Differences in leaf physiology among juvenile pines and oaks following high-severity wildfire in an Arizona Sky Island Mountain range

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ABSTRACT

Recent increases in wildfire severity are converting pine-oak (*Pinus-Quercus*) woodland to oak shrubland in many sites in the southwestern United States. A key mechanism underlying this transition is the vigorous resprouting capacity of oaks compared to low regeneration rates in pines following wildfire. Differences among species in leaf physiological characteristics may also contribute to such vegetation type conversions, especially in the context of recent increased regional aridity. To that end, we evaluated variation in leaf functional traits in post-fire recruits five years after the 2011 Horseshoe Two in the Chiricahua Mountains, Arizona, USA. We measured a suite of functional traits in two pines (*Pinus engelmannii* and *P. leiophylla*) and two oaks (*Quercus hypoleucoides* and *Q. arizonica*), including leaf gas exchange, leaf pigment concentrations, leaf spectral reflectance, and wood xylem δ^{13}C, δ^{18}O isotopes, and integrated water use efficiency ($_i$WUE). The four study species displayed a range of plant functional traits tied to desiccation tolerance. *P. engelmannii* seedling recruits presented invariably low maximum photosynthetic rate (A_{max}), stomatal conductance (g_s), and transpiration (E), and high relative leaf water content during the peak of the May-June drought, a response strongly indicative of a desiccation-avoidant leaf that prioritizes water conservation over carbon fixation in arid conditions. In contrast, resprouts of both oaks displayed leaf desiccation tolerance, with high levels of g_s and E and low relative leaf water content. Gas exchange in *P. leiophylla* resprouts was more similar to the oaks, except for relative water content, which was similar to that of *P. engelmannii*. Compared to the other two species, *P. engelmannii* and *Q. hypoleucoides* exhibited significantly higher δ^{13}C, δ^{18}O and $_i$WUE values—a pattern that appears to have arisen from different mechanisms in the two species. In desiccation-avoidant *P. engelmannii*, low instantaneous g_s and high δ^{18}O suggested that low stomatal conductance rather than high photosynthetic rates led to high $_i$WUE, whereas lower δ^{18}O and very high pigment concentrations in *Q. hypoleucoides* suggest a more important role for A_{max} *in this species*. Neither fire severity nor physiography influenced the physiological responses in any of the four species, suggesting that the expression of resprout and seedling functional traits is fixed. These results raise the possibility that differences in leaf physiological characteristics contribute to the regeneration success of some oak species and the poor seedling establishment of obligate seeder pines, such as *P. engelmannii*, after high-severity wildfire in the American Southwest.

