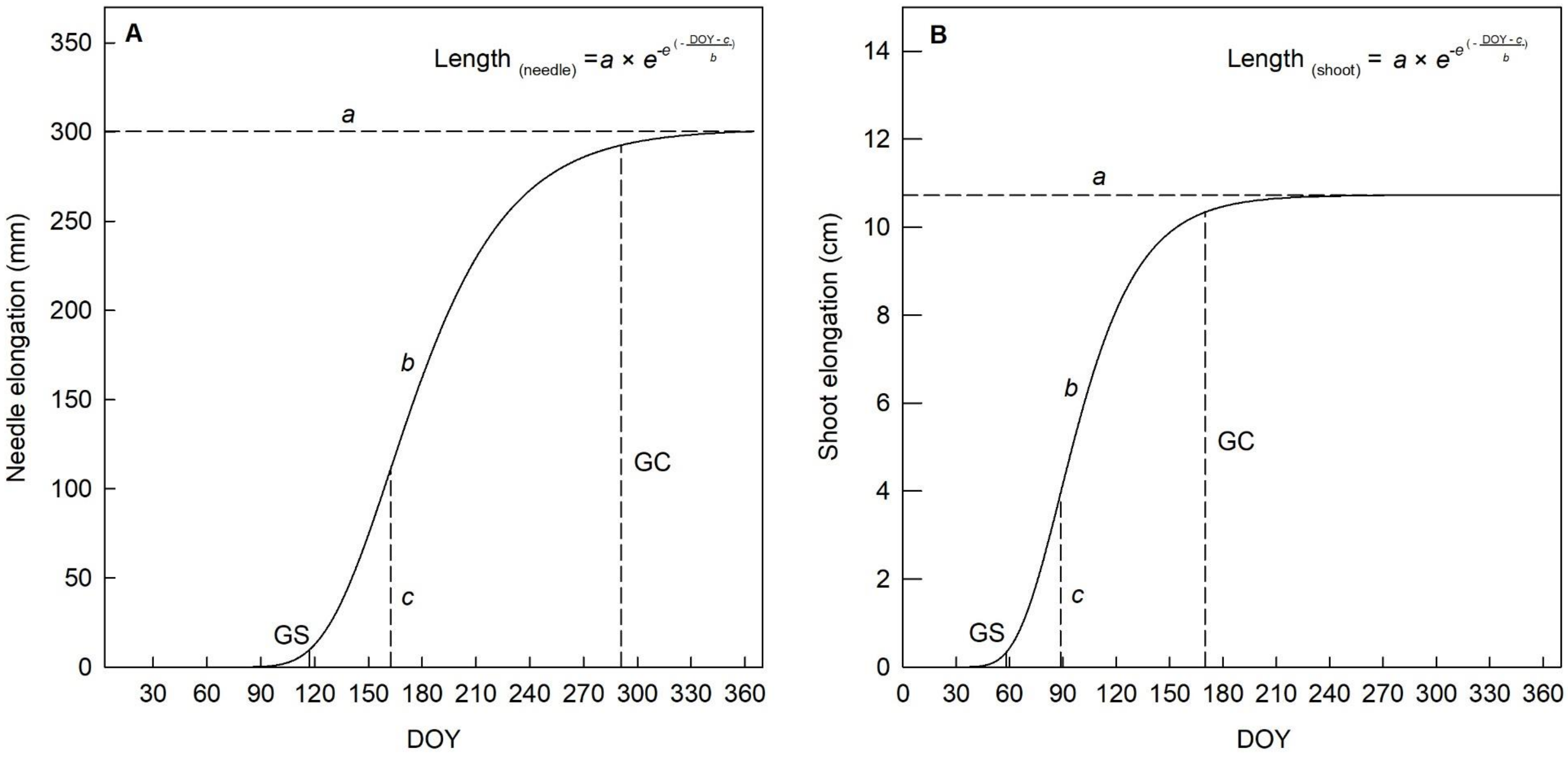

Figure 2. Schematic representation of the needle (A) and shoot (B) elongation curves used to describe the phenological development patterns along the year (i.e., day of the year – DOY) in a longleaf pine plantation in Marion County, Georgia, USA. The parameters were as follows: parameter '*a*': estimated final length of the needle (mm) or shoot (cm); parameter '*b*': slope of the linear part of the growth curve (also an estimate of linear growth rate); parameter '*c*': DOY when needle or shoot length reached the inflection point of the curve; GS: growth start, the day by which 3% of total needle or shoot growth had occurred; and GC, growth cessation, the day by which 97% of total shoot or needle growth had occurred.

3. Results

3.1. Environmental conditions

Annual precipitation at the site was 1234 mm in 2017, 1451 mm in 2018, and 1232 mm in 2019 (Figure 3). Compared to the 30-year precipitation average for the location of the experiment (1245 mm), 2017 and 2019 had slightly lower annual precipitation than the 30-year average, while 2018 had above-average precipitation (~17% more rain than the 30-year precipitation average for the area). In the 40% throughfall reduction treatment, residual rainfall was estimated to be 740 mm in 2017, 871 mm in 2018, and 739 mm in 2019. During shoot development (mid-February through October), total rainfall varied among the years: 843 mm in 2017, 1044 mm in 2018, and 822 mm in 2019.

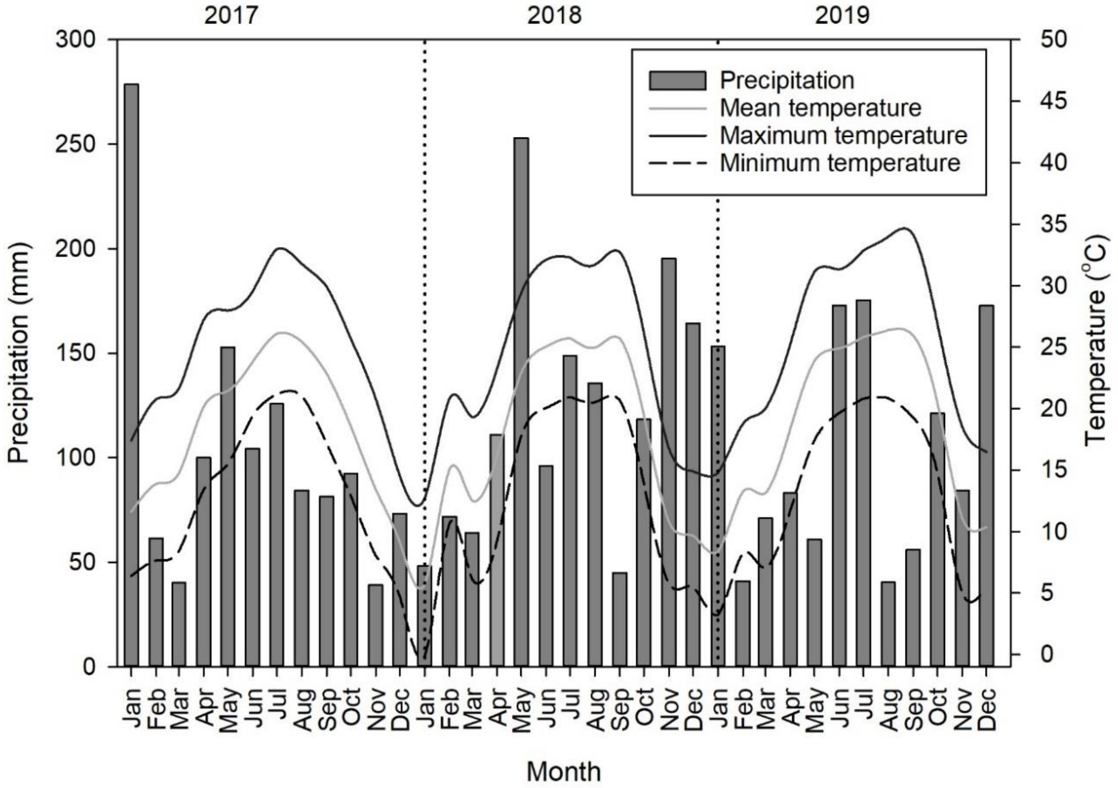

Figure 3. (A) Monthly precipitation (bars) and monthly mean maximum, mean, and mean minimum temperatures (lines) in a longleaf pine plantation in Marion County, Georgia, USA.

During each year of the study, annual mean, maximum, and minimum temperatures were similar and averaged as 18.6 °C, 25.2 °C, and 13.1 °C, respectively (Figure 3). Mean maximum temperatures of 2017 and 2019 were slightly above the average monthly maximum temperature for the study area.

3.2. Soil moisture

Mean daily soil moisture in the TR_{40} treatment (measured under throughfall exclusion trays) was often lower than in the ambient treatment (Figure 4). The difference in soil moisture between TR_{40} and TR_0 treatments generally decreased with increasing depth (Figure 4), and soil moisture was frequently lower at deeper positions within the soil profile in both treatments. Over time, soil moisture at 5, 15, 50, and 100 cm depths were on average 47, 41, 32, and 34% lower, respectively, in the TR_{40} plots compared with the TR_0 plots (Figure 4). Among years, monthly mean soil moisture at 5 cm depth varied between 7.3% and 8.8% in the TR_0 treatment and between 4.1% and 4.6% in the TR_{40} treatment. At 50 cm depth, monthly mean soil moisture varied between 4.3% and 6.5% in the TR_0 treatment and between 3.8% and 4.5% in the TR_{40} treatment.

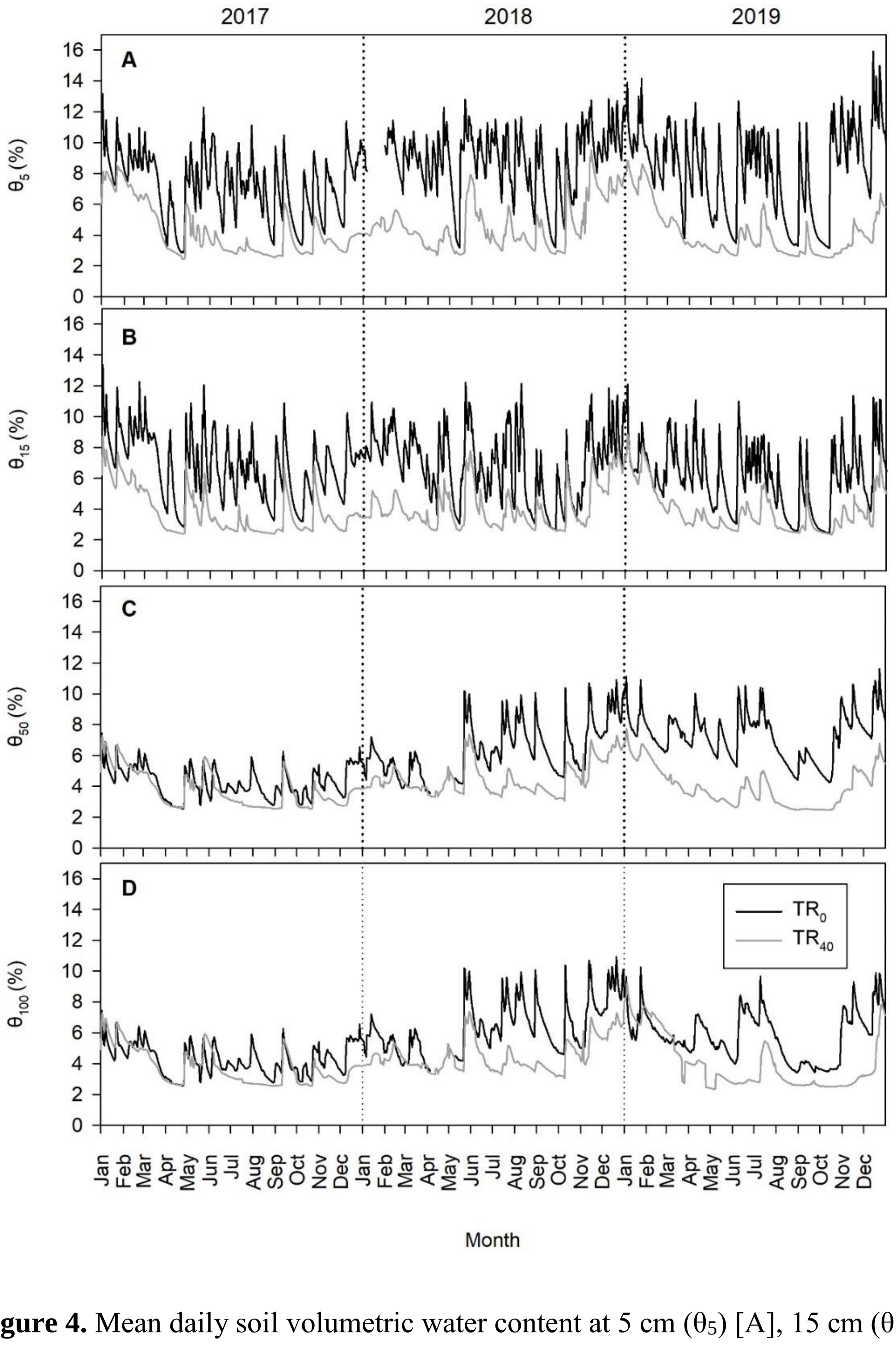

Figure 4. Mean daily soil volumetric water content at 5 cm (θ_5) [A], 15 cm (θ_{15}) [B], 50 cm (θ_{50}) [C], and 100 cm (θ_{100}) [D] depth in a longleaf pine plantation in response to throughfall reduction treatment (TR_{40}) in comparison with ambient throughfall (TR_0). Soil volumetric water content in the TR_{40} was measured under throughfall exclusion trays.

3.4. Phenological development patterns

Although shoot and needle elongation co-occurred during part of the growing seasons (shoot and needle overlapping growth period: 56 days in 2018, and 43 days in 2019; Figures 5A-C and 6A-C), the majority of the needle elongation occurred after shoot elongation ended (103 and 133 days between the shoot GC to the needle GC in 2018 and 2019, respectively; Figures 5C and 6C). The difference between shoot GS and needle GS was 66 and 67 days in 2018 and 2019, respectively (Figures 5A and 6A). In turn, GD was shorter for shoot than for the needle development. Specifically, needle elongation was 36 and 66 days longer than shoot elongation in 2018 and 2019, respectively (Figures 5D and 6D).

3.4.1. Shoot Growth

The start dates (GS) for shoot elongation differed between years (Table 1, Figure 5A) but were similar between branch axes (Table 1, Figure 5A). In 2018, shoot growth started on Julian day 54 ± 2. Shoot growth started roughly 9 days later in 2019 (Julian day 63 ± 2). In contrast to our expectations, throughfall reduction did not affect shoot GS (Table 1). Averaged across treatments, shoot growth started on Julian day 59 ± 2. No interactions between years, branch axes, and treatments were detected (Table 1).

Throughfall reduction had a marginally significant effect on parameter *c*, the Julian day when shoot elongation reached the inflection point of the shoot growth curve (p=0.054, Table 1, Figure 5B). On average, trees in the throughfall reduction treatment reached the curve's inflection point 8 days earlier than trees in the ambient throughfall treatment (Julian day 93 ± 2 for TR_0 and 85 ± 2 for TR_{40}). Parameter *c* also varied between measurement years (marginally significant p-value; Table 1). In 2018, parameter *c* was 86 ± 2. In 2019, parameter *c* was 92 ± 2 (Figure 5B). No interactions between years, branch axes, and treatments were detected for parameter *c* (Table 2).

The date when shoot GC occurred was similar between treatments. Across all measurements, shoot GC occurred around Julian day 175 ± 5. Therefore, shoot growth mainly occurred from late February in 2018 or early March in 2019 (growth starts) through late June of both years. Additionally, a marginally significant effect from the year × branch axis interaction was detected for GC (p=0.091, Table 1, Figure 5C). The interaction showed that in 2018 (p=0.044), there was a 17-day difference between the GC of the shoots from primary and secondary branch axes (shoot GC occurring at Julian day 186 ± 6 and 169 ± 6 for primary and secondary branch axes, respectively). No further interactions were observed for GC.

We also observed no differences in shoot GD between treatments (average shoot GD = 117 ± 6 days). However, we found a significant interaction between year × branch axis for shoot GD (Table 1, Figure 5D). Shoot GD of the primary and secondary branch axes differed in 2018 (p=0.015) but not in 2019 (p=0.603). In 2018, shoot GD of the primary branch axes was 134 ± 6 days, while shoot GD of the secondary axes was 113 ± 6 days. In 2019, both branch axes had GD of approximately 110 days ± 6. No further interactions were detected (Table 1, Figure 5D).

Parameter *b*, which represents the linear rate of shoot growth during the middle of the growth period, did not differ between treatments (Table 1). Across both treatments, parameter *b* was 24.6 ± 1.2 cm day^{-1}. However, parameter *b* showed a significant interaction between year × branch axes (Table 1, Figure 5F). In 2018, primary shoots grew ~15% faster than secondary shoots (parameter *b* for primary shoots parameter = 28.9 ± 1.9 cm day^{-1}, parameter *b* for secondary shoots 24.34 ± 1.9 cm day^{-1} for secondary shoots). In 2019, shoot growth was similar between branch axes (parameter *b* = 23.1 ± 1.2 cm day^{-1}). No other interactions were observed (Table 1).

Lastly, final shoot lengths (i.e., parameter *a*) did not differ between measurement years or treatments (Table 1). Averaged across treatments, final shoot lengths were 10.78 ± 1.65 cm. However, we found that final shoot length differed between branch axes (Table 1, Figure 5E). On average, primary shoots were ~60% longer than secondary shoots (primary axis shoot length = 13.41 ± 1.48 cm; secondary axis shoot length 8.14 ± 1.47 cm).

Table 1. Observed probability values (p-values) for analysis of variance results for the effects of measurement year (Y), treatment (T), branch axis (BA), and their interactions on the phenological characteristics of shoots on a longleaf pine forest exposed to a 40% throughfall reduction treatment. The table also includes the numerator (*n*) and denominator (*d*) degrees of freedom (*d.f.*). Bold text indicates a statistically significant difference with a p-value less than 0.05 or marginally significant difference with a p-value between 0.05 and 0.1.

		Shoot Elongation					
		a (cm)	*b* (cm day^{-1})	*c* (Julian day)	Growth start (Julian day)	Growth cessation (Julian day)	Growth duration (days)
P>F	*d.f.* *(n,d)*						
Y	1,4	0.228	0.161	**0.066**	**0.017**	0.521	0.166
T	1,4	0.323	0.564	**0.054**	0.121	0.183	0.529
BA	1,4	**0.044**	0.100	0.617	0.629	0.131	**0.068**
Y x T	1,4	0.379	0.942	0.115	0.161	0.523	0.884
Y x BA	1,4	0.115	**0.046**	0.748	0.192	**0.091**	**0.030**
T x BA	1,4	0.404	0.135	0.908	0.673	0.220	0.124
Y x T x BA	1,4	0.159	0.256	0.509	0.751	0.298	0.204

Parameter descriptions: *a*, parameter estimate from fitted Gompertz curve - represents upper asymptote or final shoot length; *b*, parameter estimate from fitted Gompertz curve - represents the growth-rate coefficient (which affects the slope of the linear part of the curve); *c*, parameter estimate from fitted Gompertz curve - represents the Julian day at inflection; growth start: Julian day by which 3% of upper asymptote (*a*); growth cessation: Julian day by which 97% of upper asymptote (*a*); and growth duration: number of days between growth start and cessation.

