Turkey Oak (*Quercus laevis* W.) Seedlings Experience Primarily Competitive Pressures, not Facilitation, from the Overstory in a Longleaf Pine (*Pinus palustris* M.) Ecosystem

by

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Abstract

At a site dominated by longleaf pine (*Pinus palustris* Mill.) in southwestern Georgia, silvicultural plans designed to encourage ecosystem-level tolerance to climate changes - namely increased water stress - are under evaluation. One approach is to shift the hardwood component towards more xeric species, including turkey oak (*Quercus laevis* Walt.). This study addresses the feasibility of regenerating turkey oak seedlings in a longleaf ecosystem by investigating the relationships between overstory metrics and seedling leaf gas exchange measured over one growing season. Seedling physiological performance was negatively correlated with increased overstory levels and more stressful environmental conditions. I conclude that seedlings were negatively impacted by the overstory, with little evidence of facilitation. Efforts to transition a longleaf pine ecosystem towards greater drought tolerance may therefore be most effective when planting of turkey oak seedlings is concentrated in canopy openings. Such improvements in management techniques may aid in conserving this threatened ecosystem.

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List of Abbreviations

A	Leaf-level Net Photosynthesis
AIC	Akaike's Information Criterion
ASCC	Adaptive Silviculture for Climate Change
CO	Canopy Openness
DBH	Diameter at Breast Height
g_s	Leaf-level stomatal conductance
HL	Hydraulic Lift
LAI	Leaf Area Index
NCI	Neighborhood Competition Index
OAI	Overstory Abundance Index
PAR	Photosynthetically Active Radiation
USA	United States of America
VPD	Vapor Pressure Deficit
VWC	Volumetric Water Content

1.0 Project Background

Longleaf pine (*Pinus palustris* Mill.) ecosystems are biodiversity hotspots, with some of the greatest species richness found outside of the tropics – some longleaf woodlands are home to upwards of 50 species of vascular plants per square meter (Walker & Peet 1983). In addition to longleaf and other southern pine species, these ecosystems can host many species of grasses, sedges, legumes, orchids, insectivorous plants, palms, and hardwood trees, particularly oaks (Peet 2007). However, the longleaf pine ecosystem is also one of the most threatened ecosystems in the United States (USA); historically, the species' range is estimated to have encompassed approximately 37 million hectares across the southeastern USA, yet as of 2007, longleaf pine forests occupied only about 2.2 % of this historic range (Frost 2007).

Increases in atmospheric greenhouse gas concentrations over the last two centuries have been correlated with alterations in temperature and precipitation patterns at global and regional scales. Climate projections indicate warming coupled with increased soil dryness in the eastern USA (Vogel et al. 2017, Hoegh-Guldberg et al. 2018). Since 1970, average annual temperature in the southeastern USA has increased by approximately 1.1 °C, and this warming trend is anticipated to continue, with projected increases of 2.5-5.0 °C by 2080 (Karl et al. 2009). While effects on precipitation vary across the region, total annual precipitation in the region has declined since 1970, particularly in the winter and spring months, with the area affected by moderate to severe drought increasing in extent by 12-14% (Karl et al. 2009). In many parts of the region that have experienced increases in precipitation, concurrent increases in evapotranspiration have resulted in net decreases in both runoff and groundwater

availability (Dore 2005, Dai 2016, Hoegh-Guldberg et al. 2018). These shifts in climate patterns towards increasing temperature and decreasing water availability may have significant negative impacts on the already threatened longleaf ecosystem.

Given the potential changes in climate patterns that are faced by forest ecosystems, and the need for integrating climate change adaptability into silvicultural planning, the Adaptive Silviculture for Climate Change (ASCC) project was established. This project is a collaborative effort across seven sites in the USA and Canada, representing an array of different forest ecosystems. Research at each site in the network is focused on developing an understanding of the efficacy of different management options designed to enable forest ecosystems to respond to predicted alterations in climate patterns. Site-specific treatments were developed based on local conditions and were tailored for local management objectives, while simultaneously following a common framework designed to answer questions regarding the responses of different forest types to future climate scenarios.

The primary objectives of the ASCC project are to: (1) develop a cross-regional study utilizing site-specific climate change adaptation treatments, following input from regional scientists and local managers; and (2) introduce forest resource managers to conceptual tools and silvicultural approaches that will assist with integrating climate change concepts into forest management plans (Nagel et al. 2017). In the case of forest management, adaptation is considered in terms of management actions that are designed to address specific climate change effects and ecosystem vulnerabilities in an effort to achieve management goals specific to each site. With the above goals in mind, three broad treatments were implemented at each ASCC study site: (1) *resistance* treatments

designed to maintain current forest conditions with relatively little change over time; (2) *resilience* treatments designed to allow variability in forest conditions but with the overarching goal of encouraging an eventual return to near-current conditions; and (3) *transition* treatments designed to actively facilitate changes intended to encourage forest adaptation to climate change effects (Nagel et al. 2017). The specific research presented here is a component of the *transition* treatment implemented at the Jones Center at Ichauway, a research center for longleaf pine ecosystems located in Baker County, Georgia, USA. *Transition* strategies have previously been effectively incorporated into forest management plans, from conifer forests in Oregon (Hemstrom et al. 2007) to mixed-pine and hardwood forests in Minnesota (Muller et al. 2019) and Wisconsin (Janowiak et al. 2014).

2.0 Turkey Oak (*Quercus laevis* W.) Seedlings Experience Primarily Competitive Pressures, not Facilitation, from the Overstory in a Longleaf Pine (*Pinus palustris* M.) Ecosystem

2.1 Introduction

Anticipated effects of a changing climate on the southeastern USA include increased duration, occurrence, and severity of drought (Burke et al. 2006, Huntington et al. 2009, Karl et al. 2009, Sheffield et al. 2009, IPCC 2014, Mitchell et al. 2014). These drought conditions may occur simultaneously with an increase in the number of high-intensity rainfall events in some areas, as well as hotter temperatures and longer growing seasons (Wetherald 2009, IPCC 2014). Since 1970, average annual temperature in the southeastern USA has increased by approximately 1.1°C and total annual precipitation in the region has declined, particularly in the winter and spring months (Karl et al. 2009). Evapotranspiration has also increased, resulting in net decreases in both runoff and groundwater availability (Dore 2005, Dai 2016, Hoegh-Guldberg et al. 2018).

Due primarily to warming temperatures, it is anticipated that about 55% of tree species in the eastern USA will show at least a 2% increase in suitable habitat, while about 14% are expected to show a decrease of at least 2% (Iverson et al. 2008). Of the three most common tree species in the southeastern USA, loblolly pine (*Pinus taeda* L.) and slash pine (*P. elliottii* Engelm.) are expected to increase in abundance, while red maple (*Acer rubrum* L.) is anticipated to experience reductions in abundance (Iverson et al. 2008). Droughts may impact forest ecosystems by initiating shifts in species composition towards species that are better able to withstand dry conditions and/or exploit wet conditions when they occur. Furthermore, in water-limited areas, drought has been shown to increase the patchiness of vegetation (Wainwright et al. 2002, Merino-

Martin et al. 2012). These patches of vegetation in turn alter soil moisture gradients by changing infiltration capacities and increasing soil water content within the patches (Maestre & Cortina 2002).

Drought may also lead to more frequent fire and higher risk of fire damage to forest communities, as a result of drier fuels (Huntington et al. 2009). Dukes et al. (2009) suggest that increases in global temperatures may favor the expansion of the ranges of insect pests, pathogens, and invasive species, thereby endangering native forest ecosystems. Increases in evapotranspiration, and thus water stress, are also anticipated (Huntington 2006, Hayhoe et al. 2007). This increased stress may, in turn, increase susceptibility to insects and other pests (Huntington et al. 2009). An increase of 3°C in air temperatures can result in a 45% increase in vapor pressure deficit (VPD), the difference between saturation vapor pressure and actual vapor pressure at any given temperature (Will et al. 2013). Because VPD is a driving force of transpiration in plants, increases in VPD due to higher temperatures and drought conditions are likely to increase physiological stress on plants (Williams et al. 2013, Will et al. 2013). Major storms may also increase in frequency and intensity (Trenberth et al. 2007, IPCC 2014), which could lead to more frequent and more damaging disturbances to forest ecosystems.

Longleaf pine forests can be found on a wide range of sites across the southeastern USA, from flatwoods with poorly-drained soils to xeric sandhills known as the "desert in the rain" due to abundant precipitation but well-drained soils that dry quickly and hold very little water (Boyer 1990, Brockway & Outcalt 1998). Naturally occurring gaps in longleaf pine forests are, on average, larger than in other forest types (Gagnon et al. 2004). Canopy closure has been found to average approximately 50%, and

can be as low as 20-30% (Palik & Pederson 1996), with forests on xeric sites typically having a more open canopy than those located in more mesic areas (Dyson et al. 2012). Therefore, in the longleaf ecosystem, water (rather than light) is frequently the more limiting resource.

Longleaf pine ecosystems commonly have an oak (*Quercus* spp.) component. In frequently burned areas, this component is typically a suppressed understory; however, in the absence of frequent fire, oaks are well-adapted to become dominant species in the longleaf ecosystem (Brockway & Lewis 1997, Shelton & Cain 1999, Pecot et al. 2007, Schnurr & Collins 2007). Climate change may increase the significance of oaks in this ecosystem, given predictions that drought will become an increasingly important climatological feature of the southeastern USA. Forests with a greater frequency of species that are adapted to more xeric conditions will likely be more resilient to climate changes. In longleaf ecosystems, this drought resilience is likely to depend at least in part on the species composition of the oak component.

Oaks as a group are generally well adapted to environments with high water stress, for several reasons: (1) they tend to have deep roots, enabling deep water access during most droughts; (2) they generally have thick leaves and small stomata, which increases water use efficiency; (3) their ring-porous xylem allows sustained movement of sap even in drought conditions; and (4) they have higher rates of photosynthesis than most co-occurring species at low water potentials and high VPD (Abrams 1990). However, some oak species common in the longleaf pine ecosystem are more efficient water users than others. Turkey oak (*Q. laevis* Walt.) is one of the most efficient oak water users in these forests, with better access to deep soil moisture and a highly

conservative water use strategy (Donovan et al. 2000). It is therefore proposed that transitioning longleaf ecosystems towards greater drought tolerance can be achieved using silvicultural treatments that change the composition of the oak component to reduce more mesic species and increase turkey oak. There is little understanding, however, of the feasibility of regenerating turkey oak in a longleaf pine ecosystem, particularly in regards to the effects of facilitative and competitive interactions of established overstory trees on turkey oak seedlings.

In facilitation, one plant improves the microenvironment of nearby plants and thus increases the survival of those plants or improves their physiological functioning (Loudermilk et al. 2016). It is therefore an opposing process to competition. Facilitation has been observed in various plant communities worldwide (Callaway et al. 2002, Brooker et al. 2008, de la Luz Avendano-Yanez et al. 2014), but is particularly common in high-stress environments (Callaway 1992, Flores & Jurado 2003). Nurse plants – those that provide facilitative benefits to others - may provide shade, thereby reducing water stress in the plants they facilitate via reductions in evaporative demand (Lloret et al. 2005, Sthultz et al. 2007). Nurse plants may also increase the soil moisture available to other plants through hydraulic lift (HL; Espeleta et al. 2004).

The occurrence of facilitation is strongly dependent on the species of the nurse individual. For instance, Loudermilk et al. (2016) found that longleaf pine seedling survival decreased due to competition with nearby overstory pines, but the same seedlings showed increased survival in the presence of overstory oaks. In contrast, Espeleta et al. (2004) found that longleaf pine had higher HL than either turkey oak or sand post oak (*Q. margaretta* Ashe), suggesting the potential for greater facilitation from

pines than from oaks. Furthermore, the benefits of facilitation may depend on the age of the plant being facilitated. Loudermilk et al. (2016) suggest that newly germinated longleaf seedlings may be more successful when they are facilitated by oak, but that in later stages of development, shade from overstory oak trees may inhibit longleaf seedling growth due to the relative shade intolerance of the species (Barnett 1989, Boyer 1990).

