OAK AND PINE PHYSIOLOGICAL RESPONSES TO RESOURCE AVAILABILITY

A Dissertation

by

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ABSTRACT

Large-scale drought and fire events result in extensive mortality and shifts in species' ranges. More research on responses to resource limitations is needed to predict species' success following record disturbance events and in the face of predicted increases in weather-related extremes. Therefore, the effects of resource availability were evaluated on 1) gas exchange and carbon allocation of three oak (*Quercus*) species in a controlled precipitation restriction experiment in College Station, TX, USA, and 2) loblolly pine (*Pinus taeda* L.) and oak recovery following the 2011 Bastrop County Complex Fire (BCCF), Bastrop, TX, USA.

Bur (*Quercus macrocarpa* Michx.; QUMA), Shumard (*Q. shumardii* Buckley; QUSH), and live oak (*Q. virginiana* Mill.; QUVI) saplings were subjected to two watering treatments: 1) watered, which received the equivalent of average weekly precipitation and 2) droughted, in which precipitation was reduced by 100%. Watered saplings displayed greater height increases, leaf water potential, and gas exchange rates than droughted saplings. Species differed in gas exchange rates and carbon allocation patterns. Live oak was the most drought tolerant, exhibiting 57% greater photosynthesis rates than QUSH and QUVI. Physiological changes associated with senescence and winter preparation affected foliar carbohydrate and phenolic content to a greater extent than water availability.

Following the BCCF, differences in vegetation anatomy, physiology, and age were found to affect stand recovery and resource use. Regenerating pines were shorter and less dense in severely burned than moderately burned plots. Gas exchange and pressure-volume results suggested loblolly pine seedlings preferred drought-avoidance strategies while resprouting oaks exhibited greater drought tolerance. Mature pines had greater sap flux rates (J_s) than oaks, but resprouting oaks had greater J_s on average than the regenerating pines due to declines in pine seedling J_s with reductions in shallow soil moisture. Transpiration was greatest at the moderately burned stand (2.08 mm day^{-1}), intermediate at the unburned stand (1.48 mm day^{-1}), and least for the severely burned stand (0.46 mm day^{-1}). Results suggest light to moderate burns may enhance stand transpiration through competition release and increased irradiance, while severe fires reduce stand transpiration through reductions in vegetation density in the first five years after fire.

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Natural disturbances are a regular part of ecosystem function, but extreme events are becoming more common (Easterling et al. 2000). An increase in the intensity and duration of drought events along with rising global temperatures and decreased precipitation is likely to result in species' range shifts and large-scale mortality events (Adams et al. 2009, Breshears et al. 2005). According to Manion's (1991) decline spiral model, drought may act as inciting factor that ultimately leads to mortality in trees that are already stressed by a predisposing factor such as poor edaphic condition or old age. Drought-induced tree mortality is an intricate process contingent on several interrelated mechanisms, and has been a hot topic in recent literature (McDowell et al. 2008, Van Mantgem et al. 2009, Breshears et al. 2009, Allen et al. 2010, Wang et al. 2012, Anderegg et al. 2016). McDowell et al. (2008) suggested hydraulic failure, carbon starvation, or a combination of the two, may be major drivers of drought-induced fatality. They hypothesized that hydraulic failure would occur during high intensity drought when the inadequate control of water loss results in embolism and irreversible desiccation. Carbon starvation, on the other hand, was thought be the cause of mortality during prolonged drought. Although these hypotheses have gained support, a lack of necessary evidence to rule out alternative explanations may be unwise (see Sala et al. 2010 and references within). It is important to note as well that the two hypotheses are not mutually exclusive and likely interact to drive mortality (McDowell et al. 2011, Anderegg et al. 2012). Allen et al. (2010) postulated a third mechanism that may prompt drought-induced mortality— cellular metabolism limitation. Allen et al. (2010) suggested low tissue water potentials might limit cell metabolism and prevent production and movement of carbohydrates and plant secondary compounds needed to defend against biotic attack.

Climate-induced tree mortality has been occurring in mesic regions as well as in semi-arid areas, suggesting a rise in temperature may be a greater driver than reductions in precipitation (Van Mantgem et al. 2009, Williams et al. 2013). Increases in temperature and VPD may result in prolonged stomatal closure in isohydric species which may amplify carbohydrate limitations (Breshears et al. 2009). Alternatively, greater evaporative demand may increase transpiration and risk of hydraulic failure in anisohydric species (Allen et al. 2010, Breshears et al. 2013). Extended warm temperatures increase parasite and pathogen populations (Bentz et al. 2010, Dukes et al. 2009), and weakened trees with a limited carbohydrate supply or multiple embolisms might succumb ultimately to these biotic agents (Desprez-Loustau et al. 2006).

A warmer, drier climate has resulted in increasing annual fire season length, fire frequency and size, and overall burned area in North American forests (Flannigan et al. 2005, Miller et al. 2009). Droughts and fire are intimately related. Droughted trees are more vulnerable to mortality from secondary causes, and fuel is drier and more abundant due to drought-related leaf and limb loss (Brando et al. 2014). Increases in large standing dead fuel loads as a result of fire suppression over the past century have led to greater fire size and severity as well (Pollet and Omi 2002, Miller et al. 2009). Forest fires alter resource availability through the consumption of vegetative cover, litter, and soil organic matter which can contribute to soil erosion and changes in the soil moisture regime (Kanarek 2013, Brown et al. 2014). Vegetation loss coupled with decreases in stand transpiration can augment soil moisture and watershed discharge and raise the groundwater table (Kanarek 2013, Boggs et al. 2015). An increase in light reaching the soil surface in conjunction with greater soil moisture is likely to promote regrowth. However, greater radiation levels reaching the forest floor will also result in greater soil temperatures that can actually inhibit regrowth and seedling establishment. For example, loblolly pine (*Pinus taeda* L.) root growth decreased at temperatures greater than 25ºC in a study by Barney (1951).

Disturbances, such as droughts and wildfires, and the associated changes to resource availability can have differing effects among genera, species within the same genus, and individuals in different maturity states within the same species (Cavender-Bares and Bazzaz 2000, Gracia et al. 2002, Johnstone and Kasischke 2005, Renninger et al. 2014, Moore et al. 2016). For example, droughts in the southwestern USA in recent decades have been much more detrimental to pinyon pine (*Pinus edulis* Engelm.) than one-seed juniper (*Juniperus monosperma* (Engelm.) Sarg.). Pinyon pine mortality was 6.5 times greater than juniper mortality in a study by Mueller et al. (2005). Additionally, larger pinyon pines (> 10 cm) experienced at least twice the mortality than small pinyon pines (Mueller et al. 2005). Following the drought of 2011, the driest year on record for the state of Texas (Hoerling et al. 2013), Moore et al. (2016) found a greater proportion (70%) of dead angiosperms than gymnosperms (30%) in their plots across the state. The drought also affected larger trees to a greater degree than smaller trees. Dead gymnosperms were on average 19% larger than live gymnosperms, and dead angiosperms were 17% larger than live angiosperms on average.

Forest fires also often favor the recovery of one species over another, with species displaying resprouting, serotinous cones, and/or prolific seeding characteristics typically experiencing greater success (Brose and Van Lear 1998, Outcalt 2000, Barton 2002, Rodrigo et al. 2004, Pausas et al. 2004, Ilisson and Chen 2009). However, reductions in fire frequency and an overall suppression of fire in general, have resulted in the replacement of open, park-like expanses of fire-tolerant species by closed-canopy forests characterized by shade-tolerant, fire-sensitive species (Nowacki and Abrams 2008). Although leaves and litter from fire-sensitive species are less flammable (Kreve et al. 2013), the increased density associated with fire suppression in such areas may result in fires that are more severe with greater mortality.

One major reason for the different responses among species in relation to disturbance and resource availability is inherent differences in species' anatomy, and subsequently physiology. Oaks (*Quercus* spp.) vary in distribution relative to water and nutrient availability, but many are well adapted to xeric, nutrient poor sites (Bahari et al. 1985, Abrams 1990, Johnson et al. 2009). Oaks are among the most deeply rooting species in the world (Davis and Pase 1977, Hinckley et al. 1981, Abrams 1996) which helps them maintain high water potentials and gas exchange rates during drought (Kolb and Stone 2000, Querejeta et al. 2007). Oaks are characterized by ring-porous sapwood. They have wide diameter vessels in early-wood and more dispersed, narrow vessels in late-wood (Abrams 1990, Steppe and Lemeur 2007, Taneda and Sperry 2008). The larger diameter early-wood vessels are able to move sap quickly, but are more prone to cavitation (Tyree and Dixon 1986, Cochard and Tyree 1990). Water movement will continue through the narrow late-wood vessels when the larger vessels cavitate (Granier et al. 1994). This anatomy allows rapid transpiration with high water availability, and sustained, although reduced, transpiration during drought (Abrams 1990). Oaks frequently have low osmotic potential at full turgor (Π_{FT}) and at the turgor loss point (Π_{TLP}), relative water content at the turgor loss point (RWC_{TLP}), and high capacitance at full turgor (C_{FT}) and bulk elastic modulus (ε) (Parker et al. 1982, Bahari et al. 1985, Aranda et al. 1996), which are thought to further signify drought tolerance (Tyree and Hammel 1972, Schulte and Hinckley 1985, Bartlett et al. 2012).

Similar to oaks, pines (*Pinus* spp.) cover a wide range globally and many species are known for their stress tolerance (Kolb and Robberecht 1996, Hacke et al. 2000, Cregg and Zhang 2001). Many pine species are deep rooted as well, with some reaching depths over 7 m (Canadell et al. 1996). Deep rooting may help some species maintain relatively stable water potentials during dry periods (Gyenge et al. 2003). However, pines and other gymnosperms are frequently cited as maintaining water status by using drought avoidance strategies like reducing gas exchange when water availability decreases (McDowell et al. 2008, McCulloh et al. 2010, Choat et al. 2012). In studies comparing oaks and pines, pines were more sensitive to vapor pressure deficits and decreases in soil moisture (Kolb and Stone 2000, Stoy et al. 2006, Ford et al. 2010, Meinzer et al. 2013, Renninger et al. 2015), and had lower leaf-level gas exchange rates

(Kolb and Stone 2000). Active sapwood makes up a greater portion of the cross-section of non-porous species like pines compared to ring-porous species such as oaks (Phillips et al. 1996, Cermak and Nadezhdina 1998). These larger sapwood areas and year-round gas exchange lead to greater annual water use in pines than co-occurring deciduous species (Ford et al. 2010, Renninger et al. 2015), even if they are more conservative with water use on a leaf-level basis.

Variations in structure, growth strategies, and leaf habits within species in the same genus may result in large differences in success after resource alteration. The *Quercus* genus, for example, encompasses species that exhibit a wide variety of anatomical and physiological characteristics (Cavender-Bares et al. 2004). The two primary groups of *Quercus* found in North America, red oaks (section *Lobatae*) and white oaks (section *Quercus*), have distinct ecology, habitat preferences, and wood anatomy (Abrams 1990). During drought events, red oak species exhibited lower drought avoidance and tolerance, mean net photosynthesis, leaf conductance, and leaf water potential than white oak species (Kleiner et al. 1992, Seidel 1972). Within the red and white oak groups, drought response between species may differ greatly as well. In a study by Ashton and Berlyn (1994), black oak (*Quercus velutina* Lam.) had the greatest stomatal response plasticity and lowest stomatal density while another member of the red oak group, northern red oak (*Quercus rubra* L.), had the lowest response plasticity and a high stomatal density. Such differences likely contribute to the restriction of drought-prone northern red oak to mesic sites (Ashton and Berlyn 1994). The white oak group includes some unique semi-evergreen species (e.g. *Q. virginiana* Mill., *Q. ilex* L., and *Q. geminata* Small) that maintain leaves much longer and are reported to have greater transpiration and leaf specific conductivity than deciduous oak species (Cavender-Bares and Holbrook 2001).

Different responses between species to disturbance and changes in resource availability may shift species composition at disturbed sites (Johnstone and Kasischke 2005, Moser et al. 2010). Within the state of Texas alone, we have experienced two record disturbance events in the last few years, the 2011 drought and the Bastrop County Complex Fire of 2011, the most destructive fire on record in Texas' history (Rissel and Ridenour 2013). More than 12950 ha and 1.8 million trees were burned in this fire (Rissel and Ridenour 2013). Many areas experienced subsequent erosion and topsoil loss. Nutrient loss was observed with decreases in pond pH and dissolved oxygen content (Brown et al. 2014). Visual evidence of increased soil moisture in the burned areas includes new seeps and wetter lowlands. Cardenas and Kanarek (2014) confirmed this by finding greater near-surface soil moisture in heavily burned areas of Bastrop State Park, where the majority of trees were killed, and lower near-surface soil moisture in areas that experienced low-severity burns and were still populated with pine trees.

In the wake of these events, we recognize that more research on responses to resource limitations is necessary to predict species' success following these incidents and in the face of increased weather-related extremes such as droughts and wildfires in the future. Therefore, the aim of Chapter II was to examine tradeoffs between different drought stress responses of Shumard oak (*Quercus shumardii* Buckley), bur oak (*Quercus macrocarpa* Michx.), and live oak (*Quercus virginiana* Mill.) in a controlled precipitation restriction experiment under rain-out shelters in College Station, TX, USA. Hypotheses included: 1) leaf-level gas exchange of droughted saplings would gradually decrease across the growing season with decreases in predawn leaf water potentials and soil moisture depletion (Galvez et al. 2011). 2) The three species would differ in their responses to water availability, with drought affecting the more mesic Shumard oak the most (Seidel 1972, Kleiner et al. 1992) and more xeric live oak the least (Bendevis et al. 2010). 3) Soluble sugar, non-soluble sugar, and condensed tannin concentrations would vary with degree of water stress during drought. They would likely increase in the early stages of drought as the consumption of carbohydrates for growth declines (Anuraga et al. 1993, Würth et al. 2005, Ayub et al. 2011). However, after months of drought, limited carbon reserves will likely result in decreased concentrations of soluble sugar, starch, and CT (Gutbrodt et al. 2011, McDowell 2011). 4) Saplings recovering from the previous year's drought will have gas exchange similar to that of their watered counterparts, since gas exchange rates have increased rather quickly following returns to favorable precipitation conditions in other studies (Owens and Schreiber 1992, Loik et al. 2007, Duan et al. 2013).

Chapters III and IV focused on pine and oak recovery following the 2011 wildfire in Bastrop State Park, Bastrop, TX, USA. The primary goal in Chapter III was to evaluate how ecological biotic and abiotic legacies might affect the recovery of regenerating loblolly pine seedlings. The primary hypothesis tested was that resprouting oaks would have a greater advantage initially over pine seedlings in areas with greater resource limitations. Resprouts have the advantage of utilizing remaining deep root systems from mature top-killed trees, which will help them withstand drought and support rapid growth rates through the mobilization of carbohydrates from decaying root tissue (DeSouza et al. 1986, Castell et al. 1994). Shallow-rooted regenerating pine seedlings may not be competitive with these deep-rooted resprouts for water and nutrients. Secondly, post oak (*Quercus stellata* Wangenh.) was hypothesized to be a better competitor than blackjack oak (*Quercus marilandica* Muenchh.), as a potential indicator of species dominance over time. White oak species, such as post oak, are more tolerant to drought stress than red oak species, such as blackjack oak (Seidel 1972, Abrams et al. 1990, Kleiner et al. 1992, Vivin et al. 1993), although exceptions have been reported (Wuenscher and Kozlowski 1971, Bahari et al. 1985).

The aim of the study described in Chapter IV was to determine how burn severity affected transpiration through alterations in stand structure and age in mixed pine/oak stands following the Bastrop County Complex Fire. The first hypothesis was that pines would have higher *Js* than oaks (Phillips et al. 1996, Ford et al. 2010, Renninger et al. 2015), which coupled with their large sapwood area (Cermak and Nadezhdina 1998), would result in greater transpiration in stands containing a greater number of pines. Resprouting oaks and young pines were hypothesized to have greater daily sap flux per unit sapwood than mature individuals of the same species (Yoder et al. 1994, Castell et al. 1994, Kolb and Stone 2000, Utsumi et al. 2010). The final hypothesis was that stand level transpiration would decrease in sites with greater burn severities due to reductions in vegetation density and total sapwood area (Gharun et al. 2013, Nolan et al. 2014).

CHAPTER II

PHYSIOLOGICAL RESPONSES TO PROLONGED DROUGHT DIFFER AMONG THREE OAK (QUERCUS) SPECIES

Synopsis

Plant physiological responses to water stress provide insights into which species may survive exceptional drought conditions. This study examined how drought affected the physiology of three oak species: bur oak (*Quercus macrocarpa* Michx.; QUMA), Shumard oak (*Quercus shumardii* Buckley; QUSH), and live oak (*Quercus virginiana* Mill.; QUVI). In June 2014, following a period of equal watering, three-year old saplings were subjected to two watering treatments: 1) watered (W), which received the equivalent of average weekly precipitation and 2) droughted (D), in which precipitation was reduced by 100%. Changes in growth, leaf water potential, gas exchange, and foliar biochemistry (soluble and non-soluble sugar, phenolic, and N content) were monitored across the growing season (June – October 2014). From 11 August– 14 September, I implemented a month-long short-term drought in W plots to observe recovery responses following re-watering. Stress responses were evident after only one month of induced drought. Watered saplings displayed 124% greater height increases, 48 and 21% greater pre-dawn and midday leaf water potential, respectively, and 39% greater photosynthesis rates in comparison to D saplings. Live oak exhibited 57% greater photosynthesis rates on average but similar leaf water potential to QUMA and QUSH. Droughted QUVI had gas exchange rates similar to those of W QUMA and QUSH, and W QUVI adjusted gas exchange rates most to changes in water availability during short-term drought. Species also differed in carbon allocation to carbohydrate and phenolic compounds. Soluble and non-soluble sugar contents were apt to follow changes in soil moisture and gas exchange and tended to be greater in W saplings (5 and 11% for SS and NSS, respectively). Phenolic contents were not affected by changes in water availability, suggesting control by other factors is more important. Decreases in sugar and phenolic contents in all individuals at the last measurement date imply physiological changes associated with senescence/winter preparation may trump differences in water availability at this time. Differences in species' physiological responses to drought may result in stand composition shifts in the face of future climate alterations.

Introduction

Although drought-induced plant mortality depends on complex interactions among many physiological parameters (i.e., leaf water potential, gas exchange, carbohydrate contents), few drought studies document concurrent measurements on multiple factors over time. Those that do often focus on a single species (Galvez et al. 2011, Duan et al. 2013) undergoing sustained drought without the periodic pulses of precipitation that so often offer short reprieves from dry conditions (Sala et al. 1982, Loik et al. 2007). Other studies focus on the linkage of soil water availability to multiple leaf level gas exchange parameters, but do not carry the relationship out further to see where accrued C is allocated which may be problematic when trying to assess tree health from a C storage view (Piper 2011).

The carbon starvation hypothesis (CSH) predicts that plant survival during drought is contingent on available stores of carbohydrates (McDowell et al. 2008). Carbon starvation is a valid mechanism capable of inducing mortality, but recent critics warn that prematurely accepting it as the most probable cause of drought-induced tree mortality in the absence of hydraulic failure or biotic agents, such as insects or pathogens, is unwise (Sala et al. 2010). Sala et al. (2010) cited a lack of direct evidence that trees exposed to drought, but not killed by other mechanisms, ended up dying of carbon starvation. Prior to drought-induced mortality, actual complete depletion of stored C reserves mortality has never been confirmed; severe depletion has been reported, but never a complete exhaustion (Guehl et al. 1993, Bréda et al. 2006, Arndt et al. 2008). Multiple studies described results that are compatible with McDowell et al.'s (2008) hypothesis, but did not provide necessary evidence to rule out alternative explanations (Marshall and Waring 1985, Guehl et al. 1993, Bréda et al. 2006, Adams et al. 2009). Water stress does not always lead to decreases in carbohydrate contents either (Muller et al. 2011, Piper 2011). Unchanged and increased levels of carbohydrates may occur, confirming further that identifying the ultimate cause of drought-induced mortality is complex. Additionally, Sala et al. (2010) pointed out that the CSH assumption that plants will continue to operate at optimal levels of C mobilization and translocation under drought is likely incorrect in most instances.

Drought-weakened trees are at greater risk of succumbing to insect attacks or disease outbreaks (Mattson and Haack 1987, Allen et al. 2010, Jactel et al. 2012). If foliar carbohydrate content and biochemistry shift during periods of drought, plant-herbivore interactions could shift as well, causing feedbacks between plant stress and vulnerability to herbivory. Multiple studies have examined relationships between drought and plant carbohydrate contents (Arndt et al. 2001, Bréda et al. 2006, McDowell et al. 2008, Sala et al. 2010, Adams et al. 2009, Adams et al. 2013) or drought and plant secondary compounds for defense (Peñuelas et al. 2004, Llusià et al. 2006, Tharayil et al. 2011), but few have monitored both foliar carbohydrate contents and secondary compounds in relation to drought (Pääkkönen et al. 1998). A variety of responses to drought have been reported for carbohydrate and secondary compound contents in tree and shrub species. Some studies have reported decreases in carbohydrate contents with drought (Bréda et al. 2006, Adams et al. 2013), while others have reported increases (Galvez et al. 2011, Muller et al. 2011, Piper 2011). Studies examining secondary defense compound production by trees have also found contradictory results, with some reporting increases in relation to drought (Hale et al. 2005, Tharayil et al. 2011) and others reporting decreases (Thomas and Schafellner 1999, Lavoir et al. 2009).

Condensed tannins (CT) are plant polyphenolic secondary compounds that may act as a defense against herbivory (Forkner et al. 2004). Condensed tannins are characterized by their astringency, high molecular weights, and ability to bind and precipitate proteins, warranting the moniker “protein-precipitable phenolics (PPP)” (Hagerman and Butler 1981). Condensed tannin consumption can result in reduced insect food consumption, growth, fecundity, and increased mortality (Klocke and Chan 1982, Grayer et al. 1992, Roberts and Olson 1999, Littlefield et al. 2011). Condensed tannins’ ability to bind with proteins can benefit ruminant wildlife and livestock by enhancing protein digestion and preventing bloat which can prove fatal (Min et al. 2003, Min et al. 2005). This improved protein efficiency would be especially helpful during times of drought when livestock and wildlife increase browse intake as little vegetative material is available from other sources (Holechek and Vavra 1983, Hall et al. 1992). High salivation rates and proline-rich salivary proteins increase condensed tannin tolerance of goats and other browsers. When such browsers consume plants with moderate levels of condensed tannins, palatability appears to be independent of condensed tannnin presence and concentration (Waghorn 2008; Muir 2011). Oaks and other tannin containing species make up a significant portion of browsers' diets throughout the year (McMahan 1964, Bryant et al. 1979, Wright et al. 2002). However, tannin contents above 5% of the ruminant diet can deter feeding and have negative effects on digestibility (Kumar and Vaithiyanathan 1990). Therefore, diets containing high tannin browse must be combined with other feed-stuffs in order to dilute contents and reduce deleterious effects.

This study compared the physiological responses of three oak species to summer drought in a controlled setting using rainfall manipulation. In order to compare responses from oak species with a variety of characteristics, I conducted the study on one member of the red oak group (section *Lobatae*), Shumard oak (*Quercus shumardii* Buckley; QUSH), a mesic species, and two members of the white oak group (section *Quercus*), bur oak (*Quercus macrocarpa* Michx.; QUMA), a moderately xeric species, and live oak (*Quercus virginiana* Mill.; QUVI), a semi-evergreen, xeric species. These *Quercus* species and others provide numerous services to livestock, wildlife, and invertebrates including browse from leaves, twigs, and shoots, cover and shelter from the weather, and places to nest and roost, making their responses to drought and provision of services during such a time even more interesting to study (McMahan 1964, Bryant et al. 1979, Wright et al. 2002, Russell and Fowler 2004, Ober 2011). Specific objectives were to evaluate oak water potential, gas exchange, and C partitioning responses to:

1) chronic drought across the growing season,

2) short-term drought recovery during the current growing season and

3) drought recovery following drought during the previous growing season.

For the three species in this study, I examined tradeoffs between different drought stress responses and made inferences about how leaf carbon dynamics during drought may relate to the CSH, species phenology, and/or other biological and climatic factors.

Materials and Methods

Site Description

This experiment was conducted on a remnant post oak savanna site (N 30°34″ W 96°21″, 103 m elevation) in College Station, Texas. The region has a mean annual temperature of 20.5 °C and receives an average 1018 mm precipitation annually (Volder et al. 2010, 2013). Research infrastructure at the site included four permanent 9 × 18-m rainout shelters covered with clear polypropylene film and fine mesh shade cloth to prevent wind-blown precipitation from entering the two open ends of each shelter. The open shelter sidewalls extending to 1.5 m above the ground surface, coupled with the breathable shade cloth, maintained shelter microclimatic conditions as close to ambient as possible while excluding natural precipitation. Precipitation was simulated in each shelter by an overhead irrigation system. For a more detailed description of the shelter infrastructure see Volder et al. (2013).

Long-Term Drought Experiment

In March of 2012, QUMA, QUVI, and QUSH seedlings were planted in a 9 × 17 grid pattern containing 153 trees per shelter at 1-m spacing. The oak seedlings were positioned randomly in quarter shelters bordered by water oak (*Quercus nigra* L.). Each quarter contained eight saplings per species for the three targeted oaks, along with bald cypress (*Taxodium distichum* (L.) Rich.), which was excluded from this study.

The experiment was divided into two phases. Prior to Phase I, all individuals were treated alike. Phase I took place March 2012 through May 2013 where seedlings received watering every other week. Water was purified using reverse osmosis before application. In June 2013, shelters were divided into paired plots receiving one of two treatments: 1) watered (W), receiving the equivalent of natural precipitation and 2) droughted (D), receiving 40% of natural precipitation levels. Twice per month, water was applied to W plots in amounts equivalent to the total monthly precipitation received by the city of College Station, TX, USA (NWS 2014). On occasion, watering was split into multiple consecutive days per month to allow the water to fully infiltrate the soil. From September 2013 to May 2014, all W and D plots received 100% local rainfall equivalent watering regardless of treatment in order to recover during the dormancy and green-up period. The trees were allowed to fully leaf out before reinitiating treatment in Phase II.

Phase II began 14 June, 2014 (DOY 165), and continued until 1 October, 2014 (DOY 274). For the remainder of this chapter the arbitrary term "growing season" will be used to represent the time period from DOY 165 – 274. During Phase II, I continued to deliver the equivalent of natural rainfall to W plots but stopped delivering water to D plots, effectively reducing simulated precipitation by 100%. Water was last applied to D plots on 13 June, 2014. In one of the four shelters, I applied a third treatment—"drought recovery" (D_{rec}) wherein the equivalent of normal precipitation was applied to both the previously watered plot and the plot previously droughted in the 2013 growing season (D_{rec} plot) in order to determine if prior drought treatment affected sapling physiology. From 14 June until 1 October approximately 477 mm of water were applied to W plots. The natural rainfall in College Station, TX, for the same time period was 379 mm (NWS 2014). A greater amount of simulated precipitation was applied from 14 June to 1 October than natural precipitation in an effort to catch up with year-to-date rainfall totals after falling behind earlier in the year. At the end of the experimental period, year-to-date (1 January to 1 October) simulated precipitation totaled 737 mm, while year-to-date natural precipitation totaled 769 mm.

All measurements reported for this study took place during Phase II. As saplings died during the years post establishment, they were replaced with individuals of the same species. However, only individuals which were 3 years old in 2014 were sampled during this study. Saplings located within plot perimeters were also excluded as a buffer against edge effects.

Short-Term Drought Recovery Experiment

To test recovery responses from short-term drought in the watered saplings, water was withheld from the W plots beginning on DOY 223 (11 August, 2014) for 34 days before applying water again on DOY 257 (14 September, 2014). Between DOY 224 and 254, Ψ_{PD} was reduced by 118% in the W plots.

Measurements

Soil Volumetric Water Content

To monitor soil moisture, volumetric water content was logged (θ) every 2 hours by permanently installed EC-5 Dielectric Aquameter sensors (Decagon Devices, Inc., Pullman, WA) located at 10-, 30-, and 60-cm depths. One sensor was installed at each of the three depths on both east and west sides of each half shelter for a total of six sensors per half shelter. Volumetric water content at each depth for a half shelter was calculated by averaging the respective east and west sensors.

Sapling Height and Diameter

Height and stem diameter measurements were collected on all saplings in early June 2014 prior to re-implementing watering treatments in Phase II, and again in October 2014 at the end of the second growing season. Stem diameter was measured at the base of the saplings at ground level, and height was measured at the terminal bud. I determined the percent increase of height and diameter from May to October for all individuals excluding those in half shelter perimeter rows and columns.

Leaf Water Potential

Beginning on DOY 169, I measured predawn (Ψ_{PD}) and midday (Ψ_{MD}) leaf water potential using a Scholander-type pressure chamber (PMS Instrument Company, Albany, OR USA) every 3 to 4 weeks no later than 5 days following a watering event to ensure that saplings had sufficient water to function at full capacity, except during the short-term drought experiment. Measurements were made between 500-700 h and 1100-1400 h for Ψ_{PD} and Ψ_{MD}, respectively. Within each shelter, measurements were collected on QUMA and QUSH leaves and QUVI twigs selected from the upper half of the canopy from two trees per species per plot. QUVI twigs with an average of 4 leaves each rather than individual leaves were selected since the small diameter and short length of petioles of this species' leaves makes measuring leaf water potential on a single leaf difficult.

