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Seasonal physiology and growth of planted oaks with implications for bottomland hardwood restoration

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Abstract

Afforestation and reforestation of once dominant bottomland hardwood forests in the southeastern United States can provide ecosystem services and wildlife habitat. However, challenges of prior site conditions, seasonal flooding, soil texture and lack of nearby seed sources can necessitate planting of seedlings to achieve desirable results, particularly for large-seeded species like oaks. Therefore, the objectives of this study were to compare growth and survival of two species of oaks common to southeastern and bottomland hardwood forests, cherrybark oak (*Quercus pagoda* Raf.) and willow oak (*Quercus phellos* L.) from 1-0 bareroot, conventional container (0.24 L) and large container (3.8 L) planting stocks across two growing seasons. Additionally, we sought to compare physiology across seedling types to determine the underlying differences in functioning that led to the growth responses. Despite above average rainfall, growth was modest particularly at the site that was previously pasture land and for willow oak which also exhibited net dieback. Two-year survival was adequate (> 75%) for bareroot and large container seedlings but was suboptimal (~ 50%) for conventional container seedlings. Large container seedlings had about 40% higher photosynthetic rates and 70% higher water use efficiencies compared to bareroot and conventional container seedlings. Cherrybark oak exhibited greater stomatal regulation across the growing season than willow oak, however all seedling types displayed increased stomatal conductance and decreased water use efficiency throughout the growing season. Overall, these findings highlight the importance of matching species to site conditions and providing competition control particularly on grassland sites and during above average rainfall conditions.

Keywords Afforestation · Bareroot · Container · Gulf Coastal Plain · *Quercus* · Reforestation

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Introduction

Bottomland hardwood forests once covered an extensive range across the southeastern United States (US) on the Atlantic and Gulf Coastal Plains due to the topography and erodible soils in the region (Hodges 1997). With river channelization, land use change and disturbances like hurricanes (Kupfer et al. 2008; Sharitz and Mitsch 1993), bottomland hardwood forests have dwindled in area and cover only a small portion of their original range (Battaglia et al. 2002; Kellison and Young 1997). Efforts are being made to reforest and afforest bottomland hardwoods throughout the southeastern US (King and Keeland 1999) and government programs like the Conservation Reserve Program (CRP) can assist private landowners with these efforts (Ribaudo et al. 2001). Restoring bottomland hardwood forests on land that is prone to erosion is particularly important as these forests provide a variety of ecosystem services including erosion control, buffering capacity for floodwaters (Kellison and Young 1997), nutrient removal and water quality benefits (Baker III et al. 2001; Ouyang et al. 2015), wildlife habitat (Twedt et al. 2002) and carbon sequestration potential (Bridgham et al. 2006; Shoch et al. 2009). However, sites for potential afforestation may not be in close proximity to a local seed source and will require seeds or seedlings to be planted, particularly for heavy-seeded species like oaks.

Oaks are generally more desirable than light seeded, wind-dispersed species for wildlife habitat and the potential for eventual timber production (Stanturf et al. 2000), but will need to be planted if no local seed trees are nearby. Once heavy-seeded species have established, light-seeded species will likely naturally colonize to increase the species diversity of the forest. However, afforestation can be challenging due to prior land uses and compaction that may cause changes in soil nutrients, bulk density and mycorrhizal availability as opposed to natural systems (Cambi et al. 2017; Dickie et al. 2007; Stanturf et al. 2009). In addition, marginal areas that are prime candidates for afforestation are many times also poorly drained and susceptible to seasonal flooding particularly during the late winter and early spring. Bottomland oak species have varying tolerance to flooding when in the seedling stage with overcup oak (*Quercus lyrata*), Nuttall oak (*Q. texana*), water oak (*Q. nigra*) and willow oak (*Q. phellos*) being moderately tolerant of flooding conditions and cherrybark oak (*Q. falcata*), Shumard oak (*Q. shumardii*), and swamp chestnut oak (*Q. michauxii*) being fairly intolerant (Clatterbuck and Meadows 1992; Collins and Battaglia 2008). Furthermore, moisture stress caused by poor soil conditions including heavy clay or sandy soils and environmental conditions during dry spells and hot summers can lead to reduced growth and potential mortality of newly planted seedlings (Jiménez et al. 2017). Abiotic factors along with competition and herbivory (Kellner and Swihart 2016) have led to disappointing results in terms of survival and stocking density for afforestation sites that were direct seeded with acorns (Dey et al. 2008; Stanturf et al. 2004). Oak seedlings grown for a longer period of time and/or in larger containers before outplanting are likely to have a larger, more developed root system that can reduce moisture stress and transplant shock (Davis and Jacobs 2005; Dey et al. 2012), more stored carbon for initial post-transplant growth (Sloan et al. 2018) and may contain larger internal N pools due to nursery fertilization (Vernay et al. 2018). In addition, individuals outplanted from larger containers will be taller initially, which may decrease susceptibility from herbaceous competition (Gordon et al. 1989; Löf et al. 2006; Morrissey et al. 2010), wildlife browsing (Stanturf et al. 2004) and flooding inundation (Gardiner et al. 2004). However, individuals with more aboveground biomass also have the potential for greater evaporative water losses and respiration loads (Sanz-Pérez et al. 2009; Villar-Salvador et al. 2012) which may lead to dieback after outplanting.

Oak seedlings tend to tolerate stressful conditions by allocating resources belowground initially to increase nutrient capture and access deeply available soil moisture (Grünzweig et al. 2008). Therefore, oak seedlings tend to exhibit slow aboveground growth rates initially (Shaw et al. 2003) which allows many oak species to be successful on xeric sites but rather poor competitors on more mesic sites (Dey et al. 2008). Transplant shock caused by moisture stress conditions can limit initial seedling establishment and growth (Pemán et al. 2017) with species and individuals within the oak genus exhibiting a range of suseptibility to drought conditions (Abrams 1990; Navarro-Cerrillo et al. 2018). Likewise, several strategies for surviving drought have been observed in oaks including altering root to shoot ratios (Ramírez-Valiente et al. 2018), stomatal closure under low soil moisture and/or high vapor pressure deficit, and osmotic adjustment and/or alteration of leaf tissue properties to withstand low leaf water potentials (Fotelli et al. 2000; Hamerlynck and Knapp 1994; Thomas and Gausling 2000; Xu and Baldocchi 2003). Therefore, leaf morphological and physiological properties may be more useful than growth parameters alone in determining the potential for long term success of oak planting stocks in terms of resisting stressful conditions. For example, high photosynthetic rates sustained throughout the growing season without concomitant aboveground growth may signify increased belowground allocation and/or nonstructural carbohydrate storage. Increases in leaf mass per unit area may indicate changes in tissue properties that allow leaves to withstand more negative leaf water potentials (Niinemets 2001). Greater stomatal conductance and transpiration rates that are sustained throughout the growing season may be indicative of greater resistance of water stress conditions as well as more root absorptive area to avoid drought. Together, these leaf morphological and physiological parameters provide a more complete picture of growing season stresses to oak seedlings as well as their long term potential for success.