Environmental conditions likely also play a role in the importance of facilitation to seedling survival. For instance, facilitation may be more crucial to longleaf pine seedling survival during drought periods, particularly on mesic sites (Loudermilk et al. 2016). Competitive interactions may outweigh and therefore obscure the benefits of facilitation (Stachowicz 2001, Bruno et al. 2003, Wright et al. 2015), unless environmental conditions are so unfavorable as to make facilitation the more important factor (Callaway et al. 2002, Wright et al. 2015). For instance, on days that are cool and humid, less negative plant water potentials will occur and therefore any facilitative benefits due to shading will likely be negated. On hot and dry days, however, more negative plant water potentials will dominate and the facilitative benefits of shading will be of increased importance. Wright et al. (2015) found evidence for this when studying bur oak (*Q. macrocarpa* Michx.) seedlings in a grassland in Minnesota - competition for water was outweighed by facilitative benefits in oaks planted in locations with high levels of plant biomass on hot and dry days, while on cooler and wetter days, competition dominated. They found that, for these oaks, facilitation may have been predominant for approximately 15% of the growing season, but competition was predominant for the remaining 85%. Given current climate trends towards warmer temperatures and extended

periods of drought, the importance of facilitation may increase in plant communities of the southeastern USA.

A primary way in which facilitation may occur is through HL. This is a passive process by which gradients in water potential drive the redistribution of soil moisture by root systems from deeper soil layers to shallower ones, primarily at night (Sardans & Penuelas 2014). This is proposed to have two main benefits for the lifting plant: 1) it increases moisture availability in upper soil layers where fine roots are concentrated, which is highly advantageous during drought conditions (Caldwell et al. 1998, Filella & Penuelas 2003, Zou et al. 2005, Sardans & Penuelas 2014); and 2) it improves the plant's uptake of nutrients, such as nitrogen, found in the upper soil layers (de Kroon et al. 1998, Egerton-Warburton et al. 2008, Scholz et al. 2008, Sardans & Penuelas 2014). However, some studies have found no effect of HL on nutrient availability or uptake (Caldwell & Manwaring 1994, Snyder et al. 2008).

Hydraulic lift can benefit individuals other than the lifting plant. For example, HL by deep-rooted species can facilitate survival of neighboring plants that have shallower root systems or are otherwise unable to exhibit HL activity (Zou et al. 2005, Liste & White 2008, Burgess 2011, Prieto et al. 2011, Loudermilk et al. 2016). Sardans & Penuelas (2014) reviewed various studies on HL and determined that, among those studies, the mean amount of water redistributed by HL was 40% of the total water transpired by vegetation and that the mean increase in water content in upper soil layers due to HL was 53%. Dawson (1993) found that a significant portion of hydraulically lifted water is available to species other than those that lifted the water.

Water can also be redistributed laterally between roots in the same soil layer (Sardans & Penuelas 2014). In addition, a process called downward siphoning, which is the opposite of HL, has been observed in some species when upper soil layers are wetter than deeper layers (Smith et al. 1999). This process likely increases the competitiveness of the deep-rooted plants that siphon water downward, thus prolonging water availability to them once upper soil layers dry (Schulze et al. 1998, Smith et al. 1999, Ryel et al. 2004). Ryel et al. (2003) found that downward siphoning can move 87 – 100 % of total precipitation following a storm to soils below 0.3 m. Thus, depending on current conditions, hydraulic redistribution can be either facilitative (in the case of HL) or competitive (in the case of downward siphoning) in nature. Overall, however, hydraulic redistribution is beneficial to the plant redistributing the water, particularly in locations where water availability is spatially highly heterogeneous (Penuelas et al. 2011), by reducing interspecific competition for that water (Sardans & Penuelas 2014).

Research on longleaf pine community dynamics, restoration, and silviculture has yielded mixed conclusions regarding the relative impacts of competitive and facilitative overstory interactions on longleaf seedlings. Oaks reduce the growth of longleaf seedlings in some studies (Pecot et al. 2007) and stimulate seedling growth in others (Loudermilk et al. 2016). The interactions between longleaf seedlings and mature southern pines, including longleaf and loblolly, have also varied across studies. Some studies have documented decreased seedling survival rates with increasing gap size, and hence increased distance from mature pines (Rodriguez-Trejo et al. 2003, Knapp et al. 2013), while others document no correlation between these factors (Palik et al. 1997), or

increased seedling survival at increased distances from mature trees (Brockway &
Outcalt 1998, Pecot et al. 2007).

The presence of fire further influences the relationships between mature trees and
seedlings. Prescribed fire can decrease seedling survival as distance to mature trees
decreases (Boyer 1963), even when no relationship was observed in the absence of fire
(Kara et al. 2017). Furthermore, seedling survival and growth rate can respond differently
to overstory density. For example, Knapp et al. (2013) found that root collar diameter
growth in longleaf seedlings increased from gap edges to gap centers, while survival rates
decreased along the same gradient; similarly, Pecot et al. (2007) found that seedling
biomass increased and seedling survival decreased with decreasing overstory density.

Soil moisture conditions also play an important role in the competition-facilitation
balance. For instance, Palik et al. (1997) found no relationship between longleaf pine
seedling survival and overstory density during a period of high rainfall, while Rodriguez-
Trejo et al. (2003) noted significant decreases in seedling survival as overstory density
decreased during a severe drought. It is possible that, during drought conditions, the
benefits that seedlings receive from reductions in evaporative demand due to overstory
shading may outweigh the negative effects of competition for soil water. Meanwhile,
during wetter conditions, competition may outweigh these facilitative benefits
(Loudermilk et al. 2016). Different overstory species may also have different effects on
soil moisture availability. For instance, Espeleta et al. (2004) found that longleaf pine
exhibits high levels of HL activity, while oaks show lower levels of HL activity in some
species (such as turkey oak) and no HL activity in others (such as sand post oak).

Understanding the facilitative and competitive interactions that occur in longleaf ecosystems is crucial to determining potential effects of climate alterations on these communities (Brooker et al. 2008). Given the mixed conclusions regarding this topic in previous work, further examination of competition and facilitation in longleaf pine stands is needed. In addition, previous work has concentrated on the facilitative and competitive effects of the overstory on longleaf seedlings; there is no such literature regarding the seedlings of oak species, which are likely to become more important in these communities under projected changes in climate. Furthermore, little research has been conducted on the physiology of turkey oak, outside of Donovan & Pappert (1998) and Donovan et al. (2000). The goals of this study were therefore to provide fundamental research on the physiology of turkey oak seedlings, to inform ongoing research in the ASCC program regarding transitioning the longleaf pine ecosystem in response to climate change, and to determine ideal planting conditions for turkey oak seedlings in a longleaf pine forest. The working hypotheses of the study were: (1) periods would occur during which facilitation of turkey oak seedlings from the overstory would be predominant over competitive effects; and (2) the balance between the facilitative benefits and competitive effects of the overstory on turkey oak seedlings would be influenced by environmental stressors, as well as by the proximity, species, and size of overstory trees. To test these hypotheses, seedling leaf gas exchange and microenvironmental factors were measured during one growing season and examined in relation to overstory metrics for indications of competition and facilitation.

2.2 Methods

2.2.1 Site Description and ASCC Treatments

The study was conducted at The Jones Center at Ichauway, an 11,500 ha research site located on the Gulf Coastal Plain in southwest Georgia, USA (Drew et al. 1998). This site has a humid subtropical climate, with a mean annual precipitation of approximately 1,300 mm and a mean annual temperature of 18°C (NCEI 2020). The site is composed primarily of second-growth longleaf pine savanna. In this system, the overstory is dominated by 80- to 100-year old longleaf pine, while the understory is primarily wiregrass (*Aristida stricta* Michx.), a C_4 bunchgrass. These systems have been managed with primarily dormant-season prescribed fire at 2-year intervals since 1990. Landforms on site are primarily uplands with well-drained loamy soils, but range from xeric sandhills to seasonal wetlands on poorly drained clay-textured soils. Most soils are Kandiudults or Paleudults, which have a coarse-textured surface horizon underlain by low activity clays. Dyson et al. (2012) identified the main soils on site as belonging to the Wagram series. Soils on xeric sites at The Jones Center have been described as 89.3% sand, 7.1% silt, and 3.7% clay, with a water holding capacity of 18.0 cm m^{-1}; on mesic sites, soils are described as 63.4% sand, 24.3% silt, and 12.4% clay, with a water holding capacity of 40.0 cm m^{-1} (Addington et al. 2006).

Four ASCC treatment blocks were established between January and June of 2018, each containing one control stand and three treatment stands: (1) *resistance*, in which oaks and non-longleaf pine species were removed; (2) *resilience*, in which mesic oaks and off-site pines were removed, xeric oaks were thinned to 2.3 m^2 ha^{-1}, and longleaf pine was thinned to 11.5 m^2 ha^{-1}; and (3) *transition*, in which mesic oaks and off-site pines

were removed, xeric oaks were retained at 1.15 m^2 ha^{-1}, longleaf pine was thinned to 6.9 m^2 ha^{-1}, and turkey oak seedlings and wiregrass were planted in the understory. All three treatments and the control stands continued to be managed with a 2-year burn interval.

In each of the four *transition* stands, 4,200 bare root turkey oak seedlings were planted in 150 evenly-spaced clusters of seven seedlings each. Seedlings were approximately 1 year old at time of planting and were sourced from Superior Trees (Lee, FL). Planting clusters were spaced 25 m apart. A 2 m radius circular area was treated with an herbicide mixture of Glypro (Glyphosate, Dow AgroSciences, Indianapolis, IN) and Arsenal (Imazapyr, BASF Co., Ludwigshafen, Germany) six months prior to seedling planting. Each cluster of seedlings consisted of six seedlings planted in a circular pattern around a central seedling, at 1 m triangular spacing. Planting occurred in March 2018. Prescribed burns were implemented in each of the plots in April or May 2019. Following these burns, surveys were conducted to determine seedling survival.

2.2.2 Study Seedling Selection

Two *transition* stands were selected for use in this study – one located in the Baker Woods region of the site, and one located in the Lower Pasture region. These stands were selected to represent different soil types and moisture regimes. Baker Woods is a more mesic site (primarily Norfolk series loamy sand soils), while Lower Pasture is more xeric (primarily Troup series sandy soils). Twelve seedling planting plots in each of the two stands were selected for use in the study, based on basal area measurements. Seedling plots were selected to represent a range of overstory basal area conditions. Basal area measurements were made using the variable radius plot method with a BAF 10 prism centered over the central seedling of each plot, and plots were chosen based on

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three levels of pine basal area (4.6 m^2 ha^{-1}, 9.2 m^2 ha^{-1}, or over 11.5 m^2 ha^{-1}) and two

levels of hardwood basal area (0 m^2 ha^{-1} or 2.3 m^2 ha^{-1}). Two plots representing each

possible combination of pine and hardwood basal area levels were selected in each of the

two *transition* stands. Each selected plot had at least three surviving seedlings.

2.2.3 Seedling and Microenvironment Measurements

The diameter of each seedling at root collar was measured with calipers in July

and October 2019. Heights were measured for each seedling from ground level to apical

bud in October 2019. Gas exchange measurements were recorded for each seedling eight

times over the course of the growing season, from July through October 2019 (Table 1).

