Received: 15 January 2018 | Revised: 14 September 2018 | Accepted: 11 October 2018
DOI: 10.1002/eco.2052

RESEARCH ARTICLE

WILEY

Transpiration in recovering mixed loblolly pine and oak stands following wildfire in the Lost Pines region of Texas

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Funding information
Texas Parks and Wildlife Department, Grant/Award Number: 454585

Abstract

Depending on severity, wildfire alters stand biomass, tree species distribution, and age, which may modify stand transpiration (E_t) and the amount of water available to other parts of the hydrologic cycle. Our objective was to determine how wildfire severity affected E_t in mixed pine/oak (*Pinus taeda* L./*Quercus stellata* Wangehn., *Quercus marilandica* Muenchh.) stands in the Lost Pines eco-region (Bastrop, TX, USA). Transpiration was estimated for mature pines and oaks at unburned and moderately burned sites and oak resprouts and pine saplings at a severely burned plot. On average, mature pines had 36% greater sap flux rates (J_s) than mature oaks in the unburned and moderately burned stands. Under low moisture stress, regenerating pines had greater J_s than resprouting oaks, but J_s quickly decreased as soil moisture declined. By contrast, mature pines were unaffected by dry periods. Pines contributed most to E_t at the unburned and moderate stands. Conversely, oak E_t dominated the severely burned stand, contributing over 95%. Transpiration was greatest at the moderately burned stand (2.02 mm day^{-1}), followed by the unburned (1.44 mm day^{-1}), and the severely burned stands (0.46 mm day^{-1}). Despite greater J_s in resprouts and saplings, reductions in total sapwood area resulted in lower stand-level daily E_t at the severe site. Although severe fire decreased stand transpiration through reductions in vegetation density, individual oak resprouts appear to thrive, undeterred by high vapour pressure deficit. Without pine planting, oaks will likely dominate severely burned stands that could result in shifts to local hydrology and microclimate.

KEYWORDS
loblolly pine, oak, regeneration, sap flux, transpiration, wildfire

1 | INTRODUCTION

A warmer, drier climate has resulted in increasing annual fire season length, fire frequency, and overall burned area in North American forests (Flannigan, Logan, Amiro, Skinner, & Stocks, 2005; Miller, Safford, Crimmins, & Thode, 2009). Due to fire suppression over the past century, increases in large standing dead fuel loads have also led to greater fire size and severity (Miller et al., 2009; Pollet & Omi, 2002). After high-severity fires, in particular, there may be a shift in stand structure and species composition due to alterations in resource availability (e.g., light, soil nutrients, and soil moisture; Barton, 2002; Johnstone & Kasischke, 2005; Moser, Temperli, Schneiter, & Wohlgemuth, 2010; Savage & Mast, 2005; Strom & Fulé, 2007). In turn, shifts in species composition, distribution, and vegetation age can change transpiration demands (Hadley, Kuzeja, Daley, & Phillips, 2008; Vertessy, Watson, & O'Sullivan, 2001) and water available to other parts of the hydrologic cycle (Brown, Zhang, McMahon, Western, & Vertessy, 2005; Moody & Martin, 2001).

The switch to younger vegetation, both resprouts and nonsprouting saplings, serves as the first visual indication of change to postfire stand structure. Age shifts have been shown to result in greater gas exchange and water use per unit leaf area than mature trees remaining in less severely burned areas (Castell, Terradas, & Tenhunen, 1994; Utsumi, Bobich, & Ewers, 2010). Greater water use in young individuals and resprouts may be associated with greater sapwood to leaf area ratios and stomatal conductance per unit leaf area than older individuals (Delzon & Loustau, 2005; Ewers, Gower, Bond-Lamberty, & Wang, 2005). Additionally, resprouts have greater root : shoot ratios than mature trees, which help increase hydraulic efficiency and lower leaf areas, which means individual leaves can receive more water per root area (Schafer, Breslow, Hollingsworth, Hohmann, & Hoffmann, 2014; Utsumi et al., 2010). Age difference is not the only factor affecting the hydrologic cycle of a stand. Species composition has important effects on how water resources are used. Gymnosperms and angiosperms, such as pines and oaks, respectively, differ in their rooting structure and depth (Jackson, Moore, Hoffmann, Pockman, & Linder, 1999; Renninger, Carlo, Clark, & Schäfer, 2015; Schwinning, 2008), hydraulic architecture, and leaf physiology (Choat et al., 2012; Ford, Hubbard, & Vose, 2010; Renninger et al., 2015). Additionally, differences in leaf area index, branch angles, bark surfaces, and canopy partitioning may result in large variations in throughfall, stemflow, and interception losses between deciduous and coniferous stands (Perez-Suarez, Arredondo-Moreno, Huber-Sannwald, & Serna-Perez, 2014; Augusto et al., 2015). However, cohabitation in mixed stands may cause species to deviate from typical canopy structure and subsequent evaporative losses than would be seen in monotypic stands (Pretzsch, 2014).

Of the two genera in this study, oak species are thought to exhibit smaller safety margins, progressively lowering leaf water potentials while maintaining relatively high gas exchange (Cooper, Muir, Morgan, & Moore, 2018; David et al., 2007; Pinto et al., 2012). Although pines often adopt more conservative water use strategies during drought (Choat et al., 2012; Irvine, Perks, Magnani, & Grace, 1998), they capitalize on soil moisture increases and display greater conductance and evapotranspiration than co-occurring hardwood species following precipitation events (Poyatos, Llorens, Piñol, & Rubio, 2008; Renninger et al., 2015; Zweifel, Rigling, & Dobbertin, 2009). These differences will ultimately determine their adaptability to drought events and likelihood to coexist in the same environment through multiple postfire successional events.

The “Lost Pines” area in central Texas provides an opportunity to examine possible long-term shifts in vegetation structure and species composition following wildfire and how these shifts will additionally modify vegetation water use. Prior to the 2011 Bastrop County Complex Fire, the overstory vegetation of the region predominantly consisted of loblolly pine (*Pinus taeda* L.; Stambaugh, Creacy, Sparks, & Rooney, 2017). However, post oak (*Quercus stellata* Wangenh.) and blackjack oak (*Quercus marilandica* Muenchh.) have rapidly resprouted across much of the postfire landscape, suggesting some areas may shift to oak-dominated woodlands or savannas rather than pine-dominated stands (Cooper et al., 2018). Multiple studies have evaluated sap flux responses of oaks and pines, with several studies including both genera (Phillips et al., 2003; Phillips, Oren, & Zimmermann, 1996; Poyatos et al., 2008; Poyatos, Llorens, & Gallart, 2005; Renninger et al., 2015). However, less is known about sap flux and transpiration response differences between mature trees and resprouts after fire (Ffolliott, Gottfried, Cohen, & Schiller, 2003), with the exception of a few studies focusing on *Eucalyptus* (Buckley, Turnbull, Pfautsch, Gharun, & Adams, 2012; Gharun, Turnbull, & Adams, 2013; Nolan, Lane, Benyon, Bradstock, & Mitchell, 2014; Nolan, Lane, Benyon, Bradstock, & Mitchell, 2015).