Midday Gas Exchange

Leaf gas exchange measurements were performed using a LI-6400 infrared gas analyzer system (LI-COR Inc., Lincoln, NE, USA). Rates of photosynthesis (A), transpiration (E), and stomatal conductance (g) were measured on relatively cloud-free days within 3 days of leaf water potential measurements on three trees per oak species per plot in each shelter. Leaves selected for measurements were fully expanded, sun lit, and located at the outer portions of branches in the upper half of the canopy. All gas exchange measurements were made between 1100-1430 h at ambient temperature at a fixed PAR of 2000 µmol m^{-2} s^{-1}, air flow of 500 µmol s^{-1}, and CO_2 of 400 µmol mol^{-1}. I took measurements after steady state conditions were reached, as indicated by stability of gas exchange parameters.

Soluble Sugar

Leaves were collected for soluble sugar, starch, CT, C, and N analyses within one week of midday gas exchange measurements. Within each treatment plot in every shelter, one leaf from each of nine trees per species for QUMA and QUSH and seven leaves from each of nine QUVI trees were composited within species in order to accrue sufficient dry matter material to perform laboratory analyses. I collected leaves from the upper half of the canopy and immediately placed them in a cooler. Samples were dried at 105°C for 30 minutes to stop enzymatic activity and then dried to constant mass at 75°C for 48 hours in a forced-air oven. Following drying, leaves were ground in a sheer mill (Wiley Arthur H. Thomas Co., Philadelphia, PA, USA) and the samples stored at room temperature until analysis.

Foliar soluble sugar (SS) contents were analyzed following the anthrone method described by Rose et al. (1991) and modified by Olano et al. (2006). Soluble sugars were extracted from 60 mg of dried material with 3 ml of 80% ethanol in a water bath at 80°C for 30 minutes. The extract was centrifuged at 5,000 rpm for 10 minutes and the supernatant collected for sugar determinations. This process was repeated twice for a total of three extractions, and the supernatants were combined. Three ml of anthrone reagent were added to 300 µl of combined supernatant and heated for 15 minutes at 100°C. After cooling to room temperature, sample sugar content was determined by measuring the absorbance at 620 nm on a microplate reader (BioTek Instruments, Inc., Winooski, VT, USA). Absorbances were regressed against readings from a set of standard glucose solutions, and SS contents were calculated on a dry matter basis.

Non-Soluble Sugar

Following the extraction of soluble sugar, I evaporated any excess ethanol and added 3 ml of 35% perchloric acid to the dried material to extract non-soluble sugar. After samples were placed on a shaker table for 1 hour, the extract was centrifuged at 5,000 rpm for 10 minutes. Following the soluble sugar procedure above, 3 ml of anthrone reagent was added to 300 µl of the extract and heated at 100°C for 15 minutes. After cooling to room temperature, non-soluble sugar (NSS) content was determined by measuring the absorbance at 620 nm. Absorbances were regressed against readings from a second set of standard solutions of glucose, and a correction factor of 0.9 was used to convert glucose equivalents to starch (Libby 1970). Non-soluble sugar contents were calculated on a dry matter (DM) basis.

Condensed Tannin Purification

Following Naumann et al.’s (2014) modification of Wolfe et al.’s (2008) method, condensed tannins were purified for subsequent use as a standard from each species using Sephadex LH-20 (GE Healthcare Bio-Sciences Corp., Piscataway, NJ). Plant tissue (20 g DM) was extracted with 250 ml of 7:3 (v/v) acetone:water. The aqueous portion containing CT was saved and residual acetone removed by evaporation under reduced pressure. The extract, along with enough 1:1 (v/v) methanol:water to form a slurry, was mixed with Sephadex LH-20. The slurry was washed with 1:1 (v/v) methanol:water repeatedly until the absorbance at 280 nm was negligible (absorbance ≤ 0.10). Condensed tannins bound to the Sephadex LH-20 were released by washing with 7:3 (v/v) acetone:water. Residual acetone was evaporated. The aqueous portion containing CT was then frozen at -80 °C and lyophilized. The purified CT were used to develop species-specific standards for the protein-precipitation assays (Wolfe et al. 2008).

Protein Precipitability

Protein precipitability of CT was determined using the method described by Hagerman and Butler (1978). Duplicate crude plant extracts were prepared from composite samples of each species by extracting 50 mg of plant tissue with 1 mL 1:1 (v/v) methanol:water on an orbital shaker (G10 Gyrotory® shaker, New Brunswick Scientific Co., Inc., Edison, NJ) for 30 min followed by centrifugation for 5 min at 16,070 x *g*.

To determine protein-precipitable phenolic (PPP) contents and the amount of protein bound by PPP, I combined 250 µl buffer A (0.20 M acetic acid, 0.17 M NaCl, pH 4.9), 50 µl bovine serum albumin (BSA) (5 mg ml^{-1} in buffer A), and 50 µl 1:1 (v/v) methanol:water with 50 µl of supernatant from each crude extract and incubated the mixture at room temperature for 30 min before centrifuging at 16,070 x *g* for 5 min. I removed the supernatant by vacuum aspiration and washed the protein-phenolic pellet with 250 µl buffer A before re-centrifuging and aspirating. The protein-phenolic pellet was then dissolved in 800 µl of SDS/TEA [sodium dodecyl sulfate (1% w/v)-triethanolamine (5% v/v)] before adding 200 µl $FeCl_3$ (0.01 M $FeCl_3$ in 0.01 M HCl). Absorbances were read at 510 nm after 15 min and values were converted to PPP contents using standard curves developed for the individual species.

Naumann et al.'s (2014) method was used to determine the amount of protein bound by PPP. The procedure was executed as described above, except the protein-phenolic pellet was analyzed for N to quantify grams of precipitated protein per gram of PPP. Instead of dissolving the protein-phenolic pellet in SDS/TEA, I dissolved the pellet in 500 µl of buffer A, and transferred the solution to a foil cup to dry. A Vario MACRO C-N Analyzer (Elementar Americas, Inc., Mt. Laurel, NJ) was used to assay the dried protein-phenolic residue for percent N, which was multiplied by 6.25 (Van Soest 1994) to calculate protein bound by PPP. Foliar percent N for the three species was also determined using the Vario MACRO C-N Analyzer.

Statistical Analyses

Statistical tests for treatment effects on leaf water potential, gas exchange, and biochemical parameters were performed using linear mixed-models (proc mixed procedure, SAS 9.4, SAS Institute Inc., Cary, NC, USA) with a repeated measures and random effects covariance structure. The effects of species, treatment, day of experiment, and their interactions were tested, and individual saplings within species in respective treatments and shelters were treated as subjects in models. Models for testing growth variables did not include repeated measures statements or day of experiment since I analyzed percent increase of height and diameter between two points, June and October, rather than repeated monthly measurements. Final model selection was based on corrected Akaike information criterion (AICC). When significant effects were detected in the model, the LSMEANS statement in SAS was used to estimate means. Differences between means were adjusted using Tukey's HSD post-hoc analysis. Differences were considered significant at $P \leq 0.05$.

Volumetric water content at 60-cm depth was tested as a covariate since slight differences in irrigation system application (i.e. amount of water applied by systems in individual shelters during a given watering period) (Figure 1) were observed. When 60-cm depth θ affected response variables (based on lowest AICC) it was included in final models to adjust for differences in θ. Most response variables, with the exception of PPP and NSS contents and protein bound by PPP, were affected by differences in θ, as evidenced by low AICC values. These three response variables were analyzed with ANOVA models testing species, treatment, day of experiment, and their interactions as factors. Greater AICC values for models including θ for NSS and PB which had treatment interactions (treatment x day and treatment x species x day for NSS and PB, respectively) suggest slight differences in θ within treatments were miniscule compared to overall treatment effects on these variables. Treatment had no effect on PPP contents.

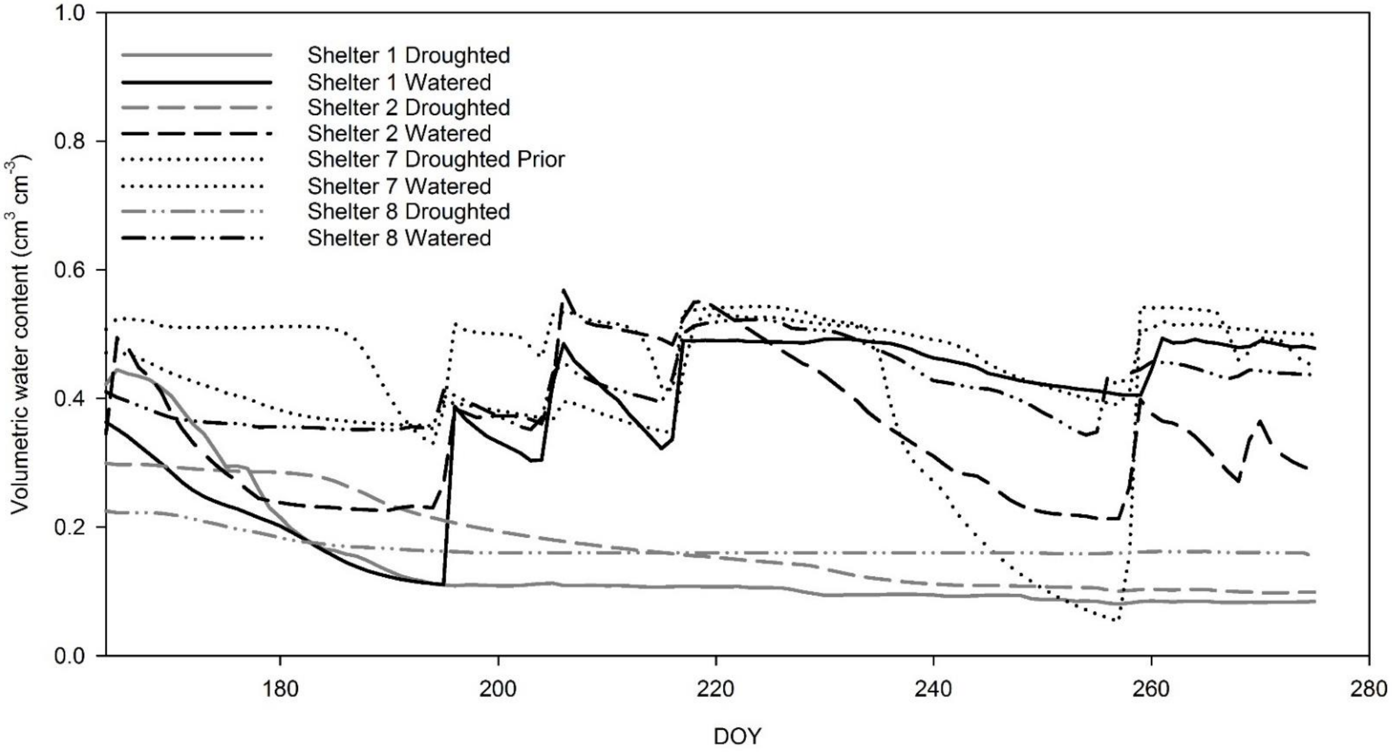


Figure 1. Average daily volumetric water content (θ; cm^3 cm^{-3}) at 60-cm depth for droughed and watered halves of each shelter from 14 June (DOY 165) to 1 October, 2014 (DOY 274).

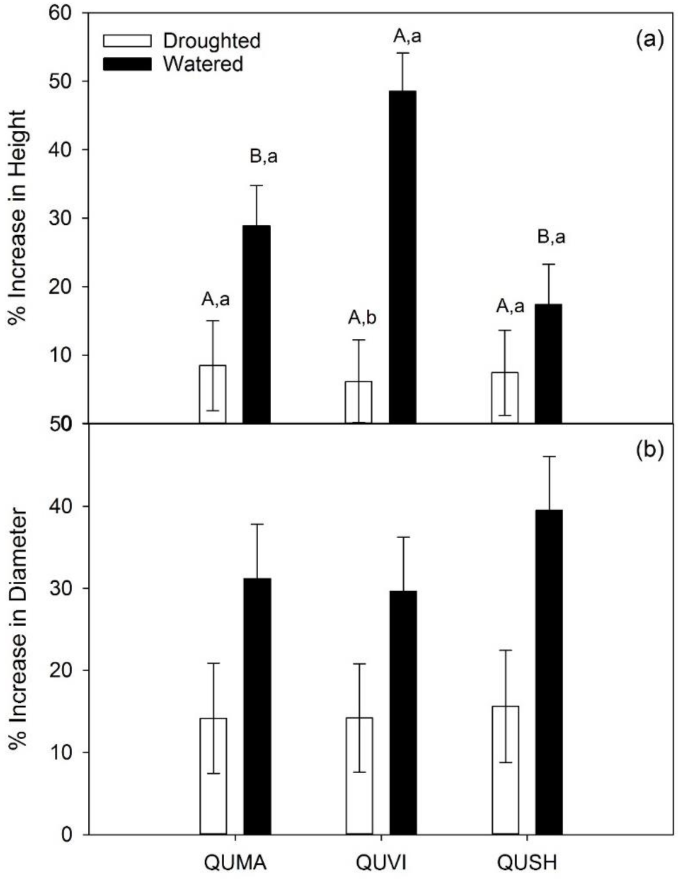


Figure 2. Average percent increase in a) height and b) diameter of droughted and watered bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings from June – October 2016. Vertical lines represent standard errors. Different uppercase letters (A) denote differences ($P \leq 0.05$) among species within a particular treatment. Different lowercase letters (a) denote differences ($P \leq 0.05$) between treatments within each species.

Statistical testing of response variables within the drought-recovery shelter followed a similar procedure as above. Individual saplings within species within a treatment (D_{rec} vs. W) were treated as subjects within models. Fully-reduced models (two-way ANOVA) with species, day of experiment, and their interaction as factors were used to analyze response variables. Models containing θ at 60 cm as a covariate had higher AICC values and were not utilized: treatment had no effect on any response variable.

Results

Height and Diameter

On average, height and diameter increased by 23% and 25%, respectively, throughout phase II, but increases in W saplings were more than double that of D saplings. In the D plots all three species had similar height growth, but in the W plots QUVI had faster height growth than QUMA and QUSH (Figure 2a) (treatment × species interaction). Although diameter growth was greater on average in W plots, percent diameter increase was not significantly greater for any species ($P = 0.07$) or treatment ($P = 0.10$) (Figure 2b).

Leaf Water Potential

At the beginning of the experiment, all individuals displayed similar Ψ_{PD} and Ψ_{MD} (Figure 3) (treatment x day interactions). By DOY 196, watering treatment effects were evident as D saplings had 0.45 MPa and 0.49 MPa, respectively, more negative Ψ_{PD} and Ψ_{MD} than W saplings. The W saplings continued to have greater Ψ_{PD} and Ψ_{MD} than the D saplings until DOY 274. The peak effect of the watering treatment occurred at DOY 224 when the Ψ_{PD} and Ψ_{MD} of D saplings were 1.11 MPa and 0.79 MPa, respectively, lower than those of the W saplings (Figures 1, 3). As a result of the short-

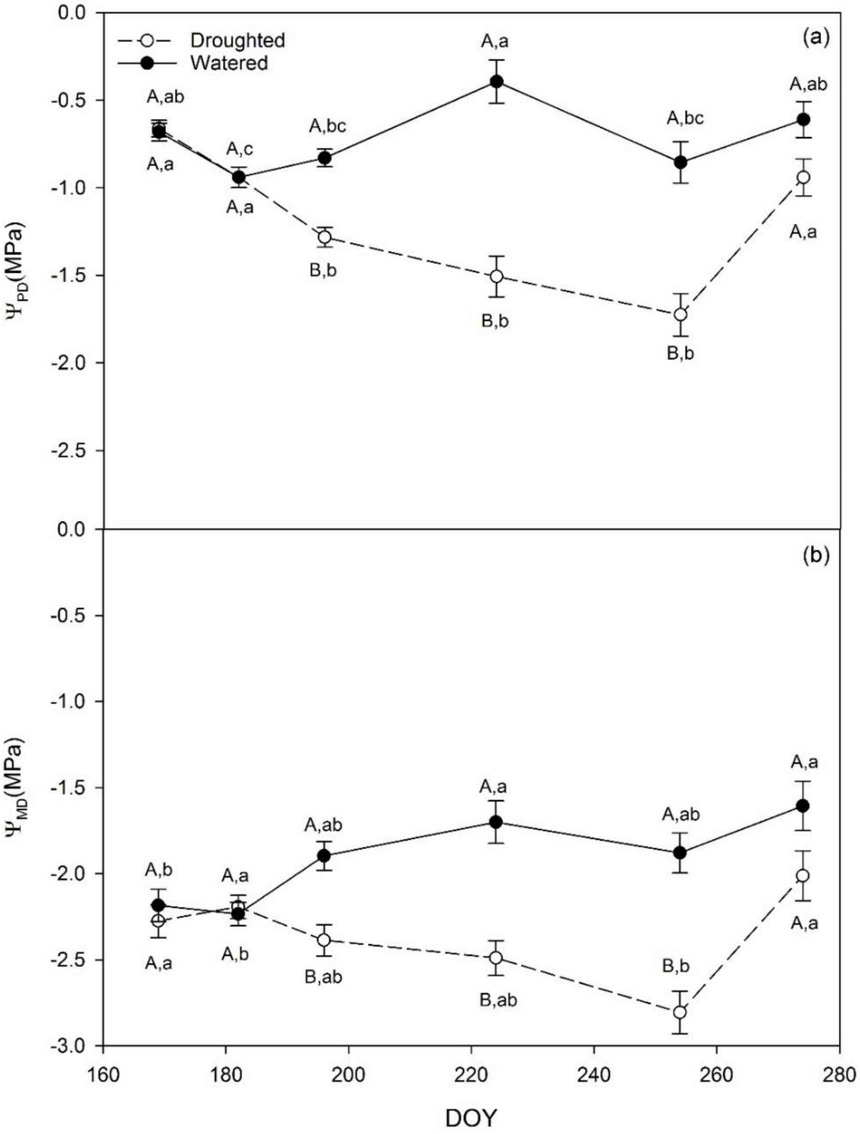


Figure 3. Predawn (Ψ_{PD}) (a) and midday (Ψ_{MD}) (b) leaf water potential of droughted and watered saplings at multiple dates across the growing season. Vertical lines represent standard errors. Different uppercase letters (A) denote differences ($P \leq 0.05$) between treatments on each measurement date. Different lowercase letters (a) denote differences ($P \leq 0.05$) among measurement dates within a particular treatment.

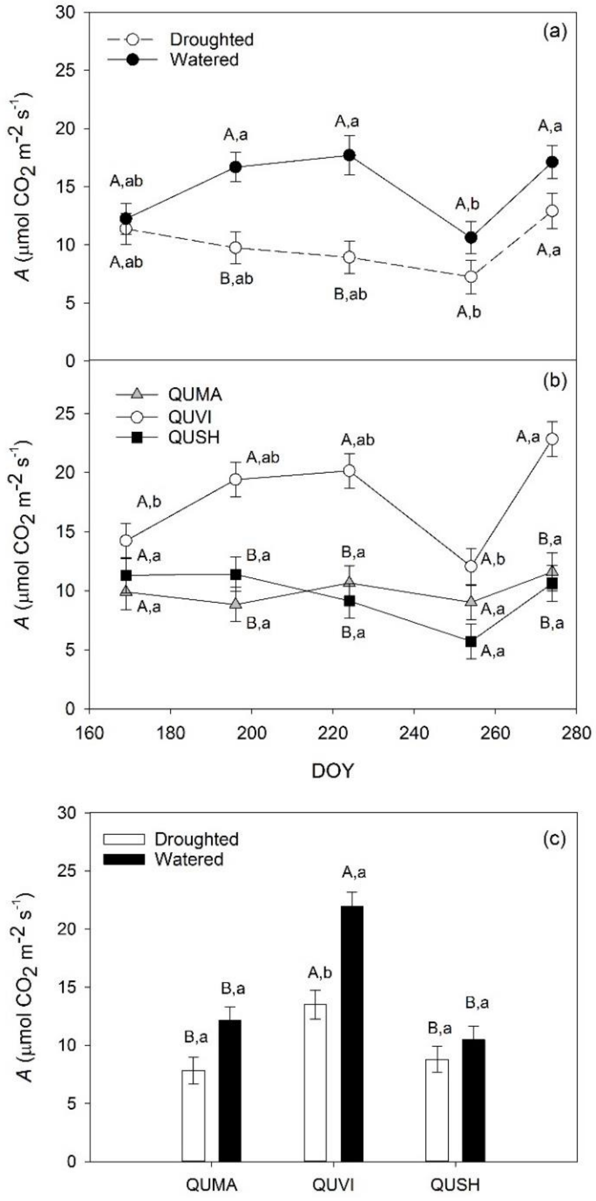


Figure 4. Net photosynthetic rates (*A*) of a) droughted and watered and b) bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season and c) the interaction of species and treatment averaged across the growing season. Vertical lines represent standard errors. Different uppercase letters (A) denote differences ($P \leq 0.05$) between treatments (Fig. 4a) or species (Fig. 4b) on each measurement date and among species within a particular treatment (Fig. 4c). Different lowercase letters (a) denote differences ($P \leq 0.05$) among measurement dates within a particular treatment (Fig. 4a) or species (Fig. 4b) and treatments within each species (Fig. 4c).

term drought experiment, W saplings' Ψ_{PD} and Ψ_{MD} values dipped (0.46 and 0.18 MPa), but were still greater than D saplings. Following re-watering, W Ψ_{PD} and Ψ_{MD} recovered to pre-micro-drought levels. Droughted saplings' Ψ_{PD} and Ψ_{MD} rose toward the end of the experiment as well; on DOY 274, D and W saplings exhibited similar Ψ_{PD} and Ψ_{MD}. All three species had similar Ψ_{PD} and Ψ_{MD} within their respective treatments.

Midday Gas Exchange

On DOY 169, all individuals exhibited similar *A*, *E*, and *g* regardless of treatment (Figures 4a, 5a, 6) (treatment × day interaction for *A* and *E*, treatment × species × day interaction for *g*). Similar to leaf water potential, W saplings demonstrated greater gas exchange approximately 1 month after initiating treatment (Phase II), and the full effect of treatment was seen around 2 months into the experiment. Species differences were evident within one month as well when QUVI began to pull away from the other two species (Figures 4b, 5b, 6). By DOY 224, QUVI had at least 62% greater *A* and 53% greater *E* than QUMA and QUSH when the differences between D and W θ were greatest as well. Stomatal conductance followed a similar trend. Due to the month-long short-term drought (Figure 1), gas exchange decreased in W saplings to levels similar to those of D saplings on DOY 254 (Figures 4a, 5a, 6). All species had similar gas exchange at DOY 254 as well (Figures 4b, 5b, 6). By DOY 274, *A* and *g* of watered saplings were back to pre- micro-drought levels, and QUVI had the greatest gas exchange rates again. Watered *E* increased 22% after DOY 254, but did not reach pre-micro-drought values.

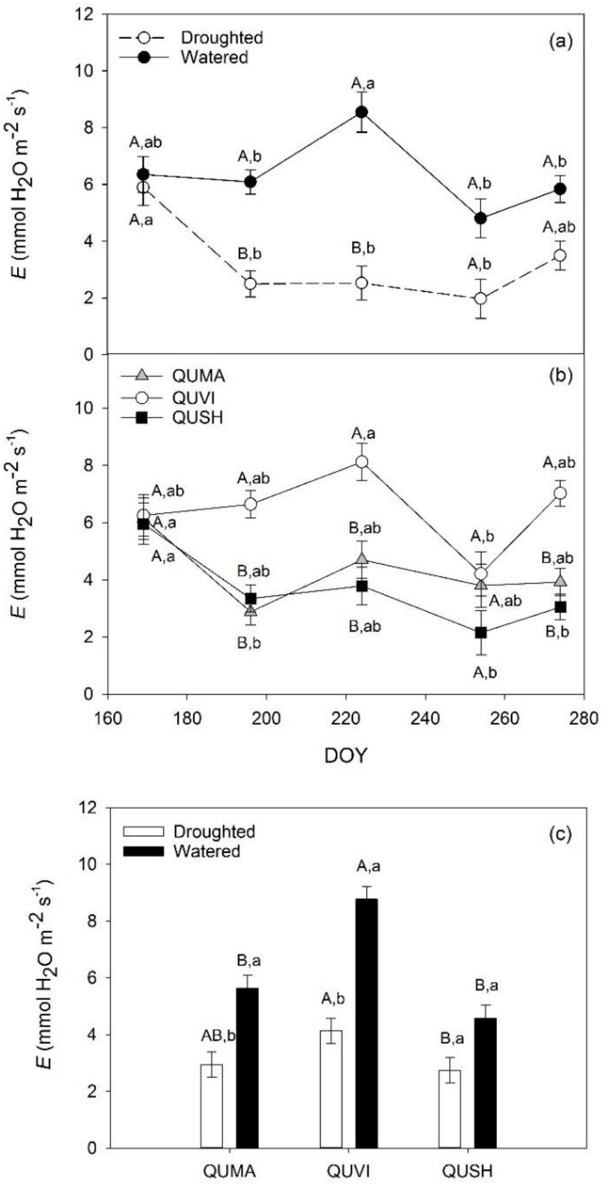


Figure 5. Transpiration rates (*E*) of a) droughted and watered and b) bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season and c) the interaction of species and treatment averaged across the growing season. Vertical lines represent standard errors. Different uppercase letters (A) denote differences ($P \leq 0.05$) between treatments (Fig. 5a) or species (Fig. 5b) on each measurement date and among species within a particular treatment (Fig. 5c). Different lowercase letters (a) denote differences ($P \leq 0.05$) among measurement dates within a particular treatment (Fig. 5a) or species (Fig. 5b) and treatments within each species (Fig. 5c).

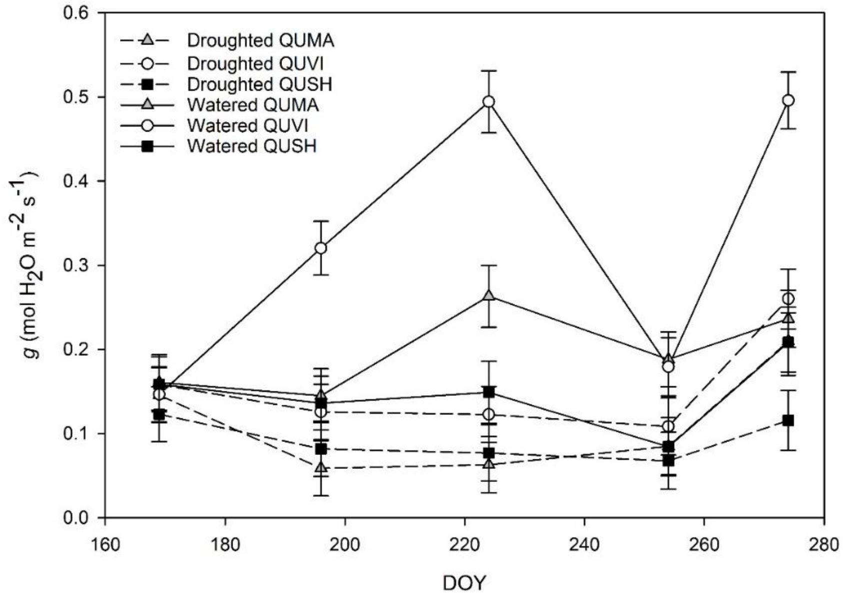


Figure 6. Stomatal conductance rates (*g*) for treatment by species interactions of droughted and watered bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season.

Bur oak and QUSH gas exchange rates were usually similar in both treatments and were generally lower than those of QUVI within their respective treatments (Figures 4c, 5c, 6). Gas exchange rates of W QUMA and QUSH were also relatively unaffected by the micro-drought; these species typically had low gas exchange rates across the entire experiment. Watered QUVI exhibited the greatest gas exchange rates, and D QUVI's gas exchange rates were comparable to those of W QUMA and QUSH.