Data were recorded between 10:00 and 14:00 with a portable photosynthesis system (LI-

6400, LI-COR Biosciences, Lincoln, NE) over the course of two days, with one block

measured per day. Clear days were targeted, and the visit order of each plot was

randomized on each day. One leaf was measured per seedling, and leaves were selected

based on size and age, with preference given to larger, older leaves. Leaves were clamped

into the cuvette so as to cover the entire 2 cm^2 chamber. Measurements were made under

ambient CO_2, relative humidity, and photosynthetically active radiation (PAR) levels for

each seedling.

Table 1. Gas exchange measurement dates in 2019, by ASCC *transition* stand.

ASCC Stand	Dates
A (Mesic)	7/18, 7/26, 8/13, 8/20, 9/5, 9/11, 9/17, 10/2
C (Xeric)	7/25, 8/14, 8/16, 8/22, 9/6, 9/12, 9/18, 10/3

On three dates between July and October 2019, at pre-dawn (within 1 hour prior to sunrise), one leaf was removed from each seedling and stored in an air-tight resealable plastic bag kept in a cooler. Leaves were transported to the lab, where their water potentials were immediately measured using a pressure chamber (PMS Instruments Co., Albany, OR). Approximately 1-2 hours elapsed between leaf collection and water potential measurement. At least five days had passed since the most recent rainfall event on all three of these dates. Weather data were collected from the on-site weather station, operated by the Georgia Automated Environmental Monitoring Network (GAEMN).

In situ PAR for each seedling was measured by the quantum sensor in the portable photosynthesis system with each gas exchange measurement. The light environment was additionally assessed using hemispherical photographs taken once within 30 minutes of sunrise using a Nikon camera (Coolpix 4500, Nikon Co., Tokyo, Japan). Photographs were processed using ImageJ software (Schneider et al. 2012) to estimate optimum threshold values, and then analyzed with Gap Light Analyzer software (Frazer et al. 2000) for light transmittance, canopy openness (CO), and leaf area index (LAI). CO is calculated by this software as the percentage of open sky not obscured by vegetation (Frazer et al. 2000). Soil moisture from 0-12 cm depth was recorded within 0.25 m of each seedling on each gas exchange measurement date, using a HydroSense Water Content Sensor (Campbell Scientific, Logan, UT) probe inserted to depth.

Seedling neighborhoods were assessed by measuring and mapping nearby trees. For overstory trees, all individuals greater than 10 cm in diameter at breast height (DBH) within a 15 m radius circular plot centered on the seedling plot were mapped. DBH and height were measured for each tree. Tree heights were assessed using a laser rangefinder

(Forestry Pro, Nikon Co., Tokyo, Japan). The species of tree, distance to the center of the

seedling plot, and azimuth from the plot center to each tree were also recorded. For

midstory trees, all individuals greater than 1.3 m in height within a 3 m radius circular

plot centered on the seedling plot were mapped. DBH, height, species, distance to the

center of the seedling plot, and azimuth to the individual from the center of the plot were

recorded for each individual. All individuals were then mapped in ArcMap 10.7.1 (ESRI,

Redlands, CA), and distances from each study seedling to each overstory and midstory

individual were calculated. Overstory Abundance Index (OAI, typically expressed as a

dimensionless value), a weighted measure of overstory competitor abundance, was also

calculated, following Palik et al. (2003). Ground-level cover around each seedling was

visually assessed within a 1 m^2 plot centered on the seedling. Ground-level cover was

divided into three categories: wiregrass, other herbaceous, and woody, and one of six

cover classes was assigned to each category (Table 2).

Table 2. Cover classes and their associated ranges used for assessing ground-level cover near each turkey oak seedling.

Cover Class	Range of Cover
1	0 – 5%
2	6 – 25%
3	26 – 50%
4	51 – 75%
5	76 – 95%
6	96 – 100%

Leaf area was measured on leaves collected for water potential measurements using a leaf area meter (LI-3100C, LI-COR Biosciences, Lincoln, NE). Leaves were dried for 72 hours at 70°C and weighed, and specific leaf weight (leaf dry weight per unit leaf area) was calculated. Dried leaves were pooled by sub-plot and across dates, and then ground for foliar nutrient analysis. Leaf N and C content were measured using an Organic Elemental Analyzer (Flash 2000, C. E. Elantech, Lakewood, NJ). Samples were sent to the Duke Environmental Stable Isotope Laboratory (DEVIL) for leaf carbon isotope discrimination analysis using an Elemental Analyzer (NA-1500, Thermo Fisher Scientific, Waltham, MA).

2.2.4 Statistical Analyses

Preliminary regression analyses used Proc Reg in SAS (v. 9.4, SAS Institute, Inc., Cary, NC). Response variables included seedling physiology and growth metrics, as well as foliar nutrients and soil moisture. All response variables were averages across all seedlings within a plot. Predictors used were overstory metrics, groundcover levels, and light environment. PAR and soil moisture were not used as predictors in the final models because early models using these variables as predictors showed high correlation between these factors and seedling physiology (as expected based on current knowledge of plant physiology). Because the final models were developed to address the effects of the overstory on seedling performance, incorporating these abiotic factors in the final models may have obscured the overstory effects that were of interest.

It was hypothesized that seedling physiology would exhibit different trends in relation to overstory metrics, depending on current environmental conditions. Under unstressed conditions, seedling performance was expected to show a linear increase with

increases in canopy openness. Conversely, under stressful conditions, facilitation was expected, and therefore changes in the slope of the relationship between CO and seedling performance were anticipated. Such changes in the relationship would indicate improved performance of more shaded plants relative to plants in more open conditions. For this reason, date was included in the models as a predictor variable. Full models including all predictor variables were run, and stepwise selection was used to select the significant variables in each model, based on R^2.

Significant predictor and response variables were then used in Proc Mixed models, with site (mesic or xeric) and plot included as random variables. Analyses indicated that these random variables had an insignificant impact on covariance, and so site was used in a by statement in all further models. Full models using leaf-level net photosynthesis (A), leaf-level stomatal conductance (g_s), and soil VWC as response variables, and CO, date, and an interaction term between CO and date as predictors, were then run. Final models were selected based on Akaike's Information Criterion (AIC). The interaction term was incorporated to discern whether differences in environmental conditions between measurement dates impacted the slope of any observed relationships between CO and A.

Additionally, neighborhood analyses were performed in R (v. 3.6, R Foundation for Statistical Computing), using custom software based on the Likelihood package (Murphy 2015), which uses simulated annealing to find maximum likelihood values for inputted parameters. Change in seedling diameter and average A were used as response variables. For change in diameter, a beta probability density function distribution was used, due to the high number of near-zero values present in the data. A normal

distribution was utilized for the net photosynthesis analyses. Neighborhood competition indices (NCI) were calculated using the formula

$$NCI = \sum_{1}^{n} \lambda \left(\frac{DBH}{100}\right)^2 \left(\frac{d}{10}\right)^{-B}$$

where n is the number of trees within 15 m of a seedling, λ is a multiplicative term estimated by the model and used to improve model fit, DBH is the diameter at breast height of each tree, d is the distance from a seedling to each tree, and B is a parameter estimated by the model that modifies the rate of decay of competitive effect with d. NCI values were allowed to decay exponentially with increasing distance from the plot center. Models taking into account NCI and tree type (coded as either longleaf pine or hardwood) were tested. Null models and both competition models were compared using AIC to select the best model for each response variable.

2.3 Results

2.3.1 Weather

Average daily temperatures during the study period ranged from 23.3-29.5 ℃, while maximum daily temperatures ranged from 28.9-39.1 ℃ and minimum daily temperatures ranged from 15.5-24.6 ℃ (Figure 1). Average daily relative humidity during the study period ranged from 59.9-93.1 %, while maximum daily relative humidity ranged from 85.7-99.8 % and minimum daily relative humidity ranged from 20.7-69.5 % (Figure 2). The highest total daily precipitation recorded during the study period was 52.6 mm on 8/3/2019; no precipitation was recorded after 9/1/2019 (Figure 3). Total precipitation recorded over the study period was 206.0 mm; total precipitation recorded over the summer months (July-September) was 256.5 mm. This total is less than the 15-year average for summer precipitation (Figure 4). Daily average VPD during the study period ranged from 0.23-2.05 kPa (Figure 5).