1. Introduction

The pine-oak forests of the Sky Island mountain ranges of southwestern North America were maintained by frequent, low-severity wildfire for centuries (Fulé and Covington, 1996; Heyerdahl and Alvarado, 2003; Kaib et al., 1996; Poulos et al., 2013; Swetnam, 1990; Swetnam et al., 2001; Trejo, 2008). Pines survive repeated wildfire via thick, insulative bark and reproduce mostly by seed on bare mineral soil during fire-free intervals (Barton, 1999; Barton et al., 2001). Chihuahua pine (*Pinus leiophylla* Schiede & Deppe) can also recover from fire via moderate resprouting after top-kill in this forest type. Oaks recruit to some degree between fire events via seed, but their principal
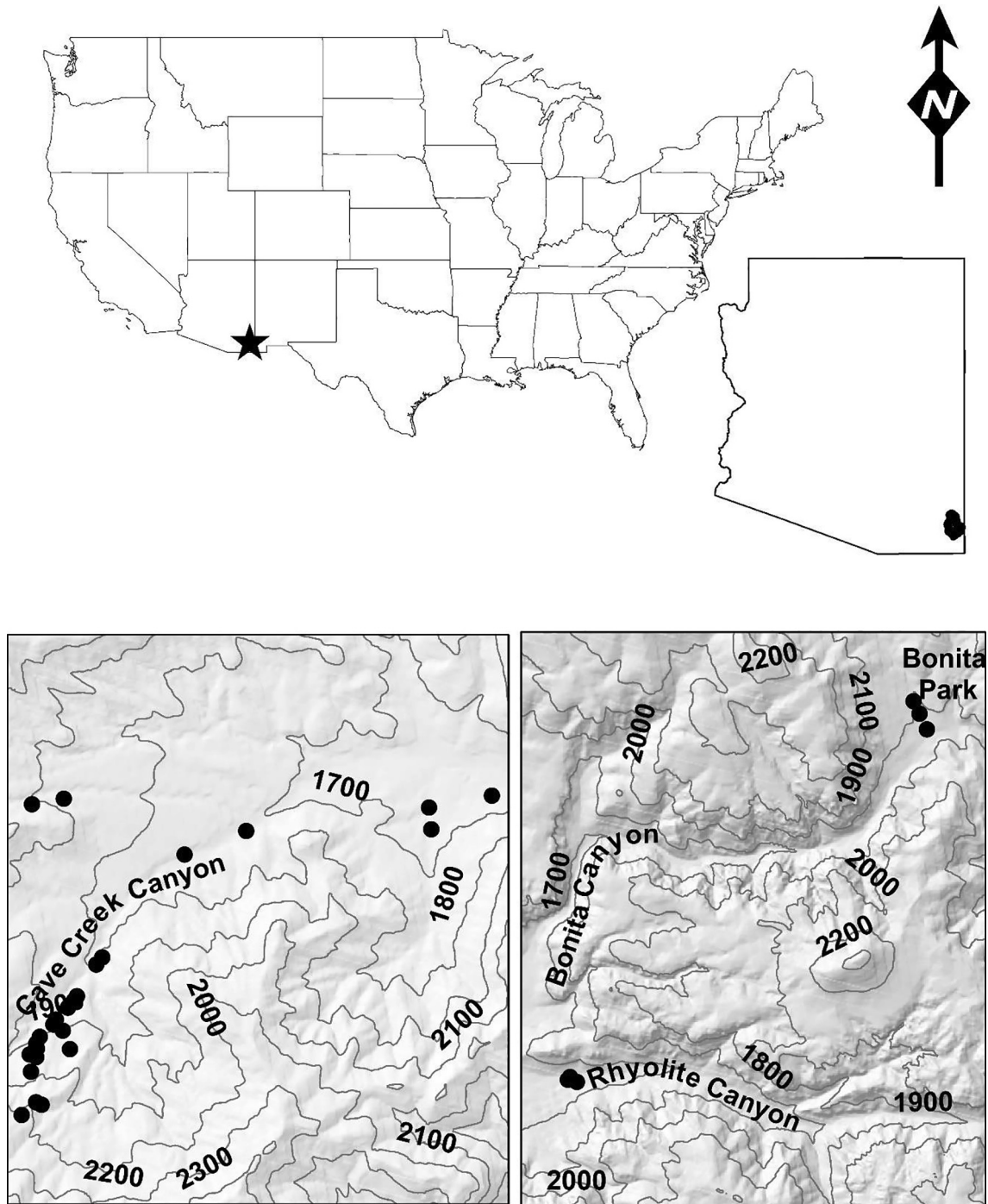
Fig. 1. Map of the Chiricahua Mountains, Arizona, USA with topographic maps showing the locations of plant sampling locations in Cave Creek Canyon (Chiricahua National Forest) and Chiricahua National Monument. Sampling locations were placed just outside the sample plot areas described in Poulos and Barton (2018).

persistence mechanism under short, low-intensity surface fire regimes is via top-kill followed by prolific post-fire resprouting from belowground tissues that survive fire (Barton, 1999; Fulé, 2000). Post-fire vegetation structure and composition, therefore, depend upon above-ground plant survival, resprouting capacity following topkill, and seedling establishment in the post-fire environment.

Historically, both resprouter and seeder persistence strategies were successful in maintaining a mixture of Sky Island tree species under pre-Euro-American fire regimes. However, over a century of grazing in the late 1800s and early 1900s, and then active fire suppression, greatly increased surface and canopy fuel loads. This, coupled with a hotter and drier climate, have triggered a transition to a new era characterized by

frequent, high-severity wildfires throughout the region (Falk et al., 2011; Fule et al., 2012; Swetnam and Betancourt, 2010). Fire strongly influences post-fire environmental site conditions through the differential combustion of biomass, soil heating, and consequent changes in irradiance, soil moisture availability, and soil biogeochemistry, all of which vary with fire intensity (Choromanska and DeLuca, 2002; DeBano et al., 1998; Johnson et al., 2007; Keeley, 2009; Neary et al., 1999; Pereira et al., 2012). Thus, the shift from a low-severity to a high-severity fire regime in the Sky Islands represents a fundamental change in the disturbance processes shaping vegetation structure, composition, and distribution.