Our primary objective was to determine how burn severity affected sap flux (J_s) and stand-level transpiration rates (E_t) through alterations in stand structure and age in mixed pine/oak stands following the Bastrop County Complex Fire. We relied on sap flux measurements at three sites differing in burn severity (unburned, moderate, and severe) and relative abundance of mature and young oaks and pines. We hypothesized that (a) E_t would decrease in sites with greater burn severities due to reductions in vegetation density and total sapwood area; (b) resprouting oaks and young pines would have greater daily J_s per unit sapwood than mature individuals of the same species; (c) mature pines would have greater J_s than mature oaks that, coupled with their large sapwood area, would result in greater transpiration in stands containing a greater number of pines; (d) oak resprouts would use more water than pine saplings because of their greater root depth and biomass; (e) pine saplings are most sensitive to changes in shallow soil moisture because their roots are closer to the surface than those of oak resprouts and mature trees.

2 | MATERIALS AND METHODS

2.1 | 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, TX, USA, within the Lost Pines eco-region. The Lost Pines represents the western-most range of loblolly pine in North America, isolated from the East Texas Piney Woods eco-region by over 160 km. These pines are thought to have been separated from the loblollies in East Texas during the Pleistocene (Al-Rabab'ah & Williams, 2004; Bryant, 1977). Loblolly pine, post oak, blackjack oak (*P. taeda* L./*Q. stellata* Wangehn., *Q. marilandica* Muenchh., respectively), 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°C to 26.5°C 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 designated the most destructive fire recorded in Texas history due to the loss of over 1,600 homes with property damage estimated at $325 million (Rissel & Ridenour, 2013). More than 12,950 ha and 1.8 million trees burned, including 96% of Bastrop State Park (Rissel & 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 & Kanarek, 2014).

Within the park, two plots were established to monitor sap flux and micrometeorological conditions. These areas were classified as (a) moderately and (b) severely burned. A third unburned control plot was established at the Griffith League Ranch located approximately 20 km north of the city of Bastrop, TX, USA. All three plots were circular with a 15-m radius (area = 707 m^2). Soils 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 confounding differences in water availability that may occur with variation in soil texture and depth to the argillic horizon (Fernandez-Illescas, Porporato, Laio, & Rodriguez-Iturbe, 2001; Hacke et al., 2000).

A full stand survey was conducted in all three plots. At the unburned site, we estimated that oaks and pines were around 11 and 16 m tall, respectively. We estimated that oaks and pines were approximately 9 and 14 m tall, respectively, at the moderate site. Heights of mature oaks and pines sampled in our study are similar to those recorded in other plots in Bastrop State Park by Stambaugh et al. (2017). Stambaugh et al. (2017) estimated that the height of 100- to 350-year-old post oaks in the park is around 10.1 m. The tallest loblolly pines measured by Stambaugh et al. were approximately 16 m at the time of measurements after the Bastrop County Complex Fire. At the severe site, resprouting oaks were around 2.7 m tall, and pine saplings were approximately 2.5 m tall. In the unburned and moderately burned sap flux plots, the relative proportion of saplings and resprouts was less than 2% of the total stand basal area. Therefore, we measured all trees with diameter at breast height (DBH) greater than 5 cm (Table 1). At the severely burned site, none of the overstory trees survived the fire. Therefore, we measured the diameter at the base of the stem (~0.1 m height; Cipollini & Whigham, 1994; Keeley & Zedler, 1978) of all resprouts and saplings with stems greater than 1 cm (Table 1).

2.2 | Sap flux and sapwood area measurements

Sap flux density (J_s) was continuously measured using heat dissipation sensors (Granier, 1987), constructed using the method described by Phillips et al. (1996), from May to October 2016. At both the unburned and moderately burned sites, two 20-mm long sensor pairs were installed in each of five mature pine trees and five mature post oak trees. Sensors were installed on the opposite sides of the trees and inserted at 1.5-m height. Oaks with sensors at the moderate site ranged from 17.6 to 39.4 cm DBH with a mean DBH of 25.0 ± 3.9 cm. The pines with sap flux sensors at the same site ranged from 39.3 to 51.0 cm DBH with a mean of 43.5 ± 2.1 cm. At the unburned site, oaks with sensors ranged from 16.4 to 32.1 cm DBH with a mean DBH of 22.5 ± 2.7 cm. Pines with sensors at the unburned site ranged from 47.5 to 62.8 cm DBH with a mean of 52.2 ± 2.8 cm. Due to the smaller statute of the resprouts and saplings (diameter < 5 cm and height < 3 m), at the severely burned site, one

TABLE 1 Number of individuals, average diameter at breast height (DBH; cm ± SEM), and total sapwood area (A_s; m^2) for each species and functional group, along with oak and pine average sapwood width (cm ± SEM) and A_s/A ratios (±SEM) in each 707 m^2 sap flux plot

	Unburned					Moderate					Severe		
Species	Number of individuals	Average DBH (cm)	Average sapwood width (cm)[a]	A_s (cm^2)/A (cm^2)[a]	Total A_s (m^2)	Number of individuals	Average DBH (cm)	Average sapwood width (cm)	A_s (cm^2)/A (cm^2)	Total A_s (m^2)	Number of Individuals[b]	Average D (cm)[c]	Total A_s (m^2)
Oak	22	18.7 ± 1.4	2.6 ± 0.09	0.37 ± 0.03	0.24	19	20.9 ± 1.5	2.6 ± 0.1	0.38 ± 0.03	0.25	38	3.9 ± 0.1	0.23
Farkleberry	3	5.6 ± 0.2			0.01	–	–			–	–	–	–
Yaupon	5	6.3 ± 0.1			0.02	–	–			–	2	4.5 ± 0.3	0.001
Willow baccharis	–	–			–	–	–			–	1	3.4 ± 0.9	0.002
Pine	13	38.0 ± 4.2	10.8 ± 1.1	0.63 ± 0.02	1.14	24	24.0 ± 2.5	6.8 ± 1.0	0.65 ± 0.06	1.02	4	5.0 ± 0.8	0.01
Eastern red cedar	11	16.9 ± 1.9			0.22	2	9.4 ± 2.2			0.01	–	–	–
Angiosperms	30				0.27	19				0.25	41		0.23
Gymnosperms	24				1.36	26				1.03	4		0.01
Total	54				1.63	45				1.28	45		0.24

[a] Average sapwood width and A_s (sapwood area)/A (basal area) ratios were derived from cored oak and pine individuals.

[b] All resprouting stems arising from the base of the same stump were collectively considered together as one "individual" plant.

[c] In the severe plot, diameters were measured at the base of the stem (~0.1 m height) for all resprouts and nonsprouting saplings.