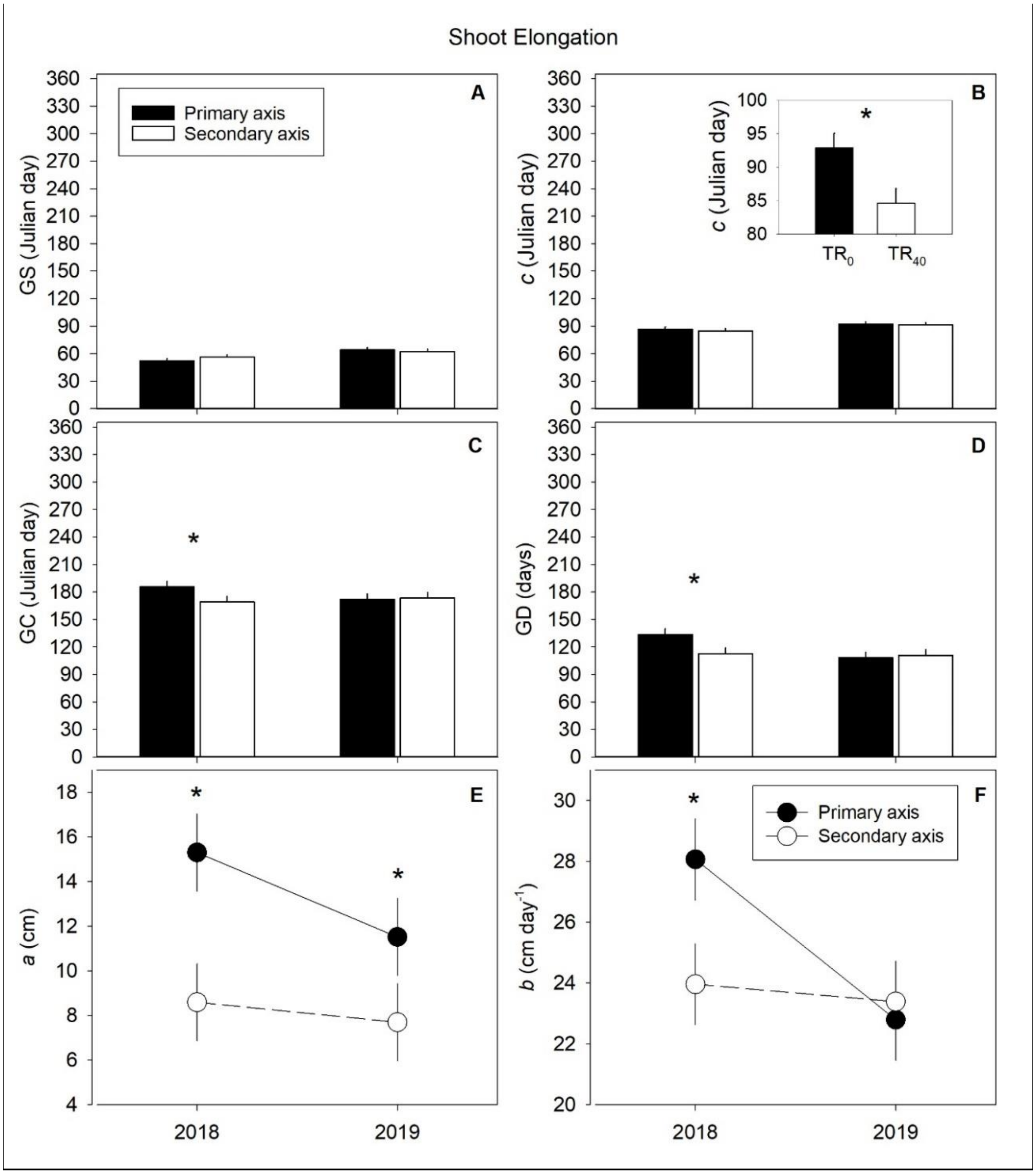

Figure 5. Mean (± standard error) values for shoot growth curve points in longleaf pine trees grown under ambient throughfall (TR_0) and reduced throughfall (TR_{40}) treatments. Growth parameters are: [A] GS, growth start: Julian day by which 3% of upper asymptote (*a*); [B] *c*, parameter estimate from fitted Gompertz curve - represents the Julian day at inflection; [C] GC, growth cessation: Julian day by which 97% of upper asymptote (*a*); [D] GD, growth duration: number of days between growth start and cessation; [E] *a*, parameter estimate from fitted Gompertz curve - represents upper asymptote or final shoot length; and [F] *b*, parameter estimate from fitted Gompertz curve - represents the growth-rate coefficient (which affects the slope of the linear part of the curve). Asterisks (*) represent the dates where differences between branch axes were observed.

3.4.2. Needle Growth

Needles along individual shoots grew simultaneously, which resulted in relatively uniform needle lengths along the shoot axis. In contrast to our expectations, all stages of needle phenological development (growth start, cessation, duration) and all parameters estimated from the growth curves (*a*, *b*, and *c*) were similar among trees growing under ambient throughfall or 40% throughfall reduction (Table 2). Averaged across treatments, needle growth on the first flush occurred between Julian day 117 ± 3 (GS) and 293 ± 9 (GD), which corresponds to the period between late April and mid-October (GD of 177 ± 9 days on both treatments). In both treatments, the inflection point of the growth curves (parameter *c*) occurred on Julian day 163 ± 3. Averaged across treatments, the estimated final needle length (parameter *a*) was 301.5 ± 6.1 mm, and the growth-rate coefficient (parameter *b*) was 36.6 ± 1.2 mm day^{-1}. No interactions between year × treatment or year × branch axis × treatment were detected (Table 2).

Parameter *a* declined each year of the study, indicating that final needle length decreased over time (Figure 6E). On average, final needle lengths in 2017, 2018, and 2019 were 322.6 ± 5.9, 301.9 ± 5.9, and 280.85 ± 5.9 mm, respectively. Parameter *a* also showed a consistent difference between branch axes (marginally significant p-value; Table 2, Figure 6E), with needles from primary and secondary branch axes differing, on average, approximately 9.8 mm in length. Final length of needles from primary and secondary branch axes were 306.4 ± 4.7 and 296.6 ± 4.7 mm long, respectively. Similarly, we also observed a pattern over the years for parameter *c*. The average Julian day at which the inflection points of the needle growth curves were reached (i.e., parameter *c*) tended to occur later over the years (Figure 6B). Averaged across treatments, mean Julian days for *c* in 2017, 2018, and

2019 were 150 ± 2, 162 ± 2 175 ± 2, respectively. Parameter *c* also showed a consistent difference between branch axes (Table 2, Figure 6B), with the inflection point occurring at Julian day 166 ± 3 and 159 ± 3 for primary and secondary branch axes, respectively. No further interactions were observed for parameters *a* and *c*.

Interactions between year × branch axis were identified for needle GS, GC (marginally significant p-values; Table 2, Figures 6A, and 6C), GD, and *b* (Table 2, Figures 6D, and 6F). However, we did not find temporal patterns in these interactions, as GS was different between branch axes in 2019 (p=0.013), and the differences between branch axes for GC, GD, and *b* occurred in 2017 (p=0.003, p=0.002 p=0.001 for GC, GD, and *b*, respectively).

Differences between branch axes for GS were minor, with GS from primary and secondary branches occurring 3 days apart. On average, GS for primary and secondary branch axes occurred at Julian day 128 ± 2 and 131 ± 2 in 2019, respectively. Needle GS did not differ between branch axes in 2017 or 2018 and occurred, on average, at Julian day 110 ± 2 in these years (Figure 6A).

Differences in the needle GC, GD, and *b* resulted from the year × branch axis interaction in 2017 were more marked. Needles from primary branch axes ceased their growth, on average, 30 days earlier than the needles from the secondary branches in 2017, with GC occurring at Julian day 280 ± 8 and 310 ± 8 for primary and secondary branch axes, respectively (Figure 6C). Also in 2017, GD was 31 days longer for the secondary branch axes than for the primary branch axes. The average GD for the primary branch axes in 2017 was 180 ± 8 days against 211 ± 8 days for the secondary branch axes (Figure 6D).

At last, needles from the primary branch axes had a steeper linear growth (i.e., faster rapid growth, or greater *b*) than the needles of the secondary branch axes. On average, *b* was 38.9 ± 1.2 mm day^{-1} for the primary branch axes and 42.5 ± 1.2 mm day^{-1} for the secondary branch axes (Figure 6F). Needle GC, GD, and *b* did not differ between branch axes in 2018 or 2019 (Figure 6C, 6D, and 6F). Averaged across 2018 and 2019, GC occurred at Julian day 293 ± 7, GD lasted 167 ± 9 days, and *b* was 34.6 ± 1.1 mm day^{-1}.

Table 2. Observed probability values (p-values) for analysis of variance results for the effects of measurement year (Y), treatment (T), branch axis (BA), and their interactions on the phenological characteristics of needles on a longleaf pine forest exposed to a 40% throughfall reduction treatment.. The table also includes the numerator (*n*) and denominator (*d*) degrees of freedom (*d.f.*). Bold text indicates a statistically significant difference with a p-value less than 0.05 or marginally significant difference with a p-value between 0.05 and 0.1.

		Needle Elongation					
		a (mm)	*b* (mm day^{-1})	*c* (Julian day)	Growth start (Julian day)	Growth cessation (Julian day)	Growth duration (days)
P>F	*d,f.* *(n,d)*						
Y	2,8	**0.001**	**0.001**	**<0.001**	**<0.001**	**0.004**	**<0.001**
T	1,4	0.441	0.487	0.205	0.379	0.836	0.897
BA	1,4	**0.060**	**0.022**	**0.022**	**0.092**	**0.027**	**0.026**
Y x T	2,8	0.350	0.818	0.581	0.535	0.699	0.811
Y x BA	2,8	0.586	**0.028**	0.592	**0.058**	**0.066**	**0.033**
T x BA	1,4	0.875	0.220	0.354	0.864	0.340	0.313
Y x T x BA	2,8	0.638	0.403	0.812	0.543	0.655	0.731

Parameter descriptions: *a*, parameter estimate from fitted Gompertz curve - represents upper asymptote or final needle length; *b*, parameter estimate from fitted Gompertz curve - represents the growth-rate coefficient (the slope of the linear part of the curve); *c*, parameter estimate from fitted Gompertz curve - represents the Julian day at inflection; growth start: Julian day by which 3% of upper asymptote (*a*); growth cessation: Julian day by which 97% of upper asymptote (*a*); and growth duration: number of days between growth start and cessation.

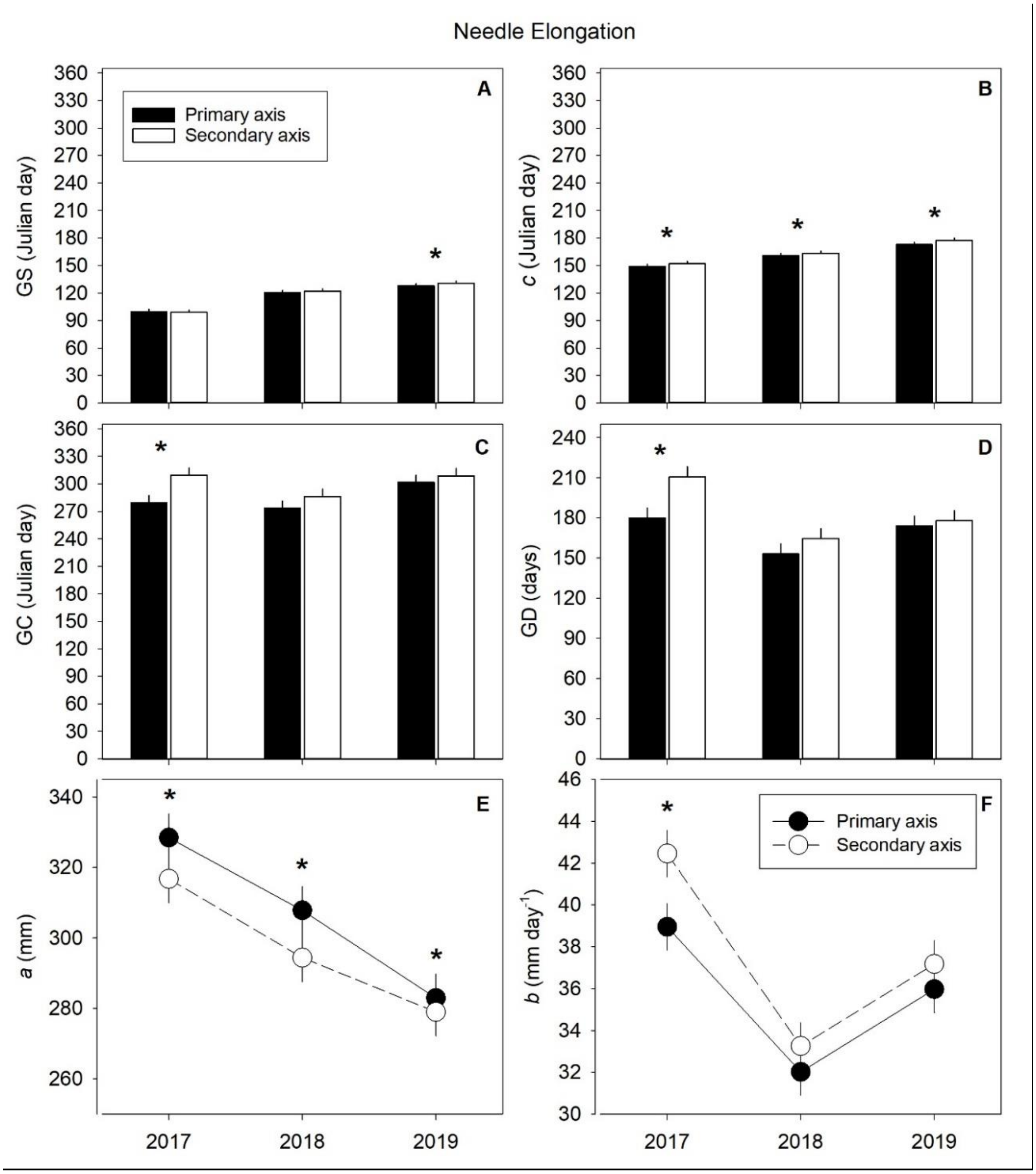

Figure 6. Mean (± standard error) values for needle growth curve points in longleaf pine trees grown under ambient throughfall (TR_0) and reduced throughfall (TR_{40}) treatments. Growth parameters are: [A] GS, growth start: Julian day by which 3% of upper asymptote (*a*); [B] *c*, parameter estimate from fitted Gompertz curve - represents the Julian day at inflection; [C] GC, growth cessation: Julian day by which 97% of upper asymptote (*a*); [D] GD, growth duration: number of days between growth start and cessation; [E] *a*, parameter estimate from fitted Gompertz curve - represents upper asymptote or final needle length; and [F] *b*, parameter estimate from fitted Gompertz curve - represents the growth-rate coefficient (which affects the slope of the linear part of the curve). Asterisks (*) represent the dates where differences between branch axes were observed.

3.5. Leaf area index (LAI)

LAI varied among measurement dates ($p<0.001$) but did not differ between treatments ($p=0.894$, Figure 7), and no interactions between date and treatment were detected ($p=0.632$). Similarly, annual peak LAI varied among years ($p<0.001$) but did not differ among treatments ($p=0.985$), and no interactions between year and treatment were detected ($p=0.572$). Thus, we found no support for our hypothesis that throughfall reduction would reduce LAI. Peak LAI occurred in August in 2017 (2.69 ± 0.1 m^2 m^{-2}), September in 2018 (3.23 ± 0.1 m^2 m^{-2}), and in August in 2019 (2.70 ± 0.1 m^2 m^{-2}). Peak LAI occurred ~3 months after shoot growth cessation and a few weeks after needle growth cessation.

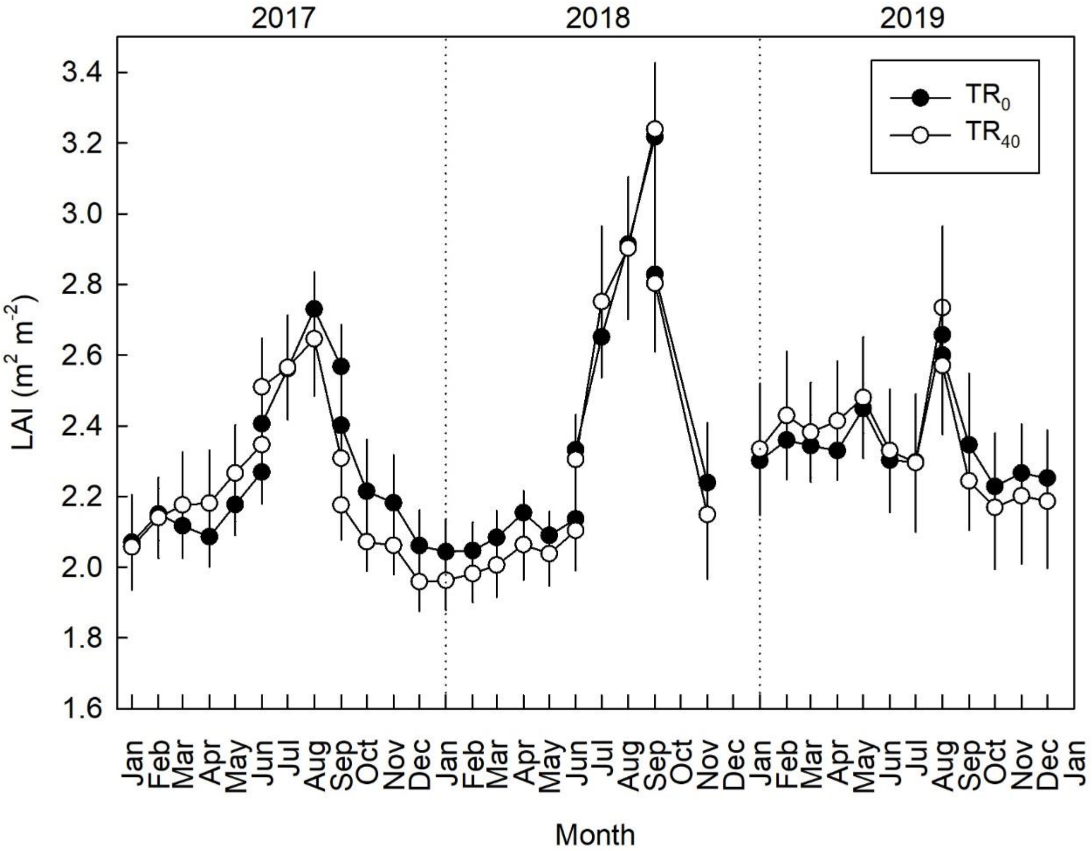

Figure 7. Mean (± standard error) values for leaf area index (LAI) in ambient throughfall (TR_0) and 40% throughfall reduction (TR_{40}) treatments in a longleaf pine plantation.

3.6. Litterfall Patterns

We found that needle fall differed between ambient and reduced throughfall treatments on some measurement dates (date × treatment interaction, *p*=0.007, Figure 8A). Interestingly, needle fall patterns were affected by throughfall reduction mainly in 2017 [four dates in 2017, one date in 2019 (August)]. The average needle fall was ~47% higher in the ambient treatment than the throughfall reduction treatment on two of these measurement dates. However, average needle fall was ~75% higher in the throughfall reduction treatment than the ambient treatment on the remaining three dates. Therefore, we did not observe any systematic difference in needle fall between the ambient and reduced throughfall treatments. Non-foliar litterfall varied among measurement dates (*p*<0.001), but did not differ between treatments (*p*=0.893), and no date × treatment effects were observed (*p*=0.743).