Soluble Sugar

I did not detect differences between D and W sapling SS across the growing season, but contents tended to follow increases and decreases in soil moisture content and gas exchange until DOY 274 (Figure 7a) (no treatment × day interaction). Although

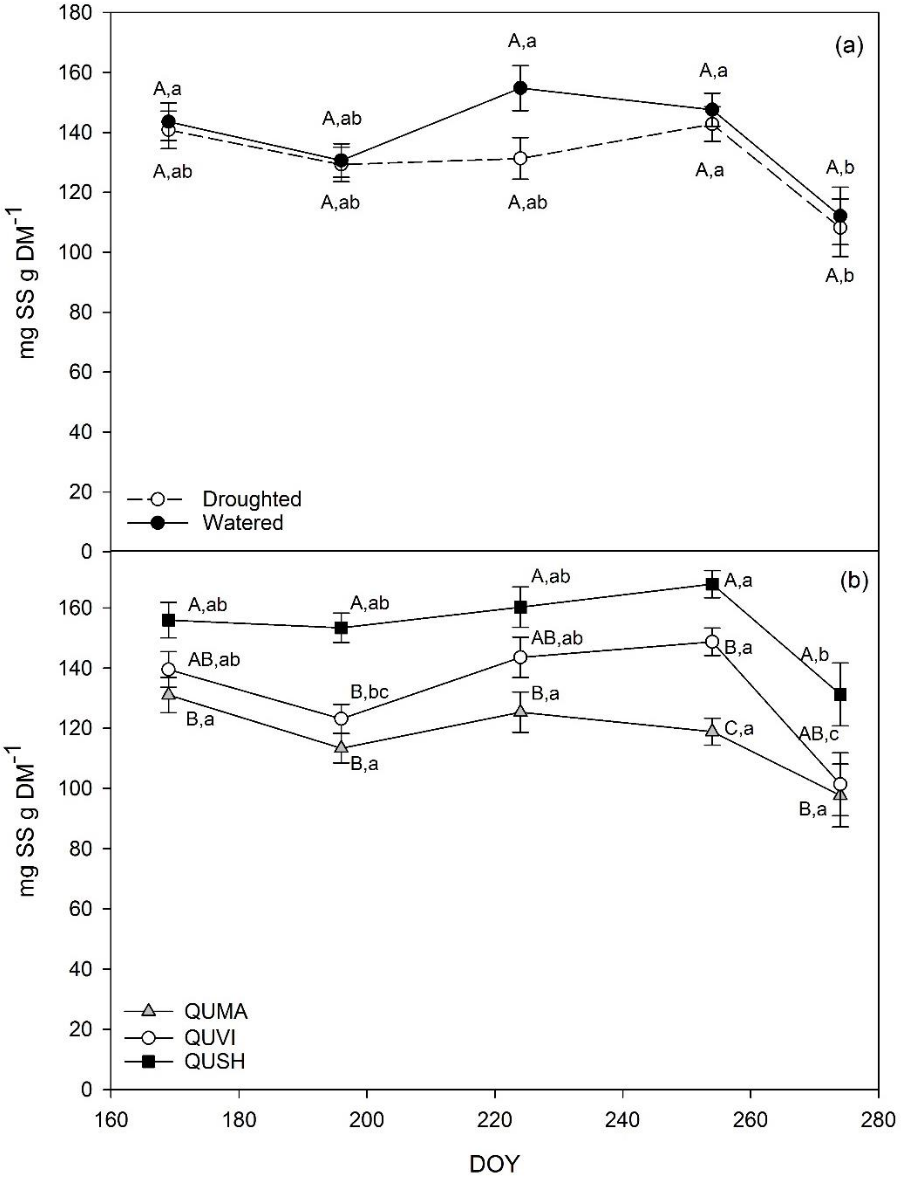


Figure 7. Soluble sugar (SS) content of a) droughted and watered and b) bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season. Different uppercase letters (A) denote differences ($P \leq 0.05$) between treatments (Fig. 7a) or among species (Fig. 7b) on each measurement date. Different lowercase letters (a) denote differences ($P \leq 0.05$) among measurement dates within a particular treatment (Fig. 7a) or species (Fig. 7b).

gas exchange rates increased to pre-micro-drought levels following re-watering (Figure 1), SS of W saplings decreased 24% to the lowest contents of the season. Soluble sugar contents of D saplings also decreased 24% at this time. Soluble sugar contents were greatest in QUSH, intermediate in QUVI, and lowest in QUMA across the entire experimental period (Figure 7b) (species × day interaction). All three species reduced leaf SS contents at the end of the growing season.

Non-Soluble Sugar

Although significant differences between D and W saplings were only detected on DOY 224 (corresponding with peak water content and gas exchange differences), NSS contents tended to be greater in W saplings across the growing season (Figure 8a) (treatment × day interaction). Non-soluble sugar contents dropped 48% in W saplings from DOY 224 to 254, likely as a result of low soil moisture at this time. Plants often convert NSS to SS for use in osmotic adjustment and to sustain exports and metabolism during times of stress (Wang and Stutte 1992, Dickson and Tomlinson 1996, Arndt et al. 2001). Non-soluble sugars were also at their lowest contents in D saplings at this time. Non-soluble sugar contents remained low in both W and D saplings at DOY 274. QUMA generally had high NSS contents followed by QUSH and QUVI respectively, but differences between the species were significant only on DOY 224 (Figure 8b) (species × day interaction).

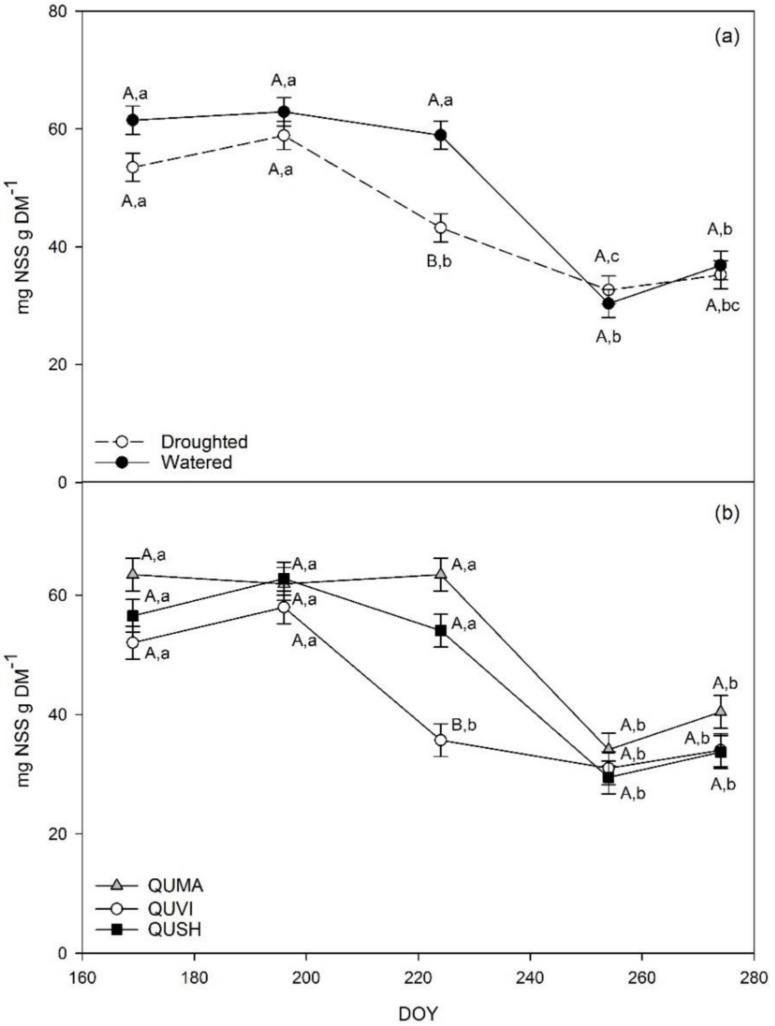


Figure 8. Non-soluble sugar (NSS) content of a) droughted and watered and b) bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season. Different uppercase letters (A) denote differences ($P \leq 0.05$) between treatments (Fig. 8a) or among species (Fig. 8b) on each measurement date. Different lowercase letters (a) denote differences ($P \leq 0.05$) among measurement dates within a particular treatment (Fig. 8a) or species (Fig. 8b).

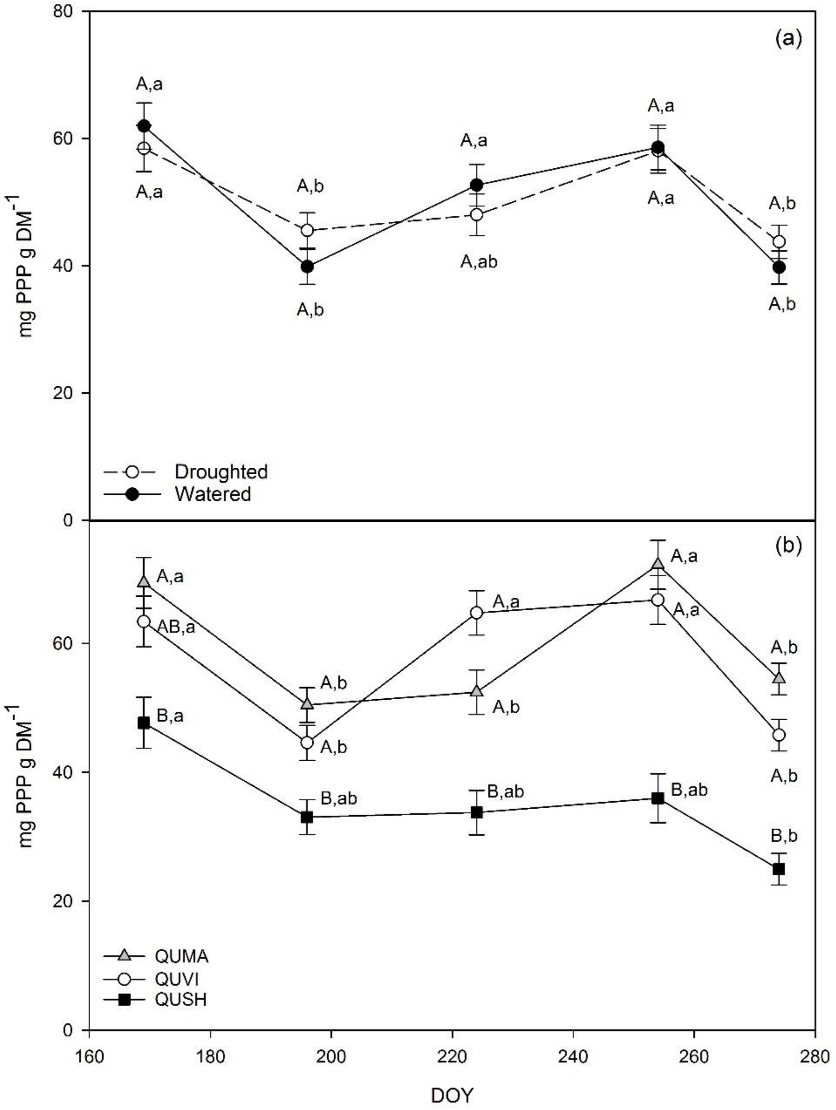


Figure 9. Protein-precipitable phenolic (PPP) content of a) droughted and watered and b) bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season. Different uppercase letters (A) denote differences ($P \leq 0.05$) between treatments (Fig. 9a) or among species (Fig. 9b) on each measurement date. Different lowercase letters (a) denote differences ($P \leq 0.05$) among measurement dates within a particular treatment (Fig. 9a) or species (Fig. 9b).

Protein-Precipitable Phenolics

Protein-precipitable phenolic contents of D and W saplings followed a similar pattern across the entire experiment (Figure 9a) (no treatment × day interaction). Contents were high initially, dropped at DOY 196, increased again until DOY 254, and then declined again at the end at DOY 274. Contents were greatest in QUMA and QUVI and least in QUSH on every measurement date (Figure 9b) (species × day interaction).

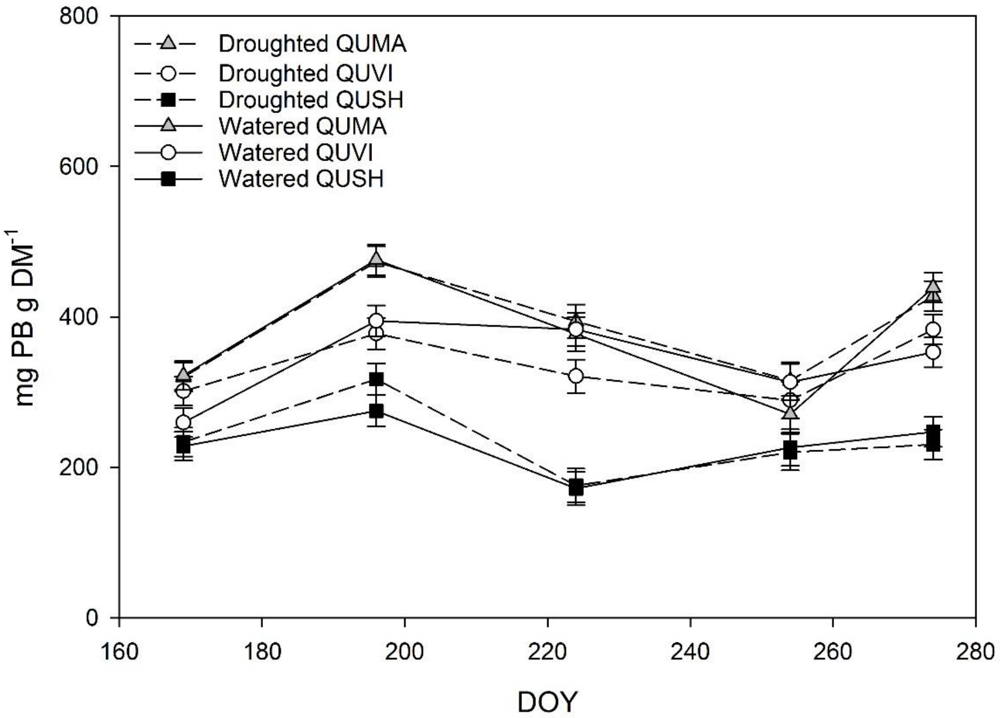


Figure 10. Amount of protein bound (PB) by PPP for treatment by species interactions of droughted and watered bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season.

Protein Bound by Protein-Precipitable Phenolics

The amount of protein bound by PPP approximately followed the pattern of PPP content in reverse: increasing at DOY 196, decreasing to DOY 254, and then increasing again at DOY 274 (Figure 10) (treatment × species × day interaction). Droughted and W saplings typically followed the same pattern within each species. Similar to PPP content, amount of protein bound was normally greatest in QUMA, intermediate in QUVI, and lowest in QUSH.

The PB:PPP ratio of D and W saplings followed a similar trend as protein bound across the experiment period (Figure 11a) (treatment × day interaction). The PB:PPP ratio of all three species were similar on all measurement dates, except DOY 224 (Figure 11b) (species × day interaction).

Nitrogen Content

Nitrogen content did not follow any particular trend across the growing season (Figure 12) (treatment × species × day interaction). Shumard oak had 2 mg g^{-1} greater N content on average than QUMA and QUVI. On each measurement date, N content was similar between W and D saplings within each species.

Drought-Recovery Experiment

Individual saplings within the D_{rec} treatment behaved similarly to their continuously W associates in gas exchange, Ψ_{PD}, and Ψ_{MD} (data not presented here). At the initiation of phase II, individuals within the continuously W plot of this shelter had

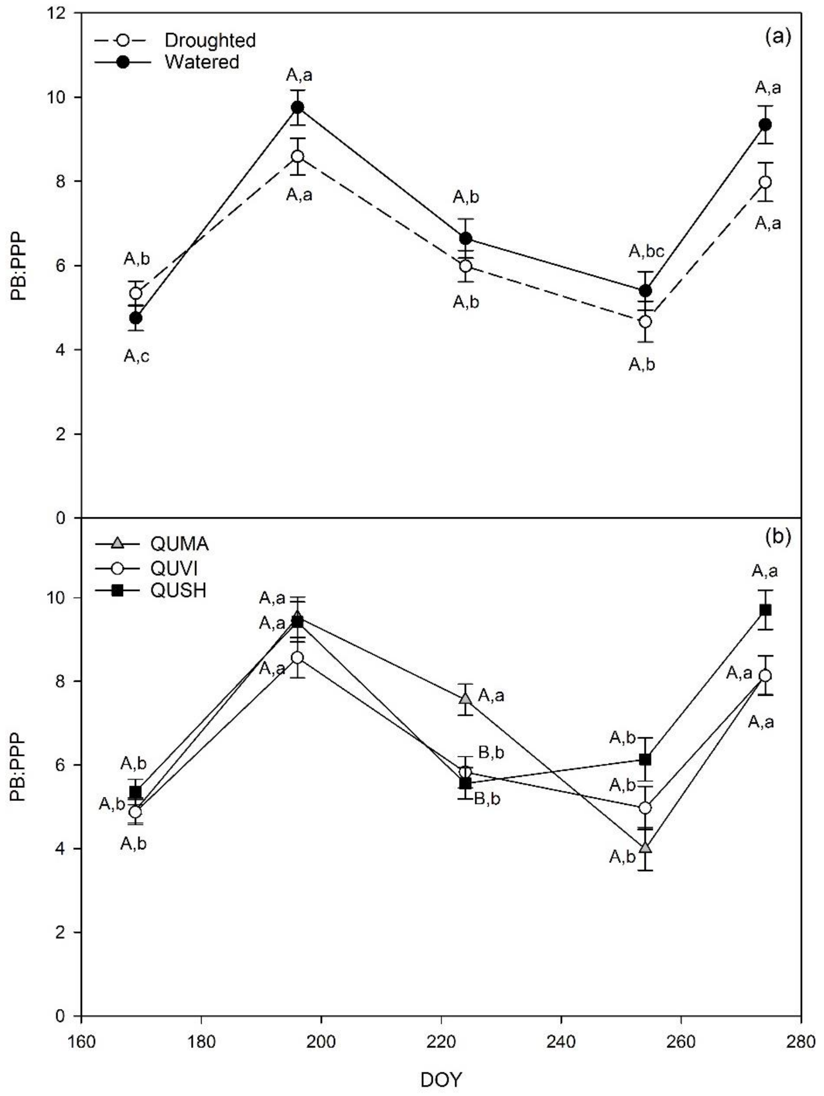


Figure 11. PB:PPP ratio of a) droughted and watered and b) bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season. Different uppercase letters (A) denote differences ($P \leq 0.05$) between treatments (Fig. 11a) or among species (Fig. 11b) on each measurement date. Different lowercase letters (a) denote differences ($P \leq 0.05$) among measurement dates within a particular treatment (Fig. 11a) or species (Fig. 11b).

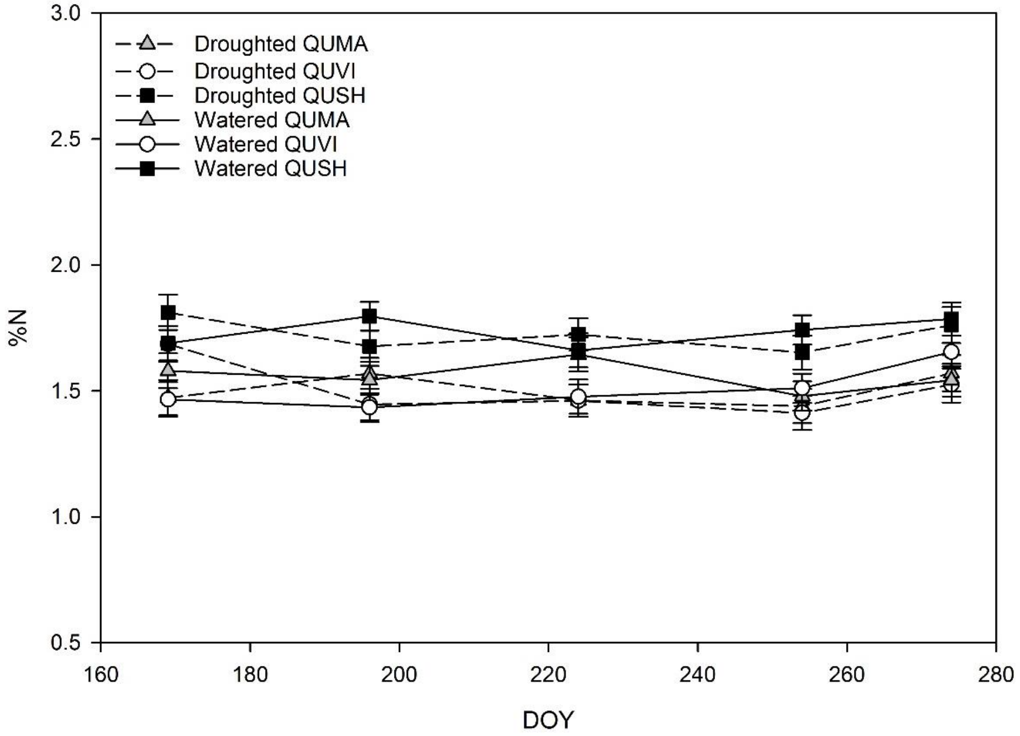


Figure 12. Leaf percent N for treatment by species interactions of droughted and watered bur oak (QUMA), live oak (QUVI), and Shumard oak (QUSH) saplings at multiple dates across the growing season.

greater heights and diameters than individuals in the plot converted from D to D_{rec}. Although percent height and diameter increases across the 2014 growing season between W and D_{rec} individuals were similar, D_{rec} individuals remained shorter and smaller in diameter due to their previous drought exposure. The larger overall size (height, diameter, crown area) of continuously W individuals may have contributed to the greater dry-down in the W plot than the D_{rec} plot in this shelter (Figure 1). Live oak's photosynthesis rates were 55% greater than those of QUMA and QUSH on average, reflecting the results seen in the other three shelters. *E* and *g* were also greater for

QUVI. The three species did not differ in Ψ_{PD} or Ψ_{MD}. Gas exchange and leaf water potential trends followed changes in θ over time. Biochemical parameter values were similar to those of the continuously W individuals of the other shelters.

Discussion

Lack of Evidence for Carbon Starvation Hypothesis

I found very little evidence to support the CSH following drought stress. Although expected reductions in growth, leaf water potential, and gas exchange in droughted saplings were documented (Hanson et al. 2001, Galvez et al. 2011, Duan et al. 2013), these did not translate into substantial differences between D and W foliar carbohydrate and phenolic contents. There was little variation in SS and NSS across the growing season and no detectable drought effect except NSS differences on DOY 224. However, SS contents tended to follow soil moisture trends, and the decrease in D sapling NSS contents over time and large drop in W sapling NSS contents at DOY 254 during the micro-drought could indicate shifts from NSS to SS. As water stress progresses, the soluble: non-soluble sugar ratio can increase as a result of starch hydrolysis and increased carbon partitioning to sucrose and other low molecular weight compounds for osmoticum and metabolism needs (Wang and Stutte 1992, Dickson and Tomlinson 1996, Arndt et al. 2001). Protein-precipitable phenolic contents appear to be even less affected by water availability differences than carbohydrate contents. Contents were similar for D and W saplings on all measurement dates, and followed no discernable pattern. Foliar N was also not affected by drought. Leaf photosynthetic capacity is often correlated with leaf N content since photosynthetic machinery (i.e. thylakoids, Rubisco, and proteins utilized in the Calvin cycle) is largely composed of N (Evans 1989, Reich et al. 1991, Springer et al. 2005). However, other studies have reported drought effects on photosynthesis with little to no change in leaf N content (Wilson et al. 2000, Xu and Baldocchi 2003) or even increases in leaf N with drought (Weih et al. 2011).

Results, particularly those from the end of the season, suggest that species phenology in relation to climatic and seasonal changes may play a larger role in determining carbohydrate and phenolic compound contents. Soluble sugar, NSS, and PPP contents decreased at the end of the season. Concomitantly D sapling gas exchange rates and leaf water potentials increased. These trends may be reflect a shift of carbohydrates towards root growth or storage at this time of the season (Isebrands and Nelson 1983, Loescher et al. 1990). Increases in leaf water potential and gas exchange in D saplings at DOY 274 appear to indicate utilization of water at deeper soil depths. Multiple studies document deeper root penetration following drying of layers at the soil surface (Wan et al. 2002, Padilla and Pugnaire 2007, Padilla et al. 2007). The greater rates of diameter increase than height increase in D saplings may also reflect that D saplings were allocating resources to root growth for water acquisition. Multiple studies reported increased root:shoot ratios for plants growing in unfavorable conditions (drought, low nutrient supply) (Michelsen and Rosendahl 1990, Kozlowski and Pallardy 2002, Leuschner et al. 2007). I measured θ in the plots only to a depth of 60 cm so I was not able to see changes in water availability below this depth. *Quercus* spp. develop deep root systems, so root depths past 60 cm for the saplings would not be unusual (Saunier and Wagle 1967, Kochenderfer 1973, Davis and Pase 1977, Hinckley et al. 1981).

The decrease in leaf SS and NSS contents later in the growing season could reflect translocation of carbohydrates to roots for necessary growth into deeper pockets of soil moisture (Lopes and Reynolds 2010). Decreases in foliar sugar, starch, and secondary compounds are often seen in the fall in preparation for leaf senescence (Lindroth et al. 2002, Kandil et al. 2004, Keskitalo et al. 2005, Acero et al. 2010). Preferential carbon allocation to roots and subsequent growth in these species could happen at this time normally. Root growth can take place throughout the year; Teskey and Hinckley (1981) noted that white oaks (*Quercus alba* L.) experienced a major period of root growth following leaf senescence while Kuhns et al. (1985) witnessed moderate to rapid black walnut (*Juglans nigra* L.) root growth at multiple depths between the initiation of senescence to complete leaf fall and during the winter.

The decrease in PPP contents at the end of the season coupled with possible resource allocation to root growth may be explained by the growth-differentiation balance hypothesis (Loomis 1932, Herms and Mattson 1982) which predicts how plants balance resource allocation between growth-related and differentiation-related processes over a range of environmental conditions. Differentiation processes, including anything that enhances the structure or function of existing cells (e.g. development of secondary compounds like condensed tannins or terpenes, trichomes, thicker cuticles, etc.), are thought to compete with growth processes for available photosynthate since simultaneous full carbon allocation to all plant functions is not possible. Reductions in condensed tannins and other secondary compounds for defense may occur as growth rates increase (Coley 1988, Hemming and Lindroth 1999, Glynn et al. 2007).

The lack of PPP content response to drought stress suggests some other climatic or biologic effect may act as a greater determinant, especially since PPP contents followed the same pattern throughout the season in both D and W treatments and all three species. For example, differences in PPP contents across the experiment period may be due to the presence of insect herbivores, changes in solar radiation, and/or the time of day when leaves were harvested on each collection date. Condensed tannins play many roles in protecting plants. They can act as plant defenses against herbivory, increasing following defoliation (Osier and Lindroth 2001, Peters and Constabel 2002, Cooper et al. 2014) and reducing insect intake, growth, and fecundity (Schultz 1989, Kopper et al. 2002). Condensed tannins also have allelopathic effects and reduce competition from neighboring species (Callaway and Ridenour 2004, Thelen et al. 2005). Condensed tannins and other phenolic compounds act as antioxidants to protect plants against high levels of PAR and UV radiation and photoinhibition as well (Close and McArthur 2002, Turtola et al. 2005, Mellway et al. 2009). Abdala-Díaz et al. (2006) found phenolic compounds were two to four times greater in the summer, when daily integrated irradiance was greatest, than during the fall and winter. They reported an exponential decrease in phenolic compounds and irradiance through November following a peak in June. Summer phenolic compounds also followed a diurnal pattern, decreasing around 1200 – 1400 hrs (Abdala-Díaz et al. 2006). Stress from photoinhibition may drive leaf phenolic level adjustment to a greater degree than herbivory (Close et al. 2003).

The amounts of protein bound by PPP and the subsequent ratio of PB:PPP followed the opposite pattern of PPP across the growing season. Similar to PPP content, amount of protein bound can also be affected by a plants' climatic and/or biotic environment. Tannin activity (e.g. protein binding, antibacterial, and/or anthelmintic capability) depends more on tannin structure than abundance (Makkar et al. 1988, Kraus et al. 2003, Halbwirth 2010). Reactivity can be affected by changes in hydroxylation pattern of the B-ring, stereochemistry, polymerization extent, substitution patterns, types of cross linkages between monomer units, etc. (Kraus et al. 2003). In an experiment by Tharayil et al. (2011), red maple (*Acer rubrum* L.) litter grown under drought conditions combined with warming had condensed tannins with reduced chain lengths and greater proportions of hydrolysable tannins. Although the integration of drought and warming resulted in double the content of condensed and hydrolysable tannins, the increase in glucosidase (protein) complexation capacity was five-fold, suggesting drought and warming increased tannin binding efficiency.

Climate related effects on biosynthesis pathways may have caused shifts in PPP hydroxylation patterns and/or changes in other structural features that led to the differences in PB and PB:PPP across the growing season. Hydroxylation pattern at the B-ring is regarded as the most significant determinant of antioxidant activity (Halbwirth 2010) and differences in light and temperature regimes bring about changes in tannin hydroxylation patterns (Jaakola et al. 2004, Jaakola and Hohtola 2010, Tharayil et al.

2011). The number and position of hydroxyl groups affect light absorption; increasing hydroxyl groups at the A and B rings shifts absorbance towards higher wavelengths (Halbwirth 2010). Shifts in hydroxylation pattern alter tannin protein binding ability as well; larger prodelphinidin/procyanidin ratios can increase condensed tannin ability to bind proteins (Hagerman 1989, Aerts et al. 1999, Andersson et al. 2006).

Had carbohydrate, nitrogen, and phenolic constituents been measured on a mass per leaf area basis rather than mass per grams of dry matter basis, results may have differed between treatments. Some studies have reported increases in leaf mass per area (LMA, g cm^{-3}) as a result of drought due to reductions in leaf expansion rates and the development of thick cell walls (Hernández et al. 2004, Poorter et al. 2009, Limousin et al. 2010). However, others have reported no difference in LMA between droughted and well-watered trees or reduced LMA in droughted trees (Thomas and Gausling 2000, Gulías et al. 2002, Ogaya and Peñuelas 2006). Plants have limited flexibility to adjust leaf morphology and anatomy after leaves have fully expanded (Poorter et al. 2009), and changes to leaf area may take long-term exposure to drought conditions over multiple years (Castro-Díez 1997, Limousin et al. 2010). Therefore we may not have seen differences in leaf area between our W and D saplings as leaves were fully expanded when we began applying different watering treatments in June 2014 and D saplings had only been exposed to one prior drought period (June to September 2013).