10-mm sensor pair each was installed at ~0.45 m above the ground surface in six post oak resprouts, four blackjack oak resprouts, and three pine saplings. Because each resprouting oak stump had at least four stems, sensors were installed in the stem with the largest girth. Data were collected every 30 s, averaged over 30-min intervals, and stored on a datalogger (CR10X, Campbell Scientific Inc., Logan, UT, USA). Temperature differences between heated and reference probes were converted to J_s ($\text{kg·m}^{-2}\text{·s}^{-1}$) using Granier's (1987) empirical calibration equation (1):

$$J_s = 0.119 \left(\frac{\Delta T_M - \Delta T}{\Delta T}\right)^{1.231} = 0.119K^{1.231}, \quad (1)$$

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

Sapwood area (A_s) was determined in the unburned and moderately burned plots using increment cores retrieved at 1.5-m height and partially immersed in safranin-fucsin dye (Gebauer, Horna, & Leushner, 2008; McDowell et al., 2002). Due to the size and age of the oak resprouts and pine saplings at the severely burned site, sapwood area was assumed to be 100% of the resprout or sapling's cross-section area minus bark width (Moore, Bond, Jones, Phillips, & Meinzer, 2004). Other studies have reported little to no heartwood in similar sized saplings (Dean & Long, 1986; Wullschleger, Hanson, & Tschaplinski, 1998). All trees with sensors at the moderate and unburned sites had a sapwood radius greater than the sensor depth of 2 cm (Table 1; Clearwater, Meinzer, Andrade, Goldstein, & Holbrook, 1999). Sapwood area of the remaining trees in the plot was calculated using linear regression equations developed from total basal area and sapwood area from the cored individuals (moderate: $n_{\text{pine}} = 10$, $n_{\text{oak}} = 10$; unburned: $n_{\text{pine}} = 7$, $n_{\text{oak}} = 7$), assuming a constant active sapwood depth in all stem directions (Figure 1; Table 1). We combined the sapwood areas obtained for all the oaks and pines from the unburned and moderately burned sites to increase our sample size and develop a more robust allometric equation. The resulting equation for pines was $A_s = 0.69A + 8.74$ ($r^2 = 0.98$) and $A_s = 0.31A + 14.31$ ($r^2 = 0.96$) for oaks, where A_s is sapwood area and A is basal area, both in square centimetre. 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. Hence, the oak regression equation was used to estimate sapwood area of other angiosperms present in the moderate and unburned stands, and the pine regression equation was applied to other gymnosperms (i.e., eastern red cedar; Moore et al., 2004).

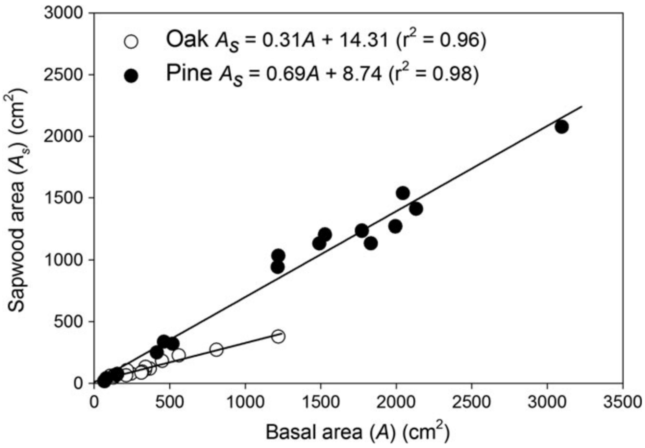


FIGURE 1 Allometric equations used to calculate sapwood area (A_s) for oak and pine individuals in the unburned and moderately burned stands

Some studies have highlighted that sap flux rates are not uniform across the entire sapwood area due to changes in conduction related to contrasting wood properties, age, and depth (Cermak & Nadezhdina, 1998; Ford, McGuire, Mitchell, & Teskey, 2004; Nadezhdina, Cermak, & Ceulemans, 2002; Phillips et al., 1996; Poyatos, Cermak, & Llorens, 2007). Hence, to avoid overestimations of stand transpiration, radial profile corrections were applied to J_s measurements (Delzon, Sartore, Granier, & Loustau, 2004; Ford et al., 2004). We monitored J_s across the sapwood profiles at multiple depths in the two largest pines (DBH = 62.8 and 52.1, A_s = 2,076.2 and 1,411.0 cm^2, respectively) and oaks (DBH = 32.1 and 23.9, A_s = 272.6 and 181.9 cm^2, respectively) 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, whereas pines had sensors installed every 2 cm from 2 to 14 cm and 2 to 16 cm into the xylem for the first and second tree, respectively. The radial profile sensors were an adapted version of James, Clearwater, Meinzer, and Goldstein (2002) variable length probes. The correction factors were calculated using the following equations, which were based on the radial profile measurements (Figure 2) and fitted using Gaussian equations (2 and 3):

$$\text{Oak } J_i/J_o = 1.03 \times \exp\left[-0.5\left(\frac{L_i/L_o - 0.04}{0.58}\right)^2\right], \quad (2)$$

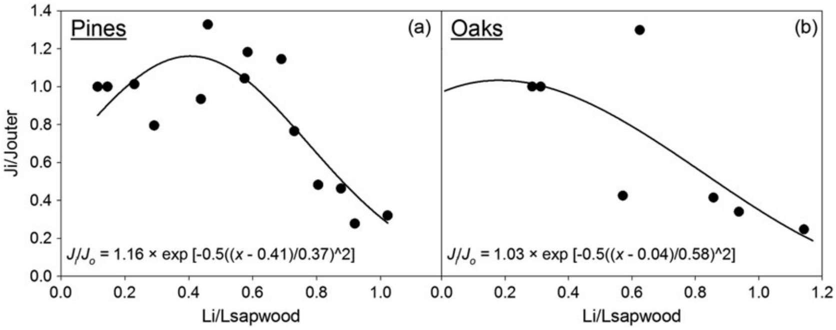


FIGURE 2 Fitted radial sap flux measurements for (a) pines and (b) oaks used to correct daily J_s ($P < 0.001$). Relative flux was calculated by normalizing the value at a given depth, J_i, to the value in the outermost depth, J_o, which was 10 mm for oak and 20 mm for pine. Relative depth was calculated by normalizing the depth of each measurement, L_i, to the total sapwood depth, L_{sapwood}, measured via core sampling

$$\text{Pine } J_i/J_o = 1.16 \times \exp^{\left[-0.5\left(\frac{L_i/L_o-0.41}{0.37}\right)^2\right]}, \quad (3)$$

where J_i/J_o is the ratio of sap flux in the *i*th depth to sap flux of the outer profile sensor (J_{o_Pine} = 2 cm; J_{o_Oak} = 1 cm) and L_i/L_o is the ratio of the *i*th sapwood depth to the total sapwood depth. We divided cross-sectional sapwood area for each tree in the moderate and unburned stands into five sections where L_i/L_o corresponded to 20% increments relative to the total sapwood depth. Within each stand, the correction factor J_i/J_o was applied to adjust the sectional sap flux per unit area (kg m^{-2}) relative to the average outer J_s from the 20-mm thermal dissipation probes for oak and pine, respectively. Daily total sap flux ($\text{kg·m}^{-2}\text{·day}^{-1}$) for each section was calculated by summing J_s values in a 24-hr period.

Daily pine E_t (mm) 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. Daily oak E_t was calculated in the same manner. E_t of species without sensors (e.g., eastern red cedar and yaupon) was calculated using the estimated sapwood area of that particular species and the adjusted daily sap flux densities of pine for gymnosperm species and oaks for angiosperm species (Moore et al., 2004). Total stand E_t was determined by summing the daily E_t of all individuals in the stand. In the severely burned stand, because daily total sap flux was assumed to be homogeneous across the entire cross-section of the resprouts and saplings, J_s was multiplied by the total sapwood area and divided by the plot area to calculate E_t 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.