The overall objectives of this study were to compare survival, growth and physiological parameters of two bottomland oak species, cherrybark oak and willow oak, from three planting stocks; 1–0 bareroot, conventional container and large container seedlings. Acorns from both of these oak species provide an important food source for wildlife and both have timber uses with willow oak wood being more suitable for oak veneer and cherrybark oak more suitable as high grade lumber for the production of furniture, flooring and lumber (Burns and Honkala 1990; Hodges et al. 2008). These planting stocks differ greatly in price, however increased growth and survival may offset additional costs of container seedlings. In addition, physiological parameters including monthly photosynthetic rates, stomatal conductance and water use efficiency indicate differences in functioning across species and planting stocks and can provide mechanistic explanations for the differences in growth seen in each seedling type. We hypothesize that seedlings with larger root systems at the time of planting (i.e. large container seedlings) will maintain greater photosynthetic rates and stomatal conductances throughout the growing season compared to seedlings with smaller root systems (bareroot and conventional container). In addition, we sought to compare seasonal physiological parameters measured in the first growing season with diameter and height growth measured in both the first and second growing seasons. These data can provide information on which physiological parameters are most important and have the most predictive power for current and future growth. Mismatches between photosynthetic rates and growth (i.e. high photosynthesis and low growth or vice versa) provide an indication of the proportion of stored carbon that is being utilized for growth. In total, these data can be used to provide recommendations for the best planting stocks to use in reforestation and afforestation projects depending on site location, soil and environmental growing conditions, desired stocking and associated costs.

Materials and methods

Site descriptions and growing conditions

Sites were planted on two privately owned properties in southern Mississippi on alluvial sites in the Gulf Coastal Plain. The first site ("Pasture") was located in Stone County, MS (30°50′29.88″ N, 89°11′32.42″ W) about 55 km north of the Gulf of Mexico on former pasture land for cattle grazing with relatively flat topography. This site previously contained woody vegetation that was impacted by Hurricane Katrina and cleared in 2005. Soils in this site did not exhibit evidence of compaction and were classified as Smithton fine sandy loam (Soil_Survey_Staff 2017). The majority of competing vegetation on this site included cypress panicgrass (*Dichanthelium dichotomum* L.) and redtop panicgrass (*Panicum agrostoides* Bosc ex Nees) both native grasses and cogongrass (*Imperata cylindrica* (L.) P. Beauv.), an exotic, invasive grass in the region. A prescribed burn was conducted in Jan 2017 prior to planting to increase precision of plot demarcation and ease of planting. The second study site ("Clearcut") was located in Lamar County, MS (31°11′18.62″N, 89°22′32.94″W) about 98 km north of the Gulf of Mexico and was previously a loblolly pine (*Pinus taeda* L.) plantation which was clearcut in 2016. All downed woody material had been cleared and no site preparation was needed prior to planting on this site. Soils in this site did not exhibit evidence of compaction and were classified as Latonia fine sandy loam (Soil_Survey_Staff 2017). The site had a relatively flat topography with a creek bordering the northern portion of the study area and an alluvial deposit of sand across the northwestern portion. The majority of competing vegetation on this site included tree and shrub seedlings of sweetgum (*Liquidambar styraciflua* L.), sassafras (*Sassafras albidum* (Nutt.) Nees), red maple (*Acer rubrum* L.), blackberry (*Rubus spp*.), winged sumac (*Rhus copallinum L.*), and yaupon (*Ilex vomitoria* Sol. Ex Aiton) and greenbriar (*Smilax spp.*) vines. Percent coverage of woody species was approximately 30% across the site. Woody vegetation was approximately 1 to 2 m tall.

Soil samples were collected randomly across both sites in the beginning of the study using a soil sampler probe to a depth of approximately 30 cm. Samples were analyzed for nutrient content, pH, organic matter percentage, and texture by the Mississippi State University (MSU) Extension Service Plant and Soil Sciences Soil Testing Lab on March 23, 2017. The Pasture site had a pH of 5.3 and a composition of 42% sand, 44% silt and 14% clay with an organic matter content of 1.6%. The Clearcut site had a pH of 4.9 and a composition of 62% sand, 26% silt and 12% clay with an organic matter content of 1.6%. Meteorological data including daily precipitation and air temperature were obtained from weather stations near the Pasture (USC00229639; Wiggins, MS, US) and Clearcut (USC00223887; Hattiesburg, MS, US) study sites from the National Oceanic and Atmospheric Administration (https://www.ncdc.noaa.gov/cdo-web/; Fig. 1a).

Study sites in 2017 received about 2.5 times more rainfall than the 30 year average for this location (Arguez et al. 2010) in January, about half the amount of average rainfall in February and March and about equal rainfall in April (Fig. 1a). From May to August, 2017, the study sites received between 2 and 3 times more rainfall than the 30 year average. In September, 2017 sites received about 10% of normal rainfall and in October they received

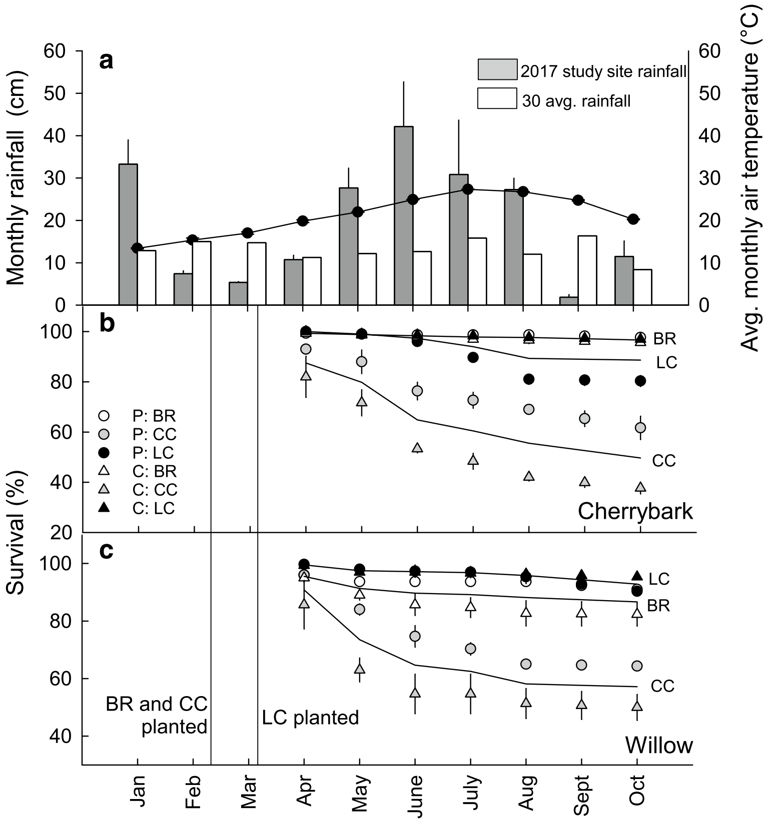

Fig. 1 **a** Meteorological parameters during the first year, 2017 growing season including monthly rainfall (cm; gray bars; average and SE of both sites), 30 year average rainfall for the study location (white bars) and average (± SE across study sites) monthly air temperature (°C; black circles). Monthly survival (%) during the first (2017) growing season for **b** cherrybark oak and **c** willow oak. Pasture site (P)—circles, Clearcut site (C)—triangles, bareroot (BR)—open symbols, conventional container (CC)—gray symbols, large container (LC)—filled symbols. Trendlines are fitted to the average monthly survival across both sites for each container type. Vertical lines indicate when seedlings of different planting stocks were planted

about 1.4 times as much rain as the 30 year average (Fig. 1a). In 2018, rainfall amounts were closer to the 30 year averages for each month although June, July and August still received about 40% more rainfall than the average for these months. In 2017, temperatures during the winter and early spring (Jan–Apr) were about 28% warmer than the 30 year average for the area. For the 2017 growing season (May–Oct), temperatures were close to the 30 year average differing by no more than 5% in any month. The 2018 winter/early spring was about 9% warmer than the 30 year average and the growing season was about 7% warmer.