Peak needle fall showed a significant year × treatment interaction (*p*=0.007). In 2017, peak needle fall occurred in September in both treatments but was 33% lower in TR_{40} (173.8 ± 20.0 kg $ha^{-}1$) than TR_0 (261.3 ± 20.0 kg h^{-1}, Figure 8A). Peak needle fall was similar between treatments in 2018 and 2019 and averaged 220.0 ± 14.2 kg ha^{-1} in October 2018 and 185.4 ± 14.2 kg ha^{-1} September 2019, respectively (Figure 8A). As peak for non-foliar needle fall was not as well defined as for needle fall, especially in 2019, no differences among years (*p*= 0.260) or between treatments (*p*=0.893) were observed, and no interactions between year and treatment were detected (*p*=0.743). Peak non-foliar litterfall occurred in September in 2017, October in 2018, and in late June in 2019, and averaged 9.04 ± 3.57 kg ha^{-1} across all years.

Total annual (cumulative) needlefall, as well as total annual non-foliar litterfall, differed among years (*p*<0.001 and *p*=0.015 for cumulative needle fall and non-foliar litterfall, respectively; Figure 8A-B). However, 40% throughfall reduction did not affect annual needlefall or non-foliar litterfall in any year (p=0.940 and p=0.694 for cumulative needle fall and non-foliar litterfall, respectively; Figure 8A-B), and no interactions between year and treatment were observed for cumulative needle fall (p=0.974) or non-foliar litterfall (p=0.731).

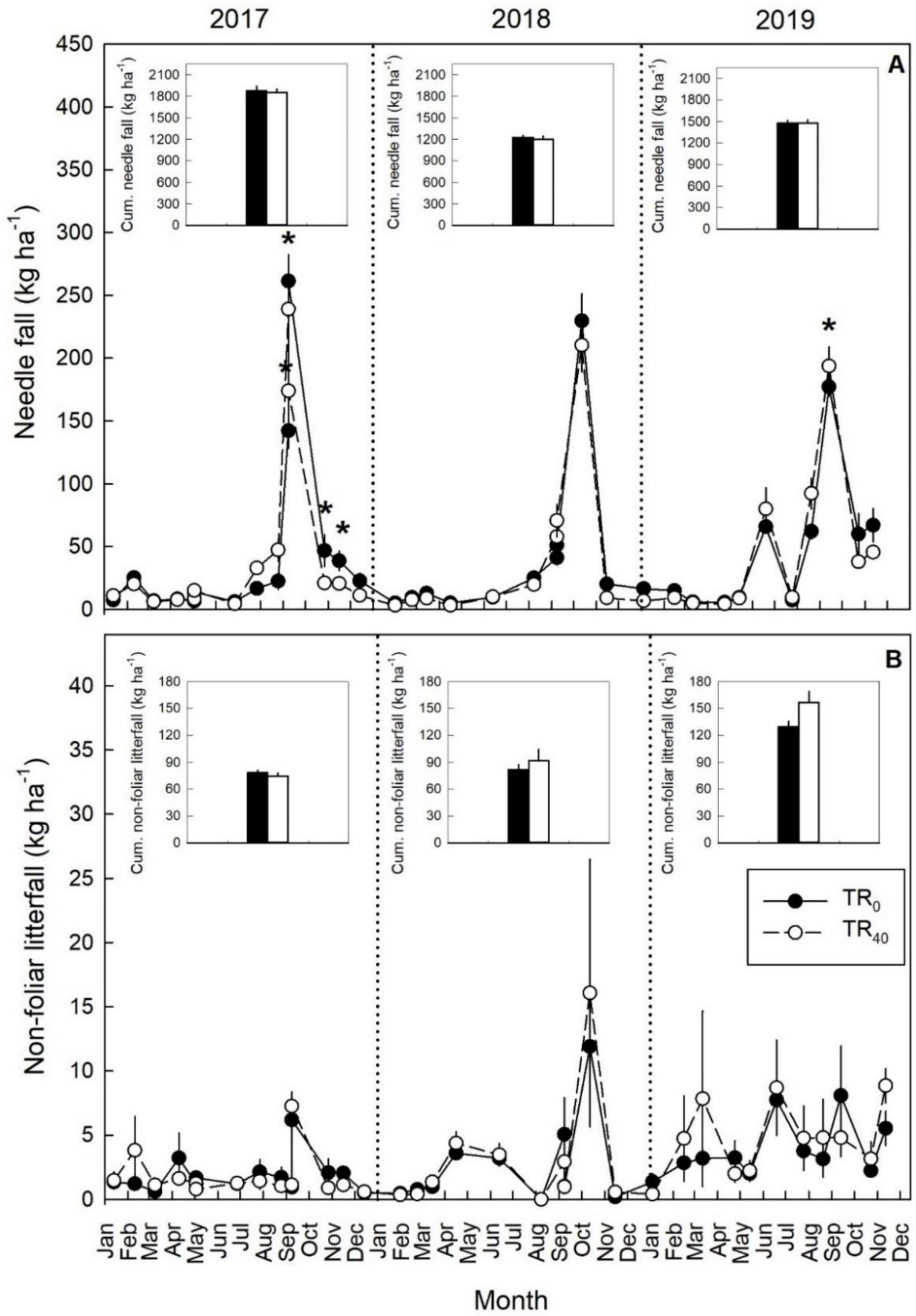

Figure 8. Mean (± standard error) values for [A] needlefall and [B] non-foliar litterfall in ambient throughfall (TR$_0$) and 40% throughfall reduction (TR$_{40}$) treatments in a longleaf pine plantation. The figure also includes the yearly cumulative needlefall and non-foliar litterfall in the TR$_0$ and TR$_{40}$ treatments in a longleaf pine plantation. Asterisks represent the dates where differences between treatments on needle/non-foliar fall were observed.

4. Discussion

Although air temperature is widely recognized as an important driver of phenological timing and growth rates in many tree species (Dougherty et al., 1994; Duputié et al., 2015; Ogaya and Penuelas, 2004), water availability also represents an essential factor regulating foliar phenology and shoot growth (Adams et al., 2015; Fatichi et al., 2014; Ogaya and Penuelas, 2004; Peñuelas et al., 2004). In this study, we determined the effects of a 40% throughfall reduction on shoot and needle elongation patterns, as well as LAI and litterfall dynamics, in a young longleaf pine plantation for three years (2017-2019). We hypothesized that throughfall reduction would delay shoot and needle elongation, shorten the period of shoot and needle growth, and reduce total shoot and needle length, as well as reduce LAI. However, during the three years of exposure to reduced water availability, we observed little effect of the 40% throughfall exclusion treatment on shoot and needle phenology and growth. The absence of throughfall reduction effects on shoot and needle phenology were also reflected in no systematic changes in LAI or litterfall fall patterns between treatments. We found, however, that needle phenology was variable across years while shoot phenology was relatively consistent across years. In particular, we found that needle growth started later each year, and needles were shorter each successive year. We also found that shoot and mainly needle phenology varied between branch axes (i.e., primary and secondary branches). Needles on primary branches tended to show earlier growth start and cessation than needles on secondary branches. Primary shoots and needles were generally longer than secondary shoots and needles. The results of this study showed that longleaf pine shoot and needle growth patterns, as well as patterns of LAI and litterfall, were similar between ambient throughfall and 40% throughfall reduction treatments. Thus, in terms of branch- and canopy-scale phenology, longleaf pine plantations may be relatively resistant to reductions in average rainfall and soil moisture.

Prolonged exposure to reduced water availability could cause trees to spend more energy or resources towards root growth, which can result in reduced shoot and foliage elongation (Dewar et al., 2011, 1994; Gholz and Cropper, 1991; Sheffield et al., 2003), and different phenological patterns (Adams et al., 2015; Borcherti, 1994; Grossiord et al., 2017). Many studies have reported that reduced water availability can reduce shoot and foliage elongation, increase foliage thickness, and reduce foliage longevity in trees (Adams et al., 2015; Grossiord et al., 2017; Sheffield et al., 2003; Stenberg et al., 1994). Initially, leaf phenological plasticity responses can be beneficial to withstand rapid environmental shifts. However, if not returned to more favorable conditions, or if drought events become repetitive, trees may show reduced physiological capacity, lower growth, longer recovery periods, and increased susceptibility to drought-induced mortality (Adams et al., 2015; Allen et al., 2015, 2010; Grossiord et al., 2017; Williams et al., 2013). Although the throughfall reduction treatment led to reduced soil moisture (~39% lower at all depths, on average), needle development was not affected. Likewise, reduced water availability had little effect on shoot phenology and growth. We observed that throughfall reduction caused an 8-day delay when shoot growth reached the inflection point, although this effect was marginally significant. In another study with longleaf pine, Sheffield et al. (2003) found differences in the timing of growth start, growth cessation, and growth duration between trees located at mesic versus xeric sites. However, these differences were generally not longer than 2 weeks; the authors concluded that these differences in phenology were relatively minor. However, Sheffield et al. (2003) also reported that final needle lengths were lower in longleaf pines grown on a xeric site relative to a mesic site. These reductions in needle growth could potentially result in lower canopy-scale C uptake and tree growth (Adams et al., 2015; Ethier et al., 2006; Warren, 2006). However, when trees are grown together on a common site, we found no evidence that throughfall reduction and lower water availability over a three-year period resulted in reduced needle or shoot growth.

The overall effects of throughfall reduction on both needle and shoot elongation processes were not as strong as we anticipated and provided no support for our hypotheses. Assuming a 40% reduction in rainfall in the throughfall treatment, trees would have received, on average, ~783 mm year^{-1} of precipitation over the three years. This amount of annual rainfall is equivalent to a 1- in 100-year drought for our site. Given this, it is surprising that the treatment effects on needle and shoot phenology were not more severe. We believe that this lack of strong effects on shoot and needle phenology, as well as shoot and needle growth, could be attributed to the relatively frequent occurrence of rainfall events. Over the course of the experiment, averaged across all years, it rained at least 1 mm on 99 days per year and the average number of days between rainfall events was ~4 days. Our results indicate that a substantial reduction in rainfall amount, without changes in rainfall frequency, is unlikely to have strong impacts on established longleaf trees and forests. Variation in rainfall seasonality, or more extended periods with no rainfall, may result in different effects, but further work is needed to quantify such effects. Our results, however, are consistent with previous findings on stand growth and physiological aspects of longleaf pine trees [Samuelson et al., 2019; Mendonça et al. (*submitted*)]. In the same study and trees, Mendonça et al. (*submitted*) found only a small reduction in leaf scale- and canopy-scale physiology in longleaf pine trees exposed to 40% throughfall reduction. Samuelson et al. (2019) also found little effect of throughfall reduction on individual tree diameter, height, or forest productivity. Therefore, it is likely that greater reductions in rainfall for prolonged periods are required to significantly alter longleaf phenology and reduce productivity, even on sandy, well-drained sites.

Drought effects on the phenology and productivity of trees at the regional scale are strongly dependent on the species and the severity and duration of the drought (Breshears et al., 2005Duan et al., 2018; Engelbrecht et al., 2017; Johnson et al., 2018). For example, Ciais et al. (2005) reported reduced physiological activity and productivity (i.e., reduced ecosystem respiration and gross primary productivity) in eastern and western European forests exposed to reduced rainfall and extreme summer heat. Kuster et al. (2014) reported changes in shoot elongation dynamics in *Quercus spp.* in Central Europe, with drought changing the frequency and intensity of shoot growth and delaying bud burst during severe summer drought. Montserrat-Martí et al. (2009) found decreases in the secondary growth, bud, and acorn growth during summer drought conditions in Mediterranean oaks. In pine species under drought conditions (either natural or experimental droughts), many studies revealed delayed phenological development and reduced needle and/or shoot growth (Adams et al., 2015; Borghetti et al., 1998; Girard et al., 2011; Grossiord et al., 2017; Sheffield et al., 2003). Even in piñon-pine (*Pinus edulis* Engelm.), a species that is naturally adapted to long periods under water stress, Adams et al. (2015) found that drought delayed phenological development and reduced foliar growth of primary axes and shoot growth. Similarly, Grossiord et al. (2016) found that trees modified their foliar traits (physiological and morphological traits) under exposure to a 45% experimental throughfall reduction. However, these effects of drought on trees species were caused by extreme drought events (with prolonged days with no or little rain) followed by, in some cases, an experimental drought treatment that exacerbated natural droughts. These extreme conditions never occurred during our three-year study. Interestingly, drought effects on physiology and biochemistry seem to be stronger than drought effects on phenology, at least in some pine species (Adams et al., 2015; Grossiord et al., 2017). Physiological and phenological responses are important for identifying plastic responses to drought, and differences in the drought sensitivity of these processes suggest that the physiological responses tend to occur faster than phenological changes (Hodge, 2006; Valladares et al., 2000a; Valladares et al., 2000b; Valladares et al., 2007).

Temporal changes in LAI and needle fall and peak LAI and needle fall were similar between treatments, highlighting similarities in shoot- and canopy-scale responses to throughfall reduction. Other studies with pine species of the southeast U.S. have indicated that LAI may shift in response to changing soil moisture availability (Bracho et al., 2012). For instance, loblolly pine (*Pinus taeda* L.) was sensitive to 30% throughfall exclusion in long-term experiments across the southeastern US, resulting in reduced LAI and growth (Bracho et al., 2012; A. Maggard et al., 2016; Samuelson et al., 2018). In longleaf pine forests, Wright et al. (2013) found that longleaf pine trees in a mesic site were generally more impacted by reductions in water availability than trees in a xeric site in southwestern Georgia (i.e., the mesic site had greater reductions in GPP and leaf area than the xeric site). Therefore, trees at water-limited xeric sites, similar to ours, may cope better with drought events than trees at mesic sites.

Patterns of shoot development often differ among species according to their environmental adaptations (Grossiord et al., 2017; Koskela, 2000; Ogaya and Penuelas, 2004). Shoot and needle elongation patterns in our study with longleaf pine appeared to be relatively similar to the general description of foliage development of other southern pines, such as loblolly pine and slash pines (*Pinus elliottii* Egelm) (Dougherty et al. 1994). Although needle elongation in our study occurred after most shoot growth had occurred, trees did show concomitant development of shoot and needles for a considerable time during the growing seasons, similar to other pines (Dougherty et al., 1994; Stenberg et al., 1994). However, shoot and needle elongation patterns generally differed from those observed in a different study with longleaf pine. In the study by Sheffield et al. (2003), shoot elongation was completed well before the growth of needles. The average interval between the completion of shoot development and the start of needle development was approximately 32 and 33 days on the xeric and mesic sites, respectively. In contrast, we found that longleaf pine trees had on average 22 and 31 days of concomitant development of shoot and needle growth in 2018 and 2019, respectively. This pattern of the concomitant shoot and needle development occurred in all years and branch types, independent of the water availability conditions imposed by the throughfall reduction treatment during our study. Future studies may help reveal whether the timing and length of concomitant shoot and needle growth varies across sites in some predictable way, depending on local conditions or other environmental cues.

The phenological development observed in trees is interpreted as a long-term evolutionary (i.e., adaptive) response to predictable or recurrent environment events (e.g., day length, seasonal temperature changes, wet seasons, irradiance; Adams et al., 2015; Cooke et al., 2012; Lieth, 1974; Piao et al., 2019; Schiestl-Aalto and Mäkelä, 2017). However, some recurrent events can vary from year to year. In our study, needle phenology and growth changed across years while shoot phenology and growth were more similar across years. Interestingly, we observed a trend of later growth start and cessation for the development of the needles and shorter needles over time. This observation could rely on the ontogeny of the trees (as trees are aging) (Williams, 1987), coupled with the responsiveness to the interannual variation in the environmental conditions (Schiestl-Aalto and Mäkelä, 2017). As demonstrated in this study, bud break tends to happen much earlier than the start of needle growth for longleaf pine. We observed that, although the needle elongation process started while the shoot was still developing, about two-thirds of the needle growth was performed after shoot growth cessation. The shoot's development ended at the beginning of the summer season (~May), while needle elongation was maintained until mid to late October. In this context, the needle development seemed to be more strongly influenced by the conditions of the current growing season. Although precipitation levels were relatively similar over the years, this strong influence of the different year-to-year environmental conditions could be attributed to differences in many other environmental factors occurring during the summer that could have substantially affected the variation in the timing of the needle development over the three years. For instance, Tang et al. (1999) found that the needle development in loblolly pine was linearly related to the previous-month irradiance and temperature. Also, specific rain events (rather than just looking at the total precipitation for the year), coupled with favorable temperatures, may have triggered or delayed needle emergence, cessation, and total growth (Ogaya and Penuelas, 2004), as well as due to other environmental factors that are related to setting the needle development, such as differences in the patterns of day length and radiation levels.

In contrast, shoot phenology and shoot growth patterns were less responsive to year-to-year variations. Needle and particularly shoot growth start are closely related to the process of dehardening and breaking of bud dormancy (Barnett et al., 2015; Schiestl-Aalto and Mäkelä, 2017), and are also strongly responsive to the conditions of different times of the year. However, the influence of the previous year's bud set in the autumn/winter is more likely to affect the dormancy release and shoot elongation process (Schiestl-Aalto and Mäkelä, 2017; Williams, 1987). In pine trees, shoot growth patterns are thought to be predetermined during the winter (i.e., overwintered growth) (Barnett et al., 2015; Williams, 1987). Therefore, shoot and needle development patterns are influenced by the conditions of different seasons, which could have resulted in different responses to the interannual environmental variations, considering that in the autumn and winter the temperature may vary more than during the summer months. However, as complete shoot observations were con ducted in just two out of the three years of the experiment, more research is needed to evaluate shoot growth responses to year-to-year environmental variations in longleaf pine trees.

5. Conclusion

Reductions in leaf development due to exposure to stresses (i.e., low soil moisture) can cause considerable reductions in leaf- and canopy-scale photosynthesis (Grossiord et al., 2017) and vigor in trees (Ethier et al. 2006, Adams et al. 2015), increasing the propensity of drought-induced tree mortality (Adams et al., 2015; Grossiord et al., 2017, McDowell et al. 2010). This study found that a 40% reduction in throughfall had little effect on shoot and needle phenology or growth. We also found that effects of throughfall reduction on LAI and litterfall were weak or inconsistent over time. Even though water availability was reduced under throughfall reduction, the number of rain events, as well as their frequency, were not altered, which may be more important in influencing this ecosystem's functionality rather than the total rainfall amount per se (Engelbrecht et al., 2017; Knapp et al., 2017, 2008; Phillips et al., 2016). Nonetheless, our results indicate that longleaf pine trees may be able to withstand potential reductions in water availability. If reductions in water availability persist over the long term, more drought-resistant species such as longleaf could be favored over less drought-resistant species, especially in more xeric sites. However, more experiments combining multiple abiotic stresses are needed to help improve our knowledge on tree functioning and the longer-term resistance of longleaf forests to climate change.

Acknowledgements

Support for this work was provided by USDA National Institute of Food and Agriculture McIntire Stennis Program (Award 1018413), the Intergovernmental Support Agreement between the U.S. Army – through the Natural Resources Branch at Fort Benning – and Auburn University (Award BENNING-IGSA-16-00), the Auburn University Intramural Grants Program (Award 180286), and the Alabama Agricultural Experiment Station – Agriculture Research Enhancement & Seed Funding Program (Award 1025522). The authors thank Thomas Stokes, Michael Ramirez, and Jake Blackstock for assistance with experiment installation and data collection, Dr. George Matusick for assistance with project funding, site selection and maintenance, the Georgia Department of Natural Resources for permitting site access and housing, and The Nature Conservancy for assisting with site maintenance and housing.