Species Differ in Phenology and Drought Tolerance

The three species in this study differed not only in leaf level gas exchange but also in how photosynthate from gas exchange is allocated to growth, carbohydrates, and phenolic compounds. Greater height growth in QUVI than QUMA and QUSH in the W treatment may reflect inherent growth rate differences between the species. Live oak seedlings are reported to grow vigorously in well-watered conditions, and may grow over 1 m in the first year (Carey 1992). Bur oak and QUSH have been reported to exhibit slow height growth rates on the other hand (Johnson 1990, Balok and St. Hilaire 2002, Drunasky and Struve 2005). Although QUVI is classified as very drought tolerant (Gilman and Watson 1994, Bendevis et al. 2010), it reduces growth, leaf water potential, and gas exchange during times of low water availability (Cavender-Bares et al. 2007, Kukowski et al. 2013), though sometimes to a lesser degree than co-occurring species (Owens 1996, Bendevis et al. 2010). Therefore, slow height and diameter growth by QUVI in D plots may be expected.

The high QUVI gas exchange values are corroborated by other studies (Owens and Schreiber 1992, Cavender-Bares et al. 2007, Bendevis et al. 2010). In studies by Owens and Schreiber (1992) and Bendevis et al. (2010), QUVI *A*, *E*, and *g* were greater than those of co-dominant Ashe juniper (*Juniperus ashei* Buchh.) across the entire measurement period, regardless of precipitation pattern. In the Owens and Schreiber (1992) study, QUVI trees were also well adapted to the extreme variability in precipitation events, taking advantage of available precipitation; *A* and *E* were six times greater during wet months. Bendevis et al. (2010) reported a maximum QUVI *A* of 21.6

μmol m^{-2} s^{-1} similar to my QUVI mean *A* of 20.1 and 22.8 μmol m^{-2} s^{-1} at DOY 224 and 274. Live oak is capable of reaching much lower leaf water potentials than seen in this experiment (Cavender-Bares et al. 2007, Schwinning 2008). Bur oak and QUSH gas exchange rates in this study were similar to those reported by Balok and St. Hilaire (2002); D and W plants had similar conductance and transpiration rates on many measurement dates and were lower than more drought tolerant species. The relatively low QUMA and QUSH gas exchange rates across the growing season may also reflect sub-optimal water availability for these species.

Carbon allocation from photosynthate differed between the three species. For example, SS contents were greatest in QUSH, intermediate in QUVI, and lowest in QUMA while PPP contents were the opposite— highest in QUMA, intermediate in QUVI, and lowest in QUSH. Live oak appears to allocate more carbon to height growth than the other two species while likely maintaining moderate leaf carbohydrate and chemical defense compounds. Shumard oak and QUMA had reduced height growth rates, so these species may have maintained greater accumulation of SS and NSS in leaves rather than translocating carbohydrates to shoots and branches for growth. Balok and St. Hilaire (2002) reported QUMA leaves were some of the thinnest and had some of the least epicuticular wax contents while QUSH had moderately thick leaves with some of the greatest epicuticular wax contents of the species they studied. Greater wax contents often reduce insect feeding and movement, and increase insect falling frequency (Eigenbrode 2004, Gentry and Barbosa 2006, Znidarcic et al. 2008). The waxy coating on QUSH leaves may help compensate for the reduced PPP contents and amounts of PB by PPP were seen in this species. Oaks produce leaves with high amounts of hydrolysable tannins (Grundhöfer et al. 2001, Salminen et al. 2004). Hydrolysable tannins are more effective than condensed tannins at deterring insect and mammal herbivory in some studies (Rossiter et al. 1988, Barbehenn et al. 2006) and, at contents over 97.7 mg tannic acid equivalent per g of dry leaves, led to 70% cattle mortality in a study by Garg et al. (1992). QUSHs may rely on greater amounts of these compounds or others for defense to a greater extent than condensed tannins. Live oak leaves are thick and have waxy coatings as well that may help deter herbivores (Knapp and Carter 1998, Cavender-Bares and Pahlich 2009). The moderate PPP contents and amounts of PB by PPP may serve as an additional defense for QUVI that must retain its leaves for most of the year.

Similarities between W and D_{rec} Saplings

Leaf gas exchange can recover within a couple days after precipitation pulses, possibly explaining why leaf water potential and gas exchange values of individuals undergoing the post-drought recovery (D_{rec}) treatment did not differ from the continuously watered saplings. Loik et al. (2007) reported that photosynthesis, transpiration, conductance, and water potential of big sagebrush (*Artemisia tridentata* Nutt.) and antelope bitterbrush (*Purshia tridentata* (Pursh.) DC) increased within one day of an experimental water pulse addition and were greatest within 2-3 days. In a study by Sala et al. (1982), pre-dawn and mid-day leaf water potential of blue grama (*Bouteloua gracilis* (H.B.K.) Griffiths) exhibited a quick response to watering, recovering to pre-drought levels after 3 days, while the response of stomatal conductance was a little slower, reaching values characteristic of non-stressed conditions after 7 days.

Foliar SS, NSS, and PPP contents were similar among D_{rec} and W saplings. Although D_{rec} and W saplings in the same shelter were exposed to different conditions prior to the experiment period discussed here (phase II), these species produce new leaves each year that, as seen in my results, may change composition fairly quickly as compounds are assembled and translocated to other tissues (Lindroth et al. 2002, Landhäusser and Lieffers 2003, Martinez-Trinidad et al. 2009).

Conclusions

I found little evidence to support that reductions in foliar carbon-based compounds (SS, NSS, PPP) occur with drought although I only monitored individuals for one growing season (approximately 5 months). Notably drought in Texas often occurs in a highly episodic manner from year-to-year, suggesting that carbon-based defense allotment by these oaks against herbivory is not inducible in response to variable drought. Phenology, other climatic, or biotic effects may have greater prevalence in driving foliar carbon allocation and translocation. Species varied in tolerance to drought and carbon allocation to growth, SS, NSS, and PPP. Of the three species studied, the differences in gas exchange following alterations to water supply suggest QUVI may be best equipped to succeed during long-term drought conditions dotted with periodic precipitation pulses. Differences between species foliar N, carbohydrate and PPP contents, and ability of PPP to bind protein may affect species utilization by insects and browsing mammals as well, which may be of particular significance during drought events when little plant material is available from other sources.

CHAPTER III

THE TORTOISE AND THE HARE: WILL RESPROUTING OAKS WIN THE RACE AGAINST REGENERATING PINES FOLLOWING A SEVERE WILDFIRE?

Synopsis

Post-fire shifts in species composition and growth are driven in part by alterations in resource availability. This study tested how loblolly pine (*Pinus taeda* L.) seedlings and resprouting oaks (*Quercus stellata* Wangenh. (post oak) and *Q. marilandica* Muenchh. (blackjack oak)) responded to various stresses following a catastrophic wildfire in the Lost Pines region in Bastrop County, TX, USA. General plant responses (heights, diameters, and density) and stress indicators (leaf water potential, gas exchange, pressure-volume parameters, and leaf biochemistry) were monitored along resource availability gradients (three burn severities and three soil types) in the summers of 2015 and 2016. Pines were 95% shorter and 137% less dense in severely burned plots than moderately burned plots in 2015. In 2016 pines were still less numerous (190% less) in severely burned plots but were similar in size to those in moderately burned plots. Pines consistently had high midday leaf water potential and low photosynthesis, transpiration, and conductance rates when compared to co-occurring oaks. Pines also tended to have greater osmotic potential at full turgor (Π_{FT}) (20%), turgor loss points (Π_{TLP}) (22%), relative water content at the turgor loss point (RWC_{TLP}) (4%), and bulk modulus of elasticity (55%) than oaks. Pines additionally had lower capacitance at full turgor (C_{FT}) (49%) and capacitance at turgor loss point (C_{TLP}) (32%)

than oaks. Loblolly pine leaf-level gas exchange and pressure-volume results suggest this species prefers a drought-avoidance strategy. Low stomatal conductance and gas exchange rates in pine seedlings may reflect greater stomatal control which could reduce cavitation risks. Alternatively, lower gas exchange rates may have arisen from reduced access to water resources by seedlings' shallow roots. Gas exchange and pressure-volume parameters of the oaks reflect greater drought tolerance than pine, with post oak being the more tolerant of the two oak species. Post oak increased gas exchange, C_{FT}, and C_{TLP} and decreased Π_{FT}, Π_{TLP}, and RWC_{TLP} as burn severity increased. Increased capacitance and reductions in Π_{TLP} extend leaf turgidity and functionality and likely contributed to the maintenance of post oak stomatal conductance and gas exchange in the more exposed severely burned areas. Differences in foliar nutrient and phenolic contents between oaks and pines may reflect differences in leaf-level gas exchange capability of the two genera. Results suggest loblolly pine regeneration may be slower in more severely burned areas, and that differences in strategies among the three species may shift stand composition to oak dominance in parts of this region following a wildfire.

Introduction

Fire has historically favored pines in environments exposed to repeated disturbances (Glitzenstein et al. 1995, Barton 1999, Rodríguez-Trejo and Fulé 2003, Pausas 2015). Prior to European settlement, fire was widespread and occurred frequently (Abrams 1992, Denevan 1992, Brose et al. 2001). Frequent, low-intensity fire favors the survival and growth of young pines and maintains pine dominance in mixed-forest stands (Waldrop et al. 1992, Gilliam and Platt 1999, Pollet and Omi 2002), while severe crownfire often results in a shift from pine- to a more oak-dominated forest, oak-shrubland, or grassland (Barton 2002, Savage and Mast 2005, Strom and Fulé 2007). Non-serotinous pines are more likely to struggle with regeneration following severe fire, so recovery of these species is not always successful and is more likely to require assistance (seedling planting and protection) (Retana et al. 2012, Carnicer et al. 2014). This combination of factors can be quite detrimental to maintaining unique mixed pine/oak ecosystems, including but not limited to the pine-mixed hardwood forests in the southeastern United States of America (USA) (Myers 1985, Frost 1993, Van Lear et al. 2005), the Mediterranean basin (Castro et al. 2004, Pausas et al. 2008), and the Sierra Occidental in north-central Mexico (Fulé and Covington 1998).

One such unique pine-oak ecosystem is the “Lost Pines” region located in Bastrop, Fayette, and Caldwell counties in central Texas, USA. The Lost Pines Ecoregion constitutes the western-most range of loblolly pine (*Pinus taeda* L.) in the USA. This 34,400 ha patch of pine-dominated forest was isolated from the East Texas Piney Woods ecoregion by over 160 km during the Pleistocene (Bryant 1977, Al-Rabab’ah and Williams 2004). The loblolly pines from this disjunct area are frequently exposed to harsh environmental conditions, receiving 250 to 500 mm less rainfall annually than the pines in east Texas (Manogaran 1975, Bilan et al. 1977), so they are often thought to be hardier than loblolly pines from other provenances. Multiple studies confirm the resilience of the loblolly pines from the Lost Pines region. For example, individuals from the Lost Pines provenance experienced lower mortality rates than those of other provenances in several studies (Goddard and Brown 1959, Rahman et al. 2003, Smith et al. 2014). Lost Pines seedlings have greater transpiration and conductance under well-watered conditions (Bongarten and Teskey 1986, Wakamiya-Noborio et al. 1999) and decrease gas exchange to a greater degree under drought conditions compared to loblolly pines from other provenances (Bilan et al. 1977, Seiler and Johnson 1988, Wakamiya-Noborio et al. 1999), all of which may help them withstand the dry conditions characteristic of the region. However, some studies have shown no differences in drought responses between Lost Pines individuals and those from other provenances, while others have suggested Lost Pines individuals are actually less drought-resistant than those from other areas (Bongarten and Teskey 1986, Retzlaff et al. 2001, Yang et al. 2002).

The thick bark of older loblolly pine trees provides some protection against light to moderate burn severity, but overall the species has limited tolerance to fire. Historically, due to this limited tolerance, loblolly pine was generally outcompeted by longleaf pine (*Pinus palustris* Mill.) and shortleaf pine (*Pinus echinata* Mill.) in sites exposed to regular fire regimes (Schultz 1997, Stewart 2015). Intense logging and fire prevention in the early 1900s allowed loblolly pine to expand past moist fringes and into more upland sites throughout its natural range (Schultz 1997). Loblolly pines do not produce serotinous cones or have a grass stage like longleaf pine which provides fire immunity, but they do possess the limited ability to sprout from dormant buds along the stem following top-kill by fire or clipping (Shelton and Cain 2002, Will et al. 2013).

Seedlings will therefore not resprout if fire kills dormant buds or if they are severed near the ground below the cotyledons (Schultz 1997, Shelton and Cain 2002).

The Bastrop County Complex Fire ignited on September 4, 2011, and was the most destructive fire in recorded Texas history. The combination of extreme summer drought, high temperatures, low relative humidity, live fuel moistures below historic lows, and strong wind gusts caused by a tropical storm contributed to prime conditions for a devastating fire (Hoerling et al. 2013, Rissel and Ridenour 2013). More than 12950 ha and 1.8 million trees were burned (Rissel and Ridenour 2013). Pine mortality was 100% in severely burned areas and many of the less burned areas also saw high stress-related tree mortality. Many areas experienced subsequent erosion and topsoil loss. Nutrient loss and export to nearby ponds was observed with decreases in the pH and dissolved O_2 content of local water bodies (Brown et al. 2014).

Prior to the Bastrop County Complex Fire, the region was dominated by loblolly pine with some areas having a significant contribution from oaks. Data from FIREMON plots suggest pine composed 75% of the combined overstory and mid-story tree basal area of Bastrop State Park prior to the wildfire, while hardwoods and juniper made up about 24% and 1%, respectively, on average (G Creacy, personal communication). In the years following the fire, post oak (*Quercus stellata* Wangenh.) and blackjack oak (*Quercus marilandica* Muenchh.) resprouts cropped up and are thriving, indicating that some areas that were previously pine-dominated may be on a trajectory toward becoming oak-dominated woodland or savanna (personal observations). These biotic “ecological legacies” persisting from the pre-fire ecosystem are likely to have major effects on vegetation recovery and succession post-disturbance (Clements 1916, Turner and Dale 1998, Franklin et al. 2002, Johnstone et al. 2016). Prolific resprouting of Gambel oak (*Quercus gambelii* Nutt.), alligator juniper (*Juniperus deppeana* Steud.), New Mexico locust (*Robinia neomexicana* A. Gray) (Strom and Fulé 2007) and silverleaf oak (*Quercus hypoleucoides*) (Barton 2002) quickly outpaced pine regeneration in previous studies, and it appears as if a similar situation may occur in some areas within the Lost Pines. Resprouting species have the advantage of utilizing remaining deep root systems from mature top-killed trees. These deeper root systems not only help resprouts withstand drought, but also support their rapid growth rates through the mobilization of carbohydrates from decaying root tissue (DeSouza et al. 1986, Castell et al. 1994, Del Tredici 2001). Shallow-rooted regenerating pine seedlings may not be competitive with these deep-rooted resprouts for water and nutrients. On the other hand, pine seedlings have the advantage of photosynthesizing and growing during the fall and winter while resprouting deciduous trees are dormant (Schultz 1997). A shift to an oak-dominated stable state could have substantial effects on ecosystem functions (Strom and Fulé 2007). Areas with light-to-moderate burn severities may retain pine dominance better than those where the fire was more severe (Gilliam and Platt 1999, Pollet and Omi 2002, Savage and Mast 2005).

Differences in leaf level gas exchange and hydraulic properties between pines and resprouting oaks may play a large role in species success following disturbance. Resprouts often have greater gas exchange rates (e.g. photosynthesis, transpiration, stomatal conductance) than mature plants of the same species (DeSouza et al. 1986, Reich et al. 1990, Castell et al. 1994) and non-sprouting individuals from other species (Thomas and Davis 1989). These greater gas exchange rates, however, may come with greater risk, especially during drought. A global analysis by Pausas et al. (2016) suggested non-sprouters were more resistant to dehydration-induced cavitation than resprouters. Many resprouting species, including oaks, are classified as drought tolerant, while pines, including loblolly, are often drought avoiders. Oaks have larger leaves, large diameter vessels with high hydraulic conductivity, and operate with small "safety margins", exhibiting progressively more negative leaf water potentials (while maintaining relatively high gas exchange) with increasing water stress and evaporative demand (Abrams 1990, Cavender-Bares and Bazzaz 2000, David et al. 2007, McCulloh et al. 2010). Pines have small evergreen leaves, use small diameter tracheids to transport water, and utilize larger hydraulic safety margins than many angiosperms (McDowell et al. 2008, McCulloh et al. 2010, Choat et al. 2012). Oaks are less sensitive to vapor pressure deficits and decreases in soil moisture (Kolb and Stone 2000, Stoy et al. 2006, Ford et al. 2010, Meinzer et al. 2013, Renninger et al. 2015), have greater leaf-level gas exchange rates (Kolb and Stone 2000), and reach maximum photosynthesis rates at lower levels of sunlight than pines (Kramer and Decker 1944, Kramer and Clark 1947). Oaks are also described as frequently having low osmotic potential at full turgor (Π_{FT}), turgor loss points (Π_{TLP}), relative water content at the turgor loss point (RWC_{TLP}), and high capacitance at full turgor (C_{FT}) as well as bulk elastic modulus (ε) (Parker et al. 1982, Bahari et al. 1985, Aranda et al. 1996), all of which further signify drought tolerance (Tyree and Hammel 1972, Schulte and Hinckley 1985, Bartlett et al. 2012).

Within the *Quercus* genus, however, leaf morphology and whole-plant structure varies greatly along with species' ability to cope with water stress (Abrams 1990, Dickson and Tomlinson 1996). White oak species, such as post oak, are more tolerant to drought stress than red oak species, such as blackjack oak (Seidel 1972, Abrams et al. 1990, Kleiner et al. 1992, Vivin et al. 1993), although exceptions have been reported (Wuenscher and Kozlowski 1971, Bahari et al. 1985). Contrasting morphology and physiological responses to water availability may not necessarily benefit one genera or species over another, however, since shifts in conditions will also change which species is favored at different times (Zweifel et al. 2009, Ford et al. 2010, Renninger et al. 2015).

In addition to biotic legacies, modifications of the physical environment by disturbance may affect regeneration success. Leaf chemical composition following disturbance may reflect resource availability to both resprouting and non-sprouting species and their degree of stress. Leaves from resprouts and young non-sprouting individuals often have greater nutrient (e.g. nitrogen (N), phosphorus (P), potassium (K), etc.) contents than mature leaves from the same species (Oechel and Hastings 1983, Reich et al. 1990, Castell et al. 1994). Fire may alter plant tissue C:N ratios due to changes in nutrient availability in burned soil (Ojima et al. 1994, Nardoto et al. 2006). Nitrogen volatilizes at relatively low temperatures and is therefore lost in greater amounts than P, K and Ca that volatilize at higher temperatures (> 500 ºC) (Boerner 1982, Caldwell et al. 2002); however, the availability of N remaining in the soil may be greatly increased following fire (Daubenmire 1968, Klopatek et al. 1990, Grogan et al.

2000, Turner et al. 2007) which may contribute to enhanced growth after fire (Christensen and Muller 1975, Ojima et al. 1994, Brockway and Lewis 1997). Plant secondary compound contents, such as condensed tannins (protein-precipitable phenolics; PPP), may also reflect stress conditions experienced by regenerating and resprouting plants due to photoxidation, high levels of PAR, and UV radiation (Fleck et al. 1998, Close and McArthur 2002, Turtola et al. 2005, Abdala-Díaz et al. 2006, Mellway et al. 2009) following canopy removal or herbivory (Bryant et al. 1983, Coley and Barone 1996, Boege and Marquis 2005). Climatic stress is reported to increase production of PPP and their reactivity (e.g. protein binding ability) (Tharayil et al. 2011).

Objectives

The goal of this study was to evaluate how ecological biotic and abiotic legacies might affect loblolly pine recovery following the Bastrop County Complex Fire. As an early indicator of post-fire success, I compared differences in size and photosynthesis rates among species to varying stress response indicators across soil type and burn severity gradients. The stress response indicators evaluated included gas exchange, pressure volume parameters, and leaf biochemistry (N, C, and PPP content). I used soil type as a surrogate for soil water and nutrient limitation, as well as burn severity, which correlates strongly with loss of topsoil and associated nutrients (Neary et al. 1999, González-Pérez et al. 2004). The primary hypothesis tested was that resprouting oaks acting as the proverbial “hare” would have a greater advantage initially over pine seedlings, the “tortoise” in this case, in areas with greater resource limitations. A secondary hypothesis tested was that post oak would be a better competitor than blackjack oak, as a potential indicator of species dominance over time. Results will provide insight into loblolly pine responses to severe fires and help guide replanting and vegetation management decisions in the Lost Pines region.

Materials and Methods

Site Description

This study was conducted within Bastrop State Park and the Griffith League Ranch, Bastrop County, Texas. Fire suppression over the past century resulted in heavy fuel loads and dense thickets of yaupon holly (*Ilex vomitoria* Sol. ex Aiton) and other shrubs (Brown et al. 2013, Brown et al. 2014). Dominant overstory species include loblolly pine, post oak, blackjack oak, and eastern red cedar (*Juniperus virginiana* L.). Yaupon holly, American beautyberry (*Callicarpa americana* L.), and farkleberry (*Vaccinium arboreum* Marshall) are common understory species. Soils in the study areas consist of sands and sandy loams from the Patilo-Demona-Silstid and Axtell-Tabor associations with some exposed areas of gravel or clay on steep, eroded slopes (Baker 1979). Temperatures in the area typically range from 12.7 – 26.5ºC annually, and the region receives around 820 mm of annual precipitation.

Following the Bastrop County Complex Fire, the Texas Parks and Wildlife Department (TPWD) mapped burn severities in Bastrop State Park using satellite imagery and ground validation. The burn severity classification used severity ratings developed by the U.S. Department of the Interior based on pre-fire vegetation density, degree of ground cover and soil organic matter consumption, changes to soil surface color, and structural aggregate stability (Parson et al. 2010, Cardenas and Kanarek 2014). Within the park, measurements were taken in areas classified by TPWD as “moderately” and “severely” burned. I wanted to extend leaf-level measurements into “lightly” burned areas as well, but these areas in in the park typically had intact, mature oaks and pines. In order to examine physiology of resprouting oaks and regenerating pine seedlings across a range of disturbance severities, additional plots were chosen to monitor leaf-level gas exchange and pressure-volume parameters at the Griffith League Ranch within an area which received a prescribed burn approximately one year prior to the Bastrop County Complex Fire (Brown et al. 2014). Following the prescribed fire and thinning of trees along the roadway for a firebreak against future fire (R Denison, personal communication), numerous blackjack and post oak resprouts and pine seedlings were growing in the area. Based on visual inspection of sites, herbaceous regrowth, and description of the prescribed fire, this area was classified as “lightly” burned.

Plot Surveys

Heights, diameters, and densities of naturally-regenerating loblolly pine seedlings and resprouting blackjack and post oaks were measured in 150 m^2 plots in Bastrop State Park in two burn severity classifications, moderate and severe, within three soil types: Edge (fine, mixed, active, thermic Udic Paleustalf), Jedd (fine, mixed, semiactive, thermic Ultic Paleustalf), and Padina (loamy, siliceous, active, thermic Grossarenic Paleustalf) soils (Soil Survey Staff 2016). Each soil type by burn severity combination was replicated three times. Measurements were conducted in July 2015 (n = 18 plots) and July 2016 (n = 18 plots) for a total of 36 plots surveyed. The Padina series is characterized by very deep fine sand (165 – over 250 cm), while the Edge and Jedd sandy loams are typically more shallow, approximately 150 and 75 cm, respectively. Of the three, Padina has the greatest water storage capacity but may drain quickly which could exacerbate drought (Hacke et al. 2000). As such, we may expect establishment to be easiest on Padina sites although individuals may still experience stress in these sites during drought which may ultimately limit recovery. Sites in the Padina soil type were selected for further leaf gas exchange comparisons since it appears the least ‘stressful’ of the three soil types. Narrow plots (50 m long and 3 m wide) were established in order to avoid edge effects from adjacent patches classified as other burn severities and to capture possible burn heterogeneity within a particular burn severity classification. I took height and diameter measurements of all loblolly pine, blackjack oak, and post oak individuals falling within a plot while documenting the number of individuals of each species within the plot. Height was measured at the terminal bud, and diameter was measured at the ground surface. Most oak resprouts had multiple stems, so I measured the diameter of the three largest stems and the height of the tallest individual stem for each resprouting individual.

Leaf Biochemical Analyses

Within each plot leaf samples were collected for N, C, and condensed tannin (CT) analyses in both 2015 and 2016. Leaves and needles were collected from the outer portions of branches in the upper half of the canopy. If the number of individuals falling within the plot was insufficient to gather an adequate quantity of material, the sampling boundary was expanded and leaves were collected from seedlings and resprouts within 5 m of the plot's center line (10-m width). Following collection, leaf material was dried at 75ºC for 48 hours in a forced-air oven, and then ground it in a sheer mill and stored it at room temperature until it was analyzed. A Vario MACRO C-N Analyzer (Elementar Americas, Inc., Mt. Laurel, NJ) was used to determine percent N and C of the ground leaf material.

Condensed tannins were purified to create standards for all three species by following Naumann's (2014) modification of the method described by Wolfe et al. (2008). Ground plant tissue (20 g DM) was extracted with 250 ml of acetone:water (700 ml l^{-1}), retaining the aqueous portion containing CT and removing residual acetone by evaporation under reduced pressure. The extract was mixed, along with enough methanol:water (500 ml l^{-1}) to form a slurry, with Sephadex LH-20 (GE Healthcare Bio-Sciences Corp., Piscataway, NJ), and repeatedly washed with methanol:water (500 ml l^{-1}) until the absorbance at 280 nm was negligible (absorbance ≤ 0.10). An acetone:water (700 ml l^{-1}) wash was used to release CT bound to the Sephadex, followed by evaporation of residual acetone by air stream/vacuum. The aqueous portion containing CT was frozen at -80 °C and lyophilized. Purified CT were then used to develop species-specific standards for the protein-precipitation assays.

Hagerman and Butler's (1978) scaled down method was modified to determine protein precipitability of CT. Duplicate crude plant extracts for each species within a plot were prepared by extracting 50 mg of plant tissue with 1 mL methanol:water (500 ml l^{-1}) on a G10 Gyrotory® shaker (New Brunswick Scientific Co., Inc., Edison, NJ) for 30 min followed by centrifugation at 16,070 x *g* for 5 min. To determine protein-precipitable phenolic (PPP) contents and the amount of protein bound (PB) by PPP, 50 µl of supernatant from crude plant extracts were combined with 250 µl buffer A (0.20 M acetic acid, 0.17 M sodium chloride, pH 4.9), 50 µl bovine serum albumin (BSA) (5 mg ml^{-1} in buffer A), and 50 µl methanol:water (500 ml l^{-1}) and the solution was incubated at room temperature for 30 min prior to centrifuging at 16,070 x *g* for 5 min. The supernatant was removed using vacuum aspiration and the protein-phenolic pellet washed with buffer A (250 µl) before re-centrifuging and aspirating again. The protein-phenolic pellet was dissolved in 800 µl of sodium dodecyl sulfate (10 g l^{-1})-triethanolamine (50 ml l^{-1}) (SDS/TEA) before adding 200 µl $FeCl_3$ (0.01 M $FeCl_3$ in 0.01 M HCl). After 15 minutes, the absorbance was read at 510 nm. Absorbances were translated to PPP contents via external standards for each species.

Following Naumann et al.'s (2014) method to determine the amount of protein bound by PPP, the procedure was performed as described above, but the protein-phenolic pellet was analyzed for N to quantify precipitated protein. Rather than dissolving the protein-phenolic pellet in SDS/TEA, the pellet was dissolved in 500 µl of buffer A and the solution was transferred into a foil cup to dry. A Vario MACRO C-N Analyzer (Elementar Americas, Inc., Mt. Laurel, NJ) was subsequently used to analyze the dried protein-phenolic residue for percent N, which was then multiplied by 6.25 (Van Soest 1994) to calculate the amount of protein bound by PPP.

Leaf-Level Physiological Measurements

Gas exchange, leaf water potential, and pressure-volume measurements were conducted on leaves from blackjack and post oak resprouts and loblolly pine seedlings in three burn severities (lightly, moderately, and severely burned) in June and early July 2016. Gas exchange and midday leaf water potential measurements were performed 15 to 17 June, and pressure-volume measurements were completed 6 – 8 July, 2016. Measurements were conducted at three plots (replications) within each burn severity. Moderate (n = 3 plots) and severe (n = 3 plots) leaf-level physiology sites were located at Bastrop State Park and corresponded with the locations of 2016 height and diameter stand survey plots in the Padina soil (Moderate x Padina and Severe x Padina). Lightly burned (n = 3) leaf-level physiology plots were established in Padina soil as well at the Griffith League Ranch. At each site, I conducted midday gas exchange measurements (930 – 1430 hrs) with an open-flow gas analyzer system (LI-6400, Li-Cor, Lincoln, NE, USA) on leaves or fascicles of needles from the upper half of the canopy of each of two individuals of both oak species and loblolly pine, respectively. Gas exchange measurements were conducted on fully expanded sunlit leaves at ambient temperature and fixed PAR of 2000 µmol m^{-2} s^{-1}, air flow of 500 µmol s^{-1}, and CO_2 of 400 µmol mol^{-1}. Measurements were collected after steady state conditions were reached, as indicated by stability of gas exchange parameters. Midday leaf water potential measurements were taken on leaves and fascicles using a Scholander-type pressure chamber (PMS Instrument Co., Corvallis, OR, USA) immediately after gas exchange measurements.