We developed site-specific equations to approximate radial variation in J_s in pine and oak trees. Equations that account for radial variation in J_s for nonporous species (Berdanier, Miniat, & Clark, 2016; Pataki, McCarthy, Litvak, & Pincetl, 2011) were found to underestimate pine J_s at deeper depths resulting in lower pine E_t compared with E_t calculated using the profile equation developed for our pines (Figure S1). Bastrop oaks decreased J_s as distance from the cambium increased but still maintained some flow at deep depths resulting in intermediate E_t values compared with those calculated using other ring-porous equations (Berdanier et al., 2016; Pataki et al., 2011). This deeper flow was also confirmed when we compared J_s measured across 10-mm in the profile oaks with J_s measured using the 20-mm long heat dissipation probes in other oaks in the unburned sap flux plot (Figure S2).

2.3 | Stand microclimate measurements

Each site was equipped with a tipping bucket rain gauge (TR-525, Texas Electronics, Inc., Dallas, TX, USA) to monitor rainfall daily totals (mm day^{-1}), and relative humidity (%) and air temperature (°C) were measured with a temperature/relative humidity probe (HMP60, Vaisala Inc., Boulder, CO, USA). Soil temperature (°C) was measured at the soil surface, below the litter layer and at 5, 10, and 30 cm deep. Three copper-constantan thermocouple sensors were installed at both the soil surface and the litter layer, and two sensors were installed at each soil profile depth, which totalled 12 soil temperature sensors at every site. A thermistor (CR10XTCR, Campbell Scientific Inc., Logan, UT, USA) was used to provide a temperature reference for the soil temperature type T thermocouples. The values from all thermocouples at a particular soil depth were averaged together for that given depth. All micrometeorological parameters were measured every 30 s and averaged over 30 min by the site datalogger (CR10X, Campbell Scientific Inc., Logan, UT, USA). Air temperature and relative humidity data were used to calculate vapour pressure deficit (VPD; Howell & Dusek, 1995).

Each site was equipped with an aluminium access tube (5.1-cm diameter) for neutron moisture gauge (CPN Model 503DR, Instrotek, Inc., Concord, CA, USA) measurements of volumetric soil water content (θ) to a depth of 1.8 m. Water content profiles were measured on nine separate occasions from March through August 2016 at 0.15-m intervals, beginning at 0.15 m below the soil surface. For each measurement depth, count ratios ($CR = N/Ns$;i.e., the number of counts in the soil [N] relative to counts in a reference standard [Ns]) were converted to θ ($\text{m}^3\ \text{m}^{-3}$) using site-specific calibrations for Padina fine sandy loam. A 32-s count interval was used. Volumetric water content at each depth was then converted to millimetre of water and summed to calculate total millimetre of water across the profile.

2.4 | Statistical analyses

Statistical tests for effects of burn severity and species interactions on daily J_s and E_t 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 E_t. Data from DOY 148 (May 27) to 286 (October 12) were analysed because this time period represents the bulk of the growing season. In the models, "day" was considered as random, whereas 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 checked using Tukey's honestly significant difference post hoc analysis. Differences were considered significant at $P \leq 0.05$. Additionally, non-linear (exponential and quadratic) equations were used to determine the effects of site-specific daily average VPD on daily J_s (Table S1). Similarly, we examined the response of daily J_s normalized for each species across sites to VPD normalized for all sites over the entire growing season. Daily VPD values from July 1 to 24 and August 1 to 12 were examined in greater detail with respect to effects on regenerating pine J_s at the severely burned site when shallow soil moisture was depleted. We also used linear regression (proc reg procedure, SAS 9.4) to assess the relationship of site-specific soil moisture (θ, mm) between 0 and 150 cm depth and daily sap flux rates. All model fits were evaluated based on coefficient of determination (r^2) and P values.

3 | RESULTS

3.1 | Stand density and transpiration postfire

The unburned plot had the largest number of mature trees (n = 54) and basal area (A = 2.72 m^2), followed by the moderately burned site

(n = 45, A = 2.10 m^2) and the severely burned site (n = 0, A = 0.29 m^2; Table 1). Even though the fire moved through the moderately burned site and killed a few mature pines in the surrounding area, no mature trees had been killed within the plot, and very few pine seedlings had germinated in the understory. By contrast, the severely burned site had no remaining mature trees but had numerous resprouting oak stumps (n = 38) with five stems (diameter > 1 cm) resprouting from each stump on average. In addition, there were few naturally regenerating pine saplings (n = 4), yaupon (n = 2), and willow baccharis (*Baccharis salicina* Torr. & A. Gray; n = 1) in the severely burned site.

Due to the large reduction in live tree abundance and basal area, E_t was only 0.46 mm day^{-1} on average at the severely burned site. However, E_t at the unburned and moderately burned stands was three to four times greater, with 1.44 and 2.02 mm day^{-1} on average. Although the total sapwood area was 24% greater in the unburned than the moderately burned stand, the unburned stand's total E_t was 34% lower (Figure 3c), and the diameter distribution and relative abundance of pines and oaks differed between sites (Table 1).

Stand E_t in unburned and moderately burned sites was dominated by pine water use for the duration of the study (Figures 3b and 4a,b). At the unburned site, pine E_t contributed 77% of the stand's daily E_t, whereas oak E_t was only responsible for 9%. There were more oaks (n = 22) than pines (n = 13) at the unburned site, but many of the pines were larger (six between 45 < DBH < 65 cm) and had considerable amounts of sapwood (Table 1). At the moderately burned site, pines (n = 24) and oaks (n = 19) were responsible for 88 and 11% of E_t, respectively. Oak E_t was 158% and 156% less than pine E_t at the unburned and moderately burned sites, respectively. Transpiration from species other than oak and pine (i.e., eastern red cedar, yaupon holly, and farkleberry) represented ~14% of daily E_t at the unburned site. Contrastingly, due to extensive resprouting at the severely burned site, oak E_t made up 95% of total daily E_t. Very few individuals of other species (pine or otherwise) were present at the severely burned site, so their contribution to total E_t was negligible (~1%, Figure 4; Table 1). In fact, daily pine E_t at this site was less than 0.02 mm on average, which was 187% less than oak E_t. Total stand sapwood area of oaks in the severely burned stand was fairly similar to that of the oaks in the other two stands (Table 1).