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CHAPTER IV

PARAMETERIZATION AND VALIDATION OF THE 3-PG MODEL FOR LONGLEAF PINE (*Pinus palustris* Mill.) STANDS IN THE SOUTHEASTERN UNITED STATES

Abstract

Forest simulation models can be used for multiple purposes, including estimating stand productivity and forest carbon stock potential and assessing the impacts of management and climate on forest production dynamics. Forest simulation models have been used to characterize and predict the production dynamics of *Pinus taeda* L. (loblolly pine) and *Pinus elliotii* Egelm. var. *elliottii* (slash pine); two commercially important pine species in the southeast United States. Forest simulation models have not been parameterized for *Pinus palustris* Mill. (longleaf pine) – a species of great conservation importance that could also play a role in climate change adaptation. In this paper, we present the procedure used to parameterize the 3-PG model for longleaf pine stands and discuss the use of the model to simulate production dynamics in this species. We used data from extensive, long-term studies (consisting of 655 individual stands) located across the natural range of longleaf pine to establish species-specific parameter estimates. Parameter estimates were used to develop algorithms for 3-PG model to estimate growth variables, such as net primary production (NPP) allocation, quadratic mean diameter, basal area, mean height, density-dependent, independent mortality, and canopy cover dynamics, and fertility rating for even-aged longleaf pine stands. Model performance was evaluated by contrasting observed data from different studies across the species' natural range against the predicted values from simulations using the set of parameter values reported in this study.

Overall, we observed an agreement between observed values and the predictions obtained through the 3-PG model, demonstrating that the application of the model allowed a good description of the growth patterns of longleaf pine stands. As 3-PG parameters are primarily species-specific and serve to distinguish different dynamics of each species (Landsberg and Sands, 2011), the application of this set of parameters represent a more accurate way to predict longleaf pine growth dynamics. The application of this model can serve as a practical tool to establish better management strategies and assess the impact of future changes in climate in longleaf pine forests.

1. Introduction

Forests provide essential ecosystems services (e.g., biodiversity protection, carbon (C) storage, nutrient cycling, wood resources) and economic benefits to society (Bonan, 2008; Canadell and Raupach, 2008; Gupta and Sharma, 2019; McKinley et al., 2011; Pan et al., 2011). Science-based forest management is a key tool for ensuring that ecosystem services and economic benefits are sustainable. Forest simulation models are one tool that forest scientists and managers use to predict forest productivity and C storage, and the potential modifying effects of site conditions (soils, resource supply) and silvicultural prescriptions (Carlos A. Gonzalez-Benecke et al., 2014b; Gonzalez-Benecke et al., 2016; Gupta and Sharma, 2019; Stape et al., 2004; Trotsiuk et al., 2020). Process-based forest models are a common type of forest simulation model used by forest managers to describe or predict production dynamics for different forest species in either natural mixed ecosystems or intensively managed plantations (Caldeira et al., 2020; Coops and Waring, 2011; Thomas et al., 2018; Tickle et al., 2001). These models rely on mathematical representations of critical physical and biological processes regulating tree growth and allometric equations that can help estimate changes in above- and belowground biomass pools over time and under different environmental conditions. Moreover, these models differ from empirical growth and yield models by including biophysical mechanisms for tree and forest productivity grounded in ecophysiological theory. In this way, processes-based models can help us understand not only *how* forest productivity varies but also *why* forest productivity varies over space and time. The inclusion of mathematical equations describing physiological mechanisms is helpful because it offers flexibility in predicting changes in forest productivity outside the range of available data. As a result, these models also have the potential to help guide forest management practices in the face of a changing climate (Carlos A. Gonzalez-Benecke et al., 2014b; Gonzalez-Benecke et al., 2016) by simulating the impacts of the anticipated site and climate conditions on aspects of forest productivity (Gupta and Sharma, 2019)

The Physiological Process Predicting Growth model (3-PG; Landsberg and Waring, 1997) is a process-based model used to predict forest growth and productivity (Landsberg and Waring, 1997; Landsberg and Sands, 2011; Sands, 2004a). Based on principles such as radiation use efficiency and carbon balance, the 3-PG model estimates the effects of various management regimes and climate conditions on stand attributes, including stand density, stand volume, mean diameter, mean height, above-ground biomass, stand transpiration, and LAI (Landsberg and Waring, 1997; Subedi et al., 2015). The 3-PG model requires three main input variables: climatic data, stand initialization data, and site-specific data (e.g., species-specific allometric relationships, canopy cover dynamics, and stem mortality and self-thinning; Landsberg and Waring, 1997). Also, the model uses species-specific attributes to quantify net primary production (NPP), biomass allocation, stand dynamics, and soil water balance (Carlos A. Gonzalez-Benecke et al., 2014b; Gonzalez-Benecke et al., 2016; Landsberg and Waring, 1997). The 3-PG model may be used for several purposes, including estimating potential site-specific production in response to projected climate change, planning prescribed fire and managing site nutrient supply. Therefore, the projections generated by 3-PG are relevant to forest managers and help define potential management strategies for improving productivity and forest carbon stocks in the future.

To ensure that 3-PG provides accurate and realistic forest growth and function predictions, species-specific parameters should be included (Borges et al., 2012; Gonzalez-Benecke et al., 2016; Sands and Landsberg, 2002). These parameters can be determined by developing allometric equations that describe biomass allocation patterns and empirical estimates of specific parameters. Species-specific modifiers can also be used to adjust key parameters. However, process-based forest models are often challenging to parameterize and validate due to the long-term data required and the variety and uncertainty of details of many fundamental processes, such as carbon allocation, canopy closure, and light interception (Battaglia and Sands, 1998; Carlos A. Gonzalez-Benecke et al., 2014b). As a result, process-based forest models are continually developing and improving, especially for species with limited data or not been evaluated. Nonetheless, the 3-PG model has been parameterized and validated for several important conifer and hardwood forestry species, including *Eucalyptus globulus* Labill. (Rodríguez-Suárez et al., 2010; Sands and Landsberg, 2002; Vega-Nieva et al., 2013), *Eucalyptus grandis* W.Hill ex Maiden (Almeida et al., 2004), *Pinus radiata* D. Don (radiata pine; Flores and Allen, 2004; Rodríguez et al., 2002), *Pinus elliottii* Egelm var. *elliottii* (i.e., slash pine; Gonzalez-Benecke et al., 2014), and *Pinus taeda* L. (loblolly pine; Bryars et al., 2013; Gonzalez-Benecke et al., 2016; Landsberg et al., 2003; Sampson et al., 2006).

In this paper, we describe the parameterization and validation of the 3-PG model for longleaf pine (*Pinus palustris* Mill.) and discuss the use of the model to simulate the growth patterns of this species. Longleaf pine is one of the most ecologically important pine species in the southeastern United States. Longleaf pine ecosystems are considered one of the most biodiverse ecosystems in the region and support several threatened or endangered plant and animal species. Historically, these ecosystems were among the most extensive ecosystems in North America (Alavalapati et al., 2007; Brockway et al., 2007; Landers et al., 1995; Samuelson and Stokes, 2011; Van Lear et al., 2005), occurring across a wide range of sites, including mesic and poorly drained flat woods, xeric sand hills, and montane uplands (Brockway et al., 2007; Landers et al., 1995; Oswalt et al., 2012). Longleaf pine forests are recognized for producing high-quality timber and providing essential ecosystem services, especially long-term above and belowground carbon storage (Brockway et al., 2007; Oswalt et al., 2012). However, over the past two centuries, logging for timber production, fire suppression, and land-use change (agricultural development, conversion to other forest types, urbanization) have substantially reduced the natural coverage of the longleaf pine ecosystem (Brockway et al., 2005). The desire for restoring longleaf pine ecosystems has risen over recent years as greater awareness of the degradation and loss of this important ecosystem has increased, and economic incentives to restoration have increased. Longleaf pine ecosystem restoration is now one of the largest conservation priorities in the southeastern United States. Longleaf pine restoration, and planting is also seen as a potential approach for climate adaptation. The species is considered one of the most drought-resistant pines in the Southeast and may be more resistant to more variable and extreme climate conditions in the future compared to related pine species (loblolly and slash pine) (Addington et al., 2006; Samuelson et al., 2019, 2014). The perceived stability of longleaf pine ecosystems has also led to the idea that these ecosystems could serve as suitable long-term carbon sinks, which would benefit climate change mitigation strategies or natural climate solutions (Samuelson et al., 2014).

Although the 3-PG model has been parameterized for other ecologically and commercially important pine species in the southeastern U.S., the model has not been parameterized or validated for longleaf pine. This is important considering that longleaf differs from related pine species in terms of growth rate, resource use, biomass allocation, and canopy development (Foster and Brooks, 2001; Gonzalez-Benecke et al., 2011a, 2010). New work is required to parameterize 3-PG for this historically important species, which is likely to be more important under changing climate conditions. With this in mind, the purpose of this study was to parameterize the 3-PG model for longleaf pine plantations using long-term growth and biomass production data collected across a wide range of sites differing in tree age, stand density, local climate conditions, and site quality. We incorporated functions for estimating canopy cover, density-independent tree mortality, fertility rating (FR), and initial biomass pools at any starting age. Validation of the model was accomplished by testing the model predictions against data from a subset of measurement plots representing the full range of stand characteristics (age, productivity, and management).

2. Materials and Methods

2.1. The 3-PG model: an overview

In this study, we used 3-PG version 3-PGpjs2.7 (Landsberg and Waring, 1997; Sands, 2010). A full description of the original model is provided by Landsberg and Waring (1997). In addition, a detailed description of the current version of the model is provided by Sands (2010). Here, we summarize some of the main aspects of the model. 3-PG combines some of the key biological and physiological determinants of tree growth (Sands, 2004b). The species-specific parameters of this model are established by determining empirical relationships from long-term studies with process-based calculations, based on well-established principles and constants (Landsberg and Waring, 1997; Sands and Landsberg, 2002). The 3-PG model calculates net primary production (NPP) as a constant portion of the total carbon fixed gross primary production (GPP), estimated from photosynthetically active radiation (PAR). Absorbed PAR are corrected and used in conjunction with canopy quantum efficiency obtained by the forest canopy. Canopy quantum efficiency determination generally accounts for specific interrelated effects, such as environmental- and site-related factors (i.e., dimensionless factors; modifiers) and aspects related to the stand age and density.

After predicting NPP, species-specific allometric ratios are used to quantify the proportion of carbon allocated above (foliage and stem) and below ground. In addition, the effects of soil fertility are also included in the carbon allocation calculations, as more or less biomass tends to be allocated below ground with decreased or increased soil fertility, according to the site-specific conditions. In summary, the 3-PG model provides a combination of key factors to determine forest growth based on crucial physiological features, enabling reliable projections. At the same time, the simplicity of this model interface also allows it to be accessible and practical to all forest managers.

The model's general structure comprises five sub-models: (1) the assimilation of carbohydrates, (2) the distribution of biomass between foliage, roots, and stems, (3) mortality, (4) soil water balance, and (5) conversion of biomass values into variables of interest to forest managers (Almeida et al., 2004; Landsberg et al., 2003; Sands and Landsberg, 2002). The model requires weather data and initial site characteristics to predict the growth of even-aged, mono-specific stands. The main input variables to run 3-PG are climate (temperature, solar radiation, vapor pressure deficit, and rainfall), soil (fertility, texture, water availability), plant (foliage, root and stem biomass at starting age, initial stand density), and physiological (such as canopy quantum efficiency, stomatal conductance). The 3-PG model can be run for years, using either actual monthly weather data or long-term monthly averages.

2.2. Parameter estimations and validation

For parameterization of the 3-PG model for longleaf pine, we used published data from long-term productivity studies of longleaf pine growing across different sites throughout the species' natural range. All the necessary parameters (Carlos A. Gonzalez-Benecke et al., 2014b; Gonzalez-Benecke et al., 2016; Landsberg and Waring, 1997) were calculated using component variables or extracted from existing literature sources. When calculated, the parameter estimates were determined by combining all datasets, except when specified (see other sections). We incorporated functions for estimating canopy cover, density-independent tree mortality, the fertility rating (FR), and initial biomass pools at different starting ages. The validation of the established parameters of the 3-PG model to longleaf pine stands was done against data from measurement plots covering a varied range in stand characteristics in the southern US, following the validation process described by Gonzalez-Benecke et al. (2016).

2.3. Study sites

The model parameterization and validation used long-term datasets from sites located across the natural range of longleaf pine (Tables 1 and 2). The parameterization dataset included data from 209 plots, while the validation dataset included 53 plots spanning the same range (Figure 1). A third dataset, containing 26 plots, was used to determine the relationship between site index and FR – an important parameter that accounts for variation in site quality (Figure 1). Datasets included long-term studies developed by U.S. Army at Fort Benning GA (FB), Harrison Experimental Forest (HEF), T. R. Miller Mill Company, the Palustris Experimental Forest (P312, P313, P329, and P410), The Nature Conservancy (TNC), Virginia Department of Forestry (VA), and the Southwide Southern Pine Seed Source Study (SSPSSS). A summary of the site and stand characteristics of the studies is presented in Tables 1 and 2. In the parameterization dataset, stands ranged from 9-83 years old, and quadratic mean diameter, basal area, stand density, and site indexes ranging from 2.90-42.59 cm, 0.29-52.10 m^2 ha^{-1}, 133-1825 trees ha^{-1}, and 11.55-33.90 m, respectively (Table 1). Likewise, stands in the validation dataset had very similar characteristics, with stand ages ranging from 7-68 years old, and quadratic mean diameter, basal area, stand density, and site indexes ranging from 3.65-39.99 cm, 0.26-42.61 m^2 ha^{-1}, 156-1663 trees ha^{-1}, and 12.07-34.01 m, respectively (Table 2).

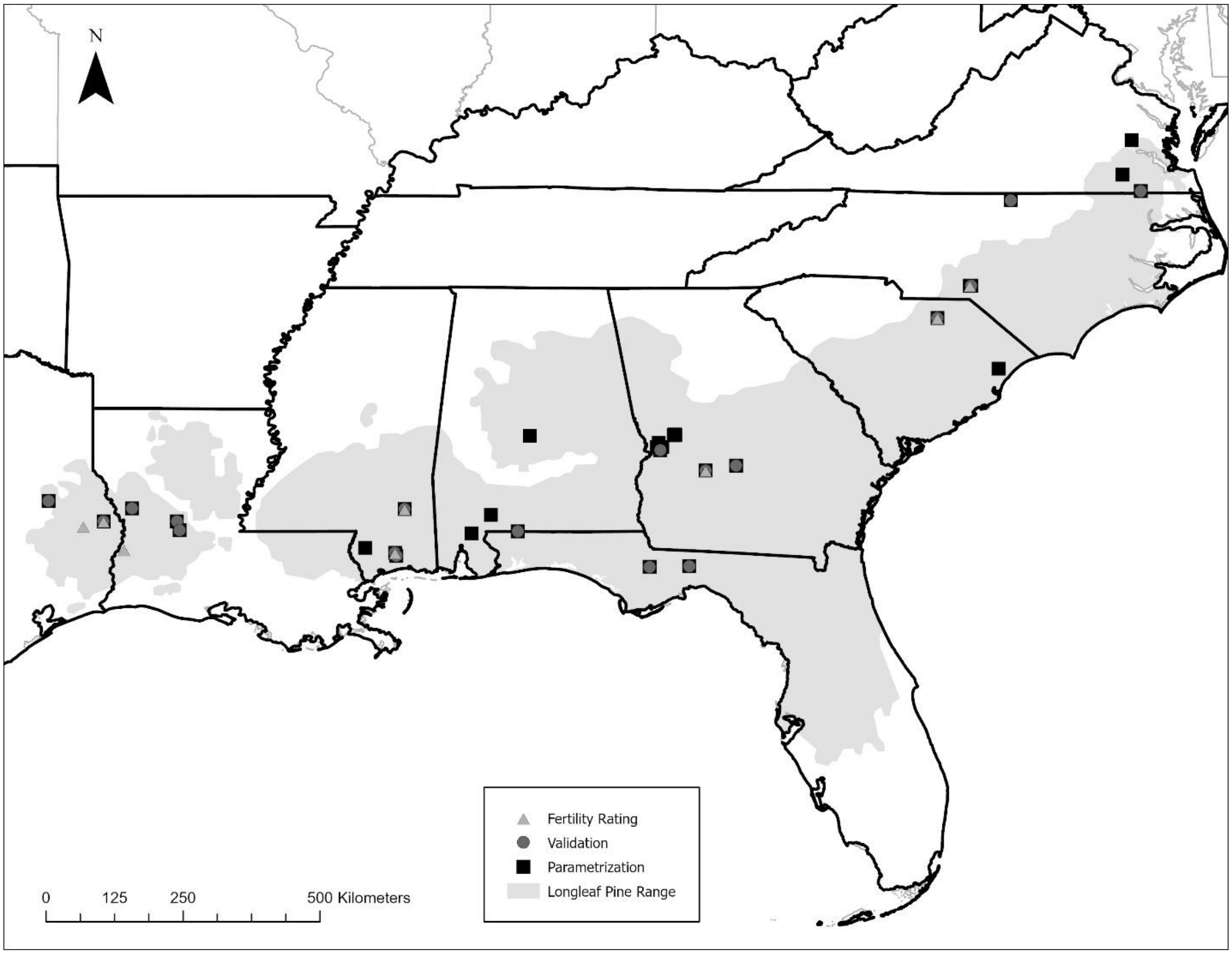

Figure 1. Location of sites used for parameterization (black squares), validation (dark grey circles), and fertility rating (light grey triangles). The shaded area represents the species natural distribution range.

2.4. Initial biomass pools

The model requires initial pools of stem, foliage and root biomass prior predictions for model initialization (i.e., initial pools required to start the predictions). As these values can be challenging to be estimated by model users, allometric relationships were provided to calculate initial foliage, stem, and root biomass (W_F, W_S, and W_R, respectively; Mg ha^{-1}) from species-specific allometric relationships, following Samuelson et al. (2016) and Gonzalez-Benecke et al. (2014b, 2014a, 2015, 2018).

For cases in which the diameter at breast height (DBH, m) of the trees in the stand were known, allometric equations for each biomass above-ground component (i.e., W_S and W_F) were obtained from a non-linear model developed by Gonzalez-Benecke et al. (2018):

Equation (2) $$W_{(F,S)} = a_1 \,.\, Ht^{a_2} \,.\, DBH^{a_3} \,.\, AGE^{a_4}$$

where W_F and W_S are the dry biomass of foliage and stem, respectively; a_1 is a constant, a_2 is the power of height (Ht, m), a_3 is the power of the DBH, and a_4 is the power of age.

For estimating W_F and W_S of seedlings during the initial state of development or during the grass stage (i.e., height < 1.37 m and unknown DBH), alternative allometric equations were obtained based on the ground line diameter (GLD, m) relationship with the above-ground biomass components (i.e., W_F and W_S), established by Samuelson et al. (2014):

Equation (3) $$W_{(F,S)} = b_1 \,.\, GLD^{b_2}$$

where W_F and W_S are the dry biomass of foliage and stem, respectively; b_1 is the constant, and b_2 is the power of the GLD.

Lastly, estimations of W_R were obtained from a model for longleaf pine stands established by Samuelson et al. (2017), which used age to estimate total live root carbon (Mg C ha^{-1}). According to the same publication, Samuelson et al. (2017) estimates that the total live root carbon (accounting for coarse and fine roots) represents about 50% of the total belowground biomass. Based on the proportion of carbon and root biomass described by Samuelson et al. (2016), total W_R was assumed to be two times the total live root carbon:

Equation (4) $W_R = (c_1 \, . \, AGE^{c_2}) \, . \, 2$

where d_1 and d_2 are curve fit parameters obtained from Samuelson et al. (2016).