2.3.2 Stand Structure

The mesic site had an average OAI of 103.3, with an average pine OAI of 92.0 and an average hardwood OAI of 11.3. In contrast, the average OAI for the xeric site was 141.9, with an average pine OAI of 130.7 and an average hardwood OAI of 11.2. Plots in the mesic site exhibited slightly greater levels of woody groundcover and significantly lower levels of wiregrass groundcover than plots in the xeric site (Table 3).
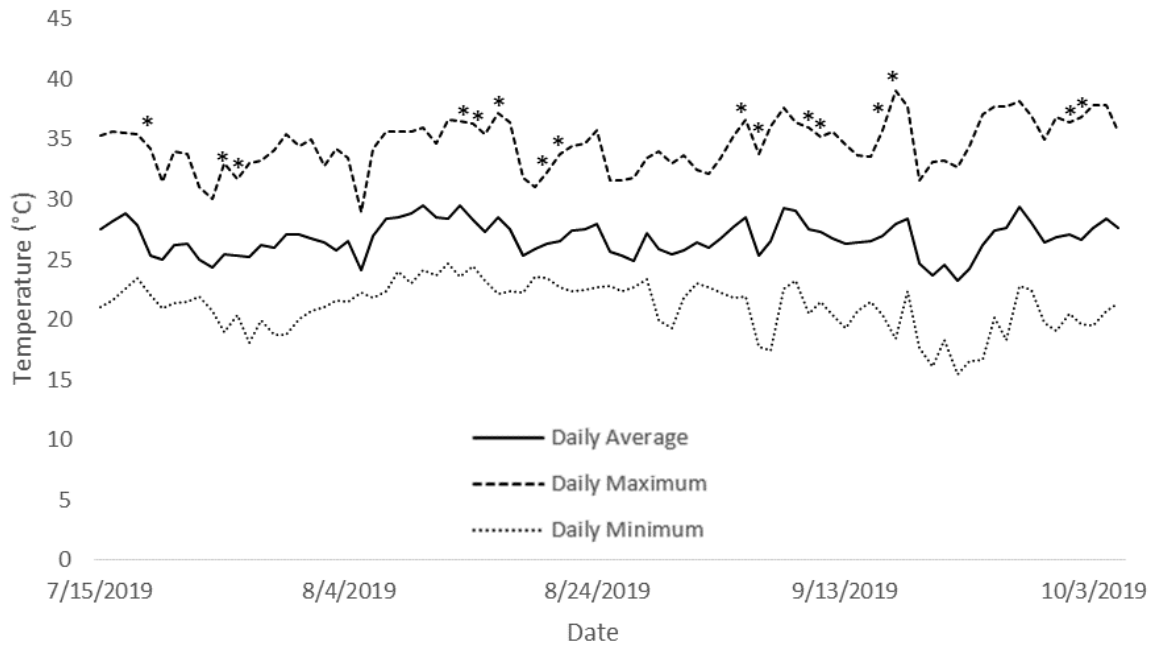
Figure 1. Daily average, maximum, and minimum temperatures at a longleaf pine site in southwest Georgia, USA in summer and fall 2019. Asterisks (*) indicate dates of seedling measurements.
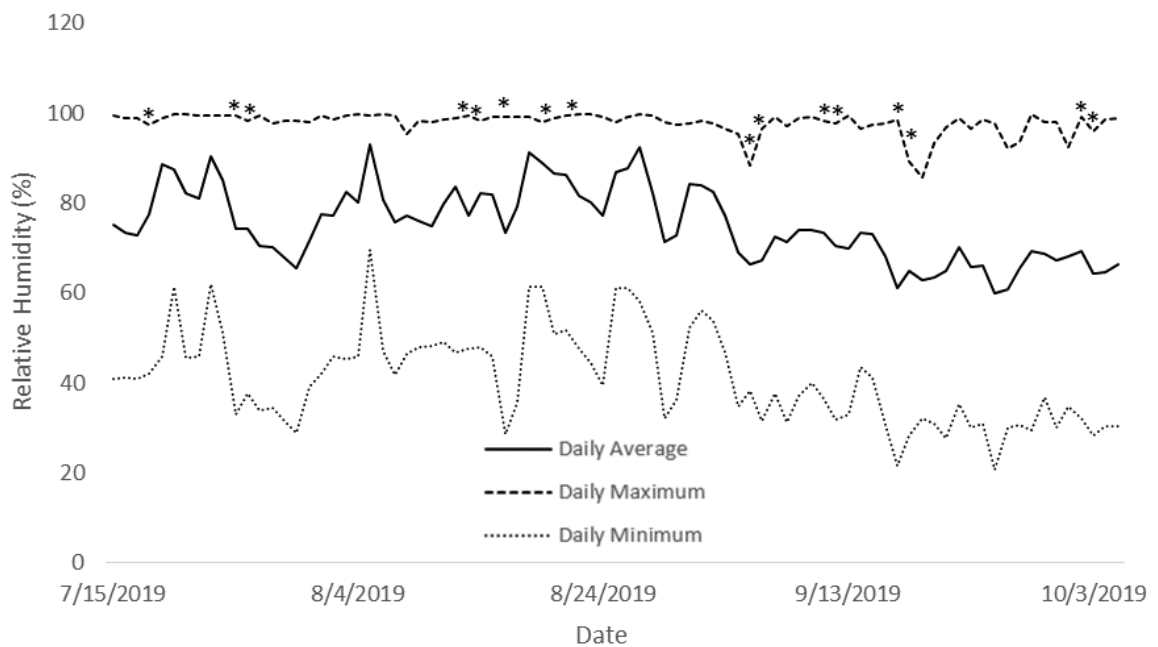
Figure 2. Daily average, maximum, and minimum relative humidity at a longleaf pine site in southwest Georgia, USA in summer and fall 2019. Asterisks (*) indicate dates of seedling measurements.
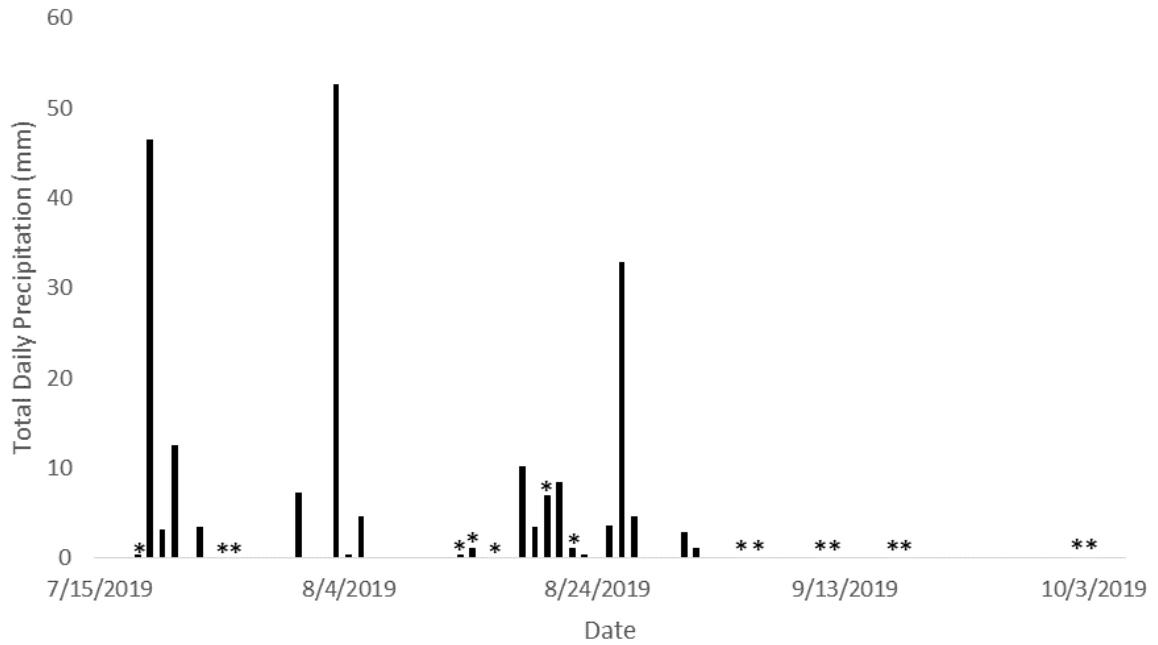
Figure 3. Daily precipitation at a longleaf pine site in southwest Georgia, USA in summer and fall 2019. Asterisks (*) indicate dates of seedling measurements.
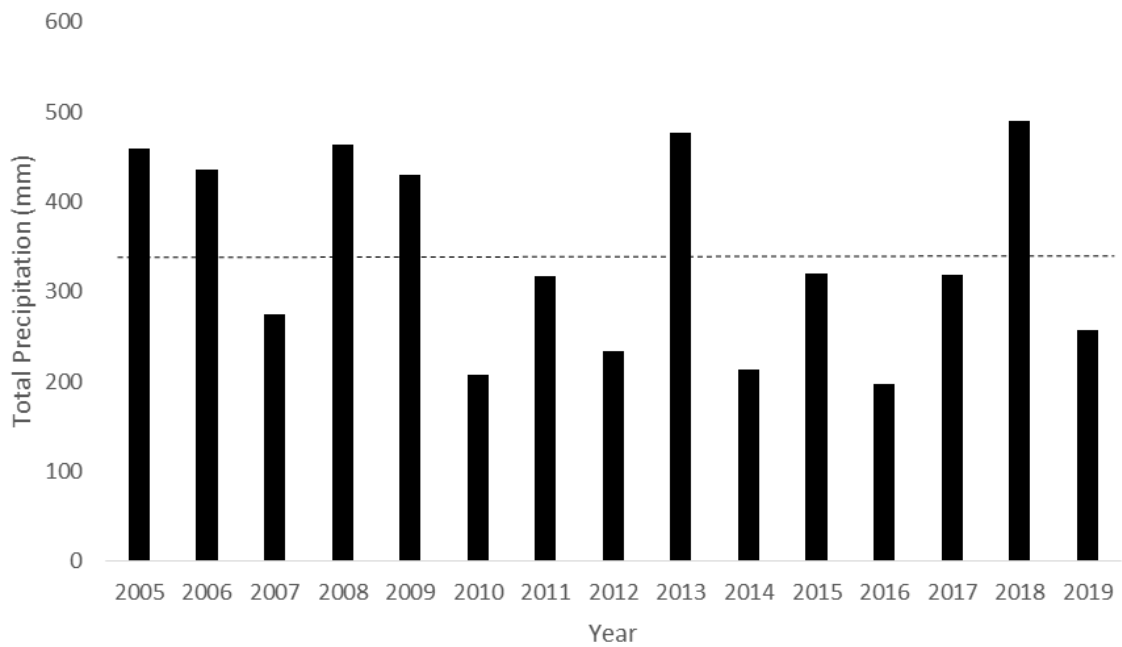
Figure 4. Total summer (July-September) precipitation at a longleaf pine site in southwest Georgia, USA for the past 15 years. The dotted line indicates the 15-year average.
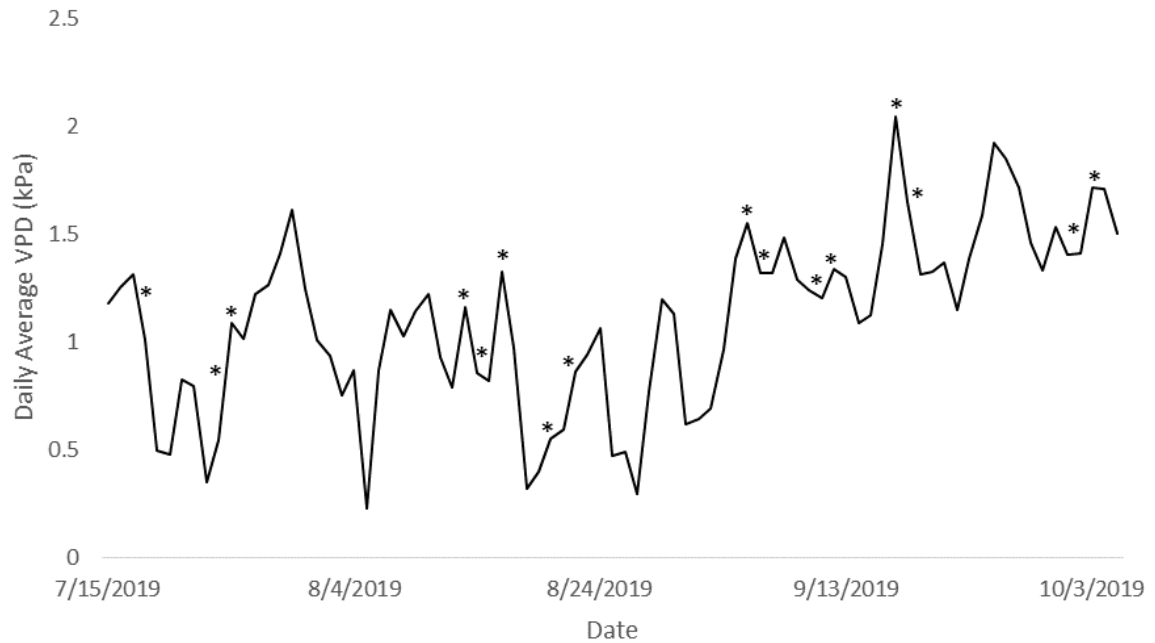
Figure 5. Daily average vapor pressure deficit (VPD) values at a longleaf pine site in southwest Georgia, USA in summer and fall 2019. Asterisks (*) indicate dates of seedling measurements.

Table 3. Average wiregrass, herbaceous, and woody groundcover in turkey oak seedling measurement plots in mesic and xeric soils at a site in southwestern Georgia, USA.

Site	Wiregrass Cover (%)	Other Herbaceous Cover (%)	Woody Cover (%)
Mesic	14.6	33.0	10.6
Xeric	26.6	30.3	8.4

Notes. Cover classes were assigned visually based on cover, as described in Table 2. Classes were then replaced with the median cover values (%) corresponding to those classes, and averages were calculated across all plots at each of the two sites.

2.3.3 Overstory Effects on Seedling Physiology

Seedling pre-dawn water potentials and specific leaf weights (Table 4), as well as

leaf nutrient levels and carbon isotope discrimination values (Table 5) were not

significantly ($\alpha = 0.05$) correlated with any overstory metrics (CO, LAI, OAI, BA) during

preliminary regression analyses. Seedling A and g_s, as well as soil VWC, were therefore

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the only response variables used in the mixed model analyses. Groundcover levels did not

significantly affect any seedling performance metrics during the preliminary analyses.

The overstory metric with the most significant effect on the response variables was CO.

Therefore, the predictors used in the mixed model analyses were CO, Date, and an

interaction term between these two variables.

Table 4. Average pre-dawn water potentials and specific leaf weights of turkey oak seedlings in mesic and xeric soils at a site in southwestern Georgia, USA.

Site	Average Pre-Dawn Water Potential (MPa)	Average Specific Leaf Weight ($g\ cm^{-2}$)
Mesic	-0.49 ($\pm$ 0.22)	0.0113 ($\pm$ 0.0014)
Xeric	-0.63 ($\pm$ 0.35)	0.0114 ($\pm$ 0.0017)

Table 5. Average percent nitrogen, percent carbon, and carbon isotope discrimination values of leaves obtained from turkey oak seedlings in mesic and xeric soils at a site in southwestern Georgia, USA.