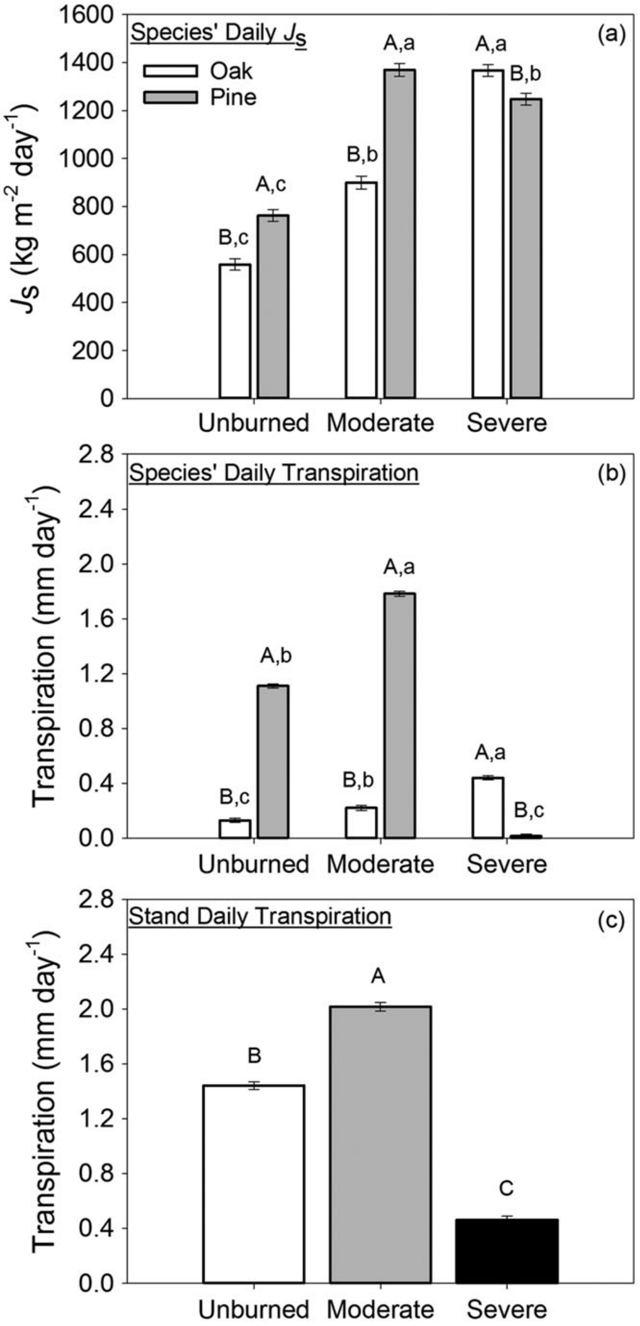


FIGURE 3 Comparison of (a) average daily total sap flux (J_s; kg·m^{-2}·day^{-1}) and (b) average daily transpiration (mm day^{-1}) for oaks and pines within the three burn severity stands along with (c) average total daily transpiration for each of the three stands for the period of May 27 to October 12, 2016. Panels a and b: different uppercase letters (A) denote differences ($P \leq 0.05$) between species within each burn severity, whereas different lowercase letters (a) denote differences ($P \leq 0.05$) among burn severities within a particular species. Panel c: differences in daily transpiration among stands are represented by uppercase letters (A)

3.2 | Differences in sap flux rates among species and responses to the environment

Differences in E_t between the three stands were also associated with differences in daily rates of J_s between pines and oaks and between young and mature trees. Within both species, daily total J_s increased as burn severity increased and was generally greater in younger individuals of each species. For example, the unburned pines had 53% lower daily total J_s on average than pines at the other two sites (Figure 3a). The resprouts had 41% and 84% greater daily J_s, respectively, than the mature oaks at the moderately burned and unburned stands. Unburned oaks had the lowest J_s rates of all species by burn severity combinations. Mature pine sap flux was greater than that of mature oaks by 31% and 41% in the unburned and moderately burned stands, respectively (Figures 3a,b and 5a). Although mature pines had greater average J_s than mature oaks, they were inclined to decrease J_s more than oaks did on rainy days (Figures 3 and 6).

We observed contrasting responses to soil water content between the three stands as well. Consistent with greater water use, soil moisture declined more quickly in the unburned and moderately burned sites compared with the severely burned site (Figure 5),

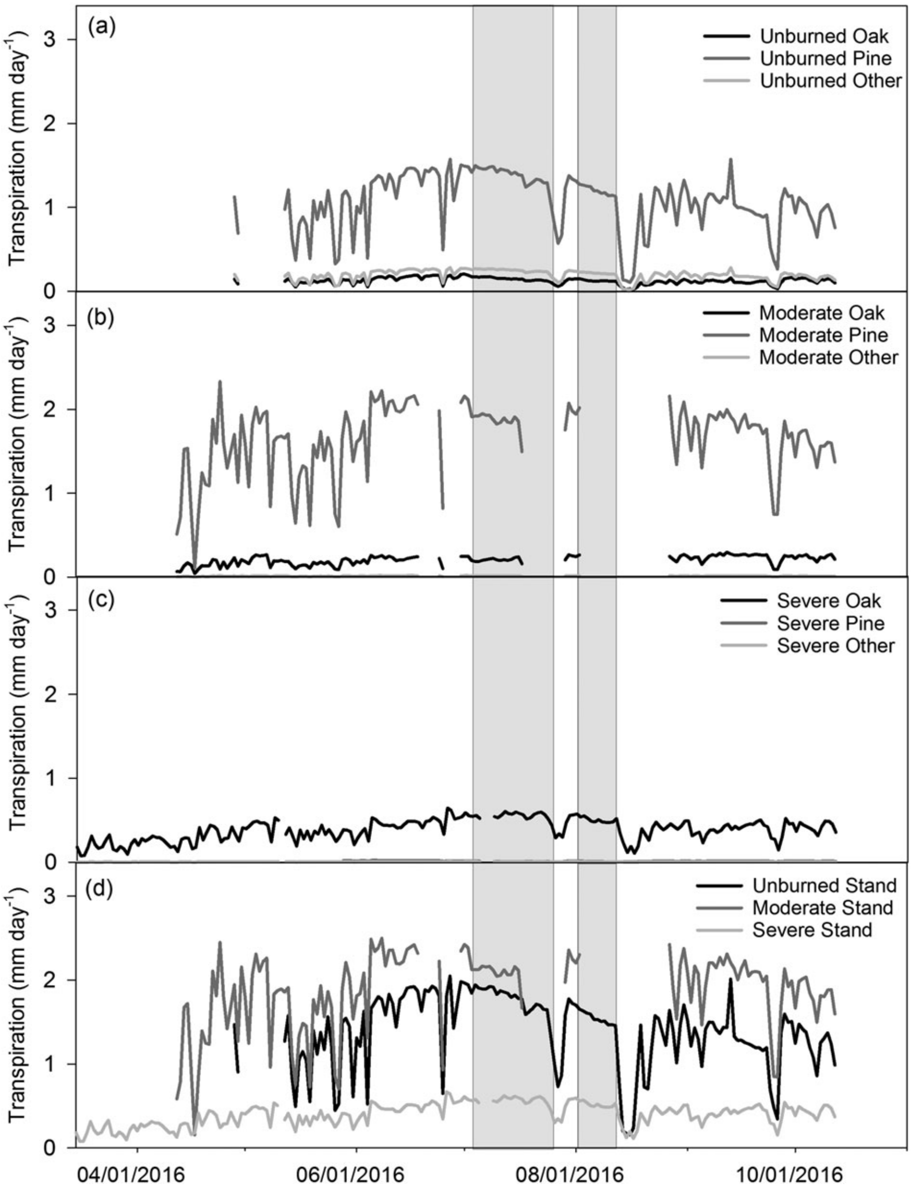


FIGURE 4 Daily transpiration (mm day^{-1}) of oaks, pines, and other species within the (a) unburned, (b) moderately burned, and (c) severely burned stands from March 15 to October 12, 2016. (d) Total daily transpiration compared among stands. Shaded portions represent periods of soil moisture dry down (July 1 to 24 and August 1 to 12, 2016)

especially in July and August. Consequently, the oak resprouts did not appear to be affected by minor reductions in θ in the top 150 cm (Figure 7b; r^2 = 0.47, $P > 0.05$) as compared with the sharp response in the pine saplings (Figure 7a; r^2 = 0.89, $P < 0.05$). During the wetter early season, regenerating pines at the severely burned site had greater J_s than the resprouting oaks, but pine J_s quickly decreased to levels below oak J_s as soil moisture in the upper soil layers was depleted (Figures 5c and 6c). Excluding a brief reprieve after rains in the last week of July, pine sapling J_s was on average 53% lower than resprouting oak J_s in the later part of the summer. Although shallow θ recovered after rains in middle to late August, regenerating pine J_s did not return to predrought levels and remained nearly equal to oak J_s throughout the later part of the growing season. In contrast, J_s of mature pines and oaks were mainly unaffected by summer dry periods despite the large decline in water availability in unburned and moderately burned sites (Figure 5a,b).