2.5. NPP partitioning

In 3-PG, parameters for NPP (Mg ha^{-1} $year^{-1}$) determination and biomass allocation are divided into three main components: foliage (Mg ha^{-1} $year^{-1}$), stem (Mg ha^{-1} $year^{-1}$), and root (Mg ha^{-1} $year^{-1}$). Using biomass equations in Samuelson et al. (2017), the biomass of these three main components was predicted for each parametrization study and site. Bark biomass was calculated from stembark equations in Gonzalez-Benecke et al. (2015). Stem biomass accounted for stem and bark biomass (woody biomass, Mg ha^{-1} $year^{-1}$). Needle fall, branch fall, and litterfall (NF, BF, and LF, Mg ha^{-1} $year^{-1}$) were calculated following Gonzalez-Benecke (2016). Plot-level basal area (BA, m^2 m^{-2}), stand density (trees ha^{-1}), and quadratic mean diameter (QMD, m) were calculated for each plot, as well as the proportion of foliage to total biomass (pF), proportion of stem to total biomass (pS) and the ratio of foliage to stem biomass(pFS), which were calculated for each plot and also for each age. Parameters were then calculated through the establishment of the relationship of pFS as a function of QMD and age, following Gonzalez-Benecke et al. (2016), and fitting the subsequent non-linear model:

Equation (1): $pFS = pFSC \,.\, QMD^{pFSQMD} \,.\, AGE^{pFSAGE}$

where pFSC is the constant in pFS relationship, pFSQMD is the QMD in the pFSAGE relationship, and a_3 is the power of age in the pFS relationship.

2.6. Allometric relationships

Estimations of QMD were established following Landsberg and Waring (1997) and Gonzalez-Benecke et al. (2016). The following non-linear model was used to predict QMD, based on its relationships with W_S, age, and stand density:

Equation (5) $QMD = a11Ws + a1Ws \,.\, W_S^{n1Ws} \,.\, AGE^{n2Ws} \,.\, DENSITY^{n3Ws}$

where a11Ws is the intercept of the relationship, a1Ws is the constant in the relationship, n1Ws is the power of W_S in the relationship, parameter n2Ws is the power of age in the relationship, and parameter n3Ws is the power of stand density in the relationship.

Height predictors were established through the relationship of height and QMD, age, density, and basal area, following Gonzalez-Benecke et al. (2014b). The same complete dataset used for the pFS relationship determination was used for establishing the parameter estimates used in height (Ht, m) predictions. The model selected to estimate mean height was:

Equation (6) $Ht = a0H + e^{(aH + aHD + QMD^{\boldsymbol{nHD}} + ln(AGE)^{\boldsymbol{aHAGE}} + ln(DENSITY)^{\boldsymbol{aHN}} + ln(BAi)^{aHBA})}$

where a0H is the intercept in the stem-height relationship, aH is the constant in the stem-height relationship, aHD is the constant of QMD in the stem-height relationship, nHD is the power of QMD in the stem-height relationship, aHAGE is the constant of age in the stem-height relationship, aHN is the constant of stand density in the stem-height relationship, and aHBA is the constant of individual basal area (BAi, m^2) in the stem-height relationship.

2.7. Stem volume

The model computes stand volume as the volume inside the bark (V_{ib}) based on W_S, stand density, and basic wood-specific gravity. Here, we followed the approach described in Gonzalez-Benecke et al. (2014a, 2016), which uses the volume ratio between the volume inside and outside the bark (V_{ratio}) to estimate V_{ib} from the volume outside the bark (V_{ob}). Both bole V_{ib} and V_{ob} were computed using the equations developed by Gonzalez-Benecke et al. (2014b). Based on the calculated V_{ratio}, we selected the following model to establish the relationship of V_{ratio} and V_{ib}, also using density and age:

Equation (7) $$V_{ratio} = aVR\,.\,V_{ib}^{nVRVi}\,.\,\,DENSITY^{nVRN}$$

where aVR, nVRVi, nVRN, and nVRAge are respectively the constant in the stem volume ratio relationship, the power of V_{ib} in the stem volume ratio relationship, the power of stocking (stand density, trees ha^{-1}) in the stem volume ratio relationship, and the power of age (years) in the stem volume ratio relationship.

2.8. Maximum canopy conductance and stomatal response to vapor pressure deficit

The maximum canopy conductance (MaxCond, m s^{-1}) and stomatal response to vapor pressure deficit between the stomatal cavity and the atmosphere (i.e., VPD) (CoeffCond, $mBar^{-1}$) were obtained using three years of data from the study developed by Samuelson et al., (2019), which is an experimental throughfall reduction established in a longleaf pine plantation in the Chattahoochee Fall Line Wildlife Management Area in Marion County, GA (32.5528˚ N, -84.776˚ W) in May 2016. A complete description of the experimental site and experimental design was previously described in Samuelson et al. (2019). Here, we briefly describe the site. The stand was 12-15 years old, with mean tree height, total basal area, and peak LAI across the three years varying from 10.2-11.7 m, 19.2-21.8 m^2 ha^{-1}, and 2.7-3.2 m^2 m^{-2}, respectively. The parameters MaxCond and CoeffCond were estimated following Gonzalez-Benecke (2014a, 2016). The dataset was obtained through meteorological measurements recorded with an automated weather station, and canopy conductance calculations followed Bartkowiak et al. (2015) – inverting the Penman-Monteith equation and assuming sap flow as transpiration. The CoeffCond (power of VPD on the equation) and MaxCond (constant) were determined fitting a linear regression to the upper boundary line (quantile = 0.95) of the transformed data.

2.9. Canopy area and cover

Canopy cover dynamics used the long-term repeated measurements of canopy cover reported by Samuelson et al. (2017), from 20 stands ranging from 5-118 years old sampled across the range of longleaf pine in Georgia (Fort Benning at the Georgia-Alabama border, Louisiana (Kisatchie National Forest), North Carolina (Camp Lejeune), and Florida (Eglin Air Force Base) managed for timber production and biodiversity. In addition to the dataset from Samuelson et al. (2016), we also used the long-term study carried at Palustris Experimental Forest, developed by the U.S. Forest Service Laboratory at Pineville, LA, which comprises permanent plots in longleaf pine plantations on a range of sites in the south-central US, with tree age in the plots ranging from 7-75 years old, and the study developed by Samuelson et al. (2019), which is an experimental throughfall reduction established in a longleaf pine plantation in Marion County, GA (32.5528° N, -84.776° W). Complete descriptions of both studies are available in Goelz and Leduc, (2002) and Samuelson et al. (2019). In all three studies, measurements included live crown, as well as height and dbh at different ages. Following Gonzalez-Benecke (2014a, 2016), and assuming an elliptical crown shape, we determined the best model fit for estimating canopy area (CA, m^2) as following:

Equation (8) $$CA = d_1 \,.\, DBH^{d_2} \,.\, BA^{d_3}$$

where d1-d3 are parameter estimates of the equation.

After estimations, the sum of each trees CA in a plot was used to determine canopy cover (CanCover, $m^2\ m^{-2}$) as a proportion of the plot area. The 3-PG model uses the maximum value of CanCover as 1 (not accounting for overlapping branches). For this reason, values of CanCover greater than 1 were assumed to be equal to 1. We followed Gonzalez-Benecke (2014a, 2016) to fit a function to describe the dynamics of CanCover before reaching full canopy closure. For longleaf pine plantations, the best set of stand attributes included just basal area, and the model finally selected to estimate mean CanCover was:

Equation (9) $$CanCover = CanBA1 . BA^{z}$$

where CanBa1 is the constant in the canopy cover estimation (representing the canopy cover at BA=1 m^2 ha^{-1}), and z is a curve fit parameter. The 3-PG model also uses the parameter estimate representing the BA at canopy cover (i.e., CanCover=1), denoted as fullCanBa, which was also calculated.

2.10. Density-dependent and density-independent tree mortality

For density-independent tree mortality (denoted as γN in 3-PG, which represents the mortality prior to intra-specific competition, % $year^{-1}$), the parameter estimates were obtained following Gonzalez-Benecke (2014a, 2016). Model simulations were obtained through the Growth and Yield Model developed by Gonzalez-Benecke et al. (2015), and simulations were run under different conditions of planting density (tree ha^{-1}) and site indexes (SI, m). A dataset was created combining the simulations and used to fit the model of Sands (2004) (maintaining parsimony in the 3-PG model structure):

Equation (10) $$\gamma N = \gamma N_1 + (\gamma N_0 - \gamma N_1) . e^{(- ln(2) . \frac{AGE}{\gamma N_t})}$$

where γN_0 is the mortality at age = 0 (i.e., seedling stage; % $year^{-1}$), γN_1 is the mortality rate at large ages (i.e., mature stands; % $year^{-1}$), γN_t is the age at which γN is the age at which mortality rate has median value (years), e is the base of natural logarithm, and ln is the natural logarithm.

Similar to Gonzalez-Benecke (2014a, 2016), density-dependent tree mortality estimates [maximum single tree stem biomass at a stand density of 1000 trees ha^{-1} (denoted as wSx1000 in 3-PG, kg tree^{-1}), and the self-thinning rule parameter (thinPower)] were computed from the parameterization dataset, after using a species-specific general biomass equation for W_S reported by Samuelson et al. (2016). Value of thinPower was determined fitting a linear regression to the upper boundary line of the transformed data of the dependent variable W_S and the independent variable stand density (trees ha^{-1}) for each year and each site. Also, the value of WSx1000 was calculated after solving the fitted equation using stand density of 1000 trees ha^{-1}.

2.11. Wood basic specific gravity

Wood basic specific gravity (SG) is needed to convert stem wood mass (Mg ha^{-1}) to V_{IB}. The relationships between age and wood specific gravity (SG) were determined using the long-term repeated measurements of canopy cover reported by Samuelson et al. (2017), from 20 stands ranging from 5-118 years old sampled across the range of longleaf pine in Georgia (Fort Benning at the Georgia-Alabama border, Louisiana (Kisatchie National Forest), North Carolina (Camp Lejeune), and Florida (Eglin Air Force Base) managed for timber production and biodiversity. Following Gonzalez-Benecke (2014a, 2016), we established a relationship between age and wood specific density and fitted the following model:

Equation (11) $$SG = \rho_1 + (\rho_0 - \rho_1) . e^{\left(-\ln(2) . \frac{AGE}{t_\rho}\right)}$$

where ρ_0 and ρ_1 are respectively the SG at age = 0 and SG of mature stands, t_ρ is the age at which SG = $\frac{1}{2}$. $(\rho_0 + \rho_1)$, and e is the base of natural logarithm.

2.12. Specific needle area

Specific needle area (SNA, m^2 kg^{-1}) estimation used the measurements of canopy cover reported by Samuelson et al. (2016). Samples included 20 different stands ranging from 5-70 years old across the range of longleaf pine in Georgia [Fort Benning at the Georgia-Alabama border, Louisiana (Kisatchie National Forest), North Carolina (Camp Lejeune), and Florida (Eglin Air Force Base)]. We fitted the model proposed by Sands (2010), maintaining parsimony in the 3-PG model structure:

Equation (12) $$SNA = SLA_1 + (SLA_0 - SLA_1) \,.\, e^{\left(-\ln(2)\,.\,\frac{AGE}{t_{SLA}}\right)}$$

where SLA_0 and SLA_1 are respectively the SNA at age = 0 and SNA of mature stands, t_{SLA} is the age at which SNA = $\frac{1}{2}$. $(SLA_0 + SLA_1)$, and e is the base of natural logarithm.

2.13. Fertility rating

Fertility rating was estimated following Gonzalez-Benecke et al. (2016), correlating fertility rating (FR) with changes in SI. The relationship between FR and SI was analyzed using data from 26 permanent plots that were separated from the parameterization and validation datasets. Sites were randomly selected to account for variability in geographic location and the range of site index. The dataset consisted of stands from 4 to 75 years old, with stand density and SI at 50 years old (SI_{50}) ranging between 133-1800 trees ha^{-1} and 15.8-35.6 m, respectively. On each plot, total above-ground biomass (AGB, Mg ha^{-1}) was determined using the general biomass function reported by Gonzalez-Benecke et al. (2018). Similar to Gonzalez-Benecke et al. (2016), after obtaining all parameter estimates required by 3-PG, we determined the value of FR that minimized the error of AGB, by recording for each plot the value that had the minimum mean square error (MSE) of the fitting between the observed and predicted AGB (including all measurements). Finally, after pooling all paired data from all 25 plots, SI was correlated with the optimum FR. Once the FR function had been developed by calibration, it was applied unchanged to the validation data set. The following exponential curve was finally selected to estimate:

Equation (13) $$FR = a \, . e^{b \, \cdot \, SI_{50}}$$

where a, and b are curve fit parameters. All other parameter estimates shown in Table X were obtained from previous reports of 3-PG parameterizations for longleaf and slash pine (Gonzalez-Benecke et al. 2014a, 2016).

2.14. Model evaluation

Model validation was conducted by comparing observed and predicted values. Predicted values were simulated with the 3-PG parameters calculated for longleaf pine forests reported in this study, running the model from age of first measurement to the age of last measurement. Initial biomass pools in the model were determined for each plot using the equations for W_F, W_S and

W_R reported in this study. The performance of 3-PG for longleaf pine was compared against independent data not used in model development. The goodness-of-fit between the observed and predicted values was evaluated using three measures of accuracy: root mean square error (RMSE), mean bias error (bias, the difference between observed and predicted values), and coefficient of determination (R^2).Variables evaluated included BA, stand density, height, AGB and VOB. For each variable, we used F-tests to determine if the relationship between predicted and observed values had a slope (i.e., β_1) different than one. All statistical analyses were performed using SAS 9.4 (SAS Inc. Cary, North Carolina, USA).

Table 1. Summary of the characteristics of the stands used for estimating parameters in 3-PG.

Study	State	County	n	Lat.	Long.	Age (years)	QMD (cm)	Density (trees ha^{-1})	BA (m^2 ha^{-1})	SI (m)
Benning	GA	Chattahoochee	4	32.332	-84.742	13-20	6.0-15.0	500-675	2.0-8.8	27.5-27.5
Benning	GA	Chattahoochee	6	32.384	-84.796	15-20	6.4-13.0	1675-1825	5.8-22.3	25.6-27.3
Benning	GA	Chattahoochee	6	32.386	-84.71	12-19	10.8-18.3	725-900	6.6-22.3	29.8-30.3
Benning	GA	Muscogee	8	32.452	-84.77	16-25	7.6-15.4	1300-1400	6.4-24.6	21.3-22.7
BLX	GA	Talbot	2	32.5752	-84.52199	31-31	15.8-16.2	889-889	17.5-18.3	20.9-20.9
BLX	GA	Talbot	2	32.5756	-84.51499	30-30	17.6-18.0	889-889	21.7-22.5	22.5-22.5
BLX	GA	Talbot	2	32.5767	-84.52295	31-31	14.0-14.2	889-911	14.0-14.1	17.7-17.7
BLX	GA	Talbot	2	32.5793	-84.50296	31-31	14.6-15.0	644-644	10.8-11.4	16.0-16.0
BLX	GA	Talbot	2	32.5817	-84.49676	30-30	16.3-17.2	633-633	13.2-14.6	18.8-18.8
BLX	GA	Talbot	2	32.582	-84.5012	29-29	18.8-20.1	500-522	14.4-15.8	25.3-25.3
BLX	GA	Talbot	2	32.5826	-84.50322	30-30	14.7-15.2	978-978	16.5-17.7	19.0-19.0
BLX	GA	Talbot	2	32.5828	-84.51535	29-29	17.3-17.8	667-667	15.7-16.6	23.0-23.0
BLX	GA	Talbot	2	32.5871	-84.50353	30-30	15.3-15.7	767-767	14.0-14.8	20.5-20.5
HEF2_1	MS	Harrison	12	30.65	-89.09	17-40	7.4-30.3	229-499	2.1-21.7	28.3-29.3
HEF2_2	MS	Harrison	8	30.65	-89.09	17-40	7.2-27.2	308-495	2.0-20.2	28.4-29.7
P_312	MS	Perry	5	31.367	-88.933	25-40	15.5-23.0	788-1200	22.6-32.5	27.7-27.7
P_313	TX	Sabine	30	31.167	-93.867	29-75	15.0-31.5	570-1590	25.0-52.1	25.4-26.5
P_329	LA	Rapides	82	31.167	-92.667	43-83	22.4-42.6	175-650	17.2-47.1	24.8-28.0
P_410	FL	Santa_Rosa	8	30.967	-87.833	10-28	5.9-21.4	644-744	1.8-25.6	29.2-29.2
SSPSSS	FL	Liberty	20	30.42	-84.92	15-30	3.0-14.8	244-844	0.3-5.7	11.6-18.6
SSPSSS	FL	Calhoun	44	30.43	-84.27	15-35	3.5-13.3	267-711	0.4-6.9	12.8-19.3
SSPSSS	MS	Harrison	66	30.6	-89.07	15-35	2.9-25.6	133-822	0.5-12.2	23.2-30.2
SSPSSS	MS	Pearl_River	43	30.73	-89.58	15-35	4.8-27.5	133-667	0.7-20.1	24.7-31.5
SSPSSS	AL	Escambia	27	31	-87.08	15-35	8.3-28.2	133-600	2.8-13.6	29.8-33.1
SSPSSS	LA	Rapides	52	31.02	-92.62	20-35	5.8-27.6	267-778	1.4-24.2	28.6-31.4
SSPSSS	AL	Monroe	2	31.27	-87.52	15-15	4.4-11.0	467-533	0.8-4.4	33.5-33.5
SSPSSS	LA	Sabine	17	31.38	-93.4	15-35	3.2-29.7	244-644	0.5-16.9	21.1-29.0
SSPSSS	TX	Nacogdoches	5	31.5	-94.77	15-35	10.1-24.8	333-733	5.8-16.1	30.1-30.1

SSPSSS	GA	Sumter	37	32	-84	15-40	9.3-23.0	267-800	3.9-18.4	23.5-30.7
SSPSSS	GA	Wilcox	20	32.08	-83.5	15-30	11.3-22.6	356-733	6.1-17.4	29.0-32.2
SSPSSS	AL	Autauga	30	32.57	-86.88	15-35	4.2-23.1	222-778	0.8-12.9	20.4-22.5
SSPSSS	SC	Georgetown	8	33.67	-79.2	15-25	9.2-21.2	400-733	4.4-16.4	30.8-33.9
SSPSSS	SC	Chesterfield	11	34.5	-80.2	15-40	8.7-22.8	133-711	3.0-11.6	18.1-19.7
SSPSSS	NC	Richmond	12	35.03	-79.67	15-40	9.5-24.3	289-600	3.3-13.4	20.0-20.5
SSPSSS	NC	Richmond	50	35.03	-79.65	15-35	8.3-22.0	400-889	3.5-18.3	17.5-20.4
SSPSSS	NC	Person	10	36.43	-79	15-30	3.6-16.1	378-689	0.7-7.7	17.9-19.6
SSPSSS	VA	Nansemond	5	36.58	-76.87	15-30	9.7-23.5	311-356	2.6-13.4	24.3-24.3
VA_GG	VA	Sussex	3	36.85	-77.1667	9-10	7.3-13.9	719-719	3.0-10.8	31.1-31.1
VA_NK	VA	New_Kent	6	37.417	-77.0167	9-10	6.9-12.4	956-988	3.7-11.6	28.8-30.0
			Total = 655			Range = 9-83	Range = 2.9-42.6	Range = 133-1825	Range = 0.3-52.1	Range = 11.6-33.9

Table 2. Summary of the characteristics of the stands used for model validation

Study	State	County	n	Lat.	Long.	Age (years)	QMD (cm)	Density (trees ha^{-1})	BA (m^2 ha^{-1})	SI (m)
BENNING	GA	Chattahoochee	4	32.332	-84.742	8-20	7.4-14.3	875-1050	4.6-14.0	28.2-28.2
HEF2_1	MS	Harrison	4	30.65	-89.09	7-40	9.1-29.0	326-505	3.3-21.6	30.3-30.3
HEF2_2	MS	Harrison	4	30.65	-89.09	7-40	7.3-26.5	371-504	2.1-20.4	29.1-29.1
P_312	MS	Perry	7	31.36667	-88.9333	20-40	12.0-19.0	1131-1663	16.3-32.4	24.9-27.1
P_313	TX	Sabine	7	31.167	-93.867	24-50	13.4-21.3	1200-1420	20.1-42.6	25.2-25.2
P_329	LA	Rapides	19	31.167	-92.667	38-68	24.8-40.0	250-525	20.5-39.9	26.3-26.9
SSPSSS	FL	Liberty	12	30.42	-84.92	10-30	3.7-12.9	244-511	0.3-4.9	15.7-16.5
SSPSSS	FL	Calhoun	7	30.43	-84.27	10-25	4.1-6.9	444-622	0.6-2.2	12.1-14.1
SSPSSS	MS	Harrison	14	30.6	-89.07	10-30	8.1-21.4	156-444	2.2-10.8	24.7-29.0
SSPSSS	AL	Escambia	21	31	-87.08	20-30	16.1-23.1	333-489	9.6-15.7	31.6-34.0
SSPSSS	LA	Rapides	4	31.02	-92.62	15-35	14.3-26.4	356-400	6.4-19.5	31.8-31.8
SSPSSS	LA	Sabine	6	31.38	-93.4	20-35	17.1-25.6	156-289	3.6-12.9	23.6-24.7
SSPSSS	TX	Nacogdoches	19	31.5	-94.77	10-35	10.9-25.4	267-711	6.6-15.0	27.2-30.1
SSPSSS	GA	Sumter	18	32	-84	20-40	15.0-23.2	289-622	9.8-16.5	23.7-27.5
SSPSSS	GA	Wilcox	3	32.08	-83.5	10-20	11.0-17.3	533-667	6.3-12.5	30.5-30.5
SSPSSS	SC	Chesterfield	16	34.5	-80.2	10-35	10.5-22.5	222-667	5.7-14.1	17.6-20.2
SSPSSS	NC	Richmond	18	35.03	-79.65	10-35	8.2-21.8	422-778	2.7-18.2	18.2-20.7
SSPSSS	NC	Person	12	36.43	-79	10-30	4.3-19.0	378-578	0.5-12.6	18.6-19.6
SSPSSS	VA	Nansemond	2	36.58	-76.87	20-25	18.7-21.6	378-378	10.4-13.8	30.1-30.105
			Total = 197			Range = 7-68	Range = 3.7-40.0	Range = 156-1663	Range = 0.3-42.6	Range = 12.1-34.0

Table 3. Description of the 3-PG parameters, units, values, and sources for longleaf pine.