Pressure-volume curve analyses were conducted on leaves and fascicles from the same individuals used in gas exchange measurements. Leaves were collected before sunrise and stored them in a dark insulated container until pressure-volume curves were completed. I used the bench dry method for pressure-volume measurements (Tyree and Hammel 1972) with non-rehydrated leaves (Kubiske and Abrams 1991). Following pressure-volume curves, oak leaf areas were measured using a leaf area meter (LI-3100) and pine fascicle areas were measured using needle length and fascicle diameter (Grace 1987, Svenson and Davies 1992). Leaf and fascicle dry mass were measured following drying for 48 hours at 70°C. From pressure-volume curves I was able to calculate leaf osmotic potential at full turgor (Π_{FT}) and at the turgor loss point (Π_{TLP}), relative water content at the turgor loss point (RWC_{TLP}), capacitance at full turgor (C_{FT}) and at the turgor loss point (C_{TLP}), and bulk elastic modulus (ε) (Koide et al. 2000).

Statistical Analyses

Statistical tests were performed for effects of burn severity and soil type on loblolly pine and oak resprout height, diameter, density, leaf nutrient, biochemical parameters (PPP, PB, and PB:PPP), leaf-level gas exchange, and pressure-volume parameters using linear mixed-models (proc mixed procedure, SAS 9.4, SAS Institute Inc., Cary, NC, USA). The effects of severity, soil type, species, and their interactions were tested for height, diameter, density, and leaf nutrient and biochemical parameters. Data from 2015 and 2016 were included together for leaf nutrient and biochemical parameters, so in those models "year" was considered a random effect. Replication within soil type × burn severity was considered random as well. To better explain observed growth differences between 2015 and 2016, I analyzed the effects of soil type, burn severity, species, and their interactions within each year, respectively, and in a second analysis compared the effects of soil type, burn severity, and year on the growth of each species.

Gas exchange and pressure-volume parameters were only monitored during summer 2016 across different burn severities on Padina soil, so "year" and soil type were not included in the model for these parameters. Replication within burn severity was considered a random effect within the model.

Differences were considered significant at $P \leq 0.05$ unless otherwise noted. When effects were detected in the model, I used the LSMEANS statement in SAS to estimate means. Differences between means were adjusted using Tukey's HSD post-hoc analysis.

Results

Variations in Oak and Pine Responses to Resource Alterations

The post-fire landscape contains both pine recruits and resprouting oaks, but differences in soil type, and especially burn severity, appear to play a large role in driving regeneration patterns. Interactions between soil type and other variables were not frequent, suggesting the three species respond fairly well to growing in all soil types that were surveyed. All three species tolerate moderately acidic conditions, shallow topsoils, and low nutrient availability (Ware et al. 1992, Abrams 1996, Schultz 1997,

Table 1. Average number of blackjack and post oak resprouts and loblolly pine seedlings in each burn severity x soil type combination in 2015 and 2016. Within each year, different uppercase letters (A) denote differences ($P \leq 0.05$) among species within a burn severity x soil type interaction. Different lowercase letters (a) denote differences ($P \leq 0.05$) within a species between the various burn severity x soil type interactions, in each year respectively.

2015							
	Moderate			Severe			
	Edge	Jedd	Padina	Edge	Jedd	Padina	SEM
Blackjack oak	$2.7^{B,a}$	$3.3^{A,a}$	$1.3^{A,a}$	$1.3^{A,a}$	$5.0^{A,a}$	$3.7^{A,a}$	5.0
Post oak	$2.3^{B,a}$	$1.0^{A,a}$	$4.7^{A,a}$	$3.7^{A,a}$	$3.0^{A,a}$	$0.7^{A,a}$	5.0
Pine	$41.0^{A,a}$	$21.0^{A,ab}$	$14.3^{A,ab}$	$7.0^{A,b}$	$3.0^{A,b}$	$4.3^{A,b}$	5.0
2016							
	Moderate			Severe			
	Edge	Jedd	Padina	Edge	Jedd	Padina	SEM
Blackjack oak	$3.7^{A,a}$	$6.7^{A,a}$	$1.7^{A,a}$	$4.0^{A,a}$	$2.7^{A,a}$	$3.7^{A,a}$	4.4
Post oak	$0.3^{A,a}$	$1.3^{A,a}$	$2.7^{A,a}$	$1.3^{A,a}$	$0.3^{A,a}$	$3.3^{A,a}$	4.4
Pine	$19.0^{A,ab}$	$8.0^{A,ab}$	$23.3^{A,a}$	$0.7^{A,ab}$	$0.3^{A,b}$	$0.3^{A,b}$	4.4

Clark and Hallgren 2003), which may explain this uniformity across different soil types. Growing conditions have been relatively mesic since the fire, and substantial drought has not been observed over the life span of the seedlings/resprouts. In the 12-mo period prior to the 2015 plot surveys, the region received approximately 1067 mm of precipitation (SRCC 2017). The region received approximately 1549 mm of precipitation in the 12-mo period prior to the plot surveys in 2016 (SRCC 2017).

In both 2015 and 2016, considerably more pine seedlings were found in moderately burned plots than severely burned plots, with many severely burned plots having no pine regeneration at all (Table 1). The ratios of pines in moderately burned

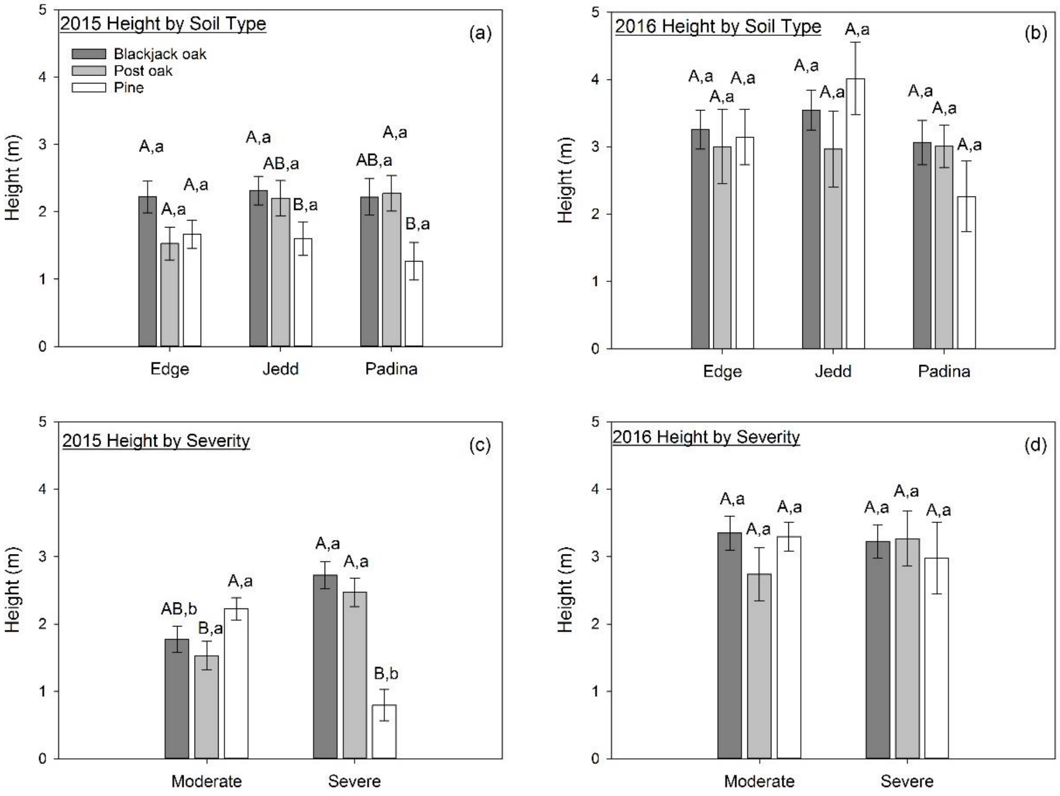


Figure 13. Blackjack and post oak resprout and loblolly pine seedling heights across soil types and burn severities in 2015 and 2016. Within the respective year, different uppercase letters (A) denote differences ($P \leq 0.05$) among species within each burn severity or soil type and different lowercase letters (a) denote differences ($P \leq 0.05$) between burn severities or soil types for a particular species.

plots to severely burned plots were on average over 5:1 and 37:1 in plots measured in 2015 and 2016, respectively. Burn severity had a greater effect on pine presence than soil type. All soil types within a particular burn severity had similar numbers of pine individuals. Oak presence was not affected by variations in burn severity or soil type, supporting the hypothesis that oaks may have a greater advantage over pines in areas with greater resource limitations after fire. However, oak growth was affected by burn

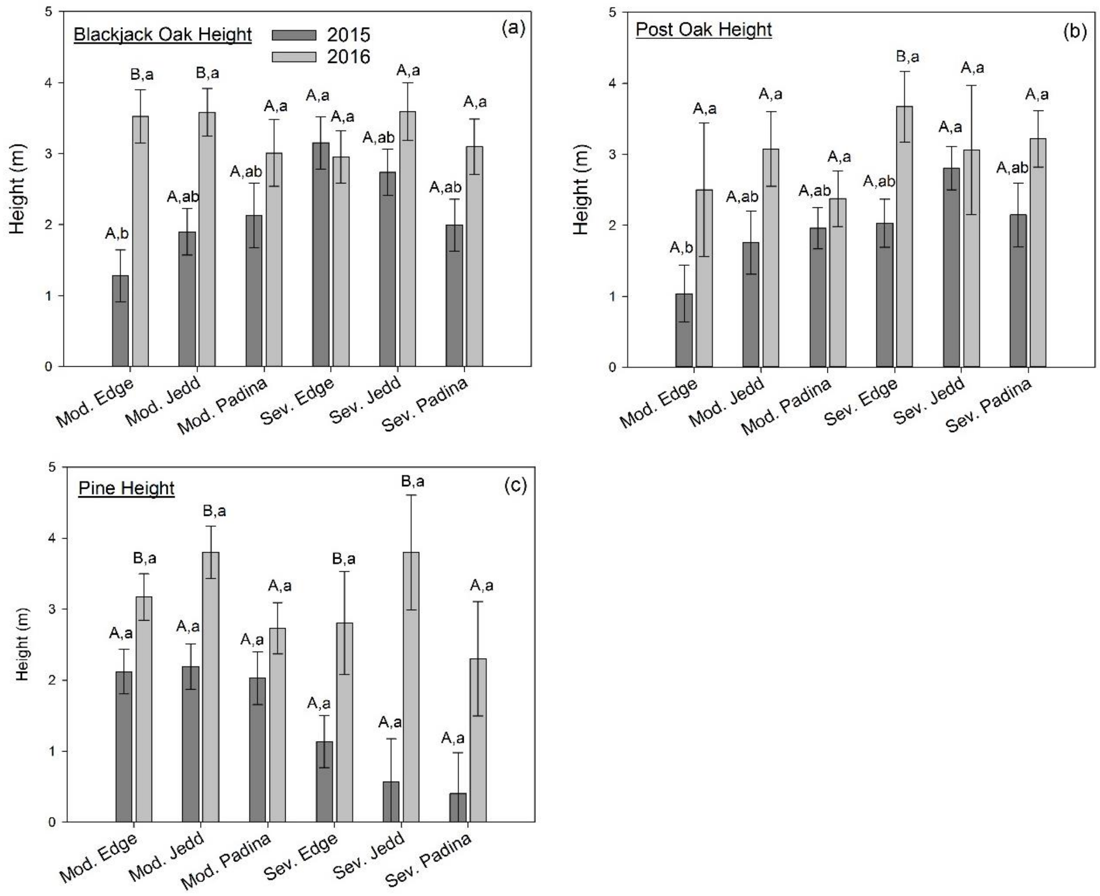


Figure 14. Comparison of blackjack and post oak resprout and loblolly pine seedling heights between 2015 and 2016 across soil type x burn severity combinations. Within each species, different uppercase letters (A) denote differences ($P \leq 0.05$) between years within each burn severity x soil type combination and different lowercase letters (a) denote differences ($P \leq 0.05$) between burn severity x soil type combinations in a particular year.

severity. In 2015, blackjack oaks and post oaks tended to be 42% and 47% taller, respectively, in severely burned plots than moderately burned plots (Figure 13, Figure 14). However for the pines, the opposite was true. The shortest pines with the smallest diameters were found in the severely burned plots in 2015 (Figure 13, Figure 14, Table 2), which was especially true in the severely burned x Padina soil combination. This

Table 2. Blackjack oak, post oak, and loblolly pine diameters (cm) within soil type and burn severity combinations in 2015 (species x severity x soil type interaction ($P \leq 0.05$)) and 2016 (species x severity x soil type interaction ($P = 0.32$)). Within 2015, different uppercase letters (A) denote differences ($P \leq 0.05$) among species within each burn severity x soil type interaction. Different lowercase letters (a) denote differences ($P \leq 0.05$) within a species between the various burn severity x soil type interactions in 2015.

2015												
	Moderate						Severe					
	Edge	SEM	Jedd	SEM	Padina	SEM	Edge	SEM	Jedd	SEM	Padina	SEM
Blackjack oak	$4.65^{A,a}$	0.52	$5.13^{A,a}$	0.49	$4.34^{A,a}$	0.61	$4.98^{A,a}$	0.54	$5.25^{A,a}$	0.53	$4.40^{A,a}$	0.53
Post oak	$2.40^{A,a}$	0.71	$4.98^{A,a}$	0.49	$3.92^{A,a}$	0.52	$5.35^{A,a}$	0.59	$4.23^{AB,a}$	0.59	$4.91^{A,a}$	0.58
Pine	$4.30^{A,a}$	0.46	$4.77^{A,a}$	0.67	$4.62^{A,a}$	0.51	$2.58^{B,ab}$	0.62	$2.32^{\mathbf{B},ab}$	0.86	$1.08^{B,b}$	0.77
2016												
	Moderate						Severe					
	Edge	SEM	Jedd	SEM	Padina	SEM	Edge	SEM	Jedd	SEM	Padina	SEM
Blackjack oak	5.48	0.55	6.18	0.51	5.02	0.66	5.06	0.55	6.13	0.62	5.08	0.57
Post oak	5.50	1.20	5.98	0.74	4.02	0.61	6.26	0.77	4.63	1.24	5.17	0.59
Pine	6.45	0.51	7.30	0.64	5.23	0.54	5.60	1.45	9.24	1.99	5.22	1.97

was likely because I only found pines in one of the three plots measured within this combination in 2015, and none of the individuals there were over 0.5 m tall or 1 cm in diameter. Therefore it appears that the pines within the severely burned areas may have

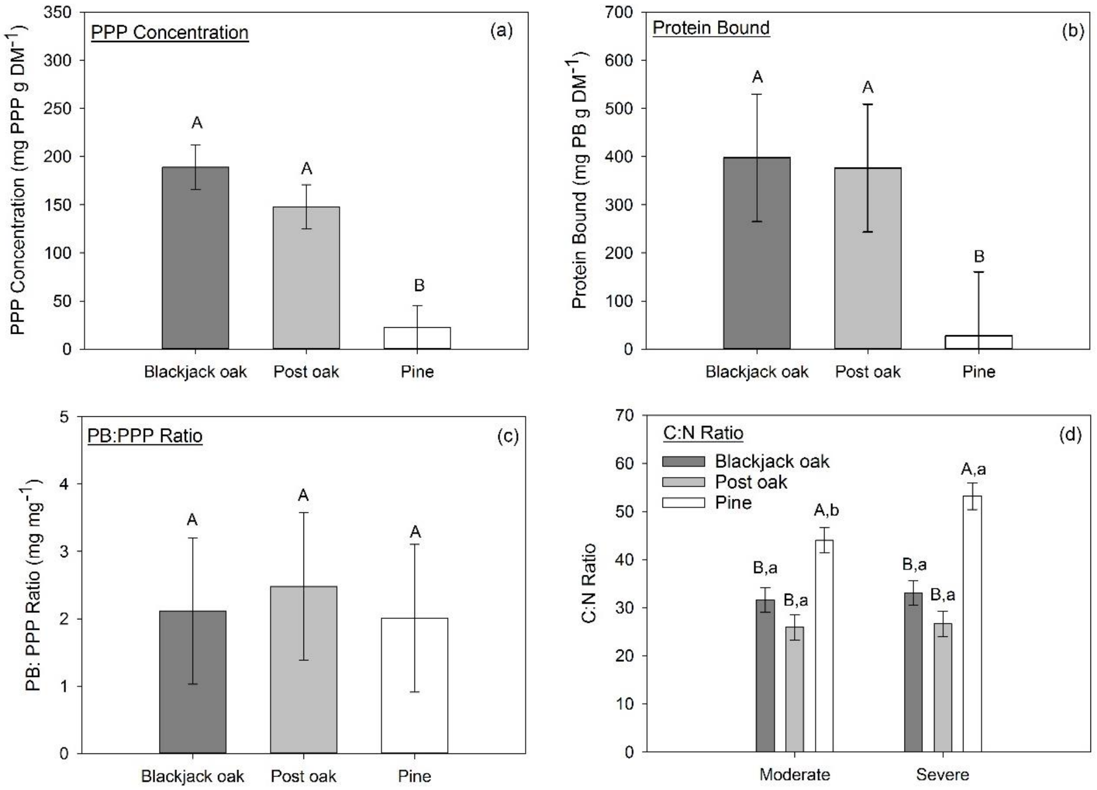


Figure 15. Blackjack and post oak resprout and loblolly pine seedling a) leaf protein-precipitable phenolic (PPP) content, b) amount of protein bound (PB) by PPP, c) PB:PPP ratio, and d) C:N ratio.   Different uppercase letters (A) denote differences ($P \leq 0.05$) among species for PPP contents, amount of protein bound, and PB:PPP ratios. For C:N ratios, different uppercase letters (A) denote differences ($P \leq 0.05$) among species within each burn severity, and different lowercase letters (a) denote differences ($P \leq 0.05$) between burn severities for a particular species.

experienced resource limitations that slowed their establishment and growth, again supporting the first hypothesis. Pine C:N ratios seem to support this. Pine foliar C:N ratios were greater in severely burned plots which could indicate N limitation (Figure 15). The reduction in heights within the oaks in the moderately burned plots in 2015 likely resulted from the competition for resources with the numerous pine seedlings in these plots (Table 1).

However, by 2016, any differences in growth between the three species within the different burn severities and soil types had disappeared (Figure 13, Figure 14, Table 2). All species within each burn severity x soil type combination had similar heights and diameters at that time. Pines still maintained dominance in moderately burned plots, while oaks maintained dominance in severely burned plots. Although pine numbers in severely burned areas continued to remain low in the 2016 plots (190% less than moderate plots), their growth suggested they were quite healthy (Figure 13, Figure 14, Table 2).

Some leaf-level physiological properties appear strongly related to differences in site "quality" post-fire, even though any effect of resource limitation on species growth as a result of severity appears to have dissipated by 2016. For example, burn severity seemed to have conflicting effects on gas exchange and leaf hydraulic properties of the three species. Pines tended to increase Ψ_{MD} and decreasing gas exchange as burn severity increased, while post oaks displayed reversed responses, lowering Ψ_{MD} and increasing gas exchange with greater severity (Figure 16). Pine pressure-volume analyses also revealed a preference for more conservative water use strategies than co-

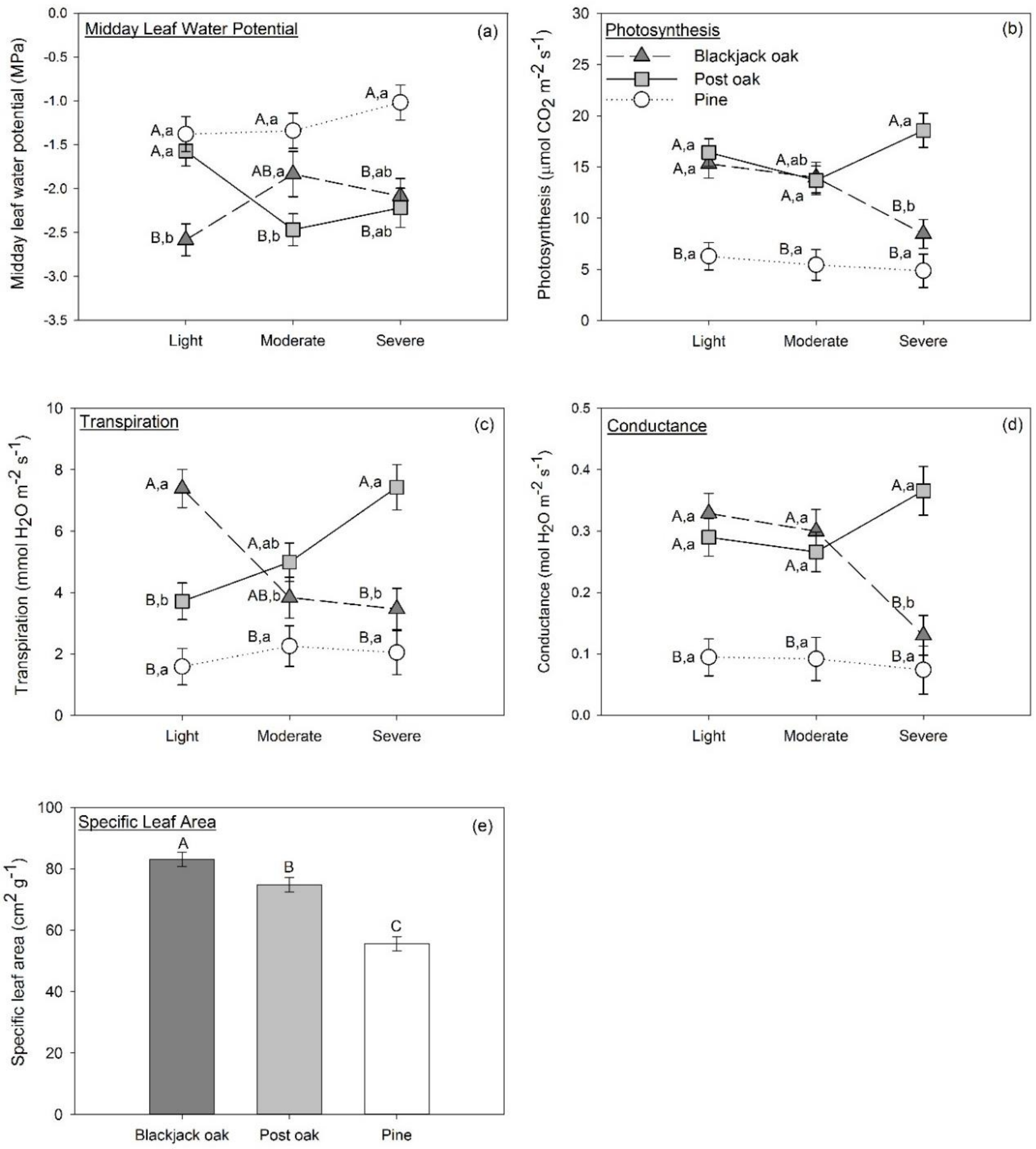


Figure 16. Blackjack and post oak resprout and loblolly pine seedling a) midday leaf water potential (Ψ_{MD}), b) net photosynthetic rates (A), c) transpiration rates (E), and d) stomatal conductance rates (g) across burn severities, e) and specific leaf area. For graphs a-d, different uppercase letters (A) denote differences ($P \leq 0.05$) among species within each burn severity, and different lowercase letters (a) denote differences ($P \leq 0.05$) between burn severities within a particular species. Differences between species specific leaf areas are represented by different uppercase letters (A).

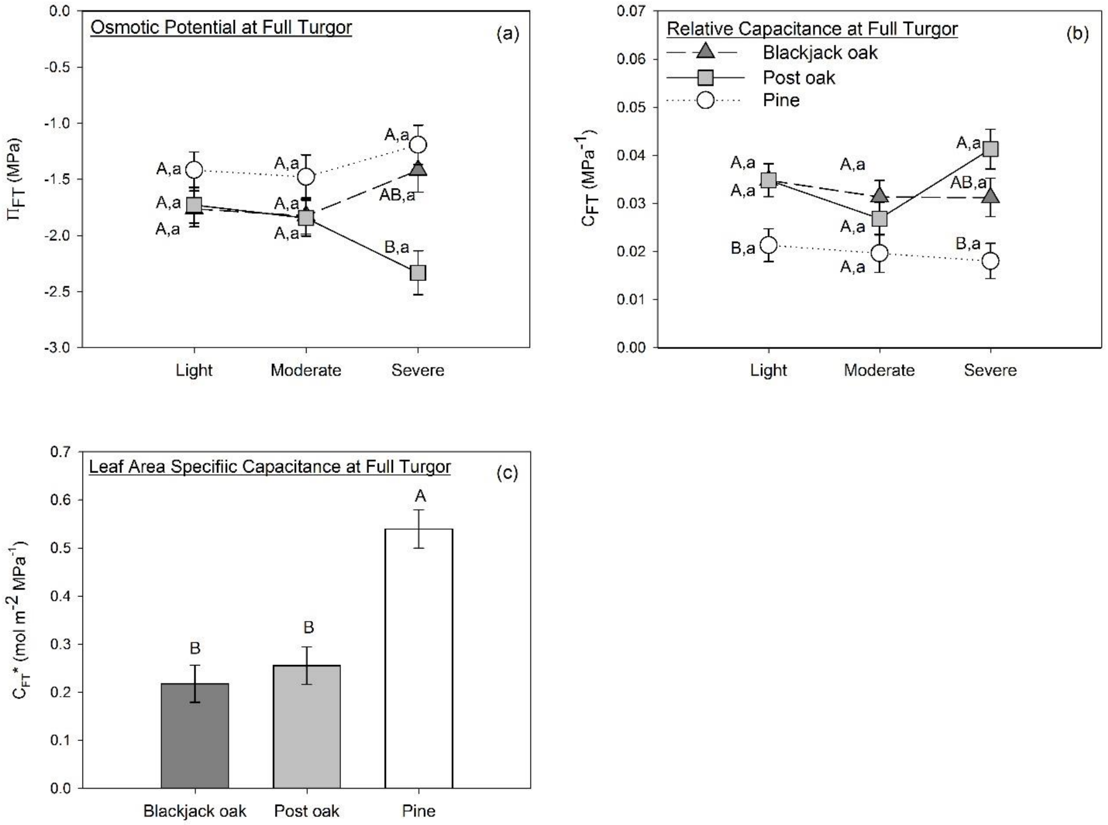


Figure 17. Blackjack and post oak resprout and loblolly pine seedling a) osmotic potential at full turgor (Π_{FT}), b) relative capacitance at full turgor (C_{FT}), and c) leaf area specific capacitance at full turgor (C_{FT*}). For graphs a and b, different uppercase letters (A) denote differences ($P \leq 0.05$) among species within each burn severity, and different lowercase letters (a) denote differences ($P \leq 0.05$) between burn severities within a particular species. Differences between species C_{FT*}, are represented by different uppercase letters (A).

occurring oaks, especially in sites with greater burn severity. Although not statistically different from the pines in less drastically burned areas, severely burned pines tended to have higher Π_{FT}, Π_{TLP}, and RWC_{TLP}, and lower C_{FT} and C_{TLP} (Figure 17, Figure 18). Leaf pressure-volume variables have been associated with hydraulic capability, and in this study they seem to have some relationship with leaf level gas exchange. For example, *A* was positively correlated with C_{FT*} in oaks and pines ($P \leq 0.05$ in post oak and pine, $P = 0.06$ in blackjack oak). C_{TLP} values were positively correlated with *E* in oak ($P \leq 0.05$ in post oak, $P = 0.06$ in blackjack oak). Pine *E* and C_{TLP} were both low but may not be related ($P = 0.28$).