One of the major responses of vegetation to this alteration in fire

regime has been a transition in some sites across from pine-oak forests to shrublands after wildfires (Barton, 2002; Barton and Poulos, 2018; Coop et al., 2016; Haffey et al., 2018; O'Connor et al., 2014). Studies characterizing high-severity wildfire impacts on pine-oak forests have examined the magnitude and type of change and plant functional trait differences among species that are likely driving these trends. Yet, mechanistic explanations, especially at the physiological level, of post-fire vegetation development remain incomplete. Both the pines and oaks in this region display considerable drought resistance in a moisture-limited environment (Barton and Teeri, 1993; Ganey and Vojta, 2011; Poulos et al., 2007a; Poulos, 2009; Poulos et al., 2007b). Fundamental differences in post-fire regeneration strategy (i.e. re-sprouting vs. regeneration via seed) between the two genera across the Southwest, however, suggest that post-fire recruits of these genera are likely to vary in the mechanisms and degree of drought resistance in sites subject to high-severity fire. At sites where few adult trees survive fire, resprouts may have an advantage over seedlings because their deeper root systems allow them to immediately access water sources and soil nutrients after the fire event, while seedlings must allocate photosynthate to both root and shoot development simultaneously after fire (Santana et al., 2012; Smith et al., 2014). This enhanced access to soil resources by resprouters provides one potential explanation for the differential post-fire success of pines vs. oaks (see Barton and Poulos, 2018).

Differences in leaf desiccation tolerance among taxa, however, may simultaneously contribute to the enhanced post-fire performance of oaks compared to pines. In the last decade, several researchers have compared plant desiccation tolerance among a wide range of taxa by demonstrating the importance of hydraulic functional traits in response to drought and plant distribution patterns (Breshears et al., 2009; Cavender-Bares and Holbrook, 2001; Choat et al., 2012; Hacke et al., 2009; Hacke et al., 2000; Jacobsen et al., 2007; Jacobsen et al., 2016; Pratt et al., 2007; Willson and Jackson, 2006). Pines are generally classified as leaf desiccation avoiders because they maintain high internal leaf water status relative to competing species, such as oaks, that maintain open stomates and high leaf gas exchange rates across a wide range of moisture circumstances, even in post-fire and drought conditions (Cavender-Bares and Bazzaz, 2000; Choat et al., 2012; Cooper et al., 2018a; Meinzer et al., 2009; Meinzer et al., 2014). While having a high internal leaf water status could be considered an advantage for staving off the effects of drought on plant performance, tight stomatal control by more isohydric taxa like pines prevents them from continuing to photosynthesize and grow under the droughty conditions that are typical of high-severity wildfire sites. Shallow roots and the maintenance of relatively high leaf water status may make pine seedlings less competitive than more deeply-rooted, desiccation-tolerant oak resprouts in the hot, dry post-fire landscape. Such differential constraints on post-fire regeneration in this new era of increased wildfire severity has the potential to dramatically alter the composition, structure, and processes of fire-dominated ecosystems within Sky Islands and around the world (Enright et al., 2015).

We investigated differences in leaf physiological traits among pines and oaks 5 years after a large, high-severity wildfire in the Chiricahua Mountains of southeastern Arizona, USA (Fig. 1). Consistent with studies elsewhere, we hypothesized that pines would exhibit desiccation avoidance, but that the oaks would display desiccation tolerance in the post-fire environment. We tested these hypotheses on post-fire recruits of the four dominant tree species within this Sky Island range: two oaks that exhibit vigorous basal resprouting in response to wildfire (*Quercus hypoleucoides* A. Camus and *Q. arizonica* Sarg.), one facultative, moderately-resprouting pine (*Pinus leiophylla* Schiede & Deppe), and one obligate seeder pine (*P. engelmannii* Carrière).

2. Methods

2.1. Study area

This study was carried out in the Chiricahua Mountains (Fig. 1) in southeastern Arizona (31°52′ N, 109°15′W), which form part of the Sky Islands mountain archipelago, a northern extension of the Sierra Madre Occidental range (DeBano et al., 1998). The mountains extend southeast to northwest for about 80 km and rise from approximately 1100 to 3000 m altitude (a.s.l.). Part of the Basin and Range Geological Province, the terrain is rugged and highly-dissected, rising from broad flat basins to rocky uplands, separated by steep-walled canyons. Soils are shallow and mostly derived from volcanic rhyolites and monzonites deposited in the early- to mid-Miocene, although pre-Tertiary rock is prominent at lower elevations (Drewes and Williams, 1973). We conducted research in evergreen Madrean pine-oak forest between 1642 and 2132 m a.s.l, mainly in Cave Creek Canyon on the east side of the Chiricahua Mountains in Coronado National Forest but also in Chiricahua National Monument on the west side (Fig. 1). Sample locations were selected within the proximity of a network of permanent geo-referenced plots that captured the range of variation in fire-severity and topography (see Barton and Poulos, 2018 for a full report on the demographic effects of the wildfire on these same species).

The climate is semiarid, with two wet seasons, one between July and September, when more than 50% of total precipitation falls, and the second between December and March (Fig. 2). A pronounced dry season usually occurs between the final winter storms in March or April and the onset of the North American Monsoon System in early July (Adams and Comrie, 1997). January average minimum and maximum temperatures are -0.2 °C and 14.7 °C, respectively; July average minimum and maximum temperatures are 17.4 and 32.8 °C, respectively. Mean annual rainfall at the Southwestern Research Station (1650 m a.s.l.), near the main study area, is 506 mm. The region experienced a long-term drought starting in 1995 and extended periods of little precipitation leading up to the Horseshoe Two Wildfire in May 2011 and for the three years following the fire (Fig. 2).