Seedling establishment and experimental design

A randomized complete block design was used for both sites in this study. Each site was divided into three blocks, with each block containing a combination of two species (cherrybark oak and willow oak) and three planting stocks (bareroot, conventional container and large container individuals) for a total of six treatments per block. For each treatment, 100 seedlings were planted on a 2.13 m by 2.13 m spacing. For both species, high quality 1–0 (1 year in the nursery bed, 0 years as an outplant) bareroot seedlings were obtained from the Weyerhaeuser nursery near Brookhaven, MS at a cost of $0.25 each. Bareroot seedlings contained at least eight first order lateral roots each (Ward et al. 2000). Number of first order lateral roots was used to estimate initial seedling quality due to its positive correlation with future growth (Dey and Parker 1997) and inclusion in one assessment of bareroot seedling quality (Mariotti et al. 2015). Bareroot cherrybark oak seedlings averaged 3.8 mm in diameter and 50 cm in height and willow oak seedlings averaged 4.1 mm in diameter and 57 cm in height. Conventional container seedlings (0.24 L pots) were obtained from Mossy Oak Nativ Nursery™ in West Point, MS at a cost of $2.00 each. Conventional container cherrybark oak seedlings averaged 4.1 mm in diameter and 33 cm in height and willow oak seedlings averaged 4.7 mm in diameter and 48 cm in height. Media for conventional container seedlings consisted of pine bark mix, commercial peat-perlite potting mix, slow release fertilizer and pasteurized poultry litter fertilizer. Large container seedlings (EKOgrown™ seedlings grown in 3.8L Rootmaker® pots) were obtained from RES Native Tree Nursery located in Montegut, LA at a cost of $15.00 each. These large container seedlings were grown at the nursery in a dry nutrient growing media using a process that promotes air pruning of the roots to develop a fibrous root system with a large volume of absorptive surface area (Dey et al. 2004). Large container cherrybark oak seedlings averaged 10.1 mm in diameter and 131 cm in height and willow oak seedlings averaged 15.4 mm in diameter and 208 cm in height.

Bareroot and conventional container seedlings were planted on Feb 11, 2017 by MSU personnel using planting shovels with approximately 35 cm long blades. No culling was implemented for conventional container seedlings, however bareroot seedlings were culled for quality control purposes. In total about 10% of bareroot seedlings fell below standards including a minimum of 0.5 m in height and a minimum of eight first order lateral roots and were not planted. This culling is in accordance with the cost differences between bareroot and conventional container planting stocks and typical restoration planting procedures. For bareroot seedlings, no root trimming was implemented during planting and on rare occasions when excessively long lateral roots were present, they were left to air prune. Large container seedlings were hand planted on March 7, 2017 by a commercial planting crew using shovels to excavate planting holes then backfilling soil around the root ball.

Herbaceous weed control was implemented once planting had concluded to suppress competing herbaceous vegetation during the initial establishment period of bareroot and conventional container seedlings. A banded application of 210 grams of Oust® XP (Bayer AG, Monheim am Rhein, Germany) per sprayed hectare was applied on Feb 25, 2017 in a 1.5 m band with the seedling as the center of the spray swath. Herbaceous weed control was repeated in the same manner on March 2, 2018 on all bareroot and conventional container seedlings. Oust® XP was chosen because it is the operational standard herbaceous weed control for oak plantings and had been shown to exhibit no negative effects on survival (Ezell and Catchot 1997; Ezell and Hodges 2001; Self et al. 2014) and in many cases, leads to increased oak seedling survival (Ezell et al. 2007). This herbicide did not control woody vegetation at the Clearcut site and was ineffective on the cogongrass at the Pasture site (for which there is currently no effective herbicide that would not also damage oak seedlings). Therefore, at the Pasture site, herbaceous weed control allowed for initial spring establishment of seedlings, however herbaceous coverage was greater than 90% by June of each growing season. On the clearcut site, woody vegetation was not controlled and had about 30% coverage across the site. Large container seedlings did not receive herbaceous weed control in either growing season because EKOgrown™ seedlings are marketed as not requiring competition control (to partially compensate for the higher costs per seedling) due to their larger root system and aboveground height at the time of planting. Therefore, each planting stock in this study was treated as it would be in an operational setting based on currently accepted forestry practices.

Survival and growth

Survival data were recorded monthly during the first growing season and at the end of the first and second growing seasons. Mortality was evaluated by scraping the bark at the base of suspected dead seedlings to check for live tissue. Trees were considered alive if they exhibited any green leaves and/or any green vascular cambium tissue. Initial groundline diameter and height measurements were recorded on March 11, 2017. Groundline diameter measurements were made directly above the root collar using Mititoyo® digital calipers and heights were measured using meter sticks to the nearest whole cm. Total height was measured from the ground to the terminal bud. If a seedling exhibited multiple stems, the tallest stem was measured. If dieback or stem breakage occurred, it was recorded and the seedling was measured to the highest point of living tissue. If complete dieback and resprouting occurred, it was noted and the resprout was measured and recorded. Heights and groundline diameters were recorded at the end of each growing season on Oct 5, 2017 and Oct 11, 2018 to determine first and second year growth estimates.

Gas exchange and leaf mass per area

A LI-COR 6400XT Portable Photosynthesis System (LI-COR Biosciences Inc., Lincoln NE, USA) with a red/blue light source was used to measure gas exchange and obtain estimates of photosynthetic rates (μmol CO_2 m^{-2} s^{-1}), stomatal conductance (mol H_2O m^{-2} s^{-1}) and transpiration rates (mmol H_2O m^{-2} s^{-1}) of selected seedlings. Intrinsic water use efficiency was calculated as the ratio of photosynthesis and stomatal conductance (μmol mol^{-1}). Monthly measurements (May–September) were made during the first growing season of the study. During each monthly period at each site, rounds of gas exchange were measured on each sampled seedling approximately every 1.5 h between 6:00 am and 12:00 pm CDT with a minimum of three rounds of measurements made during this time interval. Measurements were made in the morning to capture the period of maximum gas exchange rates. If dew was present on leaves during the early morning measurement interval, leaves were dried with a paper towel prior to data collection.