Responses to VPD also differed between pines and oaks and between young and mature trees. VPD was typically greatest at the severe site (Figure 5e). Regenerating pines actually decreased J_s at high VPD levels (~50% of the maximum VPD recorded) whereas their counterparts at the moderate and unburned stands did not (Figure 6a). However, the greatest effect of VPD on J_s was observed when shallow soil moisture was also depleted (Figures 5 and 6b). Oaks resprouts, on the other hand, continued to increase J_s with increasing VPD, whereas their counterparts at the moderate and unburned stands levelled out on days when average VPD over the entire 24-hr period was high (at ~0.9 and 1.0 kPa at the moderate and unburned sites, respectively; Figure 6c). When comparing the two species at the moderate and unburned sites, VPD was a better predictor of pine J_s (moderate: r^2 = 0.75; unburned: r^2 = 0.79) than that of oaks (moderate: r^2 = 0.63; unburned: r^2 = 0.61). At the severely burned stand, however, changes in VPD explained more variation in oak J_s (r^2 = 0.80) than pine

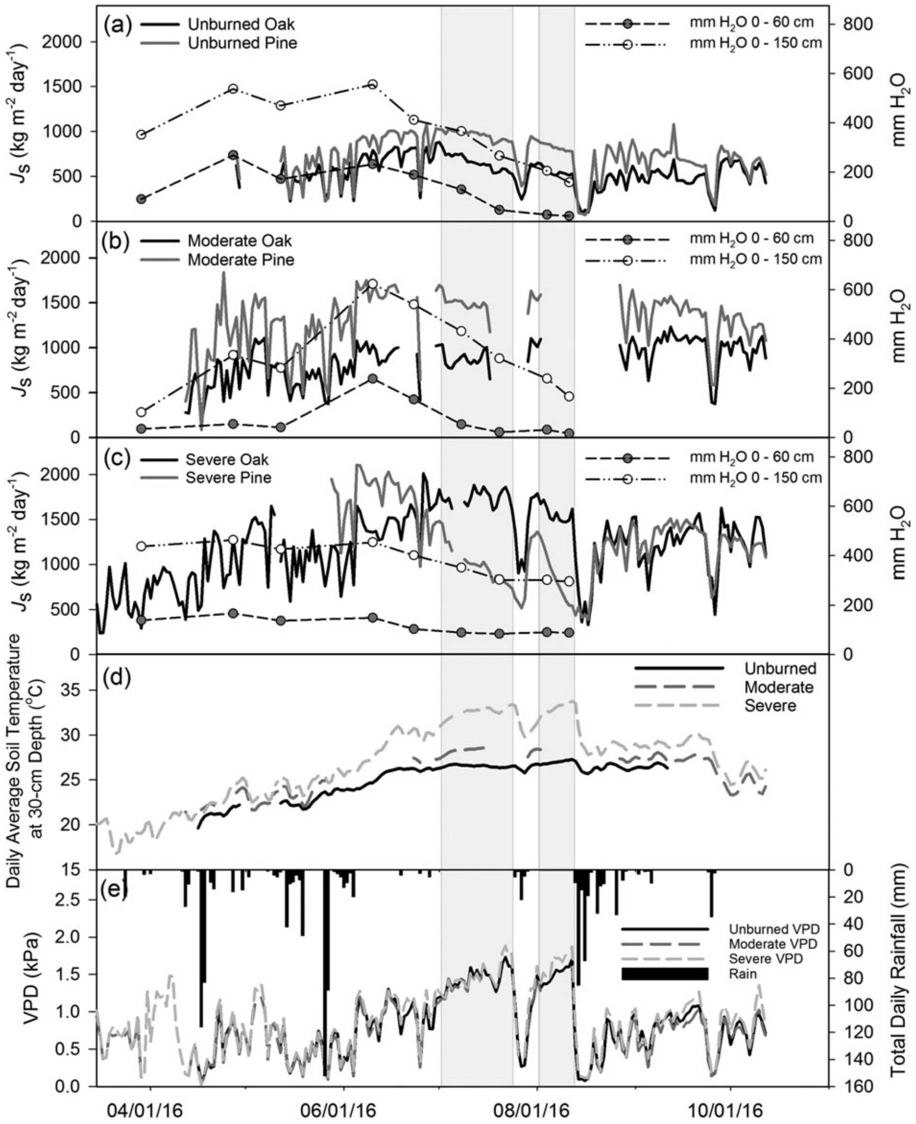


FIGURE 5 Daily total sap flux (kg·m^{-2}·day^{-1}) of oaks and pines within (a) unburned, (b) moderately burned, and (c) severely burned stands along with (d) daily average soil temperature at 30 cm below the surface at each stand, and (e) average daily vapour pressure deficit (VPD; kPa) at each stand and total daily rainfall (mm) from March 15 to October 12, 2016, at the severe site. Daily total sap flux represents that of J_o at the outer 2 and 1 cm of sapwood for the mature trees and regenerating saplings and resprouts, respectively. Shaded portions represent periods of soil moisture dry down (July 1 to 24 and August 1 to 12, 2016). For each site, total soil moisture (mm) is represented by grey and white circles for the 0–60 and 0–150 cm soil depths, respectively

J_s (r^2 = 0.49). Similar to VPD, soil temperatures were typically greatest at the severe site (Figure 5d). The soil at the severe site at 30-cm depth was 12% warmer on average than the unburned site across the study period.

4 | DISCUSSION

We acknowledge that our results and conclusions must be considered in the context of having only one plot per treatment level. Although we were not able to replicate plots with respect to fire severity, we were careful to select areas with similar soils and pine and oak densities as the surrounding region. Additionally, it is difficult to replicate in fire studies, and replication may not be as important when comparing species that are located at all plots in a study.

Our findings support the first hypothesis that stand-level transpiration would decrease in sites with high burn severities due to reductions in vegetation density and total sapwood area. Although individual resprouts and saplings had high daily J_s rates, they did not translate into large amounts of daily transpiration by the severely burned stand due to its low total sapwood area. The second hypothesis that resprouting oaks and young pines would have greater daily sap flux per unit sapwood than mature individuals of the same species was also supported by the results. However, this seems to be more contingent on shallow soil moisture availability for regenerating pines than oak resprouts. In support of our third hypothesis, our results also indicate that individual pines had greater J_s than oaks that, coupled with their larger sapwood area, led to greater transpiration in the moderate and unburned stands that contained a larger number of mature pines. We also found evidence in support of the fourth hypothesis, whereby oak resprouts had greater total daily J_s than pine saplings across the