Meaning/Comments	3-PG symbol	Units	Estimate	Sources
Biomass partitioning and turnover				
Allometric relationships & partitioning				
Constant in the pFS relationship	pFSC	-	0.4106	This study
Power of Age in the pFS relationship	pFSAge	-	0.4727	This study
Power of QMD in the pFS relationship	pFSQMD	-	-0.4453	This study
Intercept in the diam. v. stem mass relationship	a11Ws	-	3.098	This study
Constant in the diam. v. stem mass relationship	a1Ws	-	90.6038	This study
Power in the diam. v. stem mass relationship	n1Ws	-	0.5003	This study
Power of Age in the diam. v. stem mass relationship	n2Ws	-	-0.2206	This study
Power of Nha in the diam. v. stem mass relationship	n3Ws		-0.5014	This study
Maximum fraction of NPP to roots	pRx	-	0.4	Gonzalez-Benecke et al. 2014a
Minimum fraction of NPP to roots	pRn	-	0.144	Gonzalez-Benecke et al. 2014a
Litterfall & root turnover				
Maximum litterfall rate	gammaF1	month^{-1}	1	Gonzalez-Benecke et al. 2014a
Litterfall rate at t = 0	gammaF0	month^{-1}	0.733	Gonzalez-Benecke et al. 2014a
Age at which litterfall rate has median value	tgammaF	months	21.5	Gonzalez-Benecke et al. 2014a
Average monthly root turnover rate	gammaR	month^{-1}	0.018	Gonzalez-Benecke et al. 2014a
Maximum needlefall rate	gammaFmax	month^{-1}	0.13	Gonzalez-Benecke et al. 2014a
Month at which needlefall rate has maximum value	tgammaFmax	month	11	Gonzalez-Benecke et al. 2014a
Average yearly forest floor decay rate	kFF	year^{-1}	0.14	Gonzalez-Benecke et al. 2014a
NPP & conductance modifiers				
Temperature modifier (fT)				
Minimum temperature for growth	Tmin	deg. C	4	Bryars et al. 2012
Optimum temperature for growth	Topt	deg. C	25	Bryars et al. 2012

Maximum temperature for growth	Tmax	deg. C	35	Bryars et al. 2012
Frost modifier (fFRost)				
Days production lost per frost day	kF	days	1	Gonzalez-Benecke et al. 2014a
Days production lost per degree celcius below zero on frost day	kF1	days	0.178	Teskey et al. 1987
Soil water modifier (fSW)				
Moisture ratio deficit for f_q = 0.5	SWconst	-	0.7	Gonzalez-Benecke et al. 2014a
Power of moisture ratio deficit	SWpower	-	9	Gonzalez-Benecke et al. 2014a
Atmospheric CO2 modifier (fCO2)				
Assimialtion enhancement factor at 700 ppm	fCalpha700	-	1.17	Ward et al. 2014
Canopy conductance enhancement factor at 700 ppm	fCg700	-	1	Ward et al. 2014
Fertitlity effects				
Value of 'm' when FR = 0	m0	-	0	Bryars et al. 2012
Value of 'fNutr' when FR = 0	fN0	-	0.3	Bryars et al. 2012
Power of (1-FR) in 'fNutr'	fNn	-	1	Bryars et al. 2012
Age modifier (fAge)				
Maximum stand age used in age modifier	MaxAge	years	300	Sampson et al. 2006
Power of relative age in function for fAge	nAge	-	1.5	Sampson et al. 2006
Relative age to give fAge = 0.5	rAge	-	0.75	Sampson et al. 2006
Stem mortality & self-thinning				
Mortality rate for large t	gammaN1	% year^{-1}	1.63	This study
Seedling mortality rate (t = 0)	gammaN0	% year-1	0	This study
Age at which mortality rate has median value	tgammaN	years	23.2497	This study
Shape of mortality response	ngammaN	-	1	Gonzalez-Benecke et al. 2016
Max. stem mass per tree @ 1000 trees/hectare	wSx1000	kg tree^{-1}	344.12	This study
Power in self-thinning rule	thinPower	-	1.15	This study
Fraction mean single-tree foliage biomass lost per dead tree	mF	-	0	Sands and Landsberg 2002
Fraction mean single-tree root biomass lost per dead tree	mR	-	0.2	Sands and Landsberg 2002
Fraction mean single-tree stem biomass lost per dead tree	mS	-	0.4	Sands and Landsberg 2002

Canopy structure and processes				
Specific leaf area				
Specific leaf area at age 0	SLA0	m^2 kg^{-1}	4.0439	This study
Specific leaf area for mature leaves	SLA1	m^2 kg^{-1}	3.2924	This study
Age at which specific leaf area = (SLA0+SLA1)/2	tSLA	years	16.4	This study
Light interception				
Extinction coefficient for absorption of PAR by canopy	k	-	0.57	Gonzalez-Benecke et al. 2014a
Age at canopy cover	fullCanAge	years	0	This study
BA at canopy cover	fullCanBA	m^2 ha^{-1}	24.1549	This study
Canopy cover at BA=1 m2 ha-1	CanBA1	-	0.1659	This study
Maximum proportion of rainfall evaporated from canopy	MaxIntcptn	-	0.2	This study
LAI for maximum rainfall interception	LAImaxIntcptn	-	5	This study
Production and respiration				
Canopy quantum efficiency	alpha	molC molPAR^{-1}	0.05	Sampson et al. 2006
Ratio NPP/GPP	Y	-	0.47	Sands and Landsberg 2002
Conductance				
Minimum canopy conductance	MinCond	m s^{-1}	0	Gonzalez-Benecke et al. 2016
Maximum canopy conductance	MaxCond	m s^{-1}	0.01107	This study
LAI for maximum canopy conductance	LAIgcx	-	3	This study
Defines stomatal response to VPD	CoeffCond	mBar^{-1}	0.0485	This study
Canopy boundary layer conductance	BLcond	m s^{-1}	0.1	Gonzalez-Benecke et al. 2016
Wood and stand properties				
Branch and bark fraction (fracBB)				
Branch and bark fraction at age 0	fracBB0	-	0.648	Gonzalez-Benecke et al. 2014a
Branch and bark fraction for mature stands	fracBB1	-	0.24	Gonzalez-Benecke et al. 2014a
Age at which fracBB = (fracBB0+fracBB1)/2	tBB	years	4.751	Gonzalez-Benecke et al. 2014a
Basic Density				

Minimum basic density - for young trees	rho0	t m^{-3}	0.4072	This study
Maximum basic density - for older trees	rho1	t m^{-3}	0.5764	This study
Age at which rho = (rhoMin+rhoMax)/2	tRho	years	17.8767	This study
Stem height				
Intercept in the stem height relationship	a0H	-	3.3774	This study
Constant in the stem height relationship	aH	-	2.0938	This study
Constant of QMD in the stem height relationship	aHD	-	-242.9	This study
Power of QMD in the stem height relationship	nHD	-	-2.1831	This study
Constant of Age in the stem height relationship	aHAge	-	0.2767	This study
Constant of stocking in the stem height relationship	aHN	-	0.000637	This study
Constant of BA in the stem height relationship	aHBA	-	0.00817	This study
Volume Ratio				
Constant in the stem volume ratio relationship	aVR	-	1.3209	This study
Power of Vol inside bark in the stem volume ratio relationship	nVRVi	-	-0.0299	This study
Power of stocking in the stem volume ratio relationship	nVRN	-	0.0296	This study
Power of Age in the stem volume ratio relationship	nVRAge	-	0	This study
Conversion factors				
Intercept of net v. solar radiation relationship	Qa	W m^{-2}	-90	Default
Slope of net v. solar radiation relationship	Qb	-	0.8	Default
Molecular weight of dry matter	gDM_mol	gDM mol^{-1}	24	Default
Conversion of solar radiation to PAR	molPAR_MJ	mol MJ^{-1}	2.3	Default

3. Results

3.1. Model fitting

All parameter estimates for all functions used by 3-PG for longleaf pine are reported in Table 3, and for all parameters estimated from model fitting, significance level was set at $p<0.05$. Parameter estimates for NPP partitioning were determined through a model fitting that had the best fit for longleaf pine trees when based on age and QMD ($n=455$, $R^2=0.23$, $p<0.001$). Both pS and pF increased as trees aged (Figure 2A-B). Constant values for both pF and pS were reached at age 40-50 years old. In turn, even with larger increases in pS, pFS increased with both age and QMD (Figure 2A-B), and reached constant values at age 50 (Figure 3B). Values for pFS ranges from 0.28 to 0.80, and good agreement between observed and predicted values was observed (Figures 2C-D). The parameter estimates of the fitted pFS function were 0.4106, 0.4727, and -0.4453 for pFSC, pFSAge, pFSQMD, respectively.

Allometric relationships were established for QMD predictions, with the best model fit being a function of W_S, age and stand density ($n=645$, $R^2=0.99$, $p<0.001$). In general, relationship with QMD show that QMD increased with increasing age and W_S, while it decreased with increasing stand density (Figure 3A-C). For this reason, our model predicts that stands with the same age and stem biomass have smaller diameters at higher densities. The parameter estimates of the fitted QMD function were 3.0980, 90.6038, 0.5003, -0.2206, and -0.5014 for a11Ws, a1Ws, n1Ws, n2Ws, and n3Ws, respectively.

Parameters for predicting height were generated through model fitting based on QMD, age, stand density, and BA ($n=991$, $R^2=0.99$, $p<0.001$). While the relationship of height to the variables QMD, age, and BA was directly proportional (i.e., positive), stand density showed a negative relationship with height (i.e., smaller height in high-density stands; Figure 4A-D). Parameter estimates of the fitted height function were 3.3774, 2.0938, -242.9, -2.1831, 0.2767, 0.000637, and 0.00817 for a0H, aH, aHD, nHD, aHAge, aHN, and aHBA, respectively.

Stand bole volume ratio was first tested based on VIB, stand density and age. However, better model performance was detected when bole volume ratio estimations were dependent on VIB and stand density (Figure 5A-B; n=655, R^2=0.98, p<0.0001). The final parameter estimates of the fitted bole volume ratio function were -1.3209, -0.0299, and 0.0296 for aVR, nVRVi, and nVRN, respectively.

Tree mortality in 3-PG can be either density-independent (i.e., random or stress-induced), or density-dependent (i.e., self-thinning). The 3-PG model looks at density-dependent mortality by exploring the relationship between stem biomass and density (n=939, Figure 5C). The slope of the self-thinning line (thinPower) was 1.15 and the maximum stem mass per tree at 1000 trees ha^{-1} (wSx1000) was 344.12 kg. The relationship between mortality and stand density is shown in Figure 5D (n=621, R^2=0.62, p<0.001). For the model for density-independent mortality, parameter estimated were 1.63, -0.00363, and 23.2497 for γN_1, γN_0, and $t\gamma N$. The parameter γN_0 had little influence on the density-independent mortality function and was excluded from the model.

Using allometrically-based estimates of crown area, we calculated fractional canopy cover for each plot in studies used in the parameterization. We tested relationships between canopy cover and stand age and basal area, and found that basal area was directly related to the timing to reach full canopy closure (fractional canopy cover = 1), and was a better predictor of canopy cover. As any value of CanCover > 1 is assumed to be 1 in 3-PG, basal area at full canopy cover (i.e., CanBa1) in longleaf pine stands was 24.15 m^2 ha^{-1} (Figure 6A).

A negative relationship between canopy conductance and mean daily VPD was observed ($n = 413$, $R^2 = 0.23$, $p<0.001$; Figure 6B). Maximum and minimum canopy conductance (i.e., MaxCond and MinCond), and the response of canopy conductance to VPD (CoeffCond) were 0.01107 m s^{-1}, 0 m s^{-1}, and 0.0485 $mBar^{-1}$, respectively.

An exponential decay to a non-zero asymptote was fitted for getting the parameter estimates for SNA. The function describing the SNA dynamics was dependent on age ($n=120$, $p<0.001$; Figure 6C). Average SNA for young plots was about 4.5 m^2 kg^{-1}, decreasing as trees aged to values of about 3.6 m^2 kg^{-1} (Figure 6C). Parameter estimates for the SNA function were 4.0439, 3.2924, and 16.4 for SLA_0, SLA_1, and t_{SLA}, respectively. Similarly, an exponential decay to a non-zero asymptote was used to establish the parameter estimates for SG, which was also age-dependent ($n=15$, $R^2=0.97$, $p=0.002$; Figure 6D). Parameter estimates for the SG function were 0.4072, 0.5764, and 17.8767 for ρ_0, ρ_1, and t_ρ, respectively.

Estimates of the initial biomass pools required to start the model are shown in Table 4. Equations for estimating W_S or W_F were determined for trees with height below and above 3m. For taller trees (height > 3 m), biomass functions were based on DBH and age. Interestingly, the parameter estimate associated with height in the foliage biomass determination was negative, demonstrating that for the same DBH and age, taller trees had less living needle biomass than shorter trees. For trees with height < 3 m, biomass estimates (either foliage or stem) were based only on ground level diameter. For trees of all heights, W_R was only dependent on age.

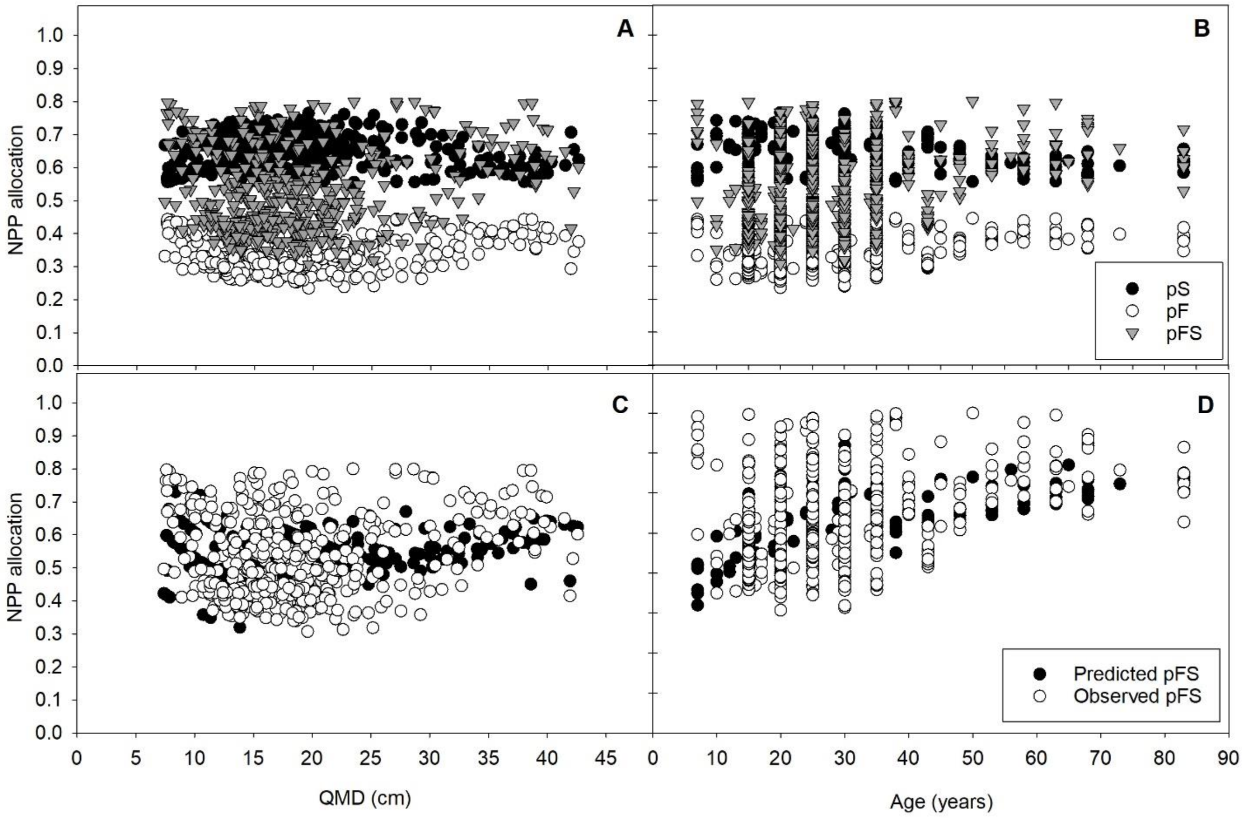

Figure 2. Panels A and C show the relationship between observed values of NPP allocation (proportion of foliage to total biomass, pF; proportion of stem to total biomass, pS; and proportion of foliage biomass to stem biomass, pFS) versus QMD [A] and age [C] for longleaf pine stands ranging age from 7 to 83 years old and QMD from 4.5 to 42.6 cm. Panels B and D show observed versus predicted values of pFS for longleaf pine stands.