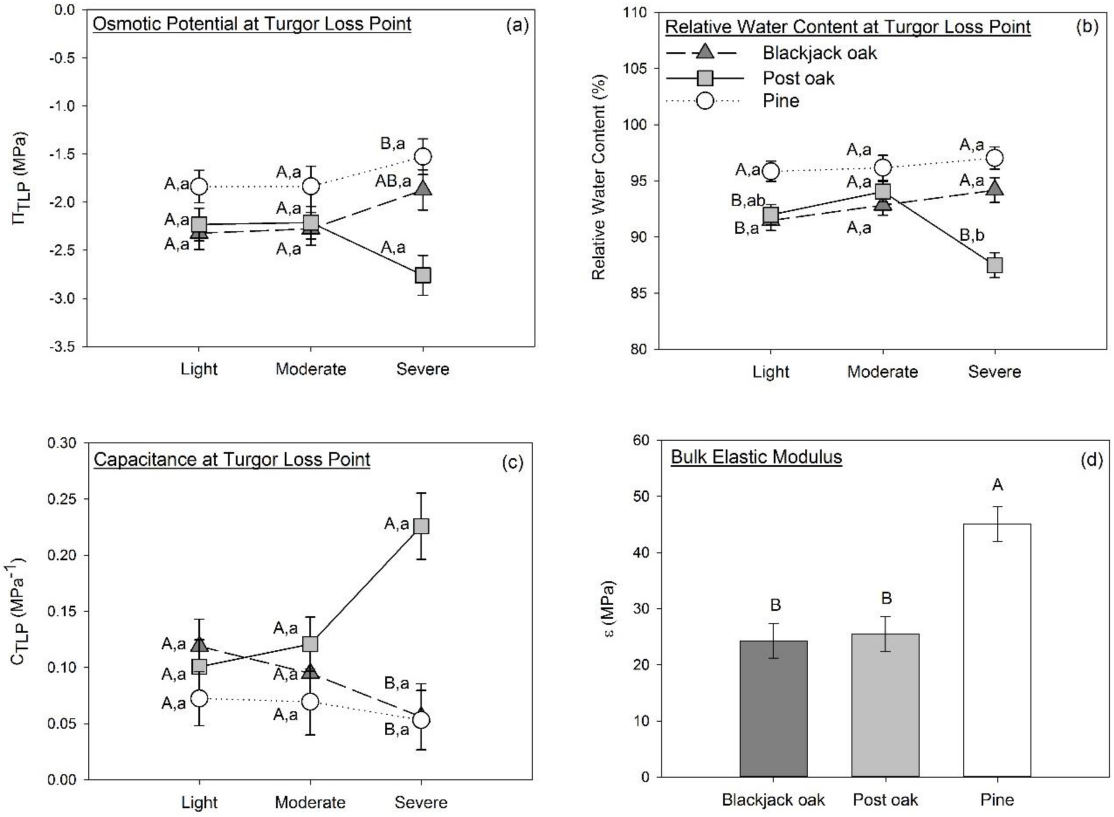


Figure 18. Blackjack and post oak resprout and loblolly pine seedling a) osmotic potential at turgor loss point (Π_{TLP}), b) relative water content at turgor loss point (RWC_{TLP}), c) capacitance at turgor loss point (C_{TLP}), and d) bulk elastic modulus (ε). For graphs a-c, different uppercase letters (A) denote differences ($P \leq 0.05$) among species within each burn severity, and different lowercase letters (a) denote differences ($P \leq 0.05$) between burn severities within a particular species. Differences between species' bulk elastic moduli are represented by different uppercase letters (A).

Several fundamental differences were documented between the physiologies of the different genera that appeared to hold true no matter the regenerating environment. For example, pines consistently had high Ψ_{MD} across all three burn severities (Figure 16). Blackjack oaks and post oaks usually had similar Ψ_{MD}, except in the lightly burned areas where blackjack oaks had lower Ψ_{MD} than post oaks. Additionally, rates of photosynthesis (*A*), transpiration (*E*), and stomatal conductance (*g*) were generally greater for oaks than pines, along with specific leaf area (Figure 16). Pines continuously had low gas exchange rates in all burn severities. Differences between oaks and pines carried over into the pressure-volume variables (Figure 17, Figure 18). Oaks tended to have lower Π_{FT}, Π_{TLP}, RWC_{TLP}, and ε than pines. C_{FT} and C_{TLP} was usually greater for the two oak species, but C_{FT} on a leaf area basis (C_{FT*}) was greater for the pines. Additionally, oak leaves had greater PPP contents and bound more protein (PB) per g DM than pine needles (Figure 15). Protein binding efficiency (g PB: g PPP) was similar among the three species, however.

Blackjack Oaks and Post Oaks Diverge in Leaf-Level Characteristics

Leaf-level gas exchange and pressure volume parameter analyses revealed disparities in post oak and blackjack oak responses to differences in burn severity. Results suggest that post oak is a better competitor than blackjack oak, supporting the second hypothesis. Post oaks generally had high gas exchange rates in all burn severities, but blackjack oaks reduced all three gas exchange parameters to rates similar to those of the pines at the severely burned sites (Figure 16). Blackjack oak gas exchange tended to decrease with burn severity, while post oak seemed to respond oppositely, exhibiting the greatest gas exchange rates within severely burned sites. Blackjack oaks also appeared to exhibit leaf hydraulic traits associated with water conservation with increasing burn severity, increasing Π_{FT}, Π_{TLP}, and RWC_{TLP} and decreasing C_{FT} and C_{TLP} like pine as burn severity increases (Figure 17, Figure 18). Again, post oaks seemed to tolerate high severity burning, exhibiting pressure-volume characteristics associated with drought tolerance in these sites. Post oaks' lowest Π_{FT}, Π_{TLP}, and RWC_{TLP} occurred in the severely burned sites along with their greatest C_{FT} and C_{TLP}. Post oak leaves also tended to have the greatest percent N, while blackjack oak leaves were intermediate between the other two species. Leaf level gas exchange and pressure volume properties give the impression that post oaks may be better competitors than blackjack oaks, particularly in severely burned areas. However, these diverging leaf-level characteristics may not ultimately determine how successful the two species will be in the future, since there were no differences between the number of individuals, heights or diameters of blackjack and post oak in any soil type x burn severity combination in 2015 or 2016.

Discussion

Evidence of Canopy Dominance Shifts in Severely Burned Areas

Results indicated that oaks may overtake pine regeneration in some areas of the Lost Pines region after the fire. For seedlings and resprouts, survival and growth are bottlenecks in species' progress to canopy occupancy (Denslow 1987, Kobe 1999, Montgomery and Chazdon 2002). It appears that site conditions in severely burned areas may have been unfavorable for the natural regeneration of loblolly pines, resulting in lower densities and slower recovery of pines in severely burned plots. Other studies have reported similar results. For example, following a wildfire in a mixed pine-oak forest of black pine (*Pinus nigra* J.F. Arnold) and Portuguese oak (*Quercus faginea* Lam.), oaks resprouted immediately and dominated the landscape during the first few years post-fire regardless of site conditions. In contrast, pine establishment occurred early in mesic plots but was delayed many years in xeric conditions (Gracia et al. 2002). Retana et al. (2002) reported that black pine and Scots pine (*Pinus sylvestris* L.) had almost disappeared from burned plots three years after wildfire and predicted that in 30 years 77 – 93% of plots dominated previously by those two species would be dominated by resprouting oak species.

High soil and air temperatures in severely burned areas reduce growth and survival of germinating pine seedlings (Barney 1951, Kramer 1957, Marx and Bryan 1971), possibly explaining low numbers and small sizes of pine individuals growing in severely burned plots. Greater radiation levels reaching the ground level in these exposed areas may have resulted in soil temperatures warm enough to inhibit seedling establishment and growth. Daily minimum temperatures 5 cm below the surface at the severely burned site were 25.1 ± 0.3 ºC, 27.7 ± 0.3 ºC, and 26.5 ± 0.3 ºC for June, July, and August respectively. Daily maximum temperatures at that depth for June, July, and August were 39.9 ± 0.8 ºC, 47.0 ± 1.0 ºC, and 40.4 ± 1.3 ºC, respectively. Daily minimum temperatures at 30-cm depth were 27.3 ± 0.3 ºC, 30.8 ± 0.2 ºC, and 29.0 ± 0.4 ºC for June, July, and August, suggesting temperatures were likely stressful across the entire root zone for the young pines. In a study by Barney (1951) loblolly pine root growth decreased at temperatures greater than 25 ºC. Kramer (1957) reported that as long as night-time air temperatures did not exceed 17 °C, 1-year old seedlings exposed to 30 °C day-time temperatures had the best height growth rates. However, the lesser the temperature difference between night and day, the slower seedlings grew.

Resprouting oaks in severely burned areas were also likely exposed to greater levels of radiation and warm soil temperatures post-fire than patches with some over-story remaining, but were able to use existing root systems to their advantage, which may be another reason why I did not see reduced growth in oaks in severely burned plots. Kanarek (2013) reported greater initial near-surface soil moisture available to surviving plants and new colonizers in severely burned areas of Bastrop State Park where the majority of trees were killed than in areas that experienced low-severity burn. However, live vegetation removal, coupled with a reduction of organic matter to further shade the surface and increase water holding capacity, can lead to rapid drying of upper soil and moisture stress to young plants with shallow root systems (Knapp 1985, Hoffman 1996).

Therefore, non-sprouting pines are at multiple disadvantages: struggling to grow roots in suboptimal soil temperatures while coping with potential drought. Loblolly pine seedlings have been reported to produce less numerous roots and root systems shorter in length with slower growth rates than hardwood species of the same age (Kozlowski and Sholtes 1948, Lee and Jose 2003). For example, Kozlowski and Scholtes (1948) reported that 1-year old loblolly pines had 30% less roots and 2.5 times shorter roots than similar aged white oaks. Post oak and blackjack oak growth rates are also relatively slow compared to other oak species and are often shorter in stature (Johnson and Risser 1973, Stahle and Hehr 1984). These species not only grow but thrive in areas with rocky terrain and relatively steep slopes and under xeric conditions, which may help them establish on the exposed rocky hillside conditions in some of the study plots (Abrams 1996, Clark and Hallgren 2003). Oaks are among the most deeply rooting species in the world (Davis and Pase 1977, Hinckley et al. 1981, Abrams 1996) so it is likely that the mature root systems of the Bastrop resprouts had access to deep soil moisture sources. Although I did not measure root depths of the oaks or pines, I observed reductions in sap flux in pine seedlings with little change in resprouting oaks during drought which provides evidence of potential disparities between rooting depths of the two genera during this stage of regeneration (Chapter IV).

Hindrances to loblolly seed dispersal that may shift species dominance must also be considered. Loblolly pine seedfall usually starts in October, and most of the seeds have been released by the end of December (Grano 1973). Seed germination begins around March when daytime temperatures range between 18 - 27ºC (Baker and Langdon 1990). The Bastrop County Complex Fire ignited on September 4, 2011, before pines could release seeds for the year. Following the combustion of most of the organic matter in severely burned patches there were likely very few seeds remaining to germinate from the previous year. Seed dispersion ranges from 61 to 91 m downwind from a seed source and only 23 to 30 m in other directions (Baker and Langdon 1990). Therefore, it may take several years before seeds are dispersed into the interior of large severely burned patches. This is likely part of the reason so few pine individuals were found in the plots. By the time other pines establish themselves, the microclimate may be too greatly altered by the resprouting oaks for successful pine regeneration.

Following the dispersal and establishment problems faced by pines, contrasting gas exchange and pressure-volume characteristics may have an effect on which species will ultimately win the race. The pines in this study consistently had low gas exchange rates, while the oaks more often than not had higher gas exchange rates. Many studies have reported lower gas exchange rates in loblolly pine than co-occurring hardwoods, particularly under conditions of low soil moisture (Kolb and Stone 2000, Springer et al. 2005, Poyatos et al. 2008, Renninger et al. 2015). Drought-avoidance strategies are reported in many conifer species (McDowell et al. 2008, Choat et al. 2012). Low gas exchange in pine seedlings in this study may reflect not only fundamental leaf-level differences between the genera, but also reduced access to resources by the shallow roots of these young individuals. Oaks continue gas exchange when leaf water potential is near or lower than -3.0 MPa (Ni and Pallardy 1991, Poyatos et al. 2008). Post and blackjack oaks are more drought tolerant than other oak species (Pastor and Post 1986, Abrams 1996), exhibiting greater gas exchange and allowing greater decreases in leaf water potential prior to stomatal closure at times of low soil moisture (Seidel 1972, Ni and Pallardy 1991).

Variability of oak and pine leaf-level properties carried over into the pressure-volume variables, with pines continuing to exhibit traits associated with drought-avoidance. Pines tended to have greater Π_{FT}, Π_{TLP}, RWC_{TLP}, and ε than oaks, hinting at the drought-avoidance strategy of the species, like gas exchange. Other studies report a coordination of gas exchange behaviors and pressure-volume parameters (Bahari et al. 1985, Sperry 2000, Brodribb and Holbrook 2003, Brodribb et al. 2003). Stomatal behavior depends on the interactions between soil and atmospheric water deficits as well as how well the vascular system supplies water. Stomata are thought to regulate water lost through transpiration to prevent water potential from falling below a threshold value that may cause xylem cavitation, reducing both xylem and leaf conductivity (Bond and Kavanagh 1999). This "threshold" may be determined by Π_{TLP}, as Π_{TLP} is considered to dictate the Ψ_{soil} below which plants are unable to take up water to recover from wilting (permanent wilting point). Π_{TLP} has been measured for decades when assessing species drought tolerance (Tyree and Hammel 1972, Schulte and Hinckley 1985). Turgor loss impacts structural integrity of cells, metabolism, and performance of the plant as a whole (Lawlor and Cornic 2002). Plants with low Π_{TLP} have an extended range of leaf turgidity and functionality, so they are able to maintain stomatal conductance, gas exchange, hydraulic conductance and growth at lower soil water potentials (Kubiske and Abrams 1991, Pita and Pardos 2001, Brodribb et al. 2003). Therefore, Π_{TLP} can be used to quantify drought tolerance, with those species exhibiting lower Π_{TLP}, like our oaks, having greater drought tolerance, while species with high Π_{TLP}, like our pines, are more likely drought avoiders, reducing gas exchange during times of low water availability. Other parameters derived from pressure-volume analyses, including RWC_{TLP}, Π_{FT}, ε, and capacitance have been correlated with drought tolerance as well (Kubiske and Abrams 1991, Clifford et al. 1998, Niinemets 2001), and many may interact with Π_{TLP}, although Bartlett et al. (2012) suggested some have a greater role in determining Π_{TLP} than others. Regardless, the loblolly pines in this study exhibited gas exchange and pressure volume characteristics associated with a drought-avoidance strategy that could reduce the risk of cavitation, but may slow recovery in severely burned areas where pines are already at a disadvantage from seed dispersal struggles, resprouting biotic legacies, and rapid soil dry-down.

Although dissimilarities in the species foliar biochemistry may simply result from innate differences between genera, nutrient and phenolic contents appear to follow other leaf-level results from the study. It is not surprising that the oak species, which tended to have greater photosynthesis rates than loblolly pine, also had greater leaf N, and that post oaks had greater leaf N contents than blackjack oaks. Leaf photosynthetic capacity is often correlated with leaf N content due to high proportion of N composing photosynthetic machinery (i.e. thylakoids, Rubisco, and proteins utilized in the Calvin cycle) (Evans 1989, Reich et al. 1991, Springer et al. 2005). Other studies comparing gas exchange of deciduous species against pines have reported greater photosynthesis and leaf N contents in the deciduous species (Reich et al. 1995, Springer et al. 2005). Protein-precipitable phenolic contents and amounts of protein bound were greater in oaks than pines. Oak leaves contain substantial amounts of phenolic compounds, including both hydrolysable and condensed tannins (Forkner et al. 2004, Salminen et al. 2004, Tharayil et al. 2011) characterized by the ability to bind large amounts of protein (Makkar et al. 1988, Tharayil et al. 2011). In addition to their ability to bind protein and enhance ruminant nutrition, CT prevent photo-oxidation and protect plants against high levels of PAR and UV radiation (Close and McArthur 2002, Turtola et al. 2005, Abdala-Díaz et al. 2006, Mellway et al. 2009). High levels of these compounds in post oak and blackjack oak could contribute to maintenance of relatively high gas exchange in individuals growing in exposed severely burned sites after canopy removal. Pines are known to contain protein-precipitating CT as well (Tiarks et al. 1989, Kraus et al. 2003), but terpenes are often produced to a greater degree (Litvak and Monson 1998, Kanerva et al. 2008). Terpenes, like phenolics, also protect against UV radiation and protect against reactive oxygen species (Zavala and Ravetta 2002, Peñuelas et al. 2005, Gil et al. 2012).

Post Oak's Competitive Ability

Between the two oak species in this study, blackjack oak seems to be the more conservative, decreasing gas exchange and exhibiting pressure-volume parameters associated with drought avoidance in more severely burned areas. Unlike blackjack oak and loblolly pine, post oak displayed its greatest gas exchange rates in severely burned sites. Pressure-volume parameters exhibited by post oak in these sites provide further evidence for this species' ability to thrive in severely burned areas where exposure to high atmospheric demand and exposed soil may limit the recovery of more sensitive species. Post oaks had their lowest Π_{FT}, Π_{TLP}, and RWC_{TLP} and highest capacitance in the severely burned sites in conjunction with their greatest A, E, and g. Nitrogen contents were greater in post oak than blackjack oak leaves, and were likely related to the greater photosynthetic rates in post oak. Johnson and Risser (1974) also reported that post oak leaves had greater N contents than blackjack oak leaves, and they had greater P which is also thought to limit photosynthesis when tissue quantities are low (Reich et al. 2009). These species differences accumulated suggest post oak is the “hare”, while blackjack oak tends to show characteristics more similar to pine in many instances. Although post oak and blackjack oak densities, heights, and diameters were similar in both measurement years, blackjack’s responses in the severely burned plots indicate this species is not as tolerant of site alteration as post oak and may not fare as well in the future.

Oak and Pine Co-Existence Up to This Point

Prior to the 2011 fire, oaks and pines co-existed in the Lost Pines environment, although pines were the more prevalent species. The Lost Pines are frequently cited for their drought hardiness. This resilience (Bongarten and Teskey 1986, Wakamiya-Noborio et al. 1999, Smith et al. 2014) is likely more a function of drought avoidance than drought tolerance, which is a strategy employed by many conifers (McDowell et al. 2008, Choat et al. 2012). Pines from this region have greater gas exchange rates than loblolly pines from more mesic regions when soil moisture levels are high, but conserve water and close stomata when soil moisture is low (Bilan et al. 1977, Wakamiya-Noborio et al. 1999). Compared to other loblolly pines, these have deeper root systems (van Buijtenen et al. 1976) and slower growth rates (Bongarten and Teskey 1987, Yang et al. 2002, Smith et al. 2014). The needles of the Lost Pines are typically short and stout with thick cuticles, deep stomatal pits, and few stomata per unit of surface area, all of which enhance their drought hardiness compared to seedlings from East Texas (Knauf and Bilan 1974, Bongarten and Teskey 1986). All of these characteristics contributed to the success of this species in the Lost Pines area prior to the fuel-accumulating management that led to the severity of the Bastrop County Complex Fire. Following the fire, post oak and blackjack oak resprouts out-number pines in much of the severely burned area and appear to utilize more drought-tolerant water use strategies which may extend the oaks' lead in those patches even more. However, it appears that pines will retain dominance in less-severely burned spaces, and physiological differences between the genera may actually foster co-existence. Loblolly pines are fairly shade intolerant (Teskey and Shrestha 1985, Schultz 1997), so they may utilize the time when oaks are dormant for growth and catching up to height gains the oaks made during the growing season.

Conclusions

Intense fire behavior like that seen in the Bastrop County Complex Fire may limit recovery of pine species like loblolly pine which are not adapted to severe fire events. The pines in this study appear to be recovering well under light to moderate burn conditions, but may require supplemental planting from additional sources to re-populate severely burned areas if park managers and landowners in the region seek to maintain pine-dominated stands. The three species included in this study exhibit unique gas exchange and pressure volume parameter responses to varying burn severity in addition to dissimilarities in leaf chemistry, all of which may play a role in stand recovery and composition following wildfire. The drought-avoidance strategies of loblolly pine appear to have worked well in maintaining pine dominance prior to the fire. However, greater gas exchange, drought-tolerant pressure-volume characteristics, and access to deeper soil moisture may allow oaks to out-pace pine recovery in severely burned patches. Local managers will need to continue to monitor regrowth over time and, in particular, closely examine species performance in relation to drought since results suggest changes in water availability may have different effects on the species studied. More frequent but less severe controlled burns may likewise favor some species over others, and comparisons of burn frequency intervals may provide best management practices.

CHAPTER IV

COMPARISON OF TRANSPIRATION ACROSS BURN SEVERITIES IN RECOVERING MIXED LOBLOLLY PINE AND OAK STANDS IN THE LOST PINES REGION OF TEXAS

Synopsis

Alterations to resource availability can cause shifts in stand structure and species composition following wildfires. In turn, changes to species makeup and distribution and shifts to younger, actively growing vegetation may modify stand transpiration and the amount of water available to other parts of the hydrologic cycle. Following the Bastrop County Complex Fire in the Lost Pines eco-region, near Bastrop, TX, USA, transpiration was monitored in mixed loblolly pine (*Pinus taeda* L.)/ oak (*Quercus stellata* Wangenh., *Quercus marilandica* Muenchh.) stands across multiple burn severities. An unburned, control stand (mature pines and oaks) was identified at the Griffith League Ranch north of the city of Bastrop, while moderately burned (mature pines and oaks) and severely burned stands (pine seedlings and oak resprouts) were selected in Bastrop State Park. Transpiration was estimated for approximately 5 months using sap flux sensors in five pine and oak trees at the unburned and moderate sites, 10 oak resprouts, and three pine seedlings at the severely burned plot. From 27 May 27 to 12 October, 2016, pines had 31% and 39% greater average sap flux rates (J_s) than oaks at the unburned and moderately burned stands, respectively. Regenerating pines at the severely burned site started the experimental period with greater J_s than the resprouting oaks, but sap flux quickly decreased as shallow soil moisture was depleted. Young pines did not recover to pre-drought levels and had 9% lower sap flux on average than the oaks at the severely burned stand. Mature pines were not affected by drought periods and maintained greater J_s than mature oaks on most days. Pine transpiration made up 75% and 86% of unburned and moderate stand daily transpiration, respectively. By contrast, oak transpiration dominated at the severely burned stand, contributing over 95% of daily transpiration. Transpiration was greatest at the moderately burned stand (2.08 mm day^{-1}), intermediate at the unburned stand (1.48 mm day^{-1}), and least for the severely burned stand (0.46 mm day^{-1}). Although resprouting oaks exhibited the greatest J_s and pine seedlings had high J_s rates as well, the reduction in total sapwood area after the severe fire resulted in low daily transpiration. Results suggest light to moderate burns may enhance stand transpiration through reductions in competition and increased irradiance, while severe fires reduce stand transpiration through reductions in vegetation density. Oaks will likely retain greater numbers at the severely burned stand and continue to dominate stand transpiration.

Introduction

A warmer, drier climate has resulted in increasing annual fire season length, fire frequency and size, and overall burned area in North American forests (Flannigan et al. 2005, Miller et al. 2009). As a result of fire suppression over the past century, increases in large standing dead fuel loads have led to greater fire size and severity (Pollet and Omi 2002, Miller et al. 2009). Alterations to resource availability (e.g. light, soil nutrients, soil moisture) post-fire, in particular after high severity fires, can result in a shift in stand structure and species composition which may be different from the pre-fire environment (Barton 2002, Savage and Mast 2005, Strom and Fulé 2007, Moser et al. 2010, Johnstone and Kasischke 2005). In turn, shifts in species composition, distribution, and vegetation age can change the amount of water available to other parts of the hydrologic cycle through alterations in transpiration. The "Lost Pines" area in central Texas provides an opportunity to examine possible long-term shifts in vegetation structure and species composition following such a wildfire, and how these shifts will additionally modify water use. Prior to the 2011 Bastrop County Complex Fire, the over-story vegetation of the region predominantly consisted of loblolly pine (*Pinus taeda* L.). However, post oak (*Quercus stellata* Wangenh.) and blackjack oak (*Quercus marilandica* Muenchh.) have rapidly resprouted across much of the post-fire landscape, suggesting shifts to oak-dominated woodlands or savannas rather than pine-dominated stands could occur in some patches.

The switch to younger vegetation, both resprouts and non-sprouting pine seedlings, serves as the first visual indication of change to the stand structure and results in greater gas exchange and water use per unit leaf area than mature trees remaining in less severely burned areas (Castell et al. 1994, Utsumi et al. 2010). Greater water use in young individuals and resprouts is associated with greater sapwood and leaf area indices and stomatal conductance per unit leaf area than older individuals (Magnani et al. 2000, Roberts et al. 2001, Vertessy et al. 2001, Ewers et al. 2005, Delzon and Loustau 2005). Increases in pressure gradient with gravity and greater hydraulic resistance in older, taller trees may play a role in reducing water use as well (Ryan and Yoder 1997, Koch et al. 2004). Although average daily transpiration and sap flow per unit area can be similar or even lower in individual resprouts compared to mature trees, in some cases, stand-level transpiration by resprouts can actually be greater due to greater total sapwood area in regenerating stands (Ffolliott et al. 2003, Buckley et al. 2012). Due to a reduction in competition, water availability can initially increase for individuals regenerating in these severely burned areas, aiding increases in transpiration (Cardenas and Kanarek 2014).

Shifts in species composition may alter stand water use to a greater degree than shifts in age within a single species (Asbjornsen et al. 2007, Hadley et al. 2008, Bradford et al. 2014). For example, angiosperms and gymnosperms in the same stand often differ in amounts of sapwood area, hydraulic conductance, and transpiration (Tyree and Ewers 1991, Brodribb and Field 2000, Moore et al. 2004). Most of the sap flow in trees with ring-porous sapwood, such as oaks, occurs in younger xylem rings, although significant flow in the older rings remains (Granier et al. 1994, Poyatos et al. 2007, Gebauer et al. 2008). In diffuse porous and non-porous trees, like pine, the sapwood area occupies a greater portion of the stem cross-sectional area and is composed of narrow conduits that are more resistant than the large vessels of ring-porous trees (Cermak and Nadezhdina 1998). Differences in rooting depth and root anatomy may also lead co-occurring angiosperms and gymnosperms to access water from different parts of the soil profile (Jackson et al. 1999, Schwinning 2008, Renninger et al. 2015). Angiosperms and gymnosperms vary in conductance, photosynthesis, and transpiration responses to alterations in water availability and evaporative demand, with gymnosperms, like pines, often utilizing more conservative water use strategies during times of low water availability (Irvine et al. 1998, Choat et al. 2012). Oak species, on the other hand, exhibit small safety margins, progressively lowering leaf water potentials while maintaining relatively high gas exchange (Abrams 1990, David et al. 2007, Pinto et al. 2012). Although pines often use conservative water use strategies during drought, they capitalize on soil moisture increases; pines have greater conductance and evapotranspiration than co-occurring hardwood species following precipitation events (Poyatos et al. 2008, Zweifel et al. 2009, Renninger et al. 2015). Some studies reported greater sap flux in pines than hardwoods as well (Phillips et al. 1996, Ford et al. 2010, Renninger et al. 2015).

Following the Bastrop County Complex Fire, we have the unique opportunity to monitor physiological differences between young and mature individuals of oak and pine, two genera known to differ in water use strategies across multiple burn severities. Multiple studies have evaluated sap flux responses of oaks and pines, with several studies including both genera (Phillips et al. 1996, Phillips et al. 2003, Poyatos et al. 2005, Poyatos et al. 2008, Renninger et al. 2015). Less is known about sap flux and transpiration responses between mature trees and resprouts after fire (Utsumi et al. 2010, Buckley et al. 2012, Gharun et al. 2013, Nolan et al. 2014, Nolan et al. 2015), especially for oaks (Ffolliott et al. 2003). This study adds to the body of knowledge by examining transpiration of mature oaks and pines along with resprouting oaks and pine seedlings across multiple burn severities.

Objectives

The primary aim of this study was to determine how burn severity affects transpiration through alterations in stand structure and age in mixed pine/oak stands following the Bastrop County Complex Fire. Stand transpiration should change with shifts in pine and oak proportions post-fire. Pines were hypothesized to have higher *Js* than oaks, which coupled with their large sapwood area, would result in greater transpiration in stands containing a greater number of pines. The second hypothesis of the study was that resprouting oaks and young pines would have greater daily sap flux per unit sapwood than mature individuals of the same species. Finally, stand level transpiration was hypothesized to decrease in sites with greater burn severities due to reductions in vegetation density and total sapwood area.

Materials and Methods

Site Description

This study was conducted at Bastrop State Park (N30°6’43.992”, W97°15’38.016”) and the Griffith League Ranch (N30°12’20.2”, W97°14’03.3”), Bastrop County, Texas, USA, within the “Lost Pines” eco-region. The “Lost Pines” represents the western-most range of loblolly pine in the United States, isolated from the East Texas Piney Woods ecoregion by over 160 km during the Pleistocene (Bryant 1977, Al-Rabab’ah and Williams 2004). Loblolly pine, post oak, blackjack oak, and eastern red cedar (*Juniperus virginiana* L.) are the dominant overstory species in the region. Common understory species include yaupon holly (*Ilex vomitoria* Sol. ex Aiton), American beautyberry (*Callicarpa americana* L.), and farkleberry (*Vaccinium arboreum* Marshall). Temperatures typically range from 12.7 – 26.5ºC annually, and the area receives around 820 mm of precipitation each year.