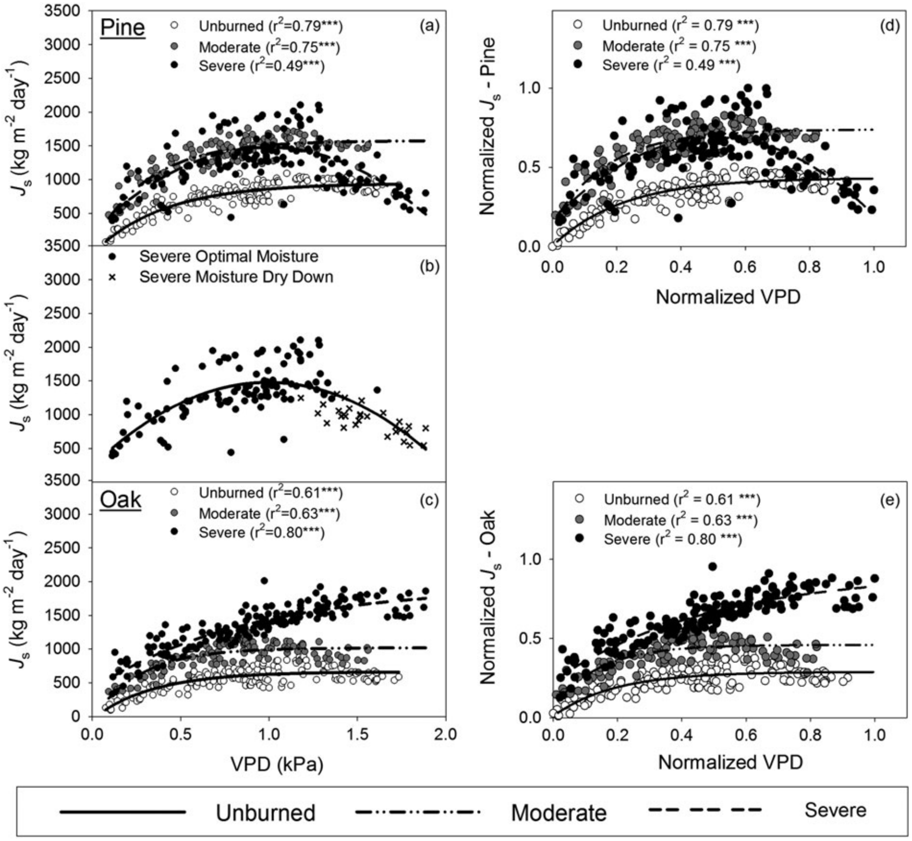
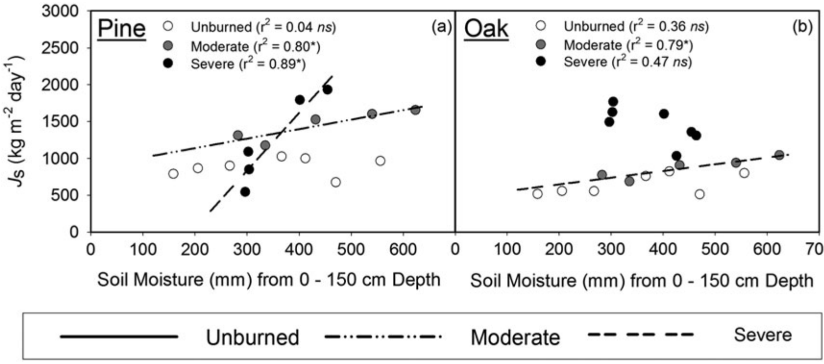


FIGURE 6 Effects of average daily VPD (kPa) on total daily sap flux of (a) pines and (c) oaks at the unburned, moderately burned, and severely burned stands. The effects of low soil moisture levels on the relationship of J_s with VPD are illustrated for pines at the severely burned site (b). The effects of normalized average daily VPD on normalized daily Js are shown for (d) pines and (e) oaks as well. Each point represents the total daily sap flux averaged from all individuals of a species within a respective stand. VPD: vapour pressure deficit

FIGURE 7 Relationships between daily total soil moisture (mm) from 0 to 150 cm depth with total daily sap flux of (a) pines and (b) oaks at the unburned, moderately burned, and severely burned stands. Only significant ($P \leq 0.05$) relationships are shown with regression lines. Each point represents the total daily sap flux averaged from all individuals of a species within a respective stand



experimental period. This was related to the fact that oak resprouts did not appear to be affected by changes to soil moisture in the upper 150 cm of soil or high VPD levels, whereas pine saplings were highly responsive to soil moisture and decreased quickly with small declines in water availability. Pine saplings were also very responsive to changes in VPD, decreasing J_s at average daily VPD levels around 1.0 kPa and confirming the final hypothesis.

4.1 | Implications for stand transpiration postfire

Wildfire affects stand water cycling and watershed-level hydrology and, potentially, regional climate (Ice, Neary, & Adams, 2004; Rogers, Randerson, & Bonan, 2013; Smith, Sheridan, Lane, Nyman, & Haydon, 2011). Wildfire drives these changes in hydrologic processes, including E_t, through alterations to stand age, species composition, and energy balance (Chambers & Chapin, 2002; Ewers et al., 2005), together with alterations in carbon cycling and net primary productivity (Dore et al., 2010; Tang et al., 2006). Consequently, changes in water and carbon fluxes following disturbances such as wildfire can have significant implications for local and regional plant growth, biomass, and climate dynamics (Ciais et al., 2005; Mitchell et al., 2014). Decreases in E_t following wildfire and, therefore, latent heat flux may in turn intensify warming trends, although this will be highly dependent on location, severity of mortality, postfire species composition, and regrowth rates (Liu, Randerson, Lindfors, & Chapin, 2005; Mitchell et al., 2014; Zhang et al., 2017). Moreover, the relative importance of changes in E_t will be timescale dependent. Postfire changes to biophysical attributes, water, and carbon fluxes may be temporary or reversible over decades of recovery (Amiro et al., 2010; Jones & Post, 2004; Lane, Feikema, Sherwin, Peel, & Freebairn, 2010).

Although sapwood area of individual trees may increase following stand thinning, large reductions in total stand sapwood area through harvest or natural disaster may result in decreases in stand E_t (Aussenac & Granier, 1988; Bréda, Granier, & Aussenac, 1995; Morikawa, Hattori, & Kiyono, 1986; Nolan et al., 2014; Whitehead & Kelliher, 1991). Other studies have reported reductions in stand-level transpiration in severely burned areas compared with lightly burned or unburned stands (Gharun et al., 2013; Nolan et al., 2014). Nolan et al. (2014) reported that transpiration of unburned mixed *Eucalyptus* stands was approximately 1.4–1.7 mm day^{-1}, whereas transpiration of severely burned stands was around 0.4 mm day^{-1}, similar to the results from our unburned (1.44 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, due to mortality of approximately half of the trees in those stands. The reduction in sapwood area at our severely burned site resulted primarily from the lack of pine sapling regeneration. The high ratio of oak resprouts to pine saplings (38:4) at the severe sap flux site (707 m^2) was comparable with those of other severely burned areas in the park. In 150-m^2 belt transects, Cooper et al. (2018) recorded ratios as low as three resprouts to one pine sapling (~14:5 per 707 m^2) and as high as 12 resprouts to no pine saplings (~56:0 per 707 m^2). Other studies have reported similar decreases in nonserotinous pines and shifts to resprouter dominance in the absence of supplemental planting (Barton, 2002; Rodrigo, Retana, & Pico, 2004; Retana et al., 2012; Carnicer et al., 2014; Barton & Poulos, 2018).