Before Euro-American settlement in the 1870s, lightning-caused, surface fires occurred frequently in Madrean pine-oak forests in the Chiricahua Mountains, with a mean fire return interval of 4.2–17.9 years; stand-replacing fires were rare (Barton et al., 2001; Kaib et al., 1996; Swetnam and Baisan, 2003). Fire was uncommon from the 1880s through the 1980s, as a consequence of intensive livestock grazing in earlier decades followed by active fire suppression (Fule et al., 2012; Leopold, 1924). During the extremely dry year of 2011 (Williams et al., 2014), the Horseshoe Two Fire burned > 90,000-ha over 49 days, from May 8 to June 25, near the end of the dry season, 38% at low severity, 29.7% at moderate severity, 12.4% at high severity, and 19.8% showing no change from before to after the fire (Arechederra-Romero, 2012).

August MODIS leaf area index data (Gao et al., 2008) reveal that Cave Creek Canyon was still in a state of vegetative recovery at the time of our study. LAI prior to the fire was 6.09 $m^2 m^{-2}$ in 2010, dropped to 4.93 $m^2 m^{-2}$ after the wildfire in 2011, and in 2016 had recovered to 5.46 $m^2 m^{-2}$. Prior to the fire, this was a closed-canopy forest site. By 5 years after the Horseshoe Two Fire, *Quercus* species had resprouted vigorously, *P. leiophylla* resprouted at low levels, and few seedlings of any species had established (Barton and Poulos, 2018). Centuries of frequent surface fires had maintained a mix of pines and oaks prior to this wildfire event, whereas, especially in sites that burned at high severity, this pine-oak forest was largely transformed to oak shrublands.

2.2. Field sampling methods

We measured a suite of physiological characteristics five years after the Horseshoe Two Fire on recruits of *P. engelmannii*, an obligate seeder, *P. leiophylla*, a seeder and weak resprouter, and two oaks, *Q. arizonica*
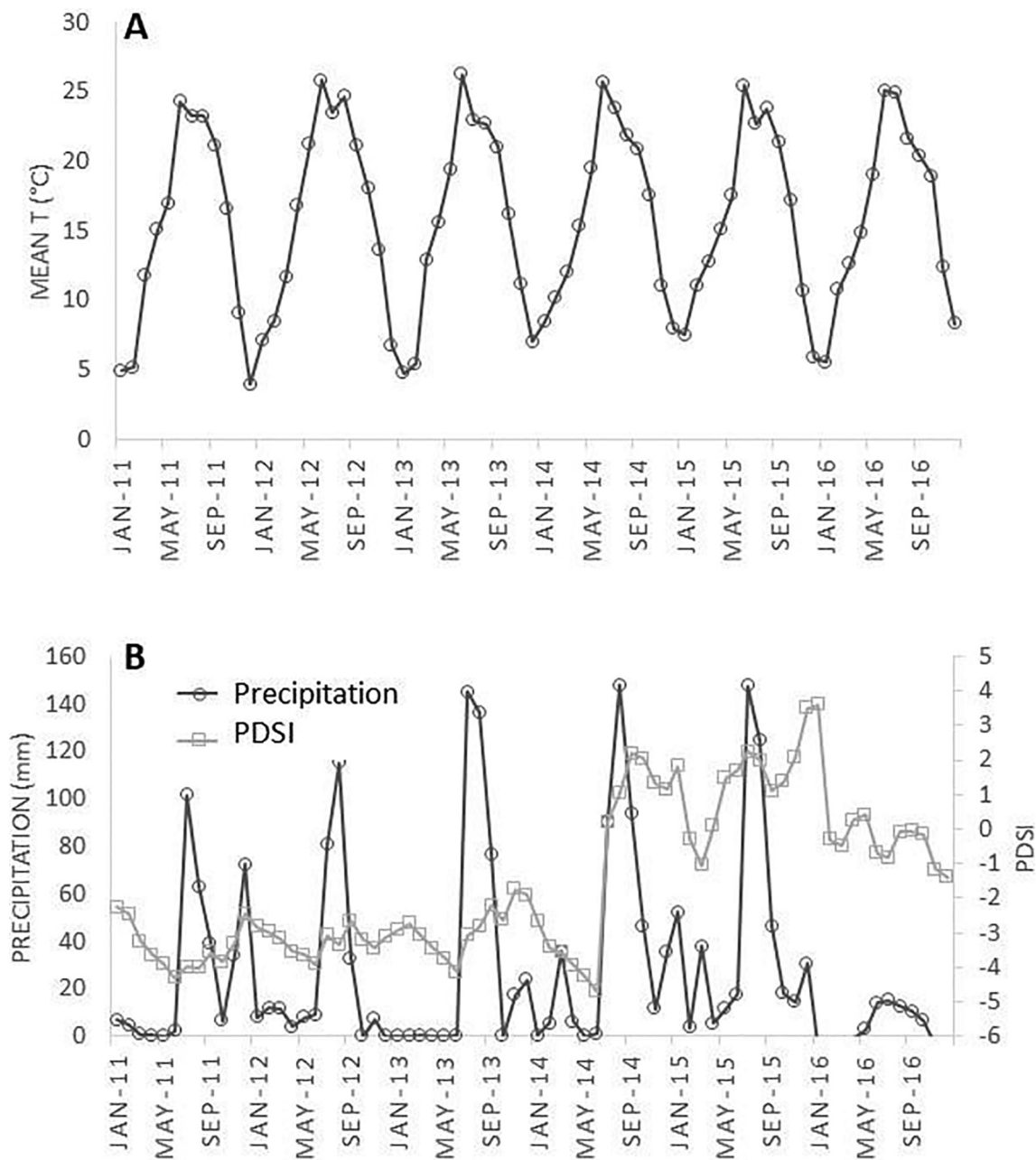
Fig. 2. (A) Mean monthly temperature (°C) and (B) precipitation (mm) and Palmer Drought Severity Index (PDSI) for each month of each year, spanning from the year of the Horseshoe Two Fire to the end of the year of the study period (January 2011-December 2016). Values for precipitation and temperature were obtained from the Western Regional Climate Center (https://wrcc.dri.edu/), and PDSI was obtained from the National Climatic Data Center (https://www7.ncdc.noaa.gov/CDO/cdo) for the Chiricahua Mountains, Arizona.