At each site, two seedlings were measured per species/planting stock combination in each block for a total of 36 seedlings per site. All measurements were made at light levels of 1500 μmol photons m^{-2} s^{-1} and CO_2 concentrations of 400 ppm and after photosynthetic rates reached equilibrium. For willow oak, leaves which were not wide enough to fill the 6 cm^2 leaf chamber were collected from each seedling during each monthly collection, placed in a plastic zip top bag and returned to the lab. The area of willow oak leaves that would have filled the chamber area was estimated using a flatbed scanner (CanoScan LiDE 210; Canon; Melville, NY, U.S.A.) and scaling factor using Image J software version 1.48 (National Institutes of Health, U.S.A., https://imagej.nih.gov/ij/). These actual chamber leaf areas were used in the LI-COR data files to correctly estimate gas exchange parameters for willow oak.

During the May, July, and September measurement periods, leaves were collected from all gas exchange sample trees, placed in zip top bags and returned to the lab. Total leaf area was determined using Image J and the procedure described above. Leaves were then placed in a 60 °C drying oven for at least 3 days and their dry weights were obtained. Fresh leaf areas and dry weights were used to estimate leaf dry mass per unit area (LMA; g m^{-2}). Leaf mass per area data were used to calculate photosynthetic rates on a per unit leaf mass basis (mass-based photosynthesis; nmol CO_2 g^{-1} s^{-1}) by dividing area-based photosynthesis by LMA. For months in which LMA was not obtained (June and August), regression equations were developed for each measured individual and used to estimate LMA for those months.

Statistical analyses

For height and diameter growth comparisons, measurements from all individuals within the study were used. Block-level averages for height and diameter growth were used to calculate standard errors and for statistical comparison between sites, species and planting stocks using analysis of variance (ANOVA) in R version 3.1.2 (R Foundation for Statistical Computing, Vienna, Austria http://www.R-project.org/). Tukey post hoc tests were used to determine which planting stocks differed significantly. Percent survival was calculated for each species*planting stock combination in each block and site and significant differences between sites, species and planting stocks were assessed using ANOVA in R. For leaf anatomical and physiological parameters, measurements made throughout the day on each individual were averaged for each month, then monthly values were averaged across the growing season. For these seasonal averages, significant differences between sites, species and planting stocks were assessed using linear mixed effect models (lme function; Pinheiro et al. (2014)) in R with replicate block included as a random effect in each model. If planting stocks were significantly different, post hoc tests were performed using the general linear hypotheses test (glht) function in the multcomp package (Hothorn et al. 2008) with Tukey contrasts in R to determine which planting stocks differed from one another.

Analyses were also performed to determine if the interaction between species*planting stock was significant using linear mixed effect models in R with site and block included as random effects. If this interaction was significant, post hoc tests with Tukey contrasts were performed as above to determine which species*planting stock combinations differed significantly from each other. In order to determine how stomatal conductances responded to vapor pressure deficits throughout the study period (i.e. stomatal sensitivity to vapor pressure deficit or g_s vs. vapor pressure deficit), the natural log of stomatal conductance for each individual was plotted versus the natural log of leaf vapor pressure deficit in the leaf chamber. Linear regressions were fitted to these data using Sigmaplot version 13 (Systat Software Inc. San Jose, CA, U.S.A.) and the slopes of these lines were compared across sites, species and planting stocks using mixed effect models and post hoc tests in R as above.

In order to determine how physiological parameters changed across the growing season, daily averages for physiological or leaf anatomical parameters for each measured individual were plotted versus the day of year (DOY) using Sigmaplot. For each individual, a slope term for this relationship (Δ Photosynthesis etc.) was estimated and comparisons across sites, species and planting stocks were made using mixed effect models and post hoc tests as above. To determine r^2 values and p-values (if slopes differed significantly from zero) for these relationships, data for each species*planting stock combination were averaged within each block at each site and these averages were plotted versus DOY. Sigmaplot was used to fit linear regression equations to these data for each species*planting stock combination. Sigmaplot was also used to determine r^2 and p-values for relationships between physiological parameters and year one and two height and diameter growth.

Results

For the 2017, year one growing season, most planting stocks, on average, exhibited dieback with negative yearly height growth except for large container cherrybark oak which exhibited modest positive height growth (Table 1). Year one height growth was significantly lower in willow oaks compared to cherrybark oaks with all planting stocks combined and was significantly lower at the Pasture site compared to the Clearcut site (− 4.4 cm vs. 1.0 cm respectively; Tables 1, 2). Comparing planting stocks, bareroot seedlings had significantly lower year one height growth than large container seedlings (Tables 1, 2). For year one diameter growth, results were similar when comparing sites and species, however large container individuals exhibited about four and six times the diameter growth for cherrybark and willow oak respectively compared to bareroot and conventional container seedlings which did not differ from one another (Tables 1, 2). Year one survival was significantly lower at the Clearcut site compared to the Pasture site (71 vs. 81% respectively) across all seedlings and was about 40% lower in conventional container seedlings compared to bareroot and large container seedlings (Table 1) which did not differ significantly from one another (Table 2). For large container cherrybark oaks, survival was lower at the Pasture site compared to the Clearcut site and decreased to the greatest extent in July and August (Fig. 1b). For conventional container cherrybark oaks, survival declined at both sites throughout the first growing season with the greatest decrease in June (Fig. 1b). Bareroot cherrybark oaks maintained high survival at both sites. For willow oaks, large container seedlings maintained high survival at both sites (Fig. 1c). Survival of willow oak bareroot seedlings was slightly lower at the Clearcut site and decreased to the greatest extent in May and June (Fig. 1c). Conventional container willow oaks also exhibited low survival with the greatest decrease in survival occurring during the beginning of the growing season (Apr–June; Fig. 1c).

At the end of the second growing season, survival results mirrored year one with conventional container individuals having significantly greater mortality than other planting stocks although differences between sites were no longer significant. Overall, seedlings experienced an additional 1.8, 4.6, and 5% mortality for bareroot, conventional container and large container seedlings respectively (Table 1). As opposed to year one height growth, large container individuals exhibited dieback and negative height growth in year two whereas bareroot and conventional container exhibited slightly positive height growth in the second growing season. Only large and conventional container stocks differed significantly with large container individuals exhibiting significantly lower second year height growth than conventional container seedlings (Table 2). For year two diameter growth, species and planting stocks were statistically similar and averaged about 0.7 mm growth during the second growing season. Sites differed significantly with the Clearcut site having greater second year diameter growth compared to the Pasture site (1.1 vs. 0.3 mm respectively).