Site	Average % Nitrogen	Average % Carbon	Average $d^{13}C$
Mesic	0.96 ($\pm$ 0.1)	49.32 ($\pm$ 1.2)	-30.66 ($\pm$ 0.26)
Xeric	0.90 ($\pm$ 0.08)	49.58 ($\pm$ 0.94)	-30.76 ($\pm$ 0.44)

Mixed model analyses suggested that the best model of overstory effect on

seedling A at the mesic site incorporated the continuous variable CO as a linear effect, as

well as an interaction term between CO and the discrete variable Date (Table 6). The CO

and CO*Date terms in this model were significant (p = 0.0107 and p < 0.0001,

respectively). Increases in A were positively correlated with increasing CO, with Date

affecting the strength of this relationship (Figure 6). Date was used as a proxy for

environmental conditions, with different dates representing a wide array in the soil VWC (Figure 7), VPD (Figure 8), and PAR (Figure 9) values measured concurrently with seedling gas exchange, though little variation in air temperature occurred (Figure 10). Thus, the data suggest that environmental conditions influenced the relationship between the overstory and A at the mesic site, with the slope of the relationship being significantly greater than the overall average on 7/26/2019 ($p = 0.0072$) and 8/13/2019 ($p = 0.0026$), and significantly lower on 9/17/2019 ($p = 0.0077$) and 10/2/2019 ($p = 0.0007$). At the xeric site, the best model of overstory effect on A incorporated only the Date variable (Table 7). While A was not significantly impacted by CO ($p = 0.2586$), differing environmental conditions on different dates did have a significant impact ($p < 0.0001$, Figure 11). A was significantly lower at this site on 9/18/2019 ($p = 0.0085$) and 10/3/2019 ($p < 0.0001$) than on any other date.

Table 6. Comparison of tested models for leaf-level net photosynthesis of turkey oak seedlings in mesic soils at a site in southwestern Georgia, USA.

Model[†]	k[‡]	Adj. R^2 [§]	AIC[‖]	ΔAIC[¶]
CO CO*Date	11	0.62	364.5	0
CO Date	11	0.62	365.1	0.6
Date	10	0.62	369.7	5.2
CO Date CO*Date	18	0.62	377.2	12.7
CO	4	0.27	402.7	38.2
Null	2	-	423.3	58.8

Notes. [†]CO = Canopy openness [‡]k = Number of estimated parameters [§]Adj. R^2 = Adjusted R^2 value, based on residual variance [‖]AIC = Akaike's Information Criterion [¶]ΔAIC = Difference in AIC between the model of interest and the model with the lowest AIC.

Figure 6. Effect of canopy openness (CO) and measurement date (Date) on leaf-level net photosynthesis (A) of turkey oak seedlings in mesic soils at a site in southwest Georgia, USA.
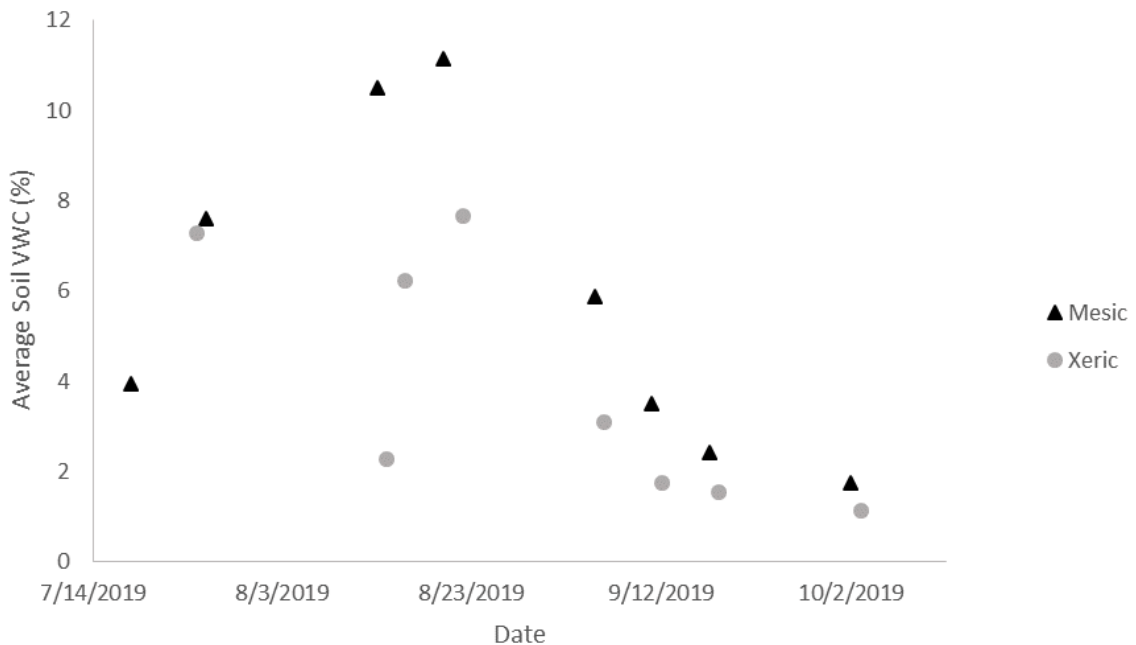
Figure 7. Variation in soil volumetric water content (VWC) across measurement dates (Date) at a mesic site and a xeric site in southwest Georgia, USA. Each point represents the average soil VWC across all plots on that date.
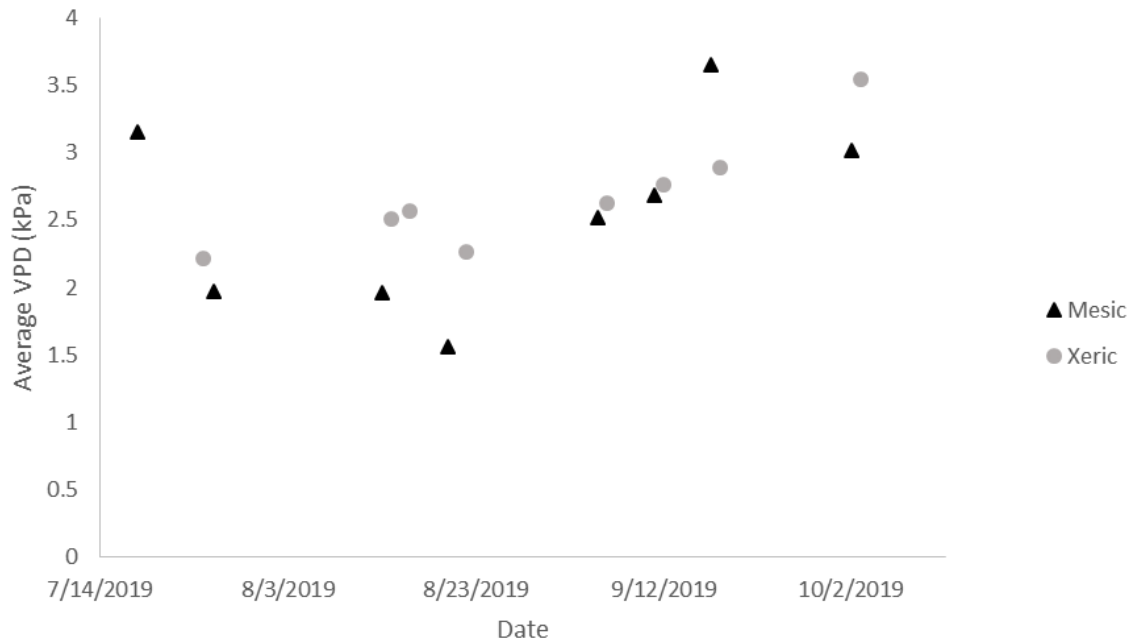
Figure 8. Variation in vapor pressure deficit (VPD) across measurement dates (Date) at a mesic site and a xeric site in southwest Georgia, USA. Each point represents the average VPD across all plots on that date.
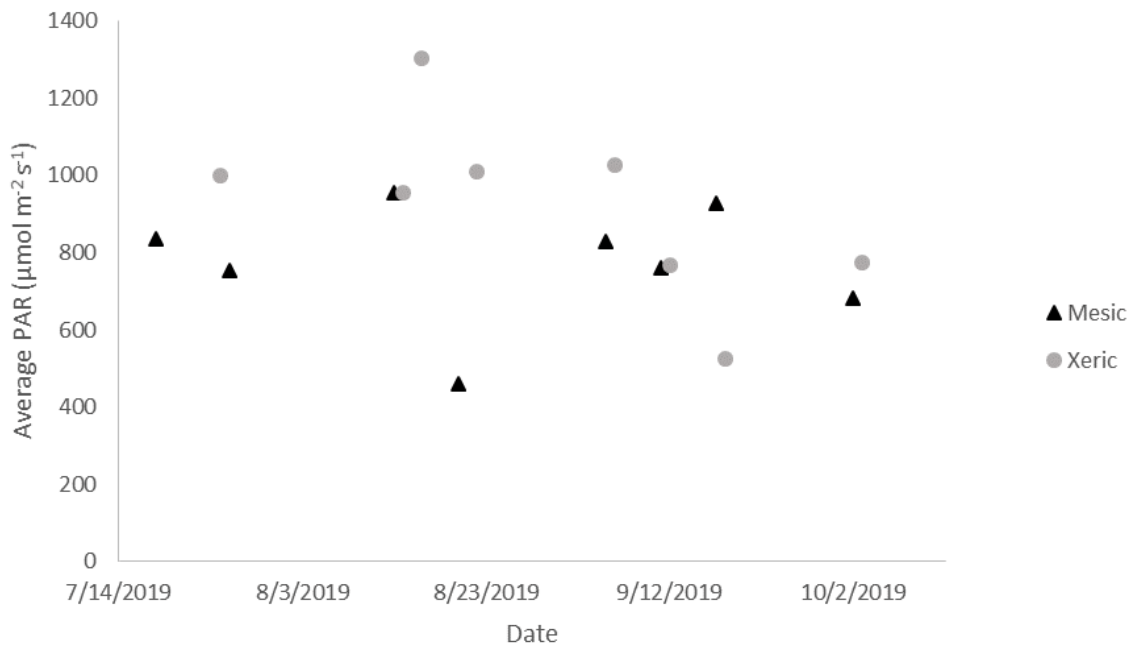
Figure 9. Variation in photosynthetically active radiation (PAR) across measurement dates (Date) at a mesic site and a xeric site in southwest Georgia, USA. Each point represents the average PAR across all plots on that date.
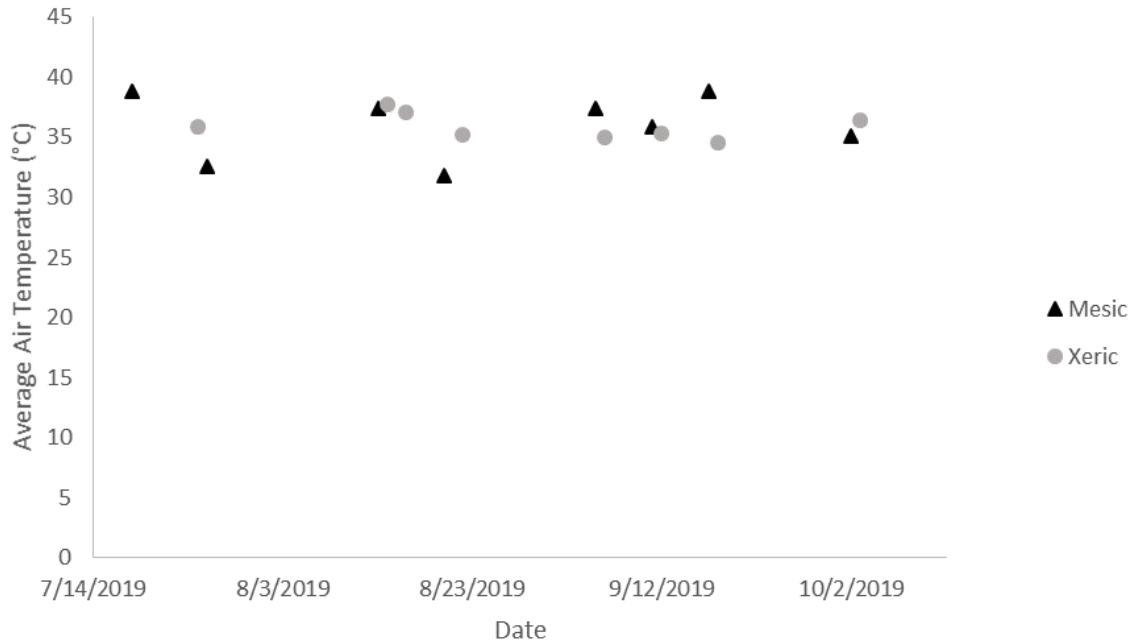
Figure 10. Variation in air temperature across measurement dates (Date) at a mesic site and a xeric site in southwest Georgia, USA. Each point represents the average temperature across all plots on that date.