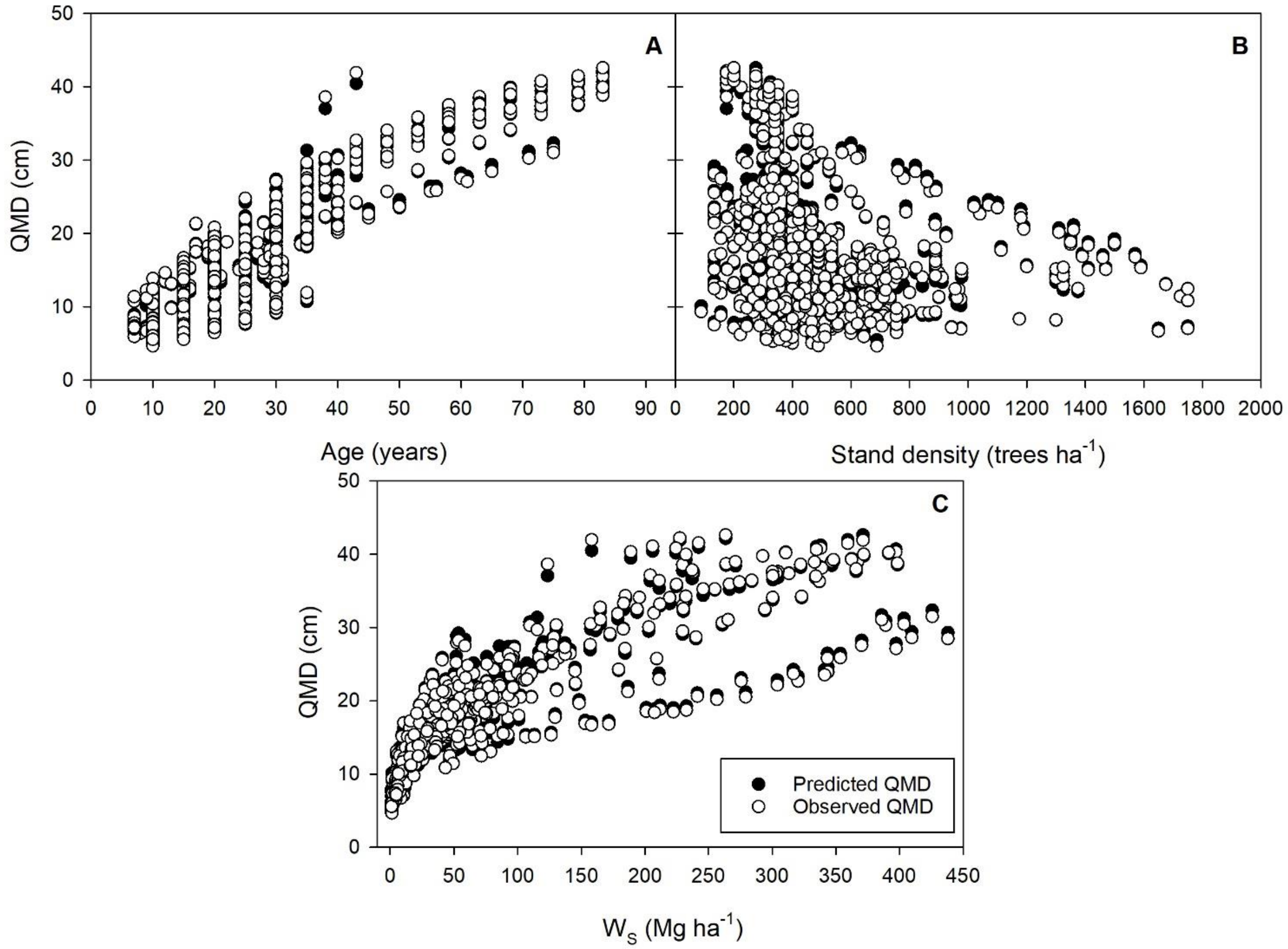

Figure 3. Observed and predicted allometric relationships for quadratic mean diameter (QMD) and age [A], stand density [B], and stem biomass (W_S) [C] for longleaf pine stands.

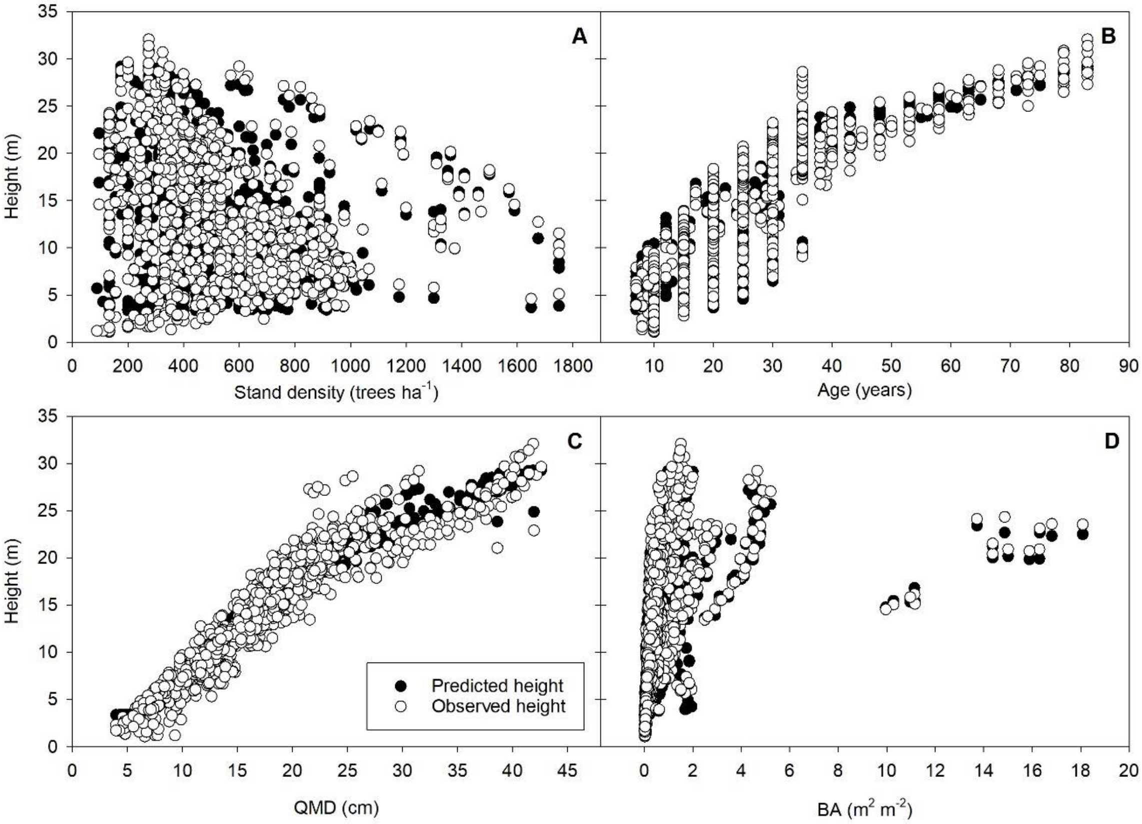

Figure 4. Observed and predicted allometric relationships for height and stand density [A], age [B], quadratic mean diameter (QMD [C], and basal area (BA) [D] for longleaf pine stands.

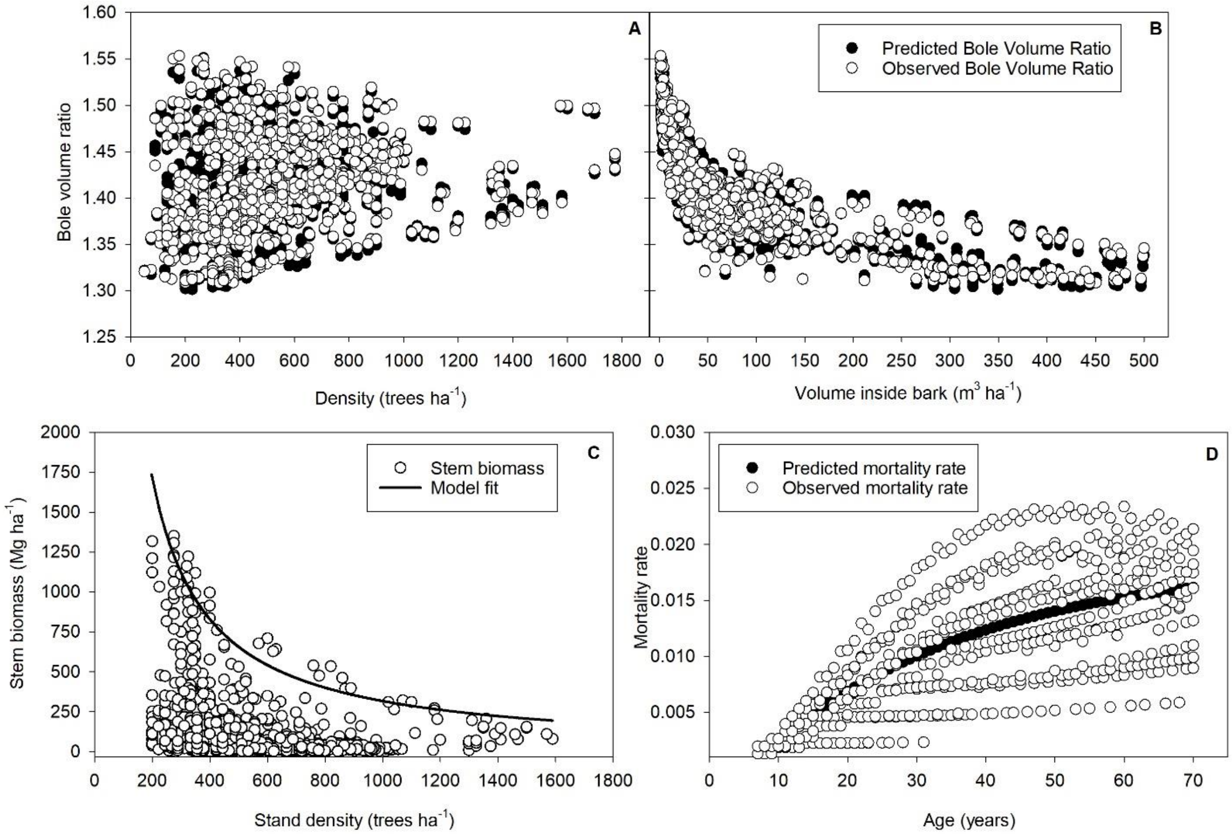

Figure 5. Panels A and B show the observed and predicted relationship for bole volume ratio and stand density [A], and volume inside the bark [B] for longleaf pine stands. Panels C and D show the observed and predicted tree mortality relationships: density-dependent mortality, based on the relationship between stem biomass and stand density, where the model fit line represents the theoretical self-thinning upper boundary [C], and relationship between density-independent mortality and age [D].

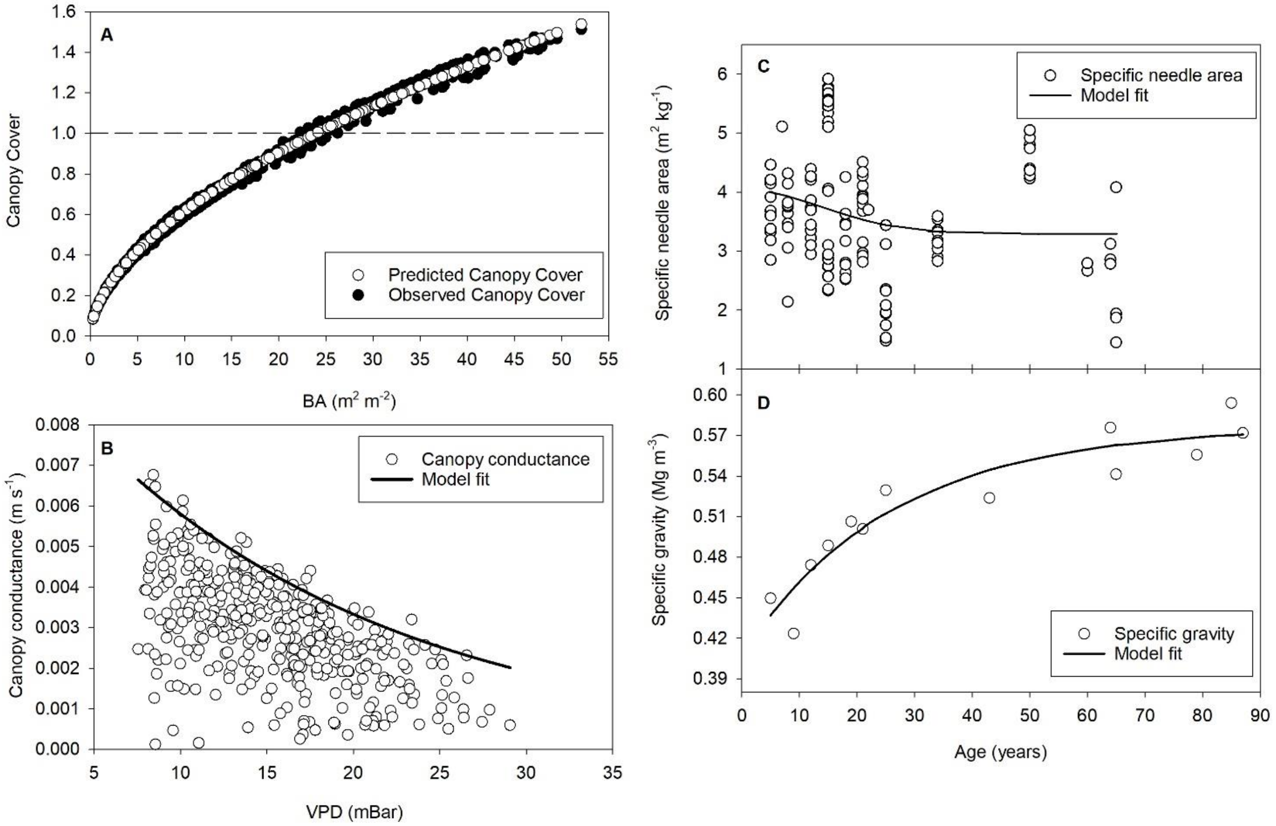

Figure 6. Observed and predicted canopy cover (expressed as fractional canopy cover) relationship versus basal area (BA) [A]; model fitting for canopy conductance sensitivity to VPD in longleaf pine trees. Data from 12-15 year-old longleaf pine plantation located in the southwestern Georgia, U.S. [B]; model fitted for age-dependent relationship between specific needle area [C] and whole-tree specific gravity [D] for longleaf pine trees.

Table 4. Parameter estimation and fitted statistics of equations for predicting initial biomass pools for longleaf pine stands growing in the southeastern United States.

	Model	Parameter	Estimate	Standard Error	Study
Height > 3	$W_F = a_1 \,.\, Height^{a2} \,.\, DBH^{a3} \,.\, Age^{a4}$	a_1	0.042	0.007	Gonzalez-Benecke et al. 2018
		a_2	-0.273	0.113	
		a_3	1.8393	0.094	
		a_4	0.1956	0.055	
	$W_S = a_1 \,.\, Height^{a2} \,.\, DBH^{a3} \,.\, Age^{a4}$	a_1	0.0156	0.001	Gonzalez-Benecke et al. 2018
		a_2	0.9285	0.051	
		a_3	1.7983	0.036	
		a_4	0.3031	0.025	
Height < 3	$W_F = b_1 \,.\, GLD^{b2}$	b_1	-3.355	0.310	Samuelson et al. 2014
		b_2	0.653	0.080	
	$W_S = b_1 \,.\, GLD^{b2}$	b_1	-5009	0.310	Samuelson et al. 2014
		b_2	1.136	0.080	
All	$WR = (c_1 \,.\, Age^{c2}) \,.\, 2$	c_1	4.068	1.156	Modified from Samuelson et al. 2016
		c_2	0.390	0.070	

Variables: W_F, foliage dry mass (kg tree^{-1}); W_S, stem dry mass (kg tree^{-1}); W_F, root dry mass (kg tree^{-1}); height, total tree height (m); DBH, tree diameter at 1.37 m from the ground line (cm)

3.2. Interactive calibration of FR

We analyzed the relationship between FR and SI through iterative calibration on 26 randomly selected plots that were previously separated from studies used in the parameterization dataset. Plots used in the FR determination were selected to cover the geographic range of longleaf pine in the southeastern U.S. (Figure 1). Selected plots represented a wide range in productivity, which resulted in SI at age 50 ranging between 23.6 and 33.4 m (Figure 7). The curve that showed the best fit and biological meaning was:

$$FR = 0.0310 \,.\, e^{0.0962 \,.\, SI_{50}} \qquad (n=26,\ R^2=0.45,\ p<0.001)$$

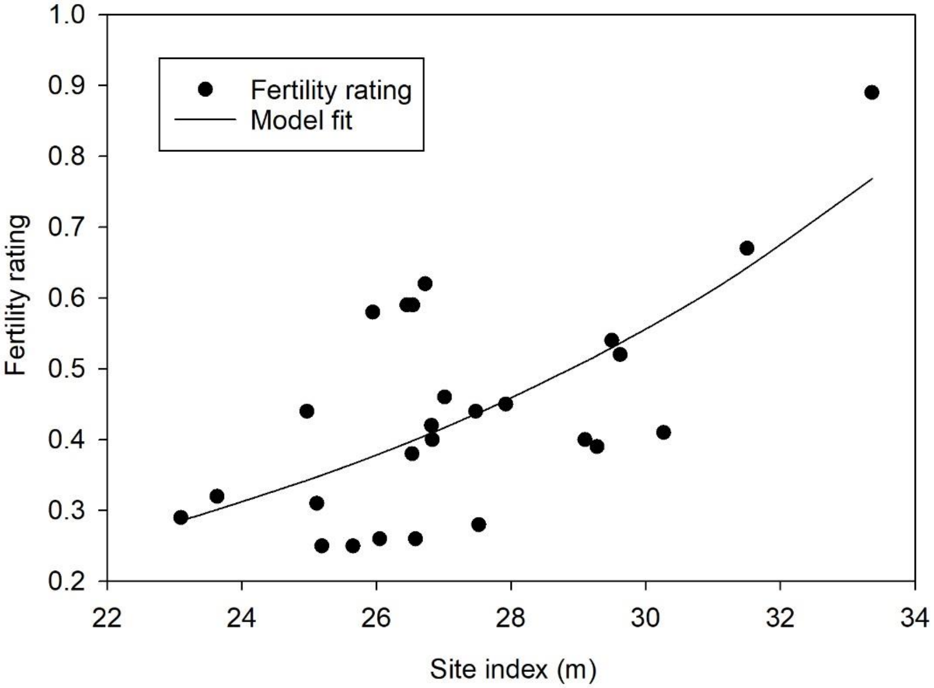

Figure 7. Relationship between fertility rating (FR) and site index (SI) after iterative calibration.

3.3. Model validation

We observed a general agreement between observed and predicted values (Figure 8A-F). However, although the model accurately predicted QMD, AGB, and stand volume well in most of the sites, in some cases, it tended to overestimate these two variables at late stages of development (Figure 8A and D). Performance tests generally showed that estimations agreed with measured values (Table 5). Across all sites, the slope of the established linear regressions between observed and predicted values was not statistically different from 1 (p=0.569). RMSE ranged between 2.06 for height predictions and 88.53 for stand density predictions (Table 5). Percent average deviation between predicted and observed values was less than 15% for most variables evaluated (Table 5). Estimated and observed values were highly correlated, with R^2 values ranging between 0.83 and 0.92 (Table 6).

Table 5. Summary of fitted statistics for model evaluation of the 3-PG model for longleaf pine stands growing in the southeastern United States. The table also includes the numerator (n) and denominator (d) degrees of freedom (*d.f.*).