Averaged across the growing season, cherrybark oak had larger leaves than willow oak (Table 2) and large container seedlings had larger leaves than bareroot or conventional

Table 1 Seasonal growth, survival, physiological parameters and changes (Δ) in parameters throughout the first growing season (slope term of parameter versus day of year (DOY; averages and SE in parentheses) for bareroot (BR), conventional container (CC) and large container (LC) planting stocks of cherrybark oak and willow oak

	Cherrybark oak			Willow oak		
	BR	CC	LC	BR	CC	LC
Year one height growth (cm)	−0.21 (1.3)	−1.3 (1.3)	2.5 (2.9)	−7.8 (2.1)	−3.9 (1.4)	−0.80 (2.1)
Year one diameter growth (mm)	0.75 (0.2)^{c}	0.42 (0.2)^{c}	2.3 (0.4)^{b}	0.74 (0.3)^{c}	0.48 (0.2)^{c}	3.9 (0.4)^{a}
Year one survival (%)	93.8 (2.4)	48.8 (6.2)	84.0 (2.5)	84.2 (3.2)	55.5 (4.8)	90.0 (0.7)
Year two height growth (cm)	1.2 (2.0)	2.4 (2.4)	−1.6 (1.8)	−0.3 (2.7)	0.4 (1.8)	−6.4 (2.8)
Year two diameter growth (mm)	0.63 (0.3)	0.26 (0.3)	0.51 (0.4)	0.89 (0.3)	0.50 (0.3)	1.15 (0.4)
Year two survival (%)	92.2 (2.5)	42.8 (4.6)	76.7 (5.4)	82.3 (3.7)	52.3 (4.6)	87.3 (1.8)
Individual leaf area (cm^{2})	21.8 (1.1)	18.3 (1.2)	31.3 (2.0)	5.5 (0.3)	5.3 (0.3)	13.3 (1.1)
Leaf mass per area (LMA; g m^{-2})	79.8 (1.1)^{c}	95.4 (3.4)^{a}	86.3 (2.1)^{bc}	81.0 (1.5)^{c}	82.8 (1.1)^{c}	91.2 (2.4)^{ab}
Mass-based photosynthesis (nmol g^{-1} s^{-1})	64.8 (5.7)	63.8 (3.2)	91.4 (4.8)	67.9 (5.7)	74.0 (4.2)	100.3 (5.7)
Transpiration rate (mmol m^{-2} s^{-1})	3.9 (0.09)^{b}	4.0 (0.1)^{b}	3.2 (0.1)^{c}	4.2 (0.2)^{ab}	4.8 (0.2)^{a}	3.2 (0.2)^{c}
Stomatal conductance (g_s; mol m^{-2} s^{-1})	0.34 (0.01)	0.40 (0.02)	0.29 (0.02)	0.29 (0.02)	0.33 (0.02)	0.21 (0.01)
Intrinsic water use efficiency (iWUE; µmol mol^{-1})	27.8 (2.4)	35.9 (2.2)	50.7 (2.3)	32.8 (2.2)	31.4 (1.6)	57.8 (3.0)
g_s versus vapor pressure deficit (ln mol m^{-2} s^{-1} ln kPa^{-1})	−1.79 (0.09)	−1.95 (0.07)	−1.86 (0.06)	−1.37 (0.1)	−1.36 (0.2)	−1.19 (0.1)
Δ Leaf mass per area versus DOY (g m^{-2} day^{-1})	0.19 (0.02)	0.045 (0.03)	0.29 (0.07)	0.23 (0.04)	0.11 (0.04)	0.32 (0.05)
Δ Photosynthesis versus DOY (nmol g^{-1} s^{-1} day^{-1})	−0.25 (0.09)	−0.28 (0.08)	−0.44 (0.2)	−0.31 (0.1)	−0.12 (0.1)	−0.24 (0.1)
Δ Stomatal conductance versus DOY (mmol m^{-2} s^{-1} day^{-1})	2.6 (0.4)	1.1 (0.5)	1.1 (0.5)	2.2 (0.5)	2.0(0.3)	1.1 (0.3)
Δ iWUE versus DOY (µmol mol^{-1} day^{-1})	−0.15 (0.03)	−0.19 (0.06)	−0.24 (0.08)	−0.25 (0.06)	−0.24 (0.04)	−0.27 (0.07)

For parameters with a significant species*planting stock interaction (Table 2), different superscript letters signify significant differences at $\alpha < 0.05$

Table 2 Analysis of variance table for seasonal morphological and physiological leaf parameters including changes (Δ) in parameters throughout the first growing season (slope term of parameter vs. day of year (DOY))

	Site	Species	BR versus CC	BR versus LC	CC versus LC	Species/planting stock interaction
Year one height growth (cm)	*	*		*		
Year one diameter growth (mm)				*	*	*
Year one survival (%)	*		*		*	
Year two height growth (cm)					*	
Year two diameter growth (mm)	*					
Year two survival (%)			*		*	
Individual leaf area (cm^2)	*	*		*	*	
Leaf mass per area (LMA; $g\ m^{-2}$)	*		*	*		*
Mass-based photosynthesis ($nmol\ g^{-1}\ s^{-1}$)				*	*	
Transpiration ($mmol\ m^{-2}\ s^{-1}$)		*		*	*	*
Stomatal conductance (g_s; $mol\ m^{-2}\ s^{-1}$)		*		*	*	
Intrinsic water use efficiency (iWUE; $\mu mol\ mol^{-1}$)				*	*	
g_s versus vapor pressure deficit ($\ln mol\ m^{-2}\ s^{-1}\ \ln kPa^{-1}$)		*				
Δ Leaf mass per area versus DOY			*		*	
Δ Mass based photosynthesis versus DOY						
Δ Stomatal conductance (g_s) versus DOY	*			*		
Δ iWUE versus DOY	*					

* signifies significant differences between sites, species (cherrybark vs. willow oak), planting stocks [bareroot (BR), conventional container (CC) and large container (LC)] and species/planting stock interaction at $\alpha < 0.05$

container seedlings which did not differ significantly from one another (Table 2). Across all seedlings, leaves were larger at the Clearcut site compared to the Pasture site (17.2 vs. 14.7 cm^2 respectively; Table 2). Despite differences in leaf size, both species maintained similar leaf mass per unit area (LMA; Tables 1, 2) averaged across all planting stocks. Averaged across individuals, the Pasture site had significantly lower LMA values compared to the Clearcut site (83.7 vs. 88.5 g m^{-2} respectively). For both cherrybark and willow oak, bareroot stocks had significantly lower LMA compared to either conventional or large container stocks (Tables 1, 2). For cherrybark oak, conventional container seedlings had the largest LMA while large container seedlings had the largest LMA in willow oak (Table 1).

Mass-based photosynthesis differed significantly across planting stocks (Table 2) with large container seedlings having about 50 and 38% higher rates than either bareroot or conventional container seedlings respectively (Table 1). In terms of transpiration rates, willow oak had higher rates compared to cherrybark oak (Table 2) and large container seedlings had lower rates than either bareroot or conventional container seedlings which tended to be similar to one another (Table 2). Results were similar for stomatal conductance with large container seedlings having about 24 and 30% lower conductances compared to bareroot and conventional container seedlings respectively (Table 1). Across planting stocks, willow oaks had significantly lower stomatal conductances compared to cherrybark oaks (Table 2). Intrinsic water use efficiency (photosynthesis/stomatal conductance) was about 70% higher in large container seedlings compared to bareroot and conventional container stocks with did not differ significantly (Table 1). For the relationship between stomatal conductance and the natural log of vapor pressure deficit (g_s vs. vapor pressure deficit), cherrybark oaks had significantly more negative slope terms compared to willow oaks, but planting stocks did not differ significantly (Tables 1, 2).