Table 7. Comparison of tested models for leaf-level net photosynthesis of turkey oak seedlings in xeric soils at a site in southwestern Georgia, USA.

Model[†]	k[‡]	Adj. R^2 [§]	AIC[‖]	ΔAIC[¶]
Date	10	0.54	427.6	0
CO Date	11	0.54	428.2	0.6
CO CO*Date	11	0.52	430.4	2.8
CO Date CO*Date	18	0.57	435.1	7.5
CO	4	0.06	473.1	45.5
Null	2	-	474.1	46.5

Notes. [†]CO = Canopy openness [‡]k = Number of estimated parameters [§]Adj. R^2 = Adjusted R^2 value, based on residual variance [‖]AIC = Akaike's Information Criterion [¶]ΔAIC = Difference in AIC between the model of interest and the model with the lowest AIC.
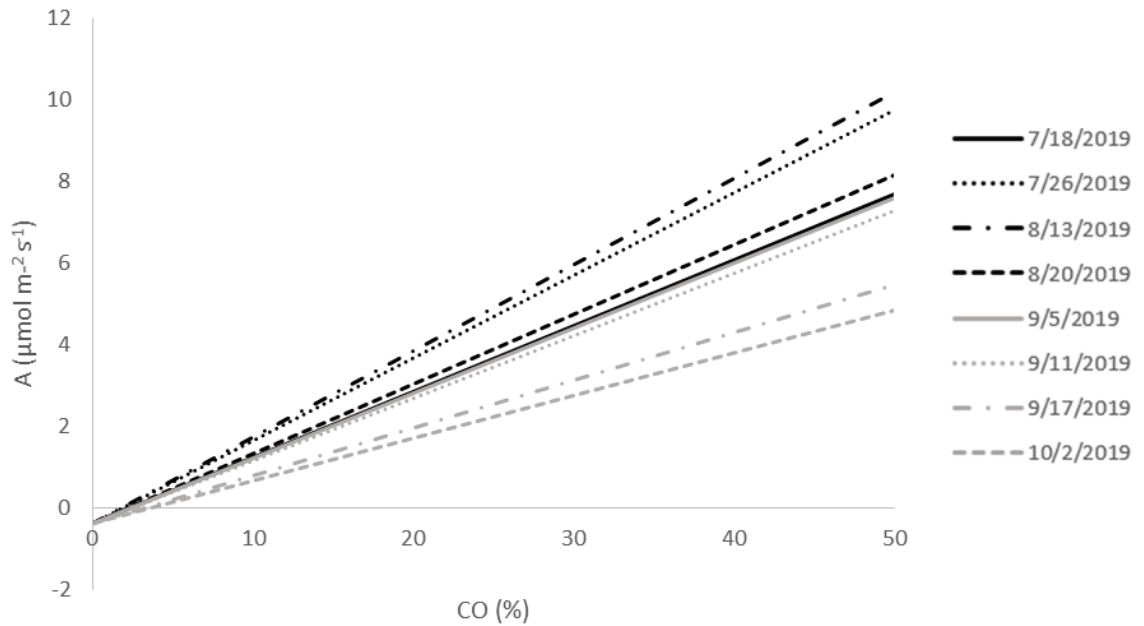
Figure 11. Effect of measurement date (Date) on leaf-level net photosynthesis (A) of turkey oak seedlings in xeric soils at a site in southwest Georgia, USA. Each point represents the average A across all plots on that date.

At the mesic site, mixed model analyses suggested that the best model of overstory effect on seedling g_s incorporated the continuous variable CO and the discrete variable Date as additive, linear effects (Table 8). Increases in g_s were positively correlated with increasing CO ($p = 0.0491$). Environmental conditions, as represented by measurement date, were also significant ($p < 0.0001$) and had a direct effect on g_s, rather than affecting the correlation between CO and g_s (Figure 12). Seedling g_s at the mesic site was significantly greater on 8/20/2019 ($p = 0.0193$), and significantly lower on 9/17/2019 ($p = 0.0098$) and 10/2/2019 ($p < 0.0001$), when compared to all other dates. The best model of overstory effect on g_s at the xeric site incorporated only the Date term (Table 9). While g_s was not significantly impacted by CO ($p = 0.7140$), differing environmental conditions on different dates were significant ($p < 0.0001$, Figure 13). Seedling g_s was

significantly greater on 8/14/2019 (p = 0.0129) and 8/16/2019 (p = 0.0172), and

significantly lower on 9/18/2019 (p = 0.0014) and 10/3/2019 (p < 0.0001).

Table 8. Comparison of tested models for leaf-level stomatal conductance of turkey oak seedlings in mesic soils at a site in southwestern Georgia, USA.

Model[†]	k[‡]	Adj. R^2 [§]	AIC[‖]	ΔAIC[¶]
CO Date	11	0.59	-390.5	0
Date	10	0.59	-388.5	2.0
CO Date CO*Date	18	0.63	-385.1	5.4
CO CO*Date	11	0.56	-385.1	5.4
CO	4	0.14	-344.7	45.8
Null	2	-	-336.7	53.8

Notes. [†]CO = Canopy openness [‡]k = Number of estimated parameters [§]Adj. R^2 = Adjusted R^2 value, based on residual variance [‖]AIC = Akaike's Information Criterion [¶]ΔAIC = Difference in AIC between the model of interest and the model with the lowest AIC.

Figure 12. Effect of canopy openness (CO) and measurement date (Date) on leaf-level stomatal conductance (g_s) of turkey oak seedlings in mesic soils at a site in southwest Georgia, USA.

Table 9. Comparison of tested models for leaf-level stomatal conductance of turkey oak seedlings in xeric soils at a site in southwestern Georgia, USA.

Model[†]	k[‡]	Adj. R^{2} [§]	AIC[‖]	ΔAIC[¶]
Date	10	0.73	-409.6	0
CO Date	11	0.73	-407.8	1.8
CO CO*Date	11	0.71	-401.2	8.4
CO Date CO*Date	18	0.74	-398.6	11.0
CO	4	0.14	-324.3	85.3
Null	2	-	-320.5	89.1

Notes. [†]CO = Canopy openness [‡]k = Number of estimated parameters [§]Adj. R^{2} = Adjusted R^{2} value, based on residual variance [‖]AIC = Akaike's Information Criterion [¶]ΔAIC = Difference in AIC between the model of interest and the model with the lowest AIC.
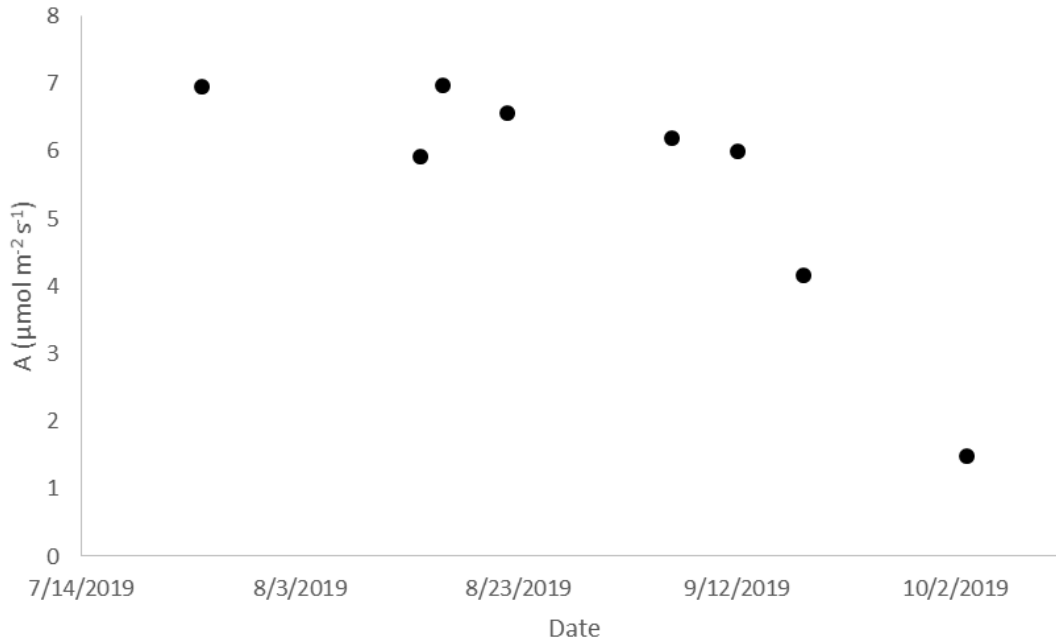

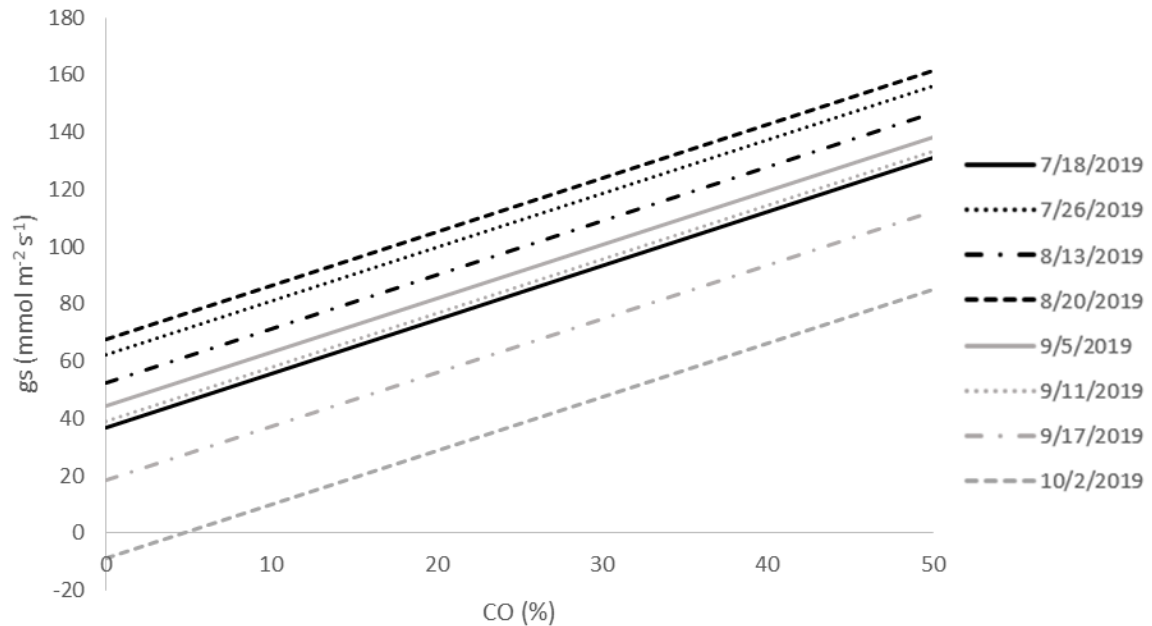
Figure 13. Effect of measurement date (Date) on leaf-level stomatal conductance (g_s) of turkey oak seedlings in xeric soils at a site in southwest Georgia, USA. Each point represents the average gs across all plots on that date.