Variable	Mean O	Mean P	*d.f.* (n,d)	RMSE	Percente average deviation	R^2
AGB	70.45	97.19	(1,203)	23.75	24.82	0.89
V_{OB}	123.97	149.15	(1,203)	38.65	14.31	0.87
QMD	17.66	18.54	(1,203)	1.99	23.66	0.92
TBA	12.77	14.76	(1,203)	3.61	6.58	0.83
Ht	15.09	16.98	(1,203)	2.06	8.31	0.89
Stand density	529.41	551.93	(1,203)	88.52	4.04	0.90

Variables: AGB, above-ground biomass (Mg ha^{-1}); V_{OB}, stand bole volume outside bark (m^3 ha^{-1}); QMD, quadratic mean diameter (cm); TBA, stand basal area (m^2 ha^{-1}); Ht: mean tree height (m); stand density (trees ha^{-1}); Mean O: mean of observed values; Mean P: mean of predicted values; RMSE: the root of mean square error (same unit as observed value); Percentage average deviation: percentage bias relative to the observed mean (%); R^2: coefficient of determination.

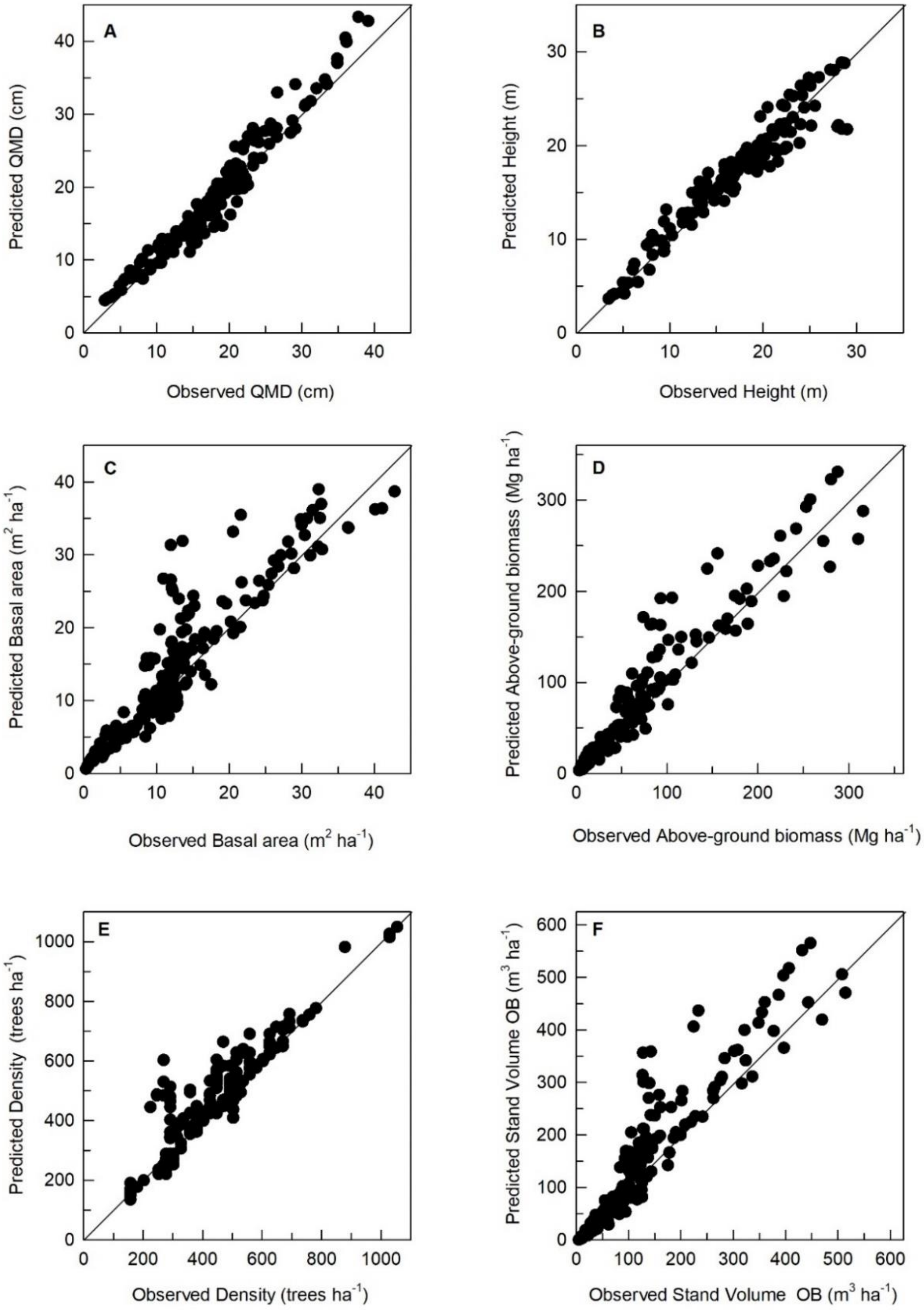

Figure 8. Model validation with observed versus predicted values (simulated with 3-PG and parameters for longleaf pine forests reported in this study). The solid line corresponds to the 1:1 relationship.

4. Discussion

In this study we provide the first parameter estimates of the 3-PG model for longleaf pine stands, using data from an extensive network of long-term studies throughout the Southeast Unites States. Parameter estimates were used to establish critical species-specific algorithms to estimate growth variables for even-aged longleaf pine stands. We used the alternative methods reported by Gonzalez-Benecke et al. (2014a, 2016) – modified from Sands and Landsberg, 2002 –, previously used in parameterizing the 3-PG model for slash and loblolly pines. Model performance was evaluated by contrasting observed data from different studies across the southeastern U.S. with predicted values from 3-PG simulations (using the species-specific set of parameter values reported in this study). Overall, we observed good agreement between observed values and the predictions, meaning that the application of the model resulted in appropriate characterization of the species' growth patterns. Nonetheless, further improvements in model performance (accuracy) are expected as new data becomes available. This study brings new insight for the parameterization of the 3-PG model to longleaf pine stands. Through this parameterization, the 3-PG model can be applied to assess growth patterns under different management regimes and to assess the possible impacts of climate change on longleaf pine stands across the southeastern United States.

The performance (accuracy) of the 3-PG model after species-specific parameterization largely depends on the quality of the data used in the calculations and on understanding the modeling procedure (Almeida et al., 2004; Sands and Landsberg, 2002; Song et al., 2013). The parameter estimates determined in this study were validated under a varied range of stand and site conditions, covering different zones within the species' natural distribution. Our model validation procedure indicated that the model showed satisfactory performance. Good agreement between observed and predicted values was observed for all tested variables. However, the model also demonstrated inaccuracies. We observed some tendency for overestimating growth variables at later stages in stand development (e.g., predictions related to AGB, and QMD, which had high percentage deviation relative to observed values). In our view, overestimations could be related to estimates of NPP and its partitioning to litterfall and root turnover. Canopy quantum efficiency, which directly impacts gross primary production (GPP), is obtained by the amount of photosynthetically active radiation (PAR) incident on the canopy (i.e., PAR and LAI through Beer's law; Landsberg et al., 2003; Sands, 2003; Sands and Landsberg, 2002). NPP is then calculated as a single constant fraction of GPP (Bryars et al., 2013; Landsberg et al., 2003; Landsberg and Waring, 1997; Law et al., 2000; Sands and Landsberg, 2002; Waring et al., 1998) which is then partitioned into root, stem, and foliage biomass pools. One potential explanation for overestimations at older ages could be the values of estimated NPP. Studies show that the proportion of GPP converted in NPP can decrease as the stand ages (Bryars et al., 2013; De Lucia et al., 2007). Therefore, different NPP to GPP fractions could account for differences throughout the years. As longleaf pine stands usually have longer rotations and are long-living pine species, this could be a critical component to review in the model. However, further studies are needed to evaluate the variability of this proportion and the applicable modifications in the model.

General climatic variations and soil properties affect the sensitivity values of most of the 3-PG model parameters. Root biomass allocation is primarily determined by soil moisture and soil nutrition (Landsberg et al., 2003). Reduced data availability prevented a specific determination of values of maximum and minimum NPP partitioning to roots in longleaf pine.

For these cases, numbers from other southern pines were assumed (Table 3; Gonzalez-Benecke et al., 2014a). However, reduced biomass allocation to roots, for example, could result in overestimations in above-ground biomass, which, consequently, may result in overestimations of basal area and stand volume. Varying amounts of biomass being allocated to foliage could also result in differences in LAI, affecting GPP and biomass going to the roots. Thus, these overestimations of LAI and GPP can result in a succession of overestimations, which would also explain the greater variation in growth variables at older ages. At the same time, there is also an inherent feedback in the model because litterfall is a fraction of current foliage mass, and is also a key factor affecting LAI estimations (Sands and Landsberg, 2002; Gonzalez-Benecke et al., 2016). Also, without data on litterfall and root turnover and dynamics, it is difficult to parameterize the relationship for root biomass partitioning (Almeida et al., 2004). Consequently, the factors involving gross and net primary production and partitioning and needlefall rate estimations need further attention as new data become available.

Although the 3-PG model showed good performance for longleaf pine, we detected some inaccuracies in predicting stand density. The overall predictions and relative deviations between observed and predicted values were satisfactory, but we visually observed that some overestimations occurred. This effect can most likely be attributed to 3-PG's use of the self-thinning rule exclusively to predict mortality (Bryars et al., 2013; Gupta and Sharma, 2019; Landsberg et al., 2003; Pinjuv et al., 2006; Sands and Landsberg, 2002). The self-thinning rule predicts mortality through allometric relationships between stand biomass and stand density, not accounting for mortality cases triggered by other causes, such as wind, diseases, or insect attacks. Further calculations that use stand density as a component, such as basal area and volume, could potentially carry on errors from stand density predictions. These miscalculations might not represent relevant errors on other species' parameterizations of the 3-PG model, such as *Eucalyptus* spp. or loblolly pine. However, over the longer rotations of longleaf pine stands, this might also be a critical component to be reevaluated in the future.

A detailed understanding of the relationship between forest growth and site characteristics is required to parameterize the 3-PG model for any given species. Fertility rating (FR) represents the soil nutritional status of the site, which is a crucial variable when estimating forest growth and directly affects 3-PG outputs. For instance, FR, along with canopy quantum efficiency and weather and soil properties, is one of the determinants of biomass production (Landsberg et al., 2003). Additionally, FR is critical in 3-PG because it directly influences the coefficient that estimates NPP partitioning to roots (Landsberg and Waring, 1997; Subedi et al., 2015). Therefore, the sensitivity of model outputs related to biomass production, such as above-ground biomass and stand volume, are closely related to FR estimates and could partly influence parameterization of the 3-PG model for longleaf pine forests. However, establishment of FR estimations are complicated (Almeida et al., 2004; Bryars et al., 2013; Carlos A. Gonzalez-Benecke et al., 2014b; Gonzalez-Benecke et al., 2016; Landsberg and Sands, 2011; Subedi et al., 2015), as it is difficult to determine a simple relationship between some single variable that simultaneously reflects soil fertility and stand productivity (Landsberg et al., 2003). For longleaf pine in particular, dynamics related to FR were challenging since this species tends to be planted in poorer sites across its natural range than other southern pines. Numerous studies have improved the FR estimations in the 3-PG model (Dye et al., 2004; Carlos A. Gonzalez-Benecke et al., 2014b; Subedi et al., 2015; Vega-Nieva et al., 2013). Here, we based our FR estimations on the method used by Gonzalez-Benecke (2016, 2014a) in the 3-PG parameterization for slash and loblolly pine stands. In this method, site index (SI) is a key factor in the FR estimation, as

FR has a positive correlation with changes in SI, and SI reflects nutrient and soil water balance through stand productivity (Gonzalez-Benecke et al., 2014a). However, the base age for site index that showed the best relationship with FR in longleaf pine stands was 50 years old, possibly because this species develops slower. Interestingly, our dataset's highest FR found among the 26 different plots used in the estimations was ~0.8, reflecting the generally poorer sites that longleaf pine stands are usually planted. This limit in FR shows the potential of the species to be more productive in better sites. We expect that the use of improved and more intensive silviculture techniques, and, perhaps, better quality sites can potentially result in higher values than those observed in this study (Fox et al., 2007b, 2007a). However, further studies are necessary to detail the production capacity of longleaf pine stands in a range of low- to high-quality sites. Also, we consider that estimates of FR could be improved as new data becomes available.

5. Conclusion

Here we present the first parameterization of the 3-PG model for longleaf pine stands. We used a large and geographically extensive long-term dataset to develop new functions for estimating important parameters for the model. The model was tested against data from stands of varying characteristics that were distributed across the southeastern United States. Although some factors need further attention as new datasets become available, the model showed good overall performance in the predictions evaluated. The parameters reported here allowed 3-PG to produce accurate estimates, with outputs matching most stand growth dynamics well. Using the 3-PG model for longleaf pine stands can help improve the predictability of this species' stands' productivity and describe the physiological dynamics of this species across a wide range of ages and stand characteristics. Notably, the use of the model for longleaf pine stands can provide a valuable tool for modeling long-term stand development, as well as serve as a practical tool to establish better management strategies and assess the impact of future changes in climate (Coops and Waring, 2011; Gonzalez-Benecke et al., 2017; Waring et al., 2011) in longleaf pine forests.

Acknowledgments

This work was supported by the Intergovernmental Support Agreement between the U.S. Army – through the Natural Resources Branch at Fort Benning – and Auburn University (Award BENNING-IGSA-16-00), the Auburn University Intramural Grants Program (Award 180286), and the Alabama Agricultural Experiment Station – Agriculture Research Enhancement & Seed Funding Program (Award 1025522).

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CHAPTER V

RESEARCH SUMMARY AND FINAL CONCLUSION

The increased anthropogenic activity and the consequent increase in the emission and accumulation of greenhouse gases in the atmosphere are altering climate patterns worldwide (Allen et al., 2015; Tian et al., 2020). Temperatures in the southeastern U.S. have progressively increased and are predicted to continue to do so in the coming years (Carter et al. 2018). Although more uncertain, precipitation patterns are also predicted to continue becoming more variable over the next decades, with the occurrence of more extreme precipitation events and more frequent and extended dry spells (Carter et al., 2018; Wang et al. 2009). Forest ecosystems represent an important component of the economy and play a critical role in regulating climate both by releasing and storing carbon. According to the United States Environmental Protection Agency (2018), carbon storage in forest ecosystems offsets approximately 10% of annual greenhouse gas emissions in the United States. However, climate change has the potential to affect and alter forest ecosystem dynamics, generating considerable modifications in forest function, composition, and distribution (Allen et al., 2010, 2011; McDowell et al., 2020). Tree water stress is expected to increase with elevated temperatures and reduced soil water availability, ultimately leading to declines in forest growth and tree survival (Adams et al., 2015; Allen et al., 2015; Breshears et al., 2013; Will et al., 2013). Decreased soil water availability may favor more drought-tolerant species and alter successional pathways. In this context, understanding the effects of a changing climate on forests and forecasting how forest ecosystems respond to reduced water availability is necessary for managing ecosystems in the face of climate change.

Longleaf pine (*Pinus palustris* Mill.) ecosystems are considered one of the most threatened ecosystems in the U.S. (Jose et al., 2007). Interest in the restoration of longleaf pine forests have increased not just because of its high natural biodiversity and the high value of timber and non-timber products (Brockway et al., 2007; Kleinman et al., 2020; Samuelson et al., 2017) but also because this species represents a potential improvement in the adaptability of southern forests to changing climate conditions (Samuelson et al., 2019, 2014). Longleaf pine is considered one of the most drought-resistant pines in the southeastern U.S. (Gonzalez-Benecke et al., 2010; Samuelson et al., 2019; Starr et al., 2016) and could serve as a suitable long-term carbon sink and key species for adapting southern forests to climate change. In this context, longleaf pine ecosystems may be an important species for mitigating climate change and increase carbon sequestration in southern forests, which increases the need to improve our knowledge and understanding about how this species will respond to future changes in climate and potential reduced water availability.

Questions remain about the sensitivity of longleaf pine to reduced water availability over extended periods. Here, we studied how three years of reduced rainfall, imposed by a throughfall reduction, impacted leaf- and canopy-scale physiology, shoot and foliage development patterns, and canopy-scale leaf area and litterfall dynamics in established longleaf pine trees. Although longleaf is considered one of the most drought-resistant tree species in the southeastern U.S., we expected significant changes in the evaluated aspects under exposure to reduced water availability. Instead, we found that a 40% reduction in throughfall resulted in small decreases in leaf- and canopy-scale function. We also found that throughfall reduction did not influence leaf- or canopy scale stomatal sensitivity to vapor pressure deficit. Similarly, we found that 40% throughfall reduction had a small effect on shoot and needle phenology or growth and LAI and litterfall dynamics. Thus, our results provide strong evidence that longleaf pine trees may withstand average reductions in total rainfall and water availability. If reductions in water availability persist over the long term, more drought-resistant species such as longleaf could be preferable over other less drought-resistant species, especially in more xeric sites.

As previously mentioned, forecasting how longleaf pine forests will respond to projected changes in climate is necessary for managing these ecosystems in the face of climate change. The use of forest simulation models, such as the 3-PG model – which uses a combination of climate, stand, and physiological parameters in its predictions – can provide a valuable tool for modeling long-term stand dynamics. Moreover, the 3-PG can also be used as an important tool for predicting the potential for carbon sequestration and serve as a practical tool to establish better management strategies and assess the impact of future climate changes (Coops and Waring, 2011; Gonzalez-Benecke et al., 2017; Waring et al., 2011). For this reason, we presented the first parameterization of the 3-PG model for longleaf pine stands. We used a large and geographically extensive long-term dataset across a species' range to develop new functions for estimating important parameters for the model. The model was tested against data from stands of varying characteristics that were distributed across the southeastern United States. Although some factors need further attention as new datasets become available, the model showed good overall performance in the predictions evaluated. The parameters reported here allowed 3-PG to produce accurate estimates, with outputs matching most stand growth dynamics well. Using the 3-PG model for longleaf pine stands can help improve the predictability of longleaf pine's stands' productivity and describe the physiological dynamics of this species across a wide range of ages and stand characteristics.

Projected increases in climate variability are expected to significantly alter forest structure and function (Knapp et al., 2017; Smith, 2011). In the first part of our study, we imposed an experimental throughfall reduction treatment based on the site’s historical precipitation records (Knapp et al., 2016). Our results showed that longleaf pine trees responded to a certain extent but were overall not strongly affected by the throughfall reduction treatment. These minor effects may indicate that longleaf pine trees may be relatively resistant to reductions in total water availability. Although the throughfall reduction treatment considerably reduced water availability for longleaf pine trees, the number of rain events and their frequency were not altered. On average, the exposure to the throughfall reduction treatment resulted in plots receiving approximately 780 mm each year. This amount is roughly equivalent to the two lowest rainfall years for the region in the 100-year record. Hence, it was unexpected that the treatment effects were not more severe. We believe that aspects related to the number, length, and seasonality of rain events dry spells may also represent significant factors influencing longleaf pine ecosystem's functionality (Engelbrecht et al., 2017; Knapp et al., 2017, 2008; Phillips et al., 2016). We consider that dry spells occurring for more extended periods with little or no rainfall, or changes in rainfall frequency, especially during warmer seasons, could impact tree function more than changes in total annual rainfall (Samuelson et al., 2019).

In conclusion, we believe that, although challenging, future experiments should rely on altering multiple aspects of rainfall timing, frequency, and amount to help advance our understanding of drought resistance in longleaf pine forests. The parameterization of the 3-PG model for longleaf pine trees may also be used to model these responses under different climatic conditions and extremes (e.g., exposure to long periods of drought or extreme dry years). The model could also help assess the performance and compare productivity and resistance among different species (e.g., other southern pines under variable climate and site conditions). Furthermore, specific to our work, it would be useful to evaluate several factors that may have influenced our results. For example, the depth of the water table and excavations to assess root extensions would help us understand if trees had access to water from additional sources other than just rainfall water. Also, evaluation of tree performance after the removal of the treatment would also bring us more information about the recovery rate after the minor effects caused by the throughfall reduction on the longleaf pine trees.

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