In determining how anatomical and physiological leaf parameters changed throughout the growing season, we found that LMA increased significantly in all seedlings except conventional container cherrybark oak ($r^2=0.04$, $p=0.42$; Fig. 2a, b). For cherrybark oak, large container seedlings exhibited the largest increase in LMA over the growing season ($r^2=0.64$, $p<0.0001$), followed by bareroot seedlings ($r^2=0.74$; $p<0.0001$; Fig. 2a). For willow oaks, large container seedlings exhibited the largest increase in LMA ($r^2=0.69$, $p<0.0001$), followed by bareroot seedlings ($r^2=0.70$, $p<0.0001$) and conventional container seedlings exhibited the smallest increases in LMA throughout the growing season ($r^2=0.41$, $p=0.004$; Fig. 2b). Species did not differ significantly in their overall changes in LMA across the growing season (Δ LMA vs. DOY), however conventional container seedlings of both species displayed the lowest changes in LMA across the growing season that were about 63% lower than bareroot seedlings and about 75% lower than large container seedlings (Tables 1, 2).

For mass-based photosynthesis, all cherrybark oak seedlings exhibited significant declines throughout the growing season with large container seedlings ($r^2=0.25$, $p=0.005$) exhibiting the greatest declines, followed by conventional container ($r^2=0.25$, $p=0.005$) and bareroot seedlings ($r^2=0.70$, $p<0.0001$; Fig. 2c). For willow oak, only bareroot seedlings ($r^2=0.17$, $p=0.02$) exhibited decreasing mass-based photosynthesis throughout the growing season and relationships were not significant for conventional container ($r^2=0.03$, $p=0.37$) or large container ($r^2=0.10$, $p=0.09$) seedlings (Fig. 2d). Neither species nor planting stocks exhibited significant differences in changes in mass-based photosynthesis throughout the growing season (Δ Photosynthesis vs. DOY; Table 2).

Stomatal conductance tended to increase throughout the growing season for willow oak but not cherrybark oak (Fig. 2e, f). For cherrybark oak, only bareroot seedlings displayed significant increases in area-based stomatal conductance across the

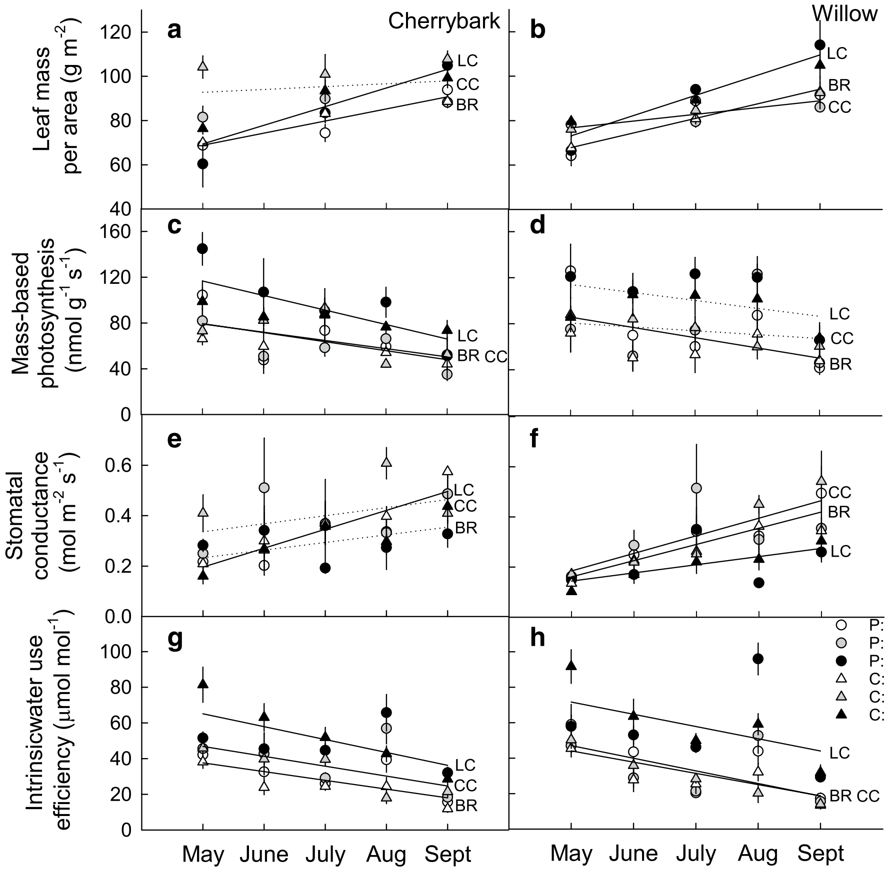

Fig. 2 Leaf-level parameters over the course of the growing season for cherrybark oak (left panels) and willow oak (right panels) including **a**, **b** leaf mass per unit area (LMA; g m^{-2}; mean and SE), **c**, **d** photosynthetic rates expressed on a per unit leaf mass basis (nmol g^{-1} s^{-1}), **e**, **f** stomatal conductance expressed on a per unit leaf area basis (mol m^{-2} s^{-1}; mean and SE), and **g**, **h** intrinsic water use efficiency (iWUE; μmol mol^{-1}). Pasture (P) site—circles, Clearcut (C) site—triangles, bareroot (BR)—open symbols, conventional container (CC)—gray symbols, large container (LC)—filled symbols. Lines are fitted for each container type (see labels) with sites averaged. Lines with slope terms that differ significantly from zero ($p < 0.05$) are solid, non significant slopes are dotted

growing season ($r^2 = 0.43$, $p < 0.0001$), whereas relationships for conventional container ($r^2 = 0.10$, $p = 0.10$) and large container seedlings ($r^2 = 0.07$, $p = 0.14$) were not significant (Fig. 2e). For willow oaks, bareroot seedlings displayed the largest increases ($r^2 = 0.51$, $p < 0.0001$) followed by conventional container ($r^2 = 0.32$; $p = 0.001$) and large container seedlings ($r^2 = 0.19$, $p = 0.02$; Fig. 2f). For both species combined, bareroot seedlings had significantly higher increases in stomatal conductance throughout the growing season (i.e. Δ Stomatal conductance vs. DOY) compared to large container seedlings (Tables 1, 2) and across all seedlings, individuals at the Clearcut site had higher increases in area-based stomatal conductance compared to individuals at the Pasture site (2.0 vs. 1.3 mmol m^{-2} s^{-1} day^{-1}; Tables 1, 2). For all species and planting stocks, intrinsic water use efficiency decreased throughout the growing season (Fig. 2g, h). For cherrybark oak, the rate of decrease (Δ iWUE vs. DOY) was similar (Table 2) across planting stocks for bareroot ($r^2 = 0.31$, $p = 0.001$), conventional container ($r^2 = 0.25$, $p = 0.004$), and large container seedlings ($r^2 = 0.31$, $p = 0.001$; Fig. 2g). Likewise for willow oaks, planting stocks did not differ from one another (Table 2) and rates of decrease in intrinsic water use efficiencies were significant in bareroot ($r^2 = 0.36$, $p = 0.0005$), conventional container ($r^2 = 0.31$, $p = 0.0013$), and large container seedlings ($r^2 = 0.17$, $p = 0.02$; Fig. 2h). For all seedling types combined, intrinsic water use efficiency decreased at a faster rate at the Clearcut site compared to the Pasture site (− 0.28 vs. − 0.17 μmol mol^{-1} day^{-1} respectively, Tables 1, 2).