2.3.4 Overstory Effects on Soil Volumetric Water Content

Mixed model analyses suggested that the best model of overstory effect on soil VWC at the mesic site incorporated the continuous variable CO as a linear effect, as well as an interaction term between CO and the discrete variable Date (Table 10). Both the CO and CO*Date terms in this model were significant ($p = 0.0193$ and $p < 0.0001$, respectively). Increases in VWC were correlated with increasing CO, but measurement date - and thus environmental conditions - affected the strength of this relationship (Figure 14). The slope of the relationship was significantly greater than the overall average on 7/26/2019 ($p < 0.0001$), 08/13 ($p < 0.0001$), and 8/20/2019 ($p < 0.0001$), while it was significantly lower on 7/18/2019 ($p < 0.0001$), 9/11/2019 ($p < 0.0001$), 9/17/2019 ($p < 0.0001$), and 10/2/2019 ($p < 0.0001$). At the xeric site, the best model of overstory effect on soil VWC incorporated the continuous variable CO and the discrete variable Date as linear, additive effects, as well as an interaction term between CO and Date (Table 11). Increases in VWC were correlated with increasing CO ($p = 0.0069$), and differing environmental conditions on different dates had a significant impact on both soil VWC ($p < 0.0001$) and the relationship between CO and VWC ($p = 0.0240$; Figure 15). The slope of the relationship was significantly lower than the overall average on 8/16/2019 ($p = 0.0321$), 9/12/2019 ($p = 0.0220$), 9/18/2019 ($p = 0.0065$), and 10/3/2019 ($p = 0.0094$), while soil VWC levels were significantly greater on 7/25/2019 ($p < 0.0001$), 8/16/2019 ($p < 0.0001$), and 8/22/2019 ($p < 0.0001$) than on the remaining dates.

Table 10. Comparison of tested models for soil volumetric water content near turkey oak seedlings in mesic soils at a site in southwestern Georgia, USA.

Model[†]	k[‡]	Adj. R^{2} [§]	AIC[‖]	ΔAIC[¶]
CO CO*Date	11	0.94	282.2	0
CO Date CO*Date	18	0.95	283.6	1.4
CO Date	11	0.93	296.9	14.7
Date	10	0.93	300.5	18.3
CO	4	0.09	505.3	223.1
Null	2	-	507.1	224.9

Notes. [†]CO = Canopy openness [‡]k = Number of estimated parameters [§]Adj. R^{2} = Adjusted R^{2} value, based on residual variance [‖]AIC = Akaike's Information Criterion [¶]ΔAIC = Difference in AIC between the model of interest and the model with the lowest AIC.
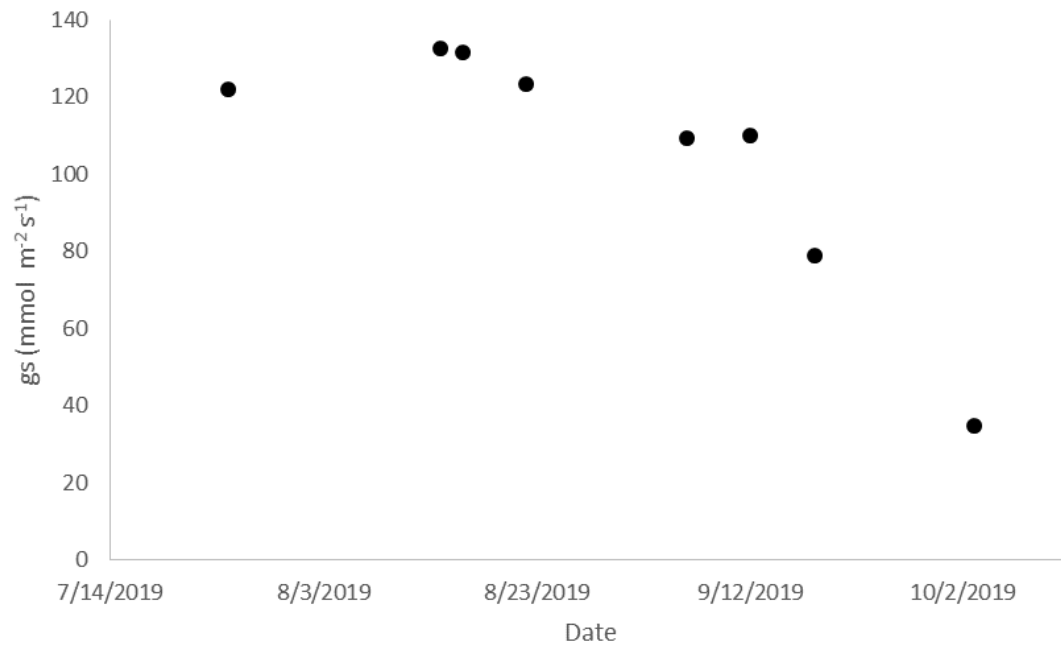

Figure 14. Effect of canopy openness (CO) and measurement date (Date) on soil volumetric water content (VWC) near turkey oak seedlings in mesic soils at a site in southwest Georgia, USA.

Table 11. Comparison of tested models for soil volumetric water content near turkey oak seedlings in xeric soils at a site in southwestern Georgia, USA.

Model[†]	k[‡]	Adj. R^{2} [§]	AIC[‖]	ΔAIC[¶]
CO Date CO*Date	18	0.96	212.7	0
CO Date	11	0.95	214.3	1.6
Date	10	0.95	214.9	2.2
CO CO*Date	11	0.92	249.4	36.7
CO	4	0.16	462.2	249.5
Null	2	-	465.3	252.6

Notes. [†]CO = Canopy openness [‡]k = Number of estimated parameters [§]Adj. R^{2} = Adjusted R^{2} value, based on residual variance [‖]AIC = Akaike's Information Criterion [¶]ΔAIC = Difference in AIC between the model of interest and the model with the lowest AIC.
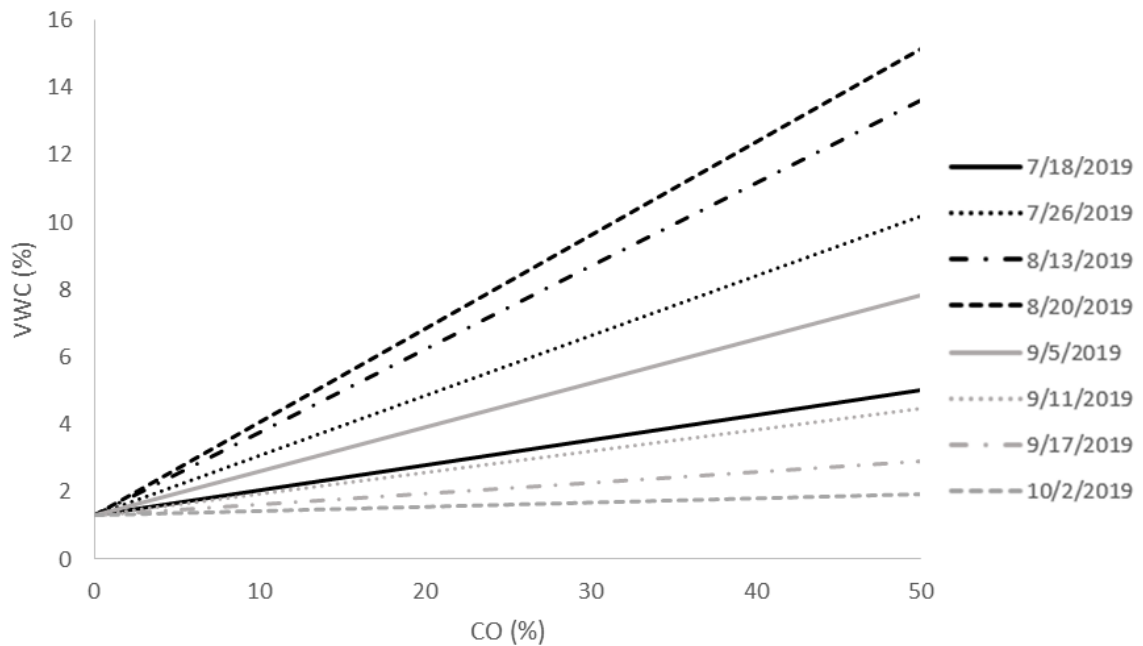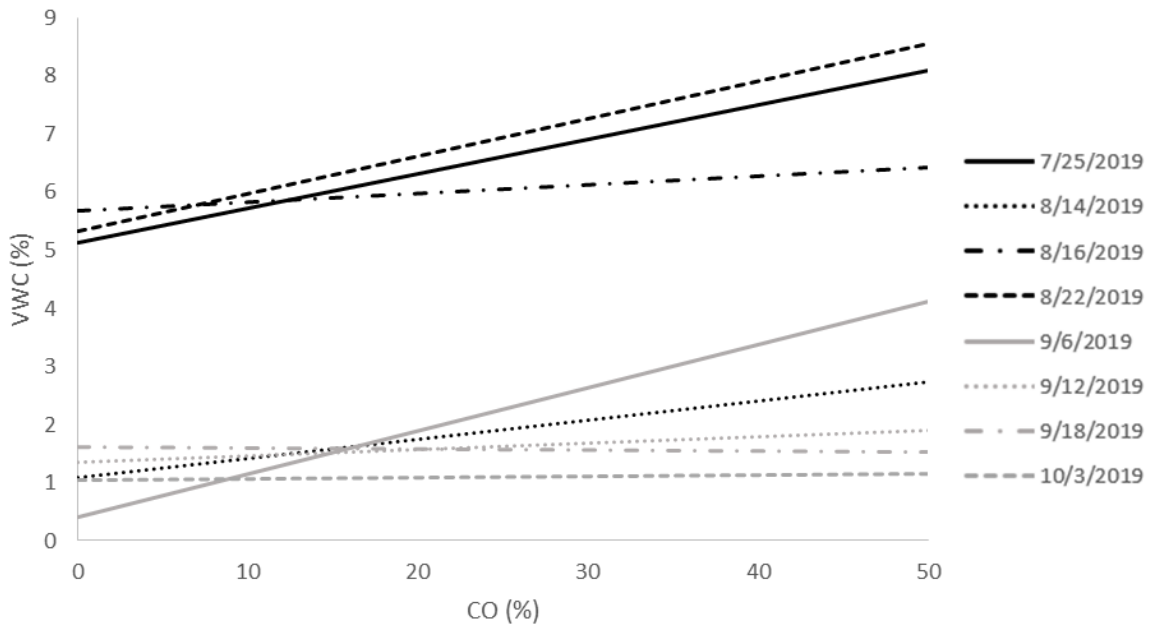

Figure 15. Effect of canopy openness (CO) and measurement date (Date) on soil volumetric water content (VWC) near turkey oak seedlings in xeric soils at a site in southwest Georgia, USA.

2.3.5 Neighborhood Effects on Seedling Physiology and Growth

Neighborhood analyses, which related seedling performance to nearby overstory

tree size and distance in a likelihood framework, suggested that the best model for

seedling relative diameter growth was the null model (Table 12). For seedling A, the best

model was the two-species neighborhood model; however, this model was not better than

the basic neighborhood model, based on AIC (Table 13). Decreases in A were correlated

with increases in NCI ($R^2 = 0.13$; Figure 16).

Table 12. Comparison of tested neighborhood models for diameter growth of turkey oak
seedlings at a site in southwestern Georgia, USA.