and *Q. hypoleucoides*, capable of vigorous resprouting. Using the sampling scheme described below, we evaluated differences among species and between genera (pine vs. oak) and the influence of fire severity and topographic position on these post-fire physiological responses. Measurements were taken during a period of pronounced moisture stress, in late May and early June 2016, prior to the onset of the North American Monsoon (Vivoni et al., 2008). We assessed four individuals of each of the four target-species in 24 permanent vegetation monitoring plots (*N* = 384 individuals). All individuals were post-fire recruits following the Horseshoe Two Fire based on subsequent destructive sampling and ring counts of 88 individuals (4 of each species) that were used for wood isotope analysis in this study. All *P. engelmannii* were seedlings, while *P. leiophylla*, *Q. arizonica*, and *Q. hypoleucoides* were resprouts. We focused exclusively on *P. leiophylla* resprouts

because we found an insufficient number of post-fire seedlings in the study area, although this species is known to be semi-serotinous and capable of regeneration via seed (Rodríguez-Trejo and Fulé, 2003, Poulos and Barton, personal observation). Measurements were taken across the fire severity gradient, spanning from low- to high-severity, and across the topographic gradient, spanning from valley bottom to ridgetop. We encountered no *P. engelmannii* seedlings in areas of high fire severity, so samples from this species were from low- and moderate-severity sites only. All specimens were sampled from just outside the Barton and Poulos (2018) vegetation plots to minimize destructive sampling effects on these long-term vegetation monitoring plots.

Maximum photosynthesis (A_{max}), stomatal conductance (g_s), and transpiration (E) were measured *in-situ* on mature, fully-expanded, healthy leaves using an open-system portable infrared gas analyzer (LI-

6400, LiCor, Lincoln, Nebraska, USA) under saturating light (800 μmol m^{-2} s^{-1}, as determined by Barton and Teeri (1993)) using the LED attachment for the LI-6400 photosynthesis system. All gas exchange measurements were taken in the morning between 8 and 11 am prior to midday stomatal closure. Air flow was kept constant at 400 μmol s^{-1} and CO_2 concentrations were also set at 400 μmol mol^{-1} for all measurements. Mean vapor pressure deficits over the sampling period were 2.35 ± 0.095 KPa and relative humidity within the sample chamber was 64.5 ± 0.56%. For the pines, we spread needles in one flat layer to fill the 2 × 3 cm chamber. Individual oak leaves were large enough to fill the chamber entirely.