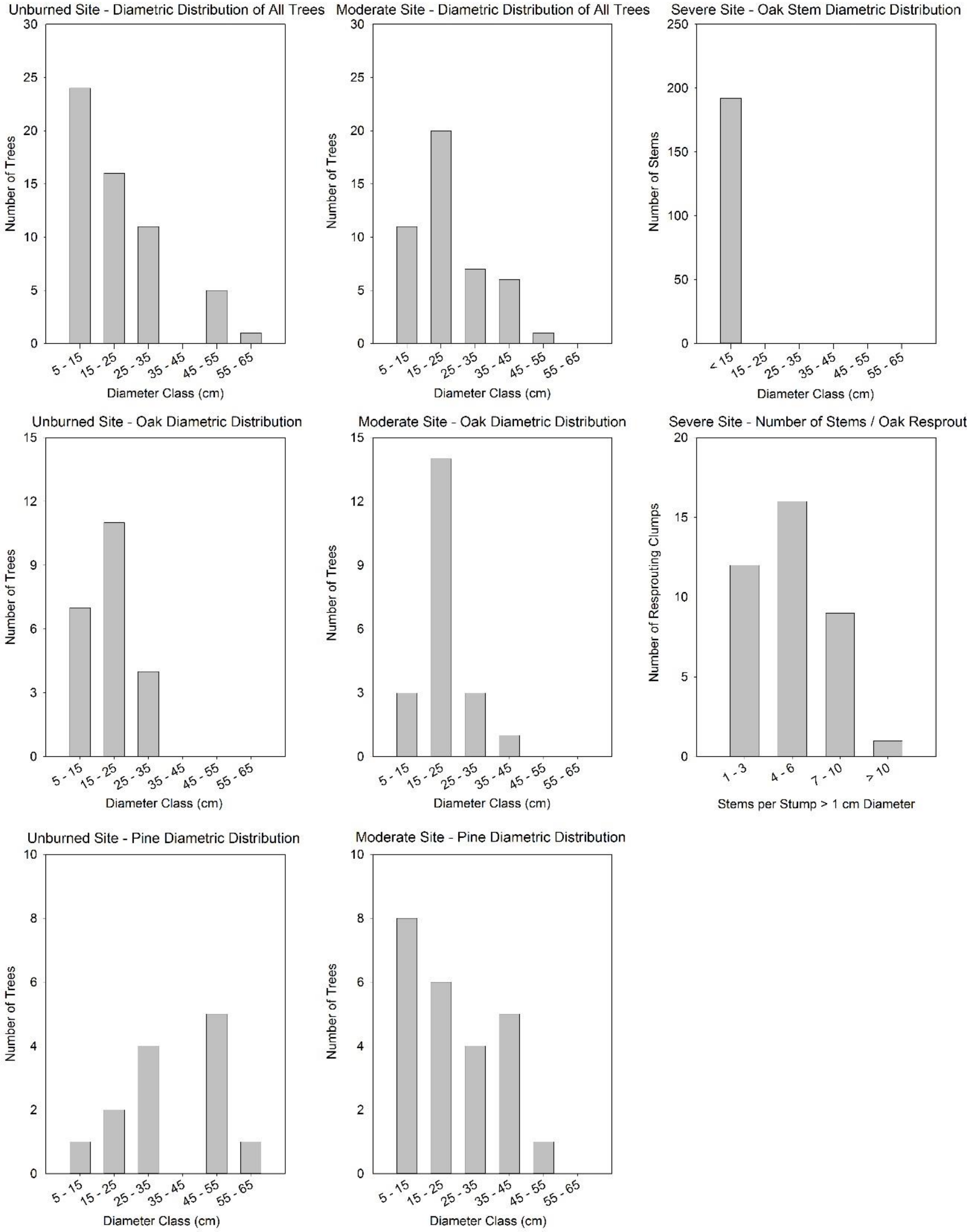
The Bastrop County Complex Fire ignited in the region on September 4, 2011, and was the most destructive fire in recorded Texas history (Rissel and Ridenour 2013). More than 12,950 ha and 1.8 million trees were burned, including 96% of Bastrop State Park (Rissel and Ridenour 2013). Pine mortality was 100% in severely burned areas and many of the lesser burned areas also saw high stress-related tree mortality. Following the Bastrop County Complex Fire, the Texas Parks and Wildlife Department mapped burn severities in Bastrop State Park using satellite imagery and ground validation following classifications developed by the U.S. Department of the Interior (Cardenas and Kanarek 2014). Within Bastrop State Park, two plots were established to monitor sap flux and micrometeorological conditions in areas classified as 1) “moderately” and 2) “severely” burned. A third unburned “control” plot was established at the Griffith League Ranch located north of the city of Bastrop. All three plots were circular with a 15-m radius (area = 707 m^2). Soils of the area consist primarily of sands and sandy loams from the Patilo-Demona-Silstid and Axtell-Tabor associations with some exposed areas of gravel or clay on steep, eroded slopes (Baker 1979). All three sites were established in areas classified as Padina fine sandy loam (loamy, siliceous, active, thermic Grossarenic Paleustalf) to prevent differences in water availability that may occur with variation in soil texture and depth to the argillic horizon (Hacke et al. 2000, Fernandez-Illescas et al. 2001).

Sap Flux and Sapwood Area Measurements

Sap flux density (J_s) was continuously measured using thermal dissipation sensors (Granier 1987) constructed using the method described by Phillips et al. (1996) starting in June 2015 until October 2016. This method utilizes an upper probe containing a constantan heating element and a lower reference probe. At both the unburned and moderately burned sites, two sensor pairs were installed in each of five mature pine trees and five mature post oak trees for a total of 20 sensor pairs per site. Sensors were installed on the north and south sides of trees and inserted in the outer 20 mm of active xylem at 1.5-m height. At the severely burned site, one sensor pair was installed in each of ten resprouting post oaks (6) and blackjack oaks (4) for a total of 10 oak sensor pairs. I also installed sensors in three pine seedlings at the severely burned site. Due to the resprouts and pine seedlings' smaller stature (diameter <5 cm and height < 3m), on these sensors were installed in the outer 10 mm of active sapwood and at ~0.45 m above the ground surface. Data were collected every 30 s, averaged over 30-min intervals, and stored on a Campbell CR10X datalogger (Campbell Scientific Inc., Logan, UT, USA). Temperature differences between heated and reference probes were converted to J_s (kg m^{-2} s^{-1}) using Granier's (1987) empirical calibration equation [equation 1]:

$$Js = 0.119\left(\frac{\Delta TM - \Delta T}{\Delta T}\right)^{1.231} = 0.119K^{1.231} \quad (1)$$

where ΔT_M is the maximum temperature difference when sap flux is assumed to be 0, and ΔT is the actual difference in temperature. Daily total sap flux density (kg m^{-2} day^{-1}) was calculated as the sum of all J_s measured in a 24-h period.


Unburned Site - Diametric Distribution of All Trees

Moderate Site - Diametric Distribution of All Trees

Severe Site - Oak Stem Diametric Distribution

Unburned Site - Oak Diametric Distribution

Moderate Site - Oak Diametric Distribution

Severe Site - Number of Stems / Oak Resprout

Unburned Site - Pine Diametric Distribution

Moderate Site - Pine Diametric Distribution

Figure 19. Distribution of tree and resprout diameters in the three 707 m^2 sap flux plots.

A full stand survey was conducted in all three sap flux plots. In the unburned and moderately burned sap flux plots, I measured all saplings and trees with diameter at breast height (DBH) greater than 5 cm (Figure 19). Unlike in the unburned and moderate plots, I measured the diameter at the base of the stem (~0.1 m) (Keeley and Zedler 1978, Cipollini and Whigham 1994) of all severe site resprouts and seedlings with stems greater than 1 cm (Figure 19). Diameters were used to calculate cross-sectional area. The unburned plot had the largest number of trees (n = 52) and basal area (A = 2.72 m^2). Although the severely burned site had numerous resprouting oaks (n = 39) with multiple stems per clump (5 on average > 1 cm) and a few individuals of other species (n = 6), the overall basal area (A = 0.294 m^2) was smaller than the other sites. Sapwood area was determined in the control and moderately burned plots using cores retrieved at 1.5-m height and immersed in safranin-fucsin dye (McDowell et al. 2002, Gebauer et al. 2008). Due to the size and age of the oak resprouts and pine seedlings at the severely burned site, sapwood area was assumed to be 100% of the seedling's cross-section area minus bark depth (Moore et al. 2004). Other studies have reported little to no heartwood in similar sized seedlings (Dean and Long 1986, Wullschleger et al. 1998). All trees with sensors at the moderate and unburned sites had a sapwood radius greater than the sensor depth of 2 cm (Clearwater et al. 1999). Sapwood area (A_s) of the remaining trees in the plot was calculated using linear regression equations developed from total basal area and sapwood area from cored individuals, assuming a constant active sapwood depth in all stem directions (Figure 20, Table 3). Data from the moderately burned and unburned sites were combined within oak and pine species, respectively, to develop models applicable to remaining trees within each species.

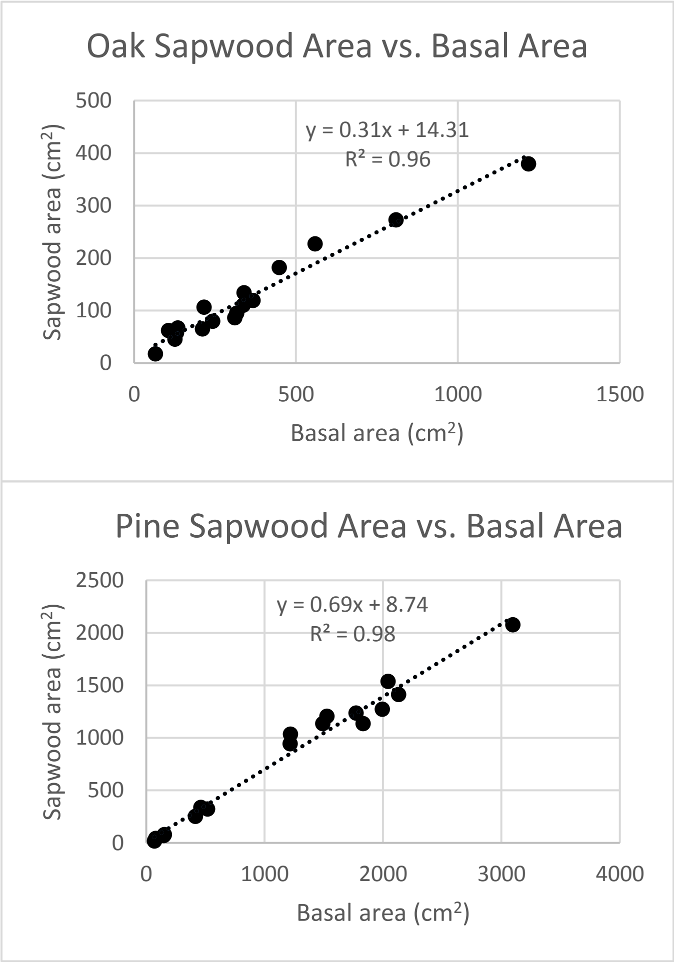


Figure 20. Regression equations used to calculate sapwood areas for a) oak and b) pine individuals in the unburned and moderately burned stands.

Table 3. Distribution of sapwood area (A_s) (m^2) among species in each 707 m^2 sap flux plot.

	Unburned Plot	Moderate Plot	Severe Plot
Oak	0.24	0.25	0.22
Farkleberry	0.01		
Yaupon	0.02		
Willow baccharis			0.01
Pine	1.14	1.02	0.01
Eastern redcedar	0.22	0.01	
Angiosperms	0.27	0.25	0.23
Gymnosperms	1.36	1.03	0.01
Total	**1.63**	**1.28**	**0.24**

For pines, $A_s = 0.69A + 8.74$ ($r^2 = 0.98$), where A_s is sapwood area and A is basal area, both in m^2. For oaks, $A_s = 0.31A + 14.31$ ($r^2 = 0.96$). The oak regression equation was used to estimate sapwood area of other angiosperms in the moderate and unburned stands, and the pine regression equation was applied to other gymnosperms (Moore et al. 2004).

Some studies have highlighted that sap flux rates are not uniform across the entire sapwood area due to changes in conduction with changes in wood proprieties, age, and depth (Phillips et al. 1996, Cermak and Nadezhdina 1998, Nadezhdina et al. 2002, Ford et al. 2004, Poyatos et al. 2007). Hence, to avoid overestimations of stand transpiration, radial profile corrections were applied to J_s measurements (Delzon et al. 2004, Ford et al. 2004). I monitored J_s across sapwood profiles at multiple depths in the two largest pine (DBH = 62.8 and 52.1, A_s = 2076.2 cm^2 and 1411.0 cm^2, respectively) and oak (DBH = 32.1 and 23.9, A_s = 272.6 cm^2 and181.9 cm^2, respectively) trees for a minimum of 9 days in the unburned site. In oak trees, profile sensors were installed at four depths: 1, 2, 3, and 4 cm into the xylem. For the pines, sensors were installed every 2 cm from 2 - 14 cm and 2 - 16 cm into the xylem for the first and second tree respectively. The radial profile sensors used were an adapted version of James et al. (2002) variable length probes. To correct for differences in conductance across the

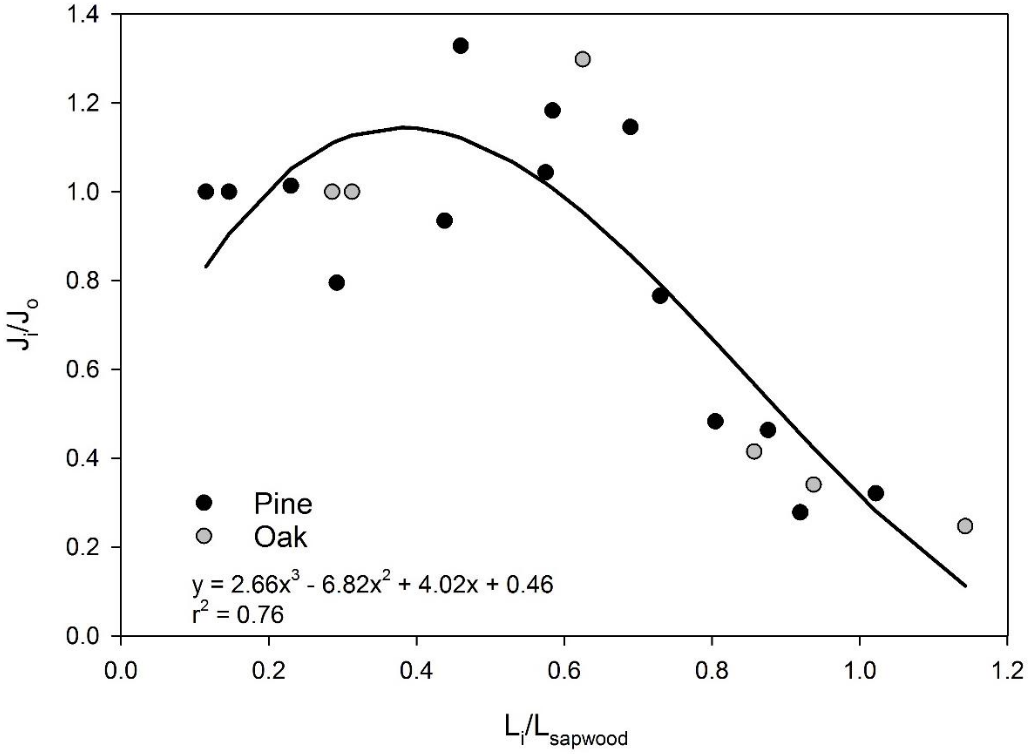


Figure 21. Radial sap flux measurements used to correct daily J_s. Relative flux was calculated by normalizing the value at a given depth, J_i, to the value in the outer 1 cm, $J_{i=1}$. Relative depth was calculated by normalizing the depth of each measurement, L_i, to the total sapwood depth, $L_{sapwood}$, measured via core sampling.

radial profile in mature oaks and pines at the moderate and unburned stands, correction factors were calculated using the following equation developed according to the radial profile measurements (Figure 21) [equation 2]:

$$\frac{Ji}{Jo} = 2.657\left(\frac{Li}{Lo}\right)^3 - 6.818\left(\frac{Li}{Lo}\right)^2 + 4.022\left(\frac{Li}{Lo}\right) + 0.455 \quad (2)$$

where Ji/Jo is the ratio of sap flux in the i^{th} depth to sap flux of the outer profile sensor and Li/Lo is the ratio of the i^{th} sapwood depth to the total sapwood depth. I divided cross-sectional sapwood area for each tree in the moderate and unburned stands into 5 sections where Li/Lo corresponded to 20% increments relative to the total sapwood depth. Within each stand the correction factor Ji/Jo was applied to adjust the sectional sap flux per unit area (kg m^{-2}) relative to the average outer J_s from the 2-cm Granier probes for oak and pine, respectively. Daily total sap flux (kg m^{-2} day^{-1}) for each section was calculated by summing J_s values in a 24-h period.

Daily pine transpiration (mm) for a stand was then calculated using the daily sap flux total for each sapwood section and multiplied by the total pine sapwood area (m^2) in that section divided by the total stand area (707 m^2). Daily oak transpiration was similarly calculated. Transpiration of species without sensors (e.g. eastern redcedar, yaupon, etc.) was calculated using the estimated sapwood area of that particular species and the adjusted daily sap fluxes of pine for gymnosperm species and oaks for angiosperm species (Moore et al. 2004). Sapwood from species other than oak and pine made up 15%, <1%, and 4% of the total sapwood area at the unburned, moderately burned, and severely burned sites, respectively. Daily total transpiration for the stand was determined by summing the daily transpiration of all individuals in the stand. In the severely burned stand, daily total sap flux was assumed to be homogeneous across the entire cross-section of the resprouts and seedlings. Hence, J_s was multiplied by the total sapwood area and divided by the plot area to calculate transpiration of each species. Similar to the moderate and unburned stands, the daily sap flux of resprouting oaks was used to calculate sap flux for other angiosperm species in the plot.

Stand Microclimate Measurements

Each site was equipped with a TR-525 tipping bucket rain gauge (Texas Electronics, Inc., Dallas, TX, USA) to monitor rainfall daily totals (mm day^{-1}) and events, while relative humidity (%) and air temperature (^{o}C) were measured with a Vaisala INTERCAP® HMP60 (Vaisala Inc., Boulder, CO, USA) probe. Soil temperature (^{o}C) was also measured at the three stands at the soil surface, below the litter layer, and at 5, 10, and 30 cm below the soil surface. Three thermocouple sensors each were installed at both the soil surface and litter layer and two sensors were installed at each soil profile depth for a total of 12 soil temperature sensors at every site. A CR10XTCR (Campbell Scientific Inc., Logan, UT, USA) was used to provide a temperature reference for the soil temperature type T thermocouples. Soil temperature, air temperature, relative humidity, and rainfall were measured every 30 seconds and averaged over 30 minutes by the site datalogger. Air temperature and relative humidity data were used to estimate vapor pressure deficit (VPD) (Murray 1967, Howell and Dusek 1995). *VPD* in kPa was computed as:

$$VPD = e^{*}(T_i)(1 - \frac{RH_i}{100}) \qquad (3)$$

where $\mathrm{e}^*(T_i) = 0.611\exp[\frac{17.27*T_i}{T_i+237.3}]$ (4)

In which $e*(T_i)$ is the saturated vapor pressure in kPa for temperature T_i in ºC and RH_i is the air relative humidity in % for the i^{th} 30-min period of each day. Vapor pressure deficit was then averaged among all measurements in a 24-h period.

Statistical Analyses

Statistical tests for effects of burn severity and species interactions on daily J_s and transpiration were performed using linear mixed-models (proc mixed procedure, SAS 9.4, SAS Institute Inc., Cary, NC, USA). The effects of severity, species, and their interactions were tested for J_s and transpiration. I focused on data from DOY 148 (27 May) to 286 (12 October) for analyses because sap flux sensors in pines at the severely burned site were not installed until May 2016. This time span (DOY 148 to 286) also represents the bulk of the growing season. In the models, “day” was considered random while species and severity were fixed effects. When significant effects were detected in the model, the LSMEANS statement in SAS was used to estimate means. Differences between means were adjusted using Tukey’s HSD post-hoc analysis. Differences were considered significant at $P \leq 0.05$. Additionally, non-linear (exponential) equations were used to determine the effects of VPD on daily sap flux rates. Model fits were evaluated based on coefficient of determination (r^2) and P-values. Daily VPD values from 1 to 24 July and 1 to 12 August were examined in greater detail with respect to effects on regenerating pine sap flux at the severely burned site when shallow soil moisture was depleted.

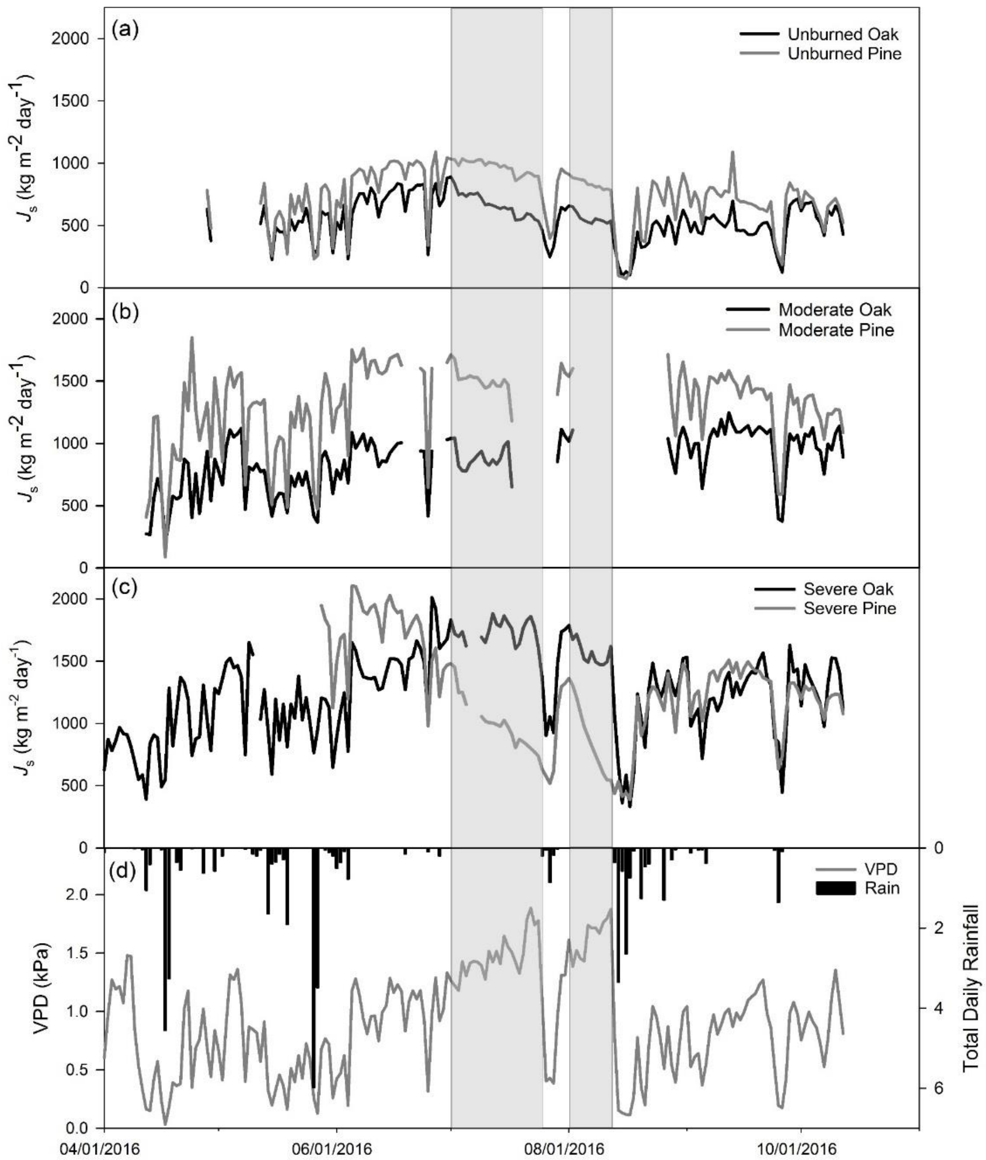


Figure 22. Daily total sap flux (kg m^{-2} day^{-1}) of oaks and pines within a) unburned, b) moderately burned, and c) severely burned stands along with d) average daily VPD and total daily rainfall from 1 April to 12 October, 2016. Daily total sap flux represents that of J_o at the outer 2 cm and 1 cm of sapwood for the mature trees and regenerating seedlings and resprouts, respectively. Periods of shallow soil moisture dry down are shaded.

Results

Sap Flux Differs Among Species and Burn Severities

Pine sap flux (J_s; kg m^{-2} day^{-1}) was greater than that of oaks in the unburned and moderately burned stands by 31 and 39%, respectively, on average from 27 May to 12 October, supporting the first hypothesis (Figures 22a and b, 23a). Pine and oak J_s tended

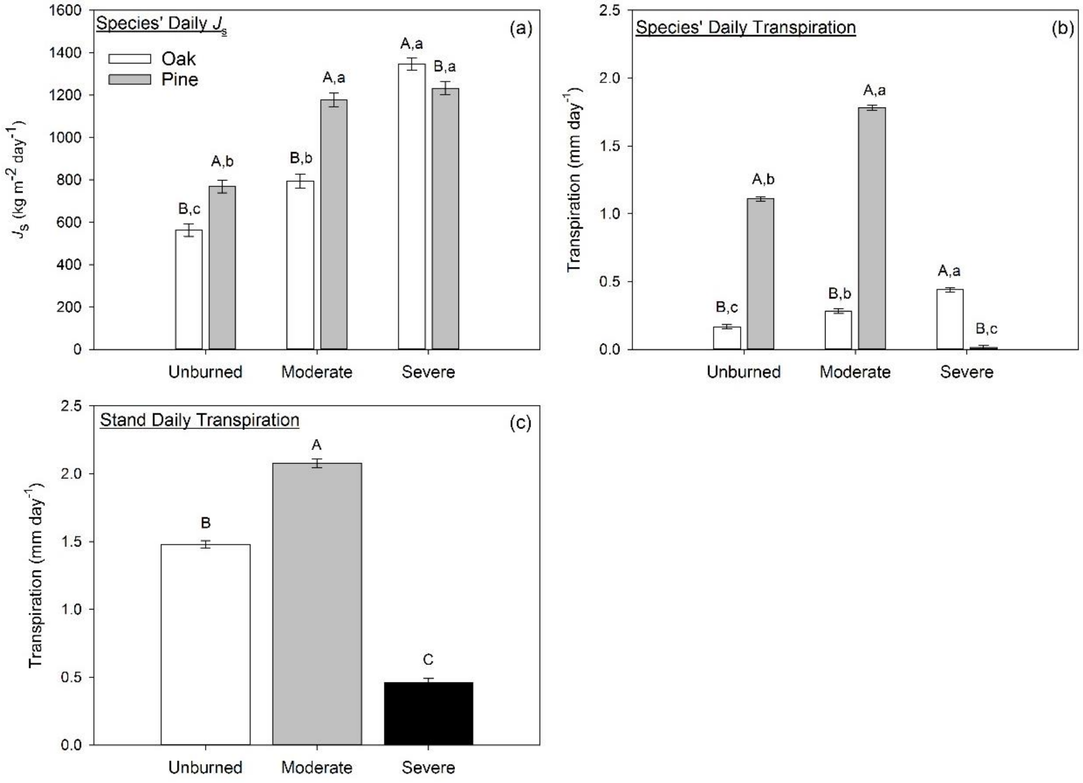


Figure 23. Comparison of a) average daily total sap flux (J_s; kg m^{-2} day^{-1}) and b) average daily transpiration (mm day^{-1}) for oaks and pines within the three burn severity stands along with c) average total daily transpiration for each of the three stands for the period of 27 May to 12 October, 2016. Different uppercase letters (A) denote differences ($P \leq 0.05$) between species within each burn severity, while different lowercase letters (a) denote differences ($P \leq 0.05$) among burn severities within a particular species for panels a and b. Differences in daily transpiration among stands are represented by uppercase letters.

to maintain their relative proportions at these two sites, although they were inclined to drop to similar levels on rainy days (Figure 24a and b). Unlike the young pines at the severely burned site, J_s of mature pines at these stands was not affected by summer dry periods. Following the wet spring of 2016, regenerating pines at the severely burned site had greater J_s than the resprouting oaks, but sap flux quickly decreased to levels below the oaks as soil moisture in the upper soil layers was depleted (Figure 22c, Figure 24c). Excluding a brief reprieve after rains in the last week of July, pine J_s was on average 53% lower than resprouting oak J_s from 1 July to 12 August. Although shallow soil moisture recovered after rains in middle to late August, regenerating pine J_s did not return to pre-drought levels and remained nearly equal to oak J_s throughout the later part of the growing season. The decreases in pine J_s with shallow soil moisture led to 9% lower sap flux on average than the oaks at the severely burned stand during the time period of 27 May – 12 October (Figure 23a).

Within both species, daily J_s tended to increase as burn severity increased and was generally greater in younger individuals of each species, confirming the second hypothesis. The resprouting oaks had 52 and 82%, respectively, greater daily J_s than the mature oaks at the moderately burned and unburned stands from 27 May – 12 October (Figure 23a). Oaks at the moderately burned site had 34% greater J_s than those at the unburned site. Daily sap flux of the regenerating pines of the severe stand and mature pines at the moderately burned stand were similar on average, but pines in these stands had at least 42% greater daily J_s than those at the unburned stand.