Similar to our study, Nolan et al. (2015) also reported that light to moderate burns increased transpiration and therefore decreased the amount of water available to other parts of the hydrologic cycle after fire. Increases in runoff and streamflow rates after severe fires have been observed, mainly in the early years of recovery (Jones & Post, 2004; Kunze & Stednick, 2006; Silins, Stone, Emelko, & Bladon, 2009). For example, Campbell, Baker, Ffolliott, Larson, and Avery (1977) reported 28, 20, and 5 mm annual runoff, on average, for the first 3 years after a fire in severely, moderately, and unburned watersheds, respectively. As vegetation grows back, increases in streamflow typically diminish over time (Jones & Post, 2004; Lane et al., 2010).

4.2 | Drivers of water use differences within and among sites

The lower daily J_s in trees at the unburned site compared with those at the moderately 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. Sampled pines at the unburned site were larger (DBH_{Unb_Pine} = 52.2 ± 2.8 cm) and likely older compared with those at the moderate site (DBH_{Mod_Pine} = 43.5 ± 2.1 cm). Tree water use often decreases with age due to declines in sapwood area, leaf area indices, and stomatal conductance (Delzon & Loustau, 2005; Ewers et al., 2005; Magnani, Mencuccini, & Grace, 2000; Martínez-Vilalta, Vanderklein, & Mencuccini, 2007; Roberts, Vertessy, & Grayson, 2001; Vertessy et al., 2001).

We recorded greater J_s in oak trees at the moderately burned than the unburned site, even though the monitored individuals were similar in size: 25.0 ± 3.9 cm and 22.5 ± 2.7 cm DBH, respectively. In addition to age differences in the pines, greater daily J_s in the moderately burned area was likely related in part to reduced competition and subsequent increases in energy and water availability per individual tree in comparison with the densely vegetated unburned stand (Asbjornsen et al., 2007; Martínez-Vilalta et al., 2007; Medhurst, Battaglia, & Beadle, 2002; Morikawa et al., 1986).

The severely burned site had the most stable water availability of the three sites across time, likely due to low total biomass and competition, but the shallow-rooted pine saplings 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 part of the profile, whereas the resprouting oaks have deep root systems remaining from mature trees (Clemente, Rego, & Coreia, 2005; Moya, de las Heras, López-Serrano, & Ferrandis, 2015; Vilagrosa, Hernandez, Luis, Cochard, & Pausas, 2014). The resprouts' greater root : shoot ratios help increase hydraulic efficiency over that of mature trees. Because resprouts have lower leaf areas, individual leaves can receive more water per root area (Kruger & Reich, 1997; Schafer et al., 2014; Utsumi et al., 2010). Reduced J_s in younger, shallow-rooted individuals compared with older, deep-rooted individuals has been reported in other studies. For example, Irvine, Law, Anthoni, and Meinzer (2002) reported similar findings when comparing J_s of a 14-year-old Ponderosa pine (*Pinus ponderosa* P. Lawson & C. Lawson) stand with an older stand (50–250 years old). Both predawn water potential and daily transpiration declined steadily in the 14-year-old stand, but the old growth stand showed no decline even though the volumetric water content was lower over the top 80 cm of soil at that site.

Decreases in soil moisture can override expected responses to VPD, especially in shallow-rooted individuals (Holscher, Koch, Korn, & Leuschner, 2005; Martínez-Vilalta et al., 2003; Oren & Pataki, 2001; Pataki, Oren, & Smith, 2000). Holscher et al. (2005) found 31–44% reductions in J_s of various deciduous species during a dry period compared with a wet period with similar VPD in a mixed, temperate forest stand. Oren and Pataki (2001) also reported a strong exponential relationship between *Quercus alba* L./*Acer rubrum* L. stand transpiration and VPD when soil moisture deficits were low (<10 mm). However, when soil moisture deficits were high (≥10 mm), VPD did not account for variability in stand transpiration.

Unlike young pines, regenerating oaks seem little affected by hot, dry conditions, because resprout J_s increased with greater VPD. This suggests that they had substantial access to water and could maintain open stomata for gas exchange at even greater levels of VPD than experienced in this study. In another study in Bastrop State Park, stomatal conductance (g_s; mol H_2O m^{-2} s^{-1}) was more than two times greater in resprouts than pine saplings (Cooper et al., 2018), indicating differences in water availability or stomatal control strategies between the two. Stress responses in that study suggest post and blackjack oak resprouts are more drought tolerant than loblolly pine saplings. Alternatively, regenerating pines may also utilize more efficient stomatal control to help reduce gas exchange during dry, hot days (Cooper et al., 2018; Irvine et al., 2002; Zang, Pretzsch, & Rothe, 2012). Once regenerating pine root systems become more established and gain access to deeper soil moisture, then these trees may have the advantage over oaks.

4.3 | Differences between oaks and pines

Other studies also reported greater J_s in pines than associated angiosperms (Ford et al., 2010; Phillips et al., 1996; Renninger et al., 2015). At the unburned site, especially, a greater portion of the pine crowns were more exposed than those of the oaks, which could have contributed to greater J_s in pines at those sites and in other studies (Granier, 1987; Jiménez, Nadezhdina, Čermák, & Morales, 2000; Köstner et al., 1992).

The amount of water lost through transpiration depends on J_s and the area of actively conducting sapwood (Granier, 1987). Not only did pines at the moderate and unburned stands have greater J_s, they also had much larger sapwood areas than the oaks (Table 1). Although maximum sap flux occurs close to the cambium and decreases towards the heartwood in oaks (Gebauer et al., 2008; Granier et al., 1994; Poyatos et al., 2007) and loblolly pine (Ford et al., 2004; Phillips et al., 1996), active sapwood makes up a greater portion of the cross-section of nonporous species, such as pines, compared with ring-porous species, such as oaks (Cermak & Nadezhdina, 1998).

As regenerating burned stands approach full canopy, they may use more water than unburned old growth stands (Kuczera, 1987; Vertessy et al., 2001). In several years, this could occur in the severely burned stands 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.

5 | CONCLUSIONS

The differences in water use strategies between the two genera in this study answer many questions about how pines and oaks interact with fire and each other in the Lost Pines region. Prior to large-scale fire suppression in the area, the relatively fire-intolerant loblolly pine persevered in sites with reduced burn occurrence or intensity. However, following this high-severity, stand replacing wildfire, loblolly pine regeneration is limited at most severely burned patches throughout the park. If oaks become the dominant species at these sites, local hydrology could shift considerably. Overall, our findings add useful information to the existent body of knowledge on the ecohydrological effects of wildfire and will further assist the development of land management strategies for effective forest restoration or improvement of local microclimate, especially after fire events.

ACKNOWLEDGEMENTS

This study was funded by the Texas Parks and Wildlife Department. We would like to thank Greg Creacy and the Bastrop State Park staff for their assistance with logistics and housing provisions while on site. We are grateful to the Boy Scouts of America and Rick Denison for allowing us to collect data on the Griffith League Ranch as well. Alex Garcia, Ashley Cross, Marco Minor, and Ajinkya Deshpande assisted with sensor installation and site maintenance. Alex Garcia collected soil moisture data for the sites.

CONFLICT OF INTEREST

We have no conflict of interest to declare.

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How to cite this article: Cooper CE, Aparecido LMT, Muir JP, Morgan CLS, Heilman JL, Moore GW. Transpiration in recovering mixed loblolly pine and oak stands following wildfire in the Lost Pines region of Texas. *Ecohydrology*. 2018;e2052. https://doi.org/10.1002/eco.2052