Leaf spectral reflectance was measured on the same leaves that were measured for gas exchange as an additional measure of May/June leaf stress. Spectral reflectance is a well-known plant stress assessment technique for a variety of metrics including plant photosynthetic potential and leaf water balance (Carter, 1993; Carter, 1994; Carter and Knapp, 2001; Peñuelas and Filella, 1998). Spectral reflectance generally increases in plants in response to a variety of stress agents (Carter, 1993), justifying our use of this technique for examining post-fire leaf vigor. Measurements were taken upon return to the lab after clipping branches of each specimen and placing them plastic bags in a cooler in the field. Leaf pigment concentrations remain stable for hours to days after branch excision according to a test by Richardson et al. (2002), which justified the use of this method. Spectral reflectance was measured using a UNIspec Spectral Analysis System (PP Systems, Haverhill, Massachusetts, USA) over the range of 400–1000 nm with a 2.0 mm diameter foreoptic and an internal 6.8 W halogen lamp within one hour upon return from the field. Standard controls were dark and a spectralon reflectance white standard. The UNIspec unit was standardized after every 10 measurements using the white reflectance standard. Leaves were held in a black polyvinyl chloride clip at a 60° angle relative to the foreoptic for scanning. For the pines, we arranged needles in a flat layer in the foreoptic leaf clip for each specimen. Oak reflectance was taken on the adaxial (top) side of the leaf. Mean spectral reflectance was compared among species over the electromagnetic spectrum between 400 and 1000 nm, and a suite of indices were also calculated to test for differences in wavelengths of pigment activation among species, fire severities, and topographic positions (Table 1).

Leaf mass per unit area (LMA) was calculated by scanning fresh leaves using the Turboscan app (Picsoft Inc.) on an iPhone6 and calculating leaf area using ImageJ software (https://imagej.nih.gov/ij/). For the pines, leaf area was estimated for 1 fascicle of needles; for the oaks, one healthy leaf was scanned for each individual. LMA was taken as leaf dry mass (DM) (after drying to a constant mass in a 70 °C oven) divided by leaf area. Leaf relative water content (RWC) was determined on one whole leaf of each individual by determining its fresh mass (FM), saturated mass (SM) after immersing them in distilled water in the dark for 24 h, and DM (described above). RWC was calculated as: RWC = (FM − DM)/(SM − DM) × 100. Leaf chlorophyll (CHL) and anthocyanin (ANTH) content were measured using hand-held meters (model CCM-300 for CHL, and model ACM-300 for ANTH, Opti-Science, Inc. USA). All measurements were taken on the same leaves to avoid variation among leaves of the same individual.

We estimated species-level changes over time in C and O isotope discrimination from 2012 to 2015 following the Horseshoe Two Fire on annual rings of 8 post-fire recruits of each of the four target species (N = 32 individuals and 128 tree-ring samples) following English et al. (2011). Individual plants from just outside each vegetation sampling plot were destructively sampled in the field with a handsaw. We selected sites randomly from plots of Barton and Poulos (2018) that fell within middle topographic positions. We chose this sampling scheme to minimize differences associated with external environmental factors for making species-level comparisons, and also because all four tree species were present at these sites since they mostly burned at moderate fire-severity. Plants were cut at the base and complete cross-sections were then sanded to a high polish for whole-wood $\delta^{13}C$ estimation in the lab following English et al. (2011), who determined that cellulose digestion was not needed for such analyses. Wood samples for each year of growth were then extracted using a dental drill under a dissecting microscope to ensure that only material for that year of growth was utilized in each sample. $\delta^{13}C$, and $\delta^{18}O$ values were then assessed at the Yale Isotope Lab (New Haven, CT). As described below, $\delta^{13}C$ can be used to estimate integrated water use efficiency ($_iWUE = $ leaf A_{max}/g_s) for each year. $\delta^{18}O$ indicates levels of g, allowing an estimation of the relative roles of A_{max} and g_s in plant water use efficiency.

Total $\Delta^{13}C$ with atmospheric corrections for wood isotope values ($\delta^{13}C_{plant}$) was used to calculate integrated water use efficiency ($_iWUE$) for each year of growth for each juvenile using the carbon isotope ratios measured in the tree rings ($\delta^{13}C_{plant}$), annual estimates of atmospheric $\delta^{13}C$ ($\delta^{13}C_{atm}$), and annual atmospheric CO_2 concentrations (C_a). $\delta^{13}C_{atm}$ values were obtained from http://www.esrl.noaa.gov/gmd/dv/data/ (accessed 12/21/17), and C_a data were taken from http://scrippsco2.ucsd.edu/data/atmospheric_co2/ (accessed 12/21/17) for each year of juvenile tree growth. $\Delta^{13}C$ discrimination was calculated using the equation by Farquhar and Sharkey (1982), $\Delta = \frac{\delta 13C_{atm} - \delta 13C_{plant}}{1 + \delta 13C_{plant}/1000}$, for each tree-ring for each plant specimen. We calculated integrated water use efficiency of the xylem ($_iWUE$) following McCarroll and Loader (2004), $iWUE = \frac{C_a * (\Delta - a)}{1.6 * (b - a)}$, where a is the constant associated with fractionation during CO_2 diffusion through the stomata (4.4$\frac{0}{00}$; (O'Leary, 1981)), b is the constant associated with fractionation during carboxylation (27$\frac{0}{00}$; (Farquhar and Richards, 1984)), and C_a is atmospheric concentration of CO_2 for that year of tree-ring growth.