Across all individuals, diameter growth in year one was correlated with more physiological parameters than height growth. Year one diameter growth was significantly correlated with all gas exchange parameters including intrinsic water use efficiency ($r^2 = 0.28$), photosynthetic rates ($r^2 = 0.22$), stomatal conductance ($r^2 = 0.19$), transpiration ($r^2 = 0.11$), as well as the relationship between stomatal conductance and vapor pressure deficit ($r^2 = 0.08$; Table 3). Diameter growth was also slightly correlated with changes in LMA and intrinsic water use efficiency across the growing season (Δ parameter vs. DOY). Year one height growth was only significantly correlated, although weakly, with the individual cross-sectional area of leaves ($r^2 = 0.15$) and the relationship between stomatal conductance and vapor pressure deficit ($r^2 = 0.04$; Table 3). Year one height growth was significantly correlated with year one diameter growth ($p = 0.02$; $r^2 = 0.08$, data not shown). In terms of the correlation between physiological parameters measured in year one with growth measured in year two, diameter growth again correlated with more parameters than height growth. Both year two diameter and height growth were significantly correlated with LMA ($r^2 = 0.08$ and 0.14 respectively) in the first growing season (Table 3). In addition, year two diameter growth was significantly correlated with changes in intrinsic water use efficiency ($r^2 = 0.07$), stomatal conductance ($r^2 = 0.05$), and LMA ($r^2 = 0.02$) throughout the first growing season (Δ parameter vs. DOY) albeit with lower r^2 values than the prior growing season (Table 3). Neither year one height growth nor diameter growth were significantly correlated with year two diameter growth ($p = 0.95$ and 0.23 respectively, data not shown).

Table 3 Significance of linear regression relationships between growth (height and ground line diameter (GLD)) as response variables and physiological and morphological parameters as explanatory variables

	Year one		Year two	
Parameter	GLD growth	Height growth	GLD growth	Height growth
Individual leaf area		***		
Leaf mass per area (LMA)			**	***
Photosynthesis	***			
Transpiration	***			
Stomatal conductance (g_s)	***			
g_s versus vapor pressure deficit	**	**		
Intrinsic water use efficiency	***		*	
Δ g_S versus DOY			**	*
Δ LMA versus DOY	*		***	
Δ iWUE versus DOY	*		**	

*Signifies $0.05 < p < 0.1$, ** signifies $0.01 < p < 0.05$, *** signifies $p < 0.01$. Δ = change in parameter across the growing season where DOY = day of year

Discussion

After two growing seasons, oaks in this study exhibited very modest growth with a total diameter growth averaging 1.5, 0.8 and 3.9 mm for bareroot, conventional container and large container seedlings across species. Height growth over 2 years averaged about 1 cm for cherrybark oaks across planting stocks and −8, −3.5 and −7 cm for bareroot, conventional container and large container willow oaks respectively. Negative height growth particularly for willow oaks, was due primarily to dieback in bareroot and conventional container seedlings and stem damage/breakage for large container seedlings. Dey et al. (2006) found that large container pin oak and swamp white oak exhibited negative height growth due to rabbit herbivory and, since they were initially taller, their height losses were greater than bareroot seedlings. In terms of dieback, Jacobs et al. (2012) found that seedling height/diameter ratios for cherrybark oak of 99 were optimal and seedlings with higher ratios were more prone to dieback and mortality. For cherrybark oak seedlings in this study, height/diameter ratios were 131, 80 and 129 respectively for bareroot, conventional and large container stocks and this higher ratio may have contributed to dieback particularly for bareroot seedlings. Willow oaks exhibited height/diameter ratios of 139, 102 and 135 respectively for bareroot, conventional and large container stocks upon planting and exhibited more extensive dieback suggesting they may require an even lower height/diameter ratio than cherrybark oak and are potentially more prone to dieback than other oak species (Day III et al. 1997).

For similar sites and planting stocks, 2 year diameter growth was between 4 and 4.5 mm for Nuttall and Shumard oak (Hall 2017) and between 6.5 and 8 mm for Shumard and swamp chestnut oak (Durbin 2018). These seedlings also ranged from 9 to almost 19 cm in 2 year height growth. The generally lower growth rates seen in seedlings in this study are surprising given that the first growing season exhibited much above average precipitation and the second growing season exhibited average precipitation for the region. However, Abrams (1996) provides evidence that oaks, as a genus, tend to be stress tolerators and can outcompete other species during stressful conditions by relying on their larger, deeper roots and stored belowground carbon. On the other hand, under optimal conditions including above average precipitation, oaks may be at a disadvantage when competing with fast growth species such as grasses. Indeed the Pasture site contained more herbaceous competition from grasses and exhibited lower growth rates than the Clearcut site in this study which exhibited less competition from primarily woody species.

There were large differences in survival for planting stocks in this study particularly for conventional container seedlings which exhibited significantly lower survival that would be considered undesirable compared to bareroot and large container seedlings. Conventional container seedlings exhibited large mortality in the beginning of the first growing season (Apr–June) which indicates a lack of initial establishment. They also did not exhibit the degree of increase in leaf mass per unit area during the first growing season seen in bareroot and large container seedlings which is similar to findings of Howell and Harrington (2004) for cherrybark oak and suggests a lack of acclimation to site conditions. Other studies comparing oaks across these planting stocks also found that survival was lower for conventional container seedlings compared to bareroot and large container seedlings (Hollis et al. 2012; Renninger et al. 2018). However, other studies comparing these planting stocks found that conventional container seedlings performed similarly in terms of survival (Conrad III et al. 2015) with other planting stocks or that either large container(Durbin 2018) or bareroot seedlings (Dey et al. 2006; Self et al. 2010) performed poorly in terms of survival.

Although root systems of container seedlings remain more intact during outplanting and the root plug can provide buffering from nutrient and moisture stress, Grossnickle and El-Kassaby (2016) found that bareroot seedlings many times have larger initial shoot systems compared with smaller container seedlings which may confer greater aboveground competitive ability compared with surrounding vegetation. Additionally, nursery practices may have led to differences in survival between planting stocks which were not the focus of this study.

In terms of physiology, large container seedlings exhibited greater photosynthetic rates and lower transpiration and stomatal conductance than bareroot or conventional container seedlings which led to higher water use efficiencies even though they received no herbaceous weed control. The larger photosynthetic rates in large container seedlings partially explain the greater first year diameter growth compared to bareroot and conventional container trees, although the extent of the growth differences likely mean that more stored carbon in large container seedlings was used for growth as well. Additionally, the nutrients in the container media of potted seedlings may have contributed to the greater photosynthetic rates and greater growth, at least initially. The differences in stomatal conductance and water use efficiency between planting stocks are similar to findings for Nuttall and Shumard oak (Renninger et al. 2018), but differ slightly from findings of Crunkilton et al. (1992) in which container northern red oak had higher stomatal conductance but similar photosynthesis and transpiration rates as bareroot seedlings although leaf area was higher for bareroot seedlings. Jacobs et al. (2009) found that large root volumes did not aid northern red oak seedlings in avoiding water stress conditions. Large container seedlings likely have more total leaf area than bareroot and conventional container seedlings and compensate for larger evaporative losses by the entire crown with higher water use efficiency at the individual leaf level (Renninger et al. 2014).