Model	$k^\dagger$	$Log(L)^\ddagger$	$AIC^\S$	$\Delta AIC^\parallel$
Null	2	-334.5	673.0	0
Basic Neighborhood	3	-402.5	813.3	140.3
Two-Species Neighborhood	4	-393.3	797.2	124.2

Notes. †k = Number of estimated parameters ‡Log(L) = Maximum log likelihood §AIC = Akaike's Information Criterion $^\parallel\Delta$AIC = Difference in AIC between the model of interest and the model with the lowest AIC

Table 13. Comparison of tested neighborhood models for leaf-level net photosynthesis of
turkey oak seedlings at a site in southwestern Georgia, USA.

Model	$k^\dagger$	$Log(L)^\ddagger$	$AIC^\S$	$\Delta AIC^\parallel$
Null	2	-245.7	495.4	9.9
Basic Neighborhood	4	-239.0	486.3	0.8
Two-Species Neighborhood	5	-237.5	485.5	0

Notes. †k = Number of estimated parameters ‡Log(L) = Maximum log likelihood §AIC = Akaike's Information Criterion $^\parallel\Delta$AIC = Difference in AIC between the model of interest and the model with the lowest AIC
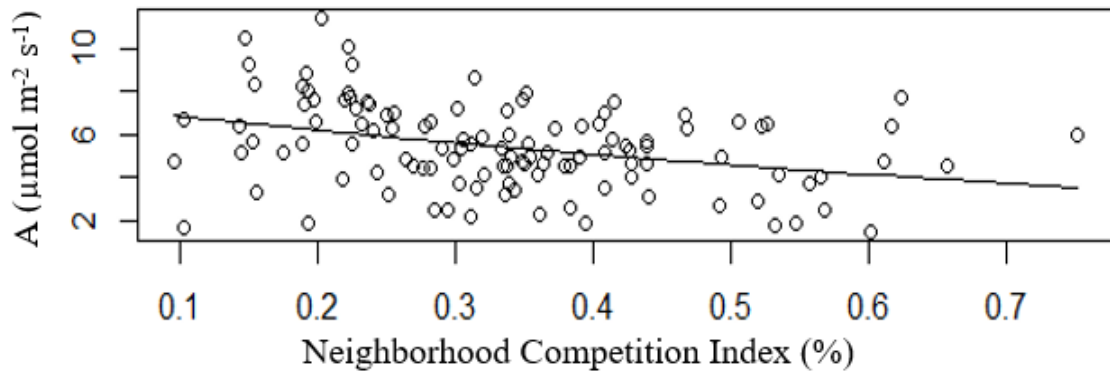
Figure 16. Relationship between neighborhood competition index and leaf-level net photosynthesis (A) of turkey oak seedlings at a site in southwest Georgia, USA.

2.4 Discussion

Average A ranged from 2.0-10.0 µmol m^{-2} s^{-1}, a range similar to those previously reported for turkey oak seedlings (Donovan et al. 2000), and in seedlings of other oak species in the southeastern USA (Donovan et al. 2000, Gardiner 2002, Schweitzer et al. 2006, Petersson et al. 2019). Average g_s ranged from 50.0-200.0 mmol m^{-2} s^{-1}, which is lower than the previously reported ranges of 160.0-250.0 mmol m^{-2} s^{-1} for turkey oak seedlings (Donovan et al. 2000), and 170.0-310.0 (Donovan et al. 2000) or 264.2-434.5 mmol m^{-2} s^{-1} (Williams & Stroupe 2002) for other oak species in the southeastern USA. However, Donovan et al. (2000) noted air temperatures were below average during their study period, and the Williams & Stroupe (2002) study seedlings were grown under greenhouse conditions with irrigation. In this study, summer 2019 exhibited the third highest average maximum daily temperature at the study site in the past 15 years (data not shown), and total precipitation at the site was approximately 80 mm less than the 15 year average (Figure 4). The differences in g_s values in comparison to previous findings may therefore be attributable to less favorable environmental conditions during this study.

The hypothesis that the turkey oak seedlings would experience periods of primarily facilitative effects from the overstory was not supported by the data. However, there is some evidence supporting the hypothesis that the balance between facilitation and competition depends on environmental conditions. Results from the mesic site indicate that the seedlings at this site were experiencing competitive pressures from the overstory, as increased overstory cover was associated with decreases in both seedling A and g_s. Similar results were found by Gardiner (2002) for seedlings of three other species of oak

(*Q. pagoda* Raf., *Q. nuttallii* Palmer, and *Q. lyrata* Walt.), which exhibited reduced levels of photosynthesis under partial light conditions. Likewise, longleaf pine seedling survival has been shown to decrease in close proximity to overstory trees (Brockway & Outcalt 1998, Pecot et al. 2007). However, at the xeric site, neither A nor g_s were significantly correlated with CO, suggesting that the overstory did not affect seedling physiological performance at this site. This may be due to the lower water availability at the xeric site, and suggests that more stressful environmental conditions may weaken any negative relationships between CO and seedling performance metrics. Such a response to stressful conditions mirrors previous findings that facilitation is particularly common in harsh environments (Callaway 1992, Flores & Jurado 2003). At the mesic site, competitive interactions outweighed any potential benefits of facilitation for the turkey oak seedlings, as has been shown previously in other systems and species (Stachowicz 2001, Bruno et al. 2003, Wright et al. 2015). However, at the xeric site, environmental conditions were so unfavorable that a competitive effect of the overstory was not evident, as suggested previously by Callaway et al. (2002) and Wright et al. (2015).

Further support for the weakening of the competitive effects of the overstory on turkey oak seedlings during stressful periods comes from the inclusion of the Date term in the mixed models, as a proxy for environmental conditions. At the mesic site, the effect of CO on A was weakened on dates with more stressful environmental conditions, and strengthened on dates with less stressful conditions. This suggests that, at this site, the competitive effects of the overstory on turkey oak seedlings may be lessened when environmental conditions are unfavorable. This may indicate that facilitation is occurring under these stressful conditions, but is not yet strong enough to outweigh the competitive

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effects. This has previously been reported by Loudermilk et al. (2016), who noted that facilitation may be more crucial to longleaf pine seedling survival during drought periods, particularly on mesic sites. Wright et al. (2015) also found evidence for this in bur oak seedlings in Minnesota grasslands – they noted that competition for water was outweighed by facilitative benefits on hot and dry days, while competition was predominant on cooler and wetter days. Similarly, Palik et al. (1997) found no relationship between longleaf pine seedling survival and overstory basal area during a period of high rainfall, but Rodriguez-Trejo et al. (2003) noted significant decreases in seedling survival as gap size increased during a severe drought, suggesting the increased importance of facilitation to longleaf seedlings during drought. Alternatively, competitive effects may be weakening during more stressful conditions, without a corresponding increase in facilitation. However, previous studies showing the occurrence of HL in longleaf ecosystems (Espeleta et al. 2004, Loudermilk et al. 2006) suggest that facilitation is likely to be a factor in these forests. However, additional measurements of seedling performance during more stressful conditions than were observed over the course of this study may provide further insight into whether overstory facilitation of turkey oak seedlings occurs in longleaf forests, and if it is more prevalent at mesic sites.

At the xeric site, stressful environmental conditions resulted in reduced A of the study seedlings without impacting the relationship between CO and A. And, at both sites, stressful environmental conditions reduced seedling g_s. Such detrimental effects of stressful conditions are consistent with the current knowledge of plant physiology and are similar to results found by Donovan et al. (2000), who noted a decrease in g_s and A in seedlings of turkey oak and two other oak species (*Q. margaretta* Ashe. and *Q. incana*

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Bartr.) during periods with lower precipitation and soil moisture. The lack of an impact of environmental conditions on the relationship between CO and seedling physiology at the xeric site further supports the conclusion made by Loudermilk et al. (2016) that facilitation may be more important on mesic sites than on xeric ones.

Average soil VWC values were lower than previously observed by Whelan et al. (2015), and total precipitation on site during the summer months was approximately 80 mm less than the average for the past 15 years. This suggests that drought conditions were prevalent during the study period. Results (Figures 14 and 15) indicate that soil VWC at both sites was negatively impacted by the overstory, with increasing levels of overstory cover resulting in decreases in soil water availability. This has been previously documented in longleaf pine forests (Dagley et al. 2002, Harrington et al. 2002). At both sites, CO had a lessened effect on soil VWC on dates with more stressful environmental conditions, and a greater effect on dates with less stressful conditions. This further indicates that facilitative effects of the overstory may be observed during periods with less favorable environmental conditions. It is possible that, during periods with unfavorable conditions, hydraulic lift was occurring at the study sites, resulting in the observed weakening of the negative effect of the overstory on soil VWC during these periods. Hydraulic lift has previously been documented in longleaf pine forests by Espeleta et al. (2004) and Loudermilk et al. (2016). The observed patterns in VWC responses to the overstory closely mirror those observed in the responses of seedling A to the overstory. This suggests that the observed effects of the overstory on seedling A may be due to overstory effects on soil water availability, likely through HL.

Likelihood analyses based on NCI indicated that seedling relative diameter growth was not affected by the nearby overstory; however, changes in seedling diameter were negligible across seedlings, and therefore likely were not great enough for effects to be observed. The negligible diameter growth observed in the seedlings is consistent with the documented growth habit of turkey oak, in which growth is initially focused belowground rather than aboveground (Harlow 1990). Meanwhile, seedling A was significantly impacted by the nearby overstory, with decreased levels of A associated with increases in NCI. These results further support the hypothesis that longleaf pine overstory trees have a competitive effect on turkey oak seedlings. Analyses did not detect a significant difference in discriminatory power between the model that distinguished between pine and hardwood overstory trees and the model which did not, suggesting that the type of overstory tree does not play an important role in turkey oak seedling performance. This contrasts with the results of Loudermilk et al. (2016), who found that longleaf pine seedlings at xeric sites experienced facilitation from overstory oaks, but not from overstory longleaf pine trees. This discrepancy is likely due to the different growth strategies and resource requirements of longleaf pine and turkey oak seedlings. Longleaf pine seedlings are particularly sensitive to water availability (McGuire et al. 2001), while turkey oak is a much more efficient water user (Donovan et al., 2000). Thus, it is likely that turkey oak seedlings would depend less on facilitation than would longleaf pine seedlings, and would potentially be affected more uniformly by differing species of overstory tree.

In summary, the results of this study indicate that turkey oak seedlings grown in a longleaf pine system experience competitive pressures from the overstory, possibly in

response to overstory effects on soil water availability. Overstory tree type (hardwood vs. longleaf pine) does not affect this relationship; however, environmental conditions do, with more stressful conditions weakening the negative impact of the overstory on seedling performance. This suggests that facilitation from the overstory may play a more significant role during environmental conditions more stressful than those observed over the course of the study period, particularly at mesic sites.

2.5 Application

The results of this study contribute to the Adaptive Silviculture for Climate Change project, which is focused on understanding the efficacy of different management plans designed to enable forest ecosystems to respond to predicted alterations in climate patterns (Nagel et al. 2017). Shifts in species composition are one tactic being explored by the ASCC project, mainly in the *transition* treatments, which aim to actively facilitate changes in forest ecosystems to encourage adaptation of those ecosystems to climate change. *Transition* strategies involving shifts in species composition have been effectively incorporated into management plans across the USA, from conifer forests in Oregon (Hemstrom et al. 2007) to mixed-pine and hardwood forests in Minnesota (Muller et al. 2019) and Wisconsin (Janowiak et al. 2014). Results from this study suggest that turkey oak seedlings will likely perform best when planted in canopy gaps within a longleaf pine forest. Such information regarding planting location will be of use to land managers and foresters interested in initiating shifts in species composition by introducing turkey oak into longleaf pine stands as a future-adapted oak species. Strategies that successfully allow for the longleaf ecosystem to adapt to future climate scenarios will be vital to the continued existence of this highly biodiverse and threatened ecosystem. This study also provides baseline information regarding the physiology of turkey oak, which is a species that has not been frequently studied.

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