We used the dual-isotope ($\delta^{13}C$ and $\delta^{18}O$) approach (sensu Barbour et al., 2002; Saurer et al., 1997; Scheidegger et al., 2000) to compare the responses of photosynthetic rate, stomatal conductance, and $_iWUE$ among the four study species. Fractionation of ^{13}C is affected by both A and g_s, leaving uncertainty about the controls on $_iWUE$. In contrast, fractionation of ^{18}O is affected by g_s, source water, and atmospheric relative humidity. Thus, the relative roles of A and g_s in $_iWUE$ (A/g_s) can be ascertained from data for both isotopes from the same wood material (tree rings in our case). However, this dual-isotope approach requires caution (Barbour and Song, 2014; Barnard et al., 2012; Roden and Siegwolf, 2012; Roden and Farquhar, 2012; Sohn et al., 2014) because, whereas fractionation in $\delta^{13}C$ is well understood, that for $\delta^{18}O$ remains somewhat uncertain because it can be affected by other factors, such as source water and relative humidity that does not necessarily affect g_s. The dual-isotope approach remains useful, nevertheless, as it provides additional information for interpreting the responses of plants to water stress (Guerrieri et al., 2019; Sohn et al., 2014). Moreover, the

Table 1

Spectral reflectance indices, formulae, and pigment activation sites used in the species-level comparisons of pine and oak juvenile plant physiology in the Chiricahua Mountains, Arizona, USA.

Description	Formula	Pigment activation	Citation
Double difference	$(R_{749} - R_{720}) - (R_{701} - R_{672})$	red edge	Le Maire et al. (2004)
Structure independent pigment index	$R_{800} - R_{445}/R_{800} - R_{680}$	chl, carotenoids	Penuelas et al. (1993)
Carotenoid reflectance index	$(R_{510} - 1) - (R_{550} - 1)$	carotenoids	Gitelson et al. (2002)
Water band index	R_{900}/R_{970}	leaf water content	Ceccato et al. (2002)

conditions of our study—consistently low humidity, the short time scale (four years), and a likely shallow water source—suggests the dual-iso-tope approach is appropriate for our study (Roden and Siegwolf, 2012).

2.3. Statistical analyses

We fit linear mixed-effects models, using the lme4 (Bates et al., 2013) package in R (R Development Core Team, 2018) to test for differences in pine and oak physiology 1) between the two tree genera (i.e. pines vs. oaks), 2) among the four individual species, 3) across low, moderate, and high fire severities, 4) among lower, middle, and upper topographic positions, and 5) for the interaction between fire severity and topographic position. Significant differences among tree genus (*Pinus* or *Quercus*) and individual species were performed by estimating differences among these groups via comparisons in their estimated marginal means in the emmeans package in R (Lenth et al., 2019). Mixed models and estimated marginal means were also used to examine temporal changes in $\delta^{13}C$, and $\delta^{18}O$ isotope discrimination and $_iWUE$ between pines vs. oaks and among species, with species nested within year. This approach accounted for the nested sampling design with multiple individuals of each species per sample site. Random effects were designated for the intercept and the slope of the sample replicate nested within sample plot.

3. Results

Our results indicated that *P. engelmannii* and *Q. hypoleucoides* occupied opposite ends of the leaf and xylem functional trait spectrum, while *P. engelmannii* and *Q. arizonica* displayed intermediate physiological responses in the post-fire landscape. Gas exchange rates were species-specific, and did not vary significantly by tree genus, topographic position, or fire severity ($P > 0.05$) (Fig. 3, SI Table 1, SI Fig. 2). The maximum photosynthetic rate (A_{max}) results were not especially telling, revealing only significantly higher A_{max} for five-year-old *P. leiophylla* seedlings compared to the other three species

($P < 0.05$) and high variation in *Q. hypoleucoides* photosynthetic rates. Transpiration (E) and stomatal conductance (g_s) were both lowest and least variable for *P. engelmannii* ($P < 0.05$), suggesting a more conservative gas exchange response for seedlings of this species compared to the resprouts of the other three species (Fig. 3, SI Table 1). As with A_{max}, there were no significant differences in E or g_s across fire severities or topographic positions (SI Table 1, SI Fig. 2). There was, however, a significant interaction between fire severity and topographic position for g_s for the two pine species, suggesting higher stomatal control by these two species compared to the oaks on more exposed, higher-fire-severity sites ($P = 0.02$, SI Table 1, SI Fig. 1). Consistent with the E and g_s results, leaf RWC also differed significantly between pines and oaks ($P < 0.0001$) and among species ($P < 0.05$) in the following order: *P. engelmannii* > *P. leiophylla* > *Q. arizonica* > *Q. hypoleucoides*. As with gas exchange, RWC did not vary significantly by topographic position or fire severity ($P > 0.05$) (SI Table 1, SI Fig. 3).