At high VPD levels J_s increased in some of the species by burn severity

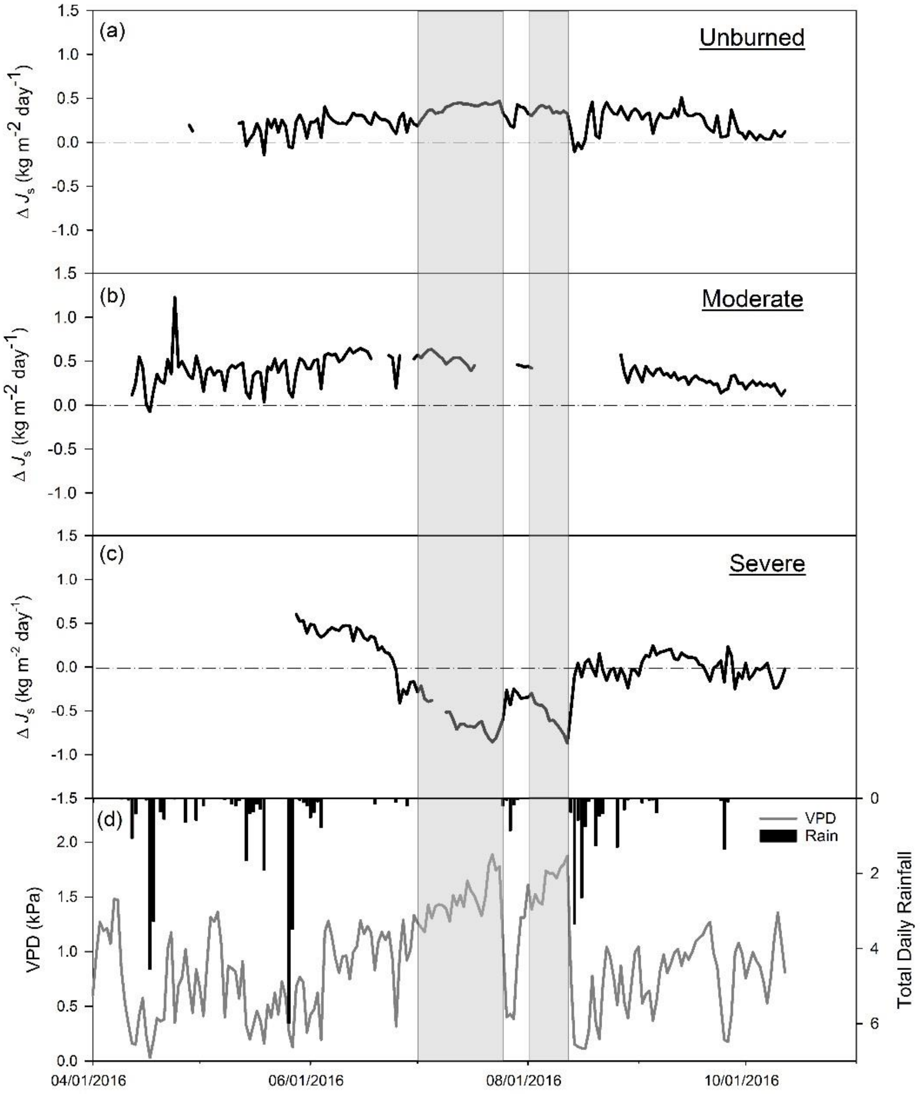


Figure 24. Relative differences between pine and oak daily total sap flux (kg m^{-2} day^{-1}) within a) unburned, b) moderately burned, and c) severely burned stands along with d) average daily VPD and total daily rainfall from 1 April to 12 October, 2016. Relative differences for each site were calculated as daily pine J_s minus daily oak J_s divided by mean pine J_s. Periods of shallow soil moisture dry down are shaded.

combinations but decreased in others (Figure 25). When comparing the two species at the moderate and unburned sites, pine J_s was better explained by changes in VPD than

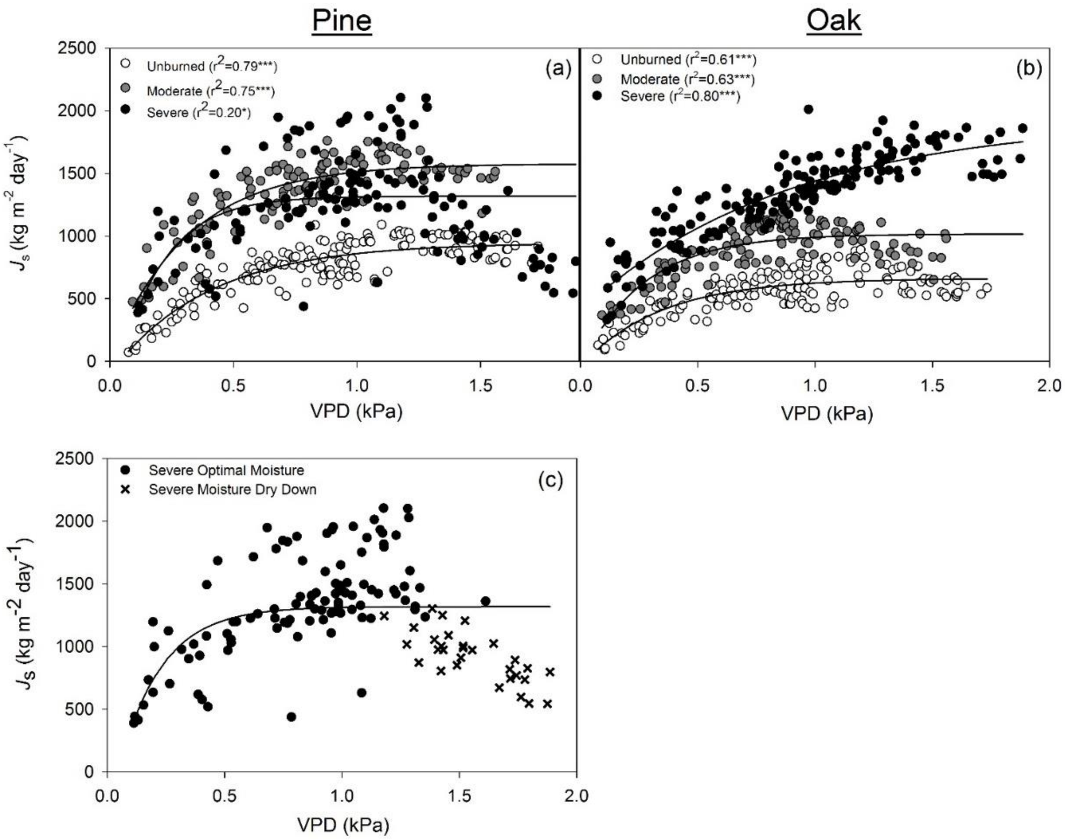


Figure 25. Effects of average daily VPD on total daily sap flux of a) pines and b) oaks at the unburned, moderately burned and severely burned stands. The effects of shallow soil moisture on the relationship of J_s with VPD are illustrated for pines at the severely burned site (c).

oaks and stabilized at greater J_s values. At the severely burned stand, however, changes in VPD explained more variation in oak J_s ($r^2 = 0.80$) than pine J_s ($r^2 = 0.20$). Severely burned pines experienced greater fluctuations in J_s across the range of VPD, going from values greater than those of the moderately burned pines to values more similar to those of the unburned pines. These regenerating pines were also much more sensitive to high VPD than their counterparts at the moderate and unburned stands. Results indicated that the regenerating pines at the severely burned site may have strong stomatal control, allowing them to reduce gas exchange during dry, hot days. However, the period of time when shallow soil moisture was depleted corresponded with the highest observed VPDs (Figure 22, 25). These soil moisture constraints may have curbed pine J_s more than the high VPD levels. Unlike the regenerating pines, resprouting oaks continued to increase J_s with increasing VPD. They did not plateau, suggesting they continue to keep stomata open for gas exchange at even greater levels of VPD than experienced in this study.

Altered Stand Transpiration Post-Fire

Stand transpiration in unburned and moderately burned sites was dominated by pine water use during the period of 27 May 27 – 12 October supporting the first hypothesis (Figure 26a and b, 23b). At the unburned site, pine transpiration made up 75% of the stand's daily transpiration while oak transpiration only made up 11%. There were more oaks (n = 22) than pines (n = 13), but the pines were large and therefore had considerable amounts of sapwood. Five of the pines were in the 45 to 55-cm DBH class and I recorded one individual (62.8 cm) in the 55 to 65-cm class. Transpiration from species other than oak and pine contributed more to the stand transpiration of the unburned site than at the other two stands (Figure 26). Together the total sapwood area from these other species (i.e. eastern red cedar, yaupon holly, and farkleberry) (0.25 m^2) was just slightly more than that of the oaks (0.24 m^2) in the stand. At the moderately burned stand, pine (n = 24) and oak (n = 17) transpiration made up 86 and 14% of the daily stand transpiration, respectively. Daily transpiration from oaks was 148 and 145% less than pines due to 130 and 120% lower sapwood and 31 and 39% lower J_s per unit

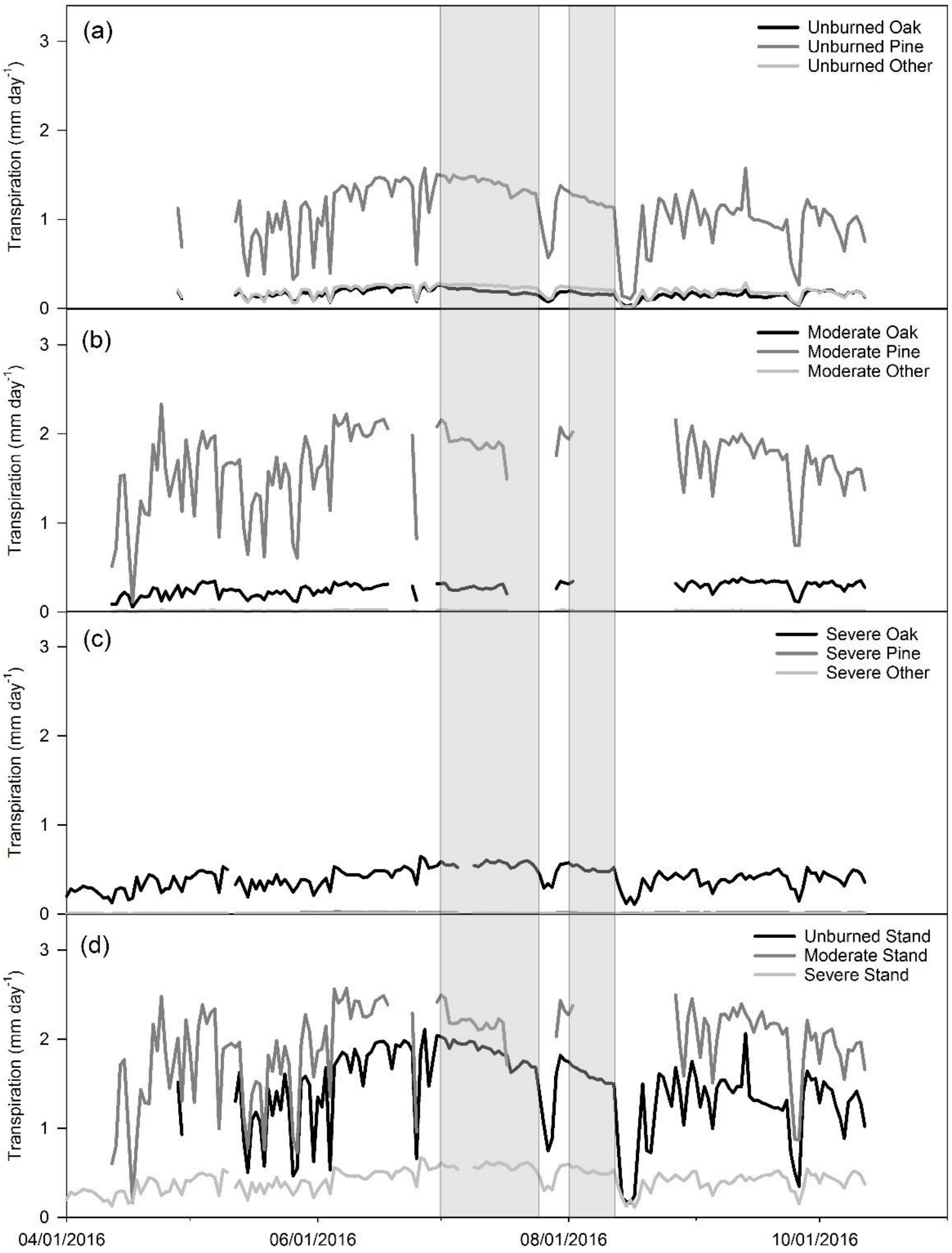


Figure 26. Daily transpiration (mm day^{-1}) of oaks, pines, and other species within the a) unburned, b) moderately burned, and c) severely burned stands from 1 April to 12 October, 2016. D) Total daily transpiration compared among stands. Periods of shallow soil moisture dry down are shaded.

sapwood at the unburned and moderately burned sites, respectively. Although the total sapwood area was 24% greater in the unburned than the moderately burned stand, the unburned stand’s total transpiration was 34% lower (Figure 23c), likely due to lower conductivity in the older trees in this stand coupled with the greater light availability and evaporative demand at the more open moderately burned site.

Transpiration was 0.46 mm day^{-1} on average at the severely burned site from 27 May to 12 October, 2016. Transpiration at the unburned and moderately burned stands was much greater, however: 1.48 and 2.08 mm day^{-1} on average. Unlike the unburned and moderate stands, oak transpiration made up over 95% of total daily stand transpiration at the severely burned stand. In this stand, I recorded very few individuals of other species, pine or otherwise, so their contribution to the stand transpiration was negligible. In fact, daily transpiration from pines at the site was less than 0.02 mm on average, which was more than 200% less than oak transpiration each day. Sapwood area of oaks in the severely burned stand was fairly similar to that of the oaks in the other two stands (Table 3) and oak daily J_s was 52 and 82% greater on average than the moderately burned and unburned stands, respectively, but the overall reduction in total sapwood area at the severely burned stand after the fire translated to 1.02 and 1.62 mm less transpiration day^{-1} on average than the sites with mature trees (Figure 23c).

Discussion

Severe Fire Alters Stand Transpiration

The high daily J_s of individual resprouts and seedlings did not translate into high amounts of daily transpiration by the severely burned stand due to its low total sapwood area. Reductions in plant density and sapwood area commonly lead to reductions in stand transpiration (Morikawa et al. 1986, Aussenac and Granier 1988, Whitehead and Kelliher 1991, Nolan et al. 2014). Other studies have reported significant reductions in stand-level transpiration in severely burned areas compared with intact, unburned stands and stands experiencing lower burn severity (Gharun et al. 2013, Nolan et al. 2014). Nolan et al. (2014) reported that transpiration of unburned stands was approximately 1.4 to 1.7 mm day^{-1} while transpiration of severely burned stands was around 0.4 mm day^{-1}, similar to the results from our unburned (1.48 mm day^{-1}) and severely burned (0.46 mm day^{-1}) stands. Unburned stands in the Nolan et al. (2014) study had 43% to 57% greater sapwood area than severely burned stands. Following mechanical thinning, Morikawa et al. (1986) and Jiménez et al. (2008) also reported greater sap flux rates for individual trees but reduced stand-level transpiration in comparison to un-thinned stands.

As indicated above, stands with greater total sapwood areas often have greater stand transpiration. However, it appears that 42% greater daily pine J_s and 34% greater daily oak J_s extrapolated across the stand resulted in greater transpiration in the moderately burned stand compared to the unburned stand, although the moderate stand had less sapwood. Nolan et al. (2015) also reported light to moderate burning increased transpiration and therefore decreased the amount of water available to other parts of the hydrologic cycle after fire. Severe fires are known to result in enhanced runoff and stream flow though, at least in the early years of recovery (Hibbert 1971, Lindley et al. 1988, Jones and Post 2004, Kunze and Stednick 2006, Silins et al. 2009). For example, Campbell et al. (1977) reported 28, 20, and 5 mm annual runoff on average for the first three years after a fire in severely, moderately, and unburned watersheds respectively. The number of runoff events was greater for the severely burned watershed (n = 25) as well compared to the unburned watershed (n = 6). Reductions in stand transpiration following severe fires may be short lived. Cerda (1998) reported a decrease in overland flow from 45% of precipitation in the first year after a wildfire to less than 6% nearly six years after the fire. As regenerating burned stands approach full canopy, they may use more water than unburned old growth stands (Kuczera 1987, Vertessy et al. 2001). This could be a possibility for the severely burned stand in several years as long as resprout densities remain high. However, when this severely burned stand reaches maturity its site water balance may differ from a similar aged pine dominated stand. Given that mature oak J_s was lower than mature pine J_s in the other two sites, a conversion to oak dominated stands in severely burned areas could result in increases in streamflow and greater water availability to other vegetation over a longer term.

Sap Flux Related to Tree Age and Abiotic Constraints

The lower daily J_s in trees at the unburned site compared to those at the moderately burned and severely burned sites could be related in part to reductions in water use and slower growth by the older, larger trees at the unburned site. Water use by trees often decreases with age due to declines in sapwood and leaf area indices and stomatal conductance in older trees (Magnani et al. 2000, Roberts et al. 2001, Vertessy et al. 2001, Ewers et al. 2005, Delzon and Loustau 2005, Martínez-Vilalta et al. 2007). Older individuals often have lower whole-tree leaf-specific hydraulic conductance and leaf-level gas exchange than young trees in the same species (Ryan et al. 1997, Niinemets 2002, Rust and Roloff 2002, Drake et al. 2010). Some of the age-related decline in water use can be attributed to increases in pressure gradient with gravity and hydraulic resistance associated with taller heights in older trees (Ryan and Yoder 1997, Koch et al. 2004), although other characteristics such as leaf:sapwood area ratio may play a greater role (Becker et al. 2000).

Greater daily sap flux in the moderate and severely burned stands was also likely related to reduced competition and subsequent increases in energy and water availability per individual tree at these sites in comparison with the densely vegetated unburned stand. These increases in light and water availability may have been the dominant factor in increasing species specific daily sap flux in the burned sites. For example, greater J_s was recorded in oak trees at the moderately burned than unburned site, although the monitored individuals were similar in size: 25.03 ± 3.88 cm and 22.48 ± 2.68 cm DBH, for the moderately burned and unburned stands, respectively. Pines with sensors at the unburned site had lower daily J_s as well but were larger in size, 52.22 ± 2.77 cm DBH, and likely older compared with those at the moderate site, 43.48 ± 2.13 cm DBH. Therefore we should not discount the possibility of age or size related decline in sapwood conductivity, but must also take increased water and light availability into consideration when determining causes of greater J_s and transpiration in the moderately burned stand. Reductions in stand density have been linked to increased sap flux in individual trees (Morikawa et al. 1986, Medhurst et al. 2002, Martínez-Vilalta et al. 2007, Asbjornsen et al. 2007). This may be in part due to increases in sapwood area or leaf area (Shelburne et al. 1993, Medhurst et al. 2002). However, Bréda et al. (1995) reported increases in sap flux and stand transpiration with density reductions without increased sapwood area or leaf area in a thinned stand.

Results suggest that regenerating pines at the severely burned site relied more on water in the upper soil layers than the resprouting oaks and mature trees of both species, and were therefore moisture limited during the hot, dry periods in the summer. The severely burned site had the most water available of the three sites due to low total biomass and competition, but the shallow rooted pines were not as able to capitalize on this advantage as the deep-rooted resprouts. The roots of regenerating pines are likely restricted to the upper few centimeters of soil, while the resprouting oaks have root systems remaining from mature trees. Shallow-rooted seedlings and young trees become water limited more quickly than mature trees during drought periods (Donovan and Ehrleringer 1994, Cavender-Bares and Bazzaz 2000, Irvine et al. 2002, Anthoni et al. 2002, Llorens et al. 2010). Irvine et al. (2002), for example, reported similar findings when comparing sap flux of a 14 year-old Ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) stand with an older stand consisting of two age classes, 50 and 250 years old. Both predawn water potential and daily transpiration declined steadily from July to October in the 14-year-old stand, but the old growth stand showed no decline although the volumetric water content was lower over the top 80 cm of soil at that site. Irvine et al. (2002) concluded that the trees at the old growth stand were getting most of their water from below 80 cm while the trees at the young stand were relying on soil moisture from the upper soil layers and also having to compete for that shallow soil moisture with co-occurring shrubs at the site.

Pine seedling J_s exhibited a downturn with high VPD levels. However, the days when VPD was the greatest also corresponded with the time periods when shallow soil moisture was at its lowest. Decreases in soil moisture are known to reduce J_s and stand level transpiration and their responses to VPD (Pataki et al. 2000, Oren and Pataki 2001, Martínez-Vilalta et al. 2003, Holscher et al. 2005). Pataki et al. (2000) and Holscher et al. (2005) reported much lower values of J_s during drought than during periods of high soil moisture, even though VPD values were similar. Oren and Pataki (2001) reported a strong exponential relationship between stand transpiration and VPD when soil moisture deficits were low (<10mm). However, when soil moisture deficits were high (≥ 10mm), VPD did not account for variability in stand transpiration. Effects were exacerbated by shallow rooting depths.

Unlike the young pines, regenerating oaks were not affected by hot, dry conditions and kept increasing J_s as VPD increased. Resprouts have access to similar or even greater water reserves than the mature oaks given the lack of competition in the severe stand. The resprouts have greater root:shoot ratios and lower leaf areas though (Utsumi et al. 2010, Schafer et al. 2014). Other studies have documented increases in leaf-specific whole-plant hydraulic conductance manifested as greater stomatal conductance in resprouts compared to mature trees, and attributed this to the reduction in leaf area without reductions in root system size (Kruger and Reich 1993, Schafer et al. 2014). The more favorable water supply to demand ratio in resprouts likely allowed them to continue gas exchange during conditions that were not optimal for their regenerating pine counterparts. Oaks exhibit small safety margins, frequently operating close to cavitation (Tognetti et al. 1998, Taneda and Sperry 2008, Li et al. 2008). However, since J_s of the resprouting oaks did not plateau under the high VPD conditions at the severely burned site, we can assume that they had enough water available to meet the evaporative demands imposed in this exposed environment and were not approaching cavitation limits.

Differences Between Oaks and Pines

Pines typically had greater daily J_s than oaks at the moderately burned and unburned sites, and the regenerating pines at the severely burned stand had greater sap flux than the oaks when soil moisture was high. Other studies also reported greater sap flux in pines than associated angiosperms (Phillips et al. 1996, Ford et al. 2010, Renninger et al. 2015). Sterck et al. (2008) and Zweifel et al. (2007) found greater stem conductivity (K_p) in pines than oaks. At the unburned site especially, a greater portion of the pine crowns were exposed than those of the oaks which could have contributed to the greater J_s in pines at those sites. Reduced irradiance on crowns of shorter trees resulted in decreased J_s in other studies (Granier 1987, Köster et al. 1992, Jiménez et al. 2000). Although growth slows as trees mature, the pines at the moderately burned stand were probably growing at a faster rate than the oaks there and using more water, which would contribute to greater J_s in the pines. Height and diameter growth of post oak and blackjack oak are usually slower than associated trees, so they are often over-shadowed by other trees, including other oak species (Stransky 1990).

The amount of water lost through transpiration depends on both J_s and the area of actively-conducting sapwood (Granier 1987). Not only did the pines at the moderate and unburned stands have greater J_s but they also had much larger sapwood areas than the oaks. Although maximum sap flow occurs close to the cambium and decreases toward the heartwood in both oaks (Granier et al. 1994, Poyatos et al. 2007, Gebauer et al. 2008) and loblolly pine (Phillips et al. 1996, Ford et al. 2004), active sapwood makes up a greater portion of the cross-section of non-porous species like pines compared to ring-porous species such as oaks (Cermak and Nadezhdina 1998). This may therefore explain the large contributions from pine to stand transpiration in the moderate and unburned stands with large pine sapwood areas.

Conclusions

Variations in sap flux and sapwood areas lead to differences in stand level transpiration following disturbance. Young, actively growing oak resprouts and pine seedlings tended to have greater sap flux per unit sapwood area than older individuals of the same species, however pine seedlings were more limited by shallow soil moisture than mature trees with deeper root systems. Less intense fire at the moderately burned site seemed to increase total stand water use, through increased water availability and greater irradiance reaching a larger portion of the canopy, even though the total sapwood area there was slightly less than that of the unburned stand. In contrast, severe fire reduced stand transpiration due to large reductions in total sapwood area. Overall, it appears like there could be more water available to other parts of the hydrologic cycle in the severely burned plot and severely burned patches throughout the region for several years while stands recover.

Although irradiance and VPD were high in these severely burned areas and enhanced daily J_s and individual plant transpiration to some degree, it appeared that conditions associated with canopy removal inhibited loblolly pine seedling gas exchange, when these were associated with low availability of shallow soil moisture. Resprouting oaks, on the other hand, were not inhibited by VPD and have deep root systems, which may allow them to suppress pine recovery. However, once regenerating pine root systems become more established and gain access to deeper soil moisture, they may have the advantage over oaks. Differences in water use strategies between the two species, various plant ages, and anatomy should be taken into account when considering post-fire management for the Lost Pines region.

CHAPTER V

CONCLUSIONS

Disturbance events such as droughts and wildfires can result in large-scale mortality events and significant shifts in vegetation composition. Following the substantial 2011 Texas drought, Bastrop County Complex Fire, and subsequent tree mortality after each of these events, we recognize the importance of increasing understanding of the interactions between physiological mechanisms and resource availability, among different genera and species within the same genus. Identifying and understanding differences in physiological responses among species will help us predict which will be more successful following such events and guide landowners and natural resource managers in proper modes of action for remediation.

This region of the state supports drought-hardy species of oak as well as phenotypic variations of loblolly pine that more adapted to drought conditions than their eastern relatives. As seen in chapters II and III, some oak species are more resilient than others and continue to exhibit high gas exchange rates under as stressful conditions while others use stress-avoidance strategies. Stress avoidance strategies are not necessarily worse than stress tolerant strategies though, and may actually save individuals from hydraulic failure in longer drought situations.

Results from Chapter III suggest loblolly pine (*Pinus taeda* L.) may not be able to overcome competition post-fire in stands with resprouting oaks (*Quercus stellata* Wangenh., *Quercus marilandica* Muenchh.) if seedlings are exposed to frequent soil moisture deficits. The pine seedlings were smaller and less numerous in severely burned areas and exhibited stronger drought-avoidance tendencies in these areas. This could limit their competitive ability during future dry periods when oak resprouts will likely continue to maintain moderate to high leaf-level gas exchange, expanding on their head-start. The fire had a bigger impact on plant abundance and competition than did soil type, and leaf-level physiology results in shallow soils were expected to be similar to those found in deeper Padina (loamy, siliceous, active, thermic Grossarenic Paleustalf) soil. However, the period of study had generally higher than normal rainfall. More severe drought conditions in the future may impact plants growing on shallow Jedd (fine, mixed, semiactive, thermic Ultic Paleustalf) and Edge (fine, mixed, active, thermic Udic Paleustalf) soils more than deep Padina soil.

As seen in Chapter IV, differences in plant abundance and competition following wildfires can lead to differences in resource availability and use that may impact water tables and stream flow. Results from the sap flux experiment indicate that severe, stand replacing fires lead to a decrease in stand level transpiration as plants recover to maturity. Following overstory mortality, individual oak resprouts and pine seedlings at the severely burned site had more water available to them and experienced high VPD conditions which resulted in high sap flux rates per unit sapwood. However, we can expect greater runoff from this area than the other two stands due to the large reduction in biomass at the site. A switch from pine to oak dominance in severely burned patches may lead to long term alterations to water fluxes and ecosystem function in the region. At the moderately burned and unburned stands, mature pines contributed more to stand transpiration than mature oaks due to greater sap flux rates per unit sapwood and greater sapwood areas. Therefore, when the oak-dominated severely burned stand matures it may use less water than pine-dominated stands of similar ages. Alterations to availability of water and other resources by the oak overstory may result in different understory plant associations than those that occurred under the previous pine-dominated regime.

Future Research Directions

Results from the long-term drought experiment expanded knowledge about foliar gas exchange and biochemistry differences between live (*Quercus virginiana* Mill.), bur (*Quercus macrocarpa* Michx.), and Shumard oak (*Quercus shumardii* Buckley), but also revealed the need to measure physiological responses from multiple plant parts. Root and stem samples taken at the same time as leaf collections would likely help explain changes in leaf N, carbohydrates, and phenolics with both drought and seasonal patterns. Since oaks are typically deep rooted, future studies examining oak drought stress should monitor changes to shallow and deep soil moisture. Both mature live oaks and bur oaks have been reported to produce roots greater than 10 m deep (Weaver and Kramer 1932, Jackson et al. 1999), and individuals of these species younger than 10 years old are known to have roots deeper than 100 cm (Holch 1931, Gilman and Harchick 2008). The use of deeper soil moisture sensors in conjunction with destructive sampling will provide information about when plants switch from relying on shallow soil moisture to water deeper in the profile and if root growth into deeper pockets of moisture has occurred.

Continual monitoring of oak resprout and pine seedling growth and climate conditions will be needed to accurately predict long-term changes to ecosystem function and the hydrologic cycle in burned areas following the Bastrop County Complex Fire. Integration of transpiration and growth data with stream flow records for nearby Copperas and Alum Creeks in the coming years will help with long-term planning for changes in water availability. This research on physiological differences between oaks and pines revealed differences in water use and highlighted interesting disparities, especially between oak resprouts and pine seedlings. Results raised questions about rooting depths and architecture and how those might differ between burn severities. Information about root structure and hydraulic properties in future studies may help explain some of the leaf level gas exchange (Chapter III) and sap flux (Chapter IV) differences between oaks and loblolly pine. Prescribed burns should also be utilized in Bastrop State Park and the Griffith League Ranch to further study oak and pine physiology and how burning on regular intervals may have led to different responses than the 2011 wildfire. Prescribed burns could also be used to direct vegetation recovery in line with park and private land management goals in the region

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