We saw significant differences in growth and survival between the Clearcut and the Pasture site likely due to differences in competition between the two sites. Competition at the Clearcut site included primarily woody tree seedlings, shrubs and vines that were lower in density than the Pasture site. The Pasture site contained cogongrass which was not controlled by the herbicide application and covered approximately 90% of the site by June of each growing season. All species/planting stock combinations exhibited negative first year height growth at the Pasture site, whereas only bareroot willow oak and conventional container planting stocks exhibited negative first year height growth at the Clearcut site. The Clearcut site exhibited higher first year mortality and this was primarily driven by the larger mortality rates in conventional container stocks and bareroot willow oak. Year two diameter growth was also lower in every species/planting stock combination at the Pasture site compared to the Clearcut site. Both height and diameter growth of red oak (*Q. rubra* L.) seedlings planted in Quebec, Canada were lower when planted in an abandoned agricultural field compared to a clearcut regardless of herbicide application (Truax et al. 1994) and lower than other planted hardwood and conifer species in the presence of herbaceous competition (St-Denis et al. 2018). In addition, *Quercus rubra* seedlings performed better in pine clearcut and shelterwood sites than in open field sites (Lesko and Jacobs 2018). For our study, seedlings at the Pasture site also exhibited lower increases in stomatal conductance across the growing season compared to seedlings at the Clearcut site suggesting they faced greater water stress due to increased belowground competition. Crunkilton et al. (1992) found that northern red oak seedlings in a clearcut had higher predawn and midday leaf water potentials than seedlings planted in a shelterwood system likely due to reduced competition for water. It is surprising that seedlings in our study faced water stress conditions given the high precipitation during the growing season. Studies of bareroot and container planting stocks of Nuttall and Shumard oak (Hall 2017) in Gulf Coastal Mississippi during drier conditions also faced competition from similar grass species as this study but exhibited higher height and diameter growth than seedlings in our study. This either suggests that Nuttall and Shumard oak were better able to compete for water and/or that increased rainfall helped the competing grasses in our study site to a greater extent than the oak seedlings.

The two oak species tested differed significantly in several parameters including first year height growth in which willow oaks exhibited net dieback across all planting stocks to a much greater extent than cherrybark oak seedlings. Both sites were located on sandy loam soils that may favor cherrybark oak which prefers drier, well drained sites (Gardiner and Hodges 1998). Willow oaks also exhibited higher transpiration rates than cherrybark oaks, particularly for bareroot and conventional container planting stocks. At the same time cherrybark oaks had higher stomatal conductances than willow oaks which were likely due to the larger boundary layer conductances of the smaller willow oak leaves. Stomatal conductance of cherrybark oak also decreased to a greater extent with increases in vapor pressure deficit suggesting willow oak maintained stomatal conductance at high atmospheric demand. However these data, coupled with the dieback seen in willow oak suggest that these oaks have differing strategies for dealing with moisture stress. Cherrybark oak appears to be more conservative in terms of regulating stomata at high vapor pressure deficit to limit transpiration rates from individual leaves. Conversely, willow oak exhibits less control over individual leaf physiology but limits water losses on a whole crown basis through branch loss and dieback to decrease total leaf area. These differences in drought strategy between cherrybark and willow oak correspond to the preferred growing locations with willow oak preferring wetter bottomland flats and cherrybark oak preferring drier bottomland ridges and terraces (Hodges 1997).

Across species and planting stocks, changes in physiological and morphological parameters occurred throughout the first growing season. Leaf mass per area increased by as much as 40% from May to September particularly in bareroot and large container planting stocks. Other studies found seasonal increases in LMA in blue oak (*Q. douglasii* Hook. & Arn.) (Xu and Baldocchi 2003) and in sessile oak (*Q. petraea* [Matt.] Liebl.) and pedunculate oak (*Q. robur* L.) (Thomas and Gausling 2000) primarily as a response to drought conditions (Niinemets 2001). Since photosynthesis on a per unit area basis remained constant throughout the growing season in most planting stocks (data not shown), mass-based photosynthesis declined across the growing season particularly for cherrybark oak. Decreased photosynthetic rates with increased LMA may be the result of increased diffusional resistance for CO_2 due to higher leaf tissue densities (Niinemets 2001) and/or self-shading of chloroplasts (Reich et al. 1999). Stomatal conductance increased across the growing season, particularly in willow oaks. This result is contrary to other studies that found decreases in stomatal conductance and increases in water use efficiency throughout the growing season in oaks (Matzner et al. 2003; Siam et al. 2009; Xu and Baldocchi 2003) due to increased drought stress. In all planting stocks, intrinsic water use efficiency decreased throughout the growing season, despite the increased competition from herbaceous vegetation and increased temperatures and vapor pressure deficits across the growing season. Similar findings of increases in stomatal conductance and decreases in intrinsic water use efficiency were also observed for Nuttall oak and shumard oak seedlings planted on the Gulf Coast (Renninger et al. 2018) despite lower summer rainfall than our current study. However, while Renninger et al. (2018) found that year one physiological parameters were strong predictors of year two height growth ($r^2 = 0.23$–0.44), the present study found better correlation between current year physiological parameters and diameter growth. Leaf mass per area was a good predictor of year two growth and was more significantly correlated than either year one height or diameter growth which were not significantly correlated with year two growth. Therefore, effects of competition in the present study may have confounded the relationships between physiological functioning and aboveground growth.

Overall, this study highlights the importance of considering prior site conditions and competition from herbaceous vegetation, particularly grasses, in determining the best planting options for oaks and competition control. We also found that above average rainfall in the first growing season did not benefit oaks in terms of growth or physiological functioning. Therefore, additional site preparation and herbicide application may be necessary during above average rainfall and/or if afforesting a prior grassland to increase initial growth rates although survival remained high for both bareroot and large container oaks after 2 years at the Pasture site. Conventional container oaks exhibited suboptimal survival for both species at both sites, but may be an option if site conditions like flooding limit access until late in the planting season (Williams and Stroupe 2002). Large container planting stocks exhibited the largest diameter growth and had the highest photosynthetic rates and water use efficiencies suggesting they are a good option for smaller plantings given their cost. Bareroot seedlings maintained adequate survival and their physiological functioning compared well with large container planting stocks suggesting that they will continue to establish and are a good option for large plantings due to their lower cost per seedling. On these sandy loam sites with herbaceous competition, cherrybark oak performed better than willow oak in terms of height growth and survival of bareroot seedlings likely due to its stronger stomatal regulation during water stress conditions. In terms of seasonal physiology, these Southern bottomland oak species exhibited similar seasonal changes as other oaks in terms of increasing LMA, however differed in terms of increasing stomatal conductance and decreasing water use efficiency across the growing season suggesting different strategies within the oak genus. In total, these findings will aid in projects aimed at afforestation and reforestation of oaks on the US Gulf Coastal Plain.

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