The leaf reflectance spectra, reflectance indices, and chlorophyll (CHL) and anthocyanin (ANTH) content analyses (Figs. 3–5, SI Table 1, SI Fig. 2) revealed important differences in photosynthetic potential: compared to the two pine species, the oaks displayed signs of leaf desiccation tolerance in all pigment concentration metrics ($P < 0.05$) except the double difference index. Overall, the pines displayed higher leaf spectral reflectance than the oaks throughout the entire electromagnetic spectrum and a red edge position at shorter wavelengths, or, in other words, we observed higher absorption by the oaks within the range of photosynthetically active radiation (Fig. 4). The pines displayed significantly higher water band index (a measure of plant water status) and structure insensitive pigment values than the oaks (where higher values indicate increased plant stress), but lower carotenoid reflectance index values ($P < 0.05$). The double difference index (a measure of red edge position) did not differ significantly between pines and oaks, due to variation in the response by *Q. hypoleucoides*. However, in the species by species comparisons, *P. engelmannii* displayed the lowest values, *Pinus leiophylla* and *Q. arizonica* were in the middle, and *Q. hypoleucoides* exhibited the highest double difference index
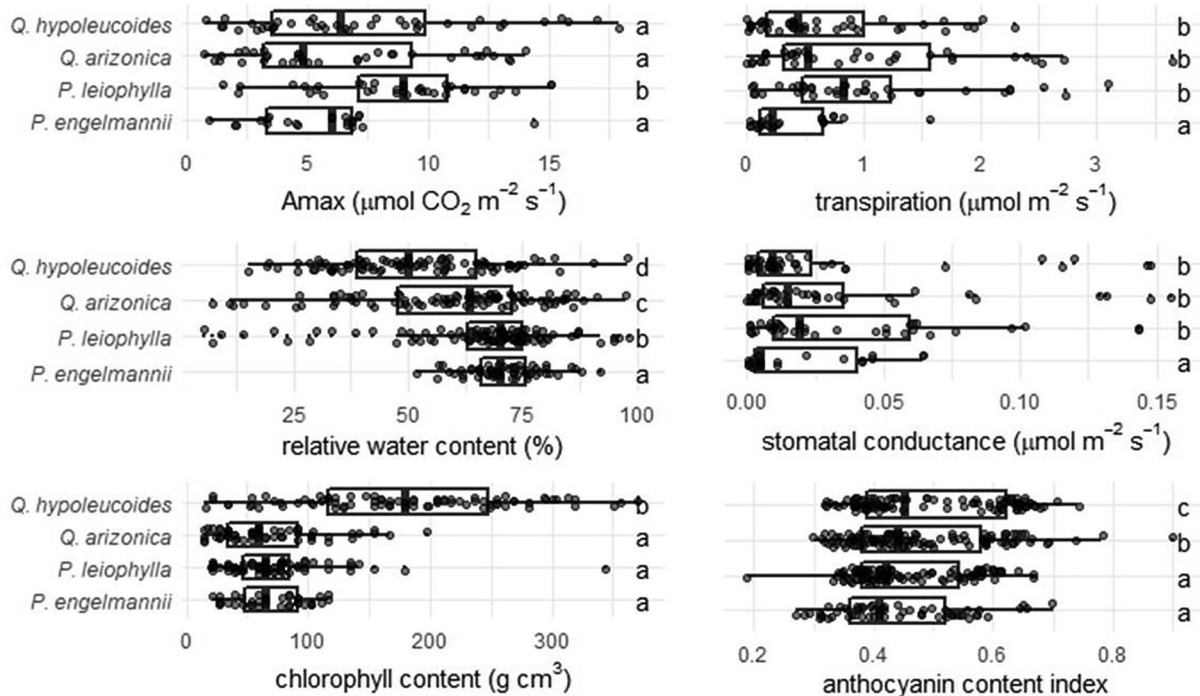
Fig. 3. Boxplots of maximum photosynthetic rate (A_{max}), leaf relative water content, transpiration rate, stomatal conductance, chlorophyll content, and anthocyanin content by species. Species are abbreviated as follows: PIEN = *Pinus engelmannii*, PILE = *P. leiophylla*, QUAR = *Quercus arizonica*, and QUHY = *Q. hypoleucoides*. All parameters differ significantly among species according to mixed-models analyses, and significant pairwise differences among species are indicated with letters. Species that do not share the same letter differ significantly at the $P < 0.05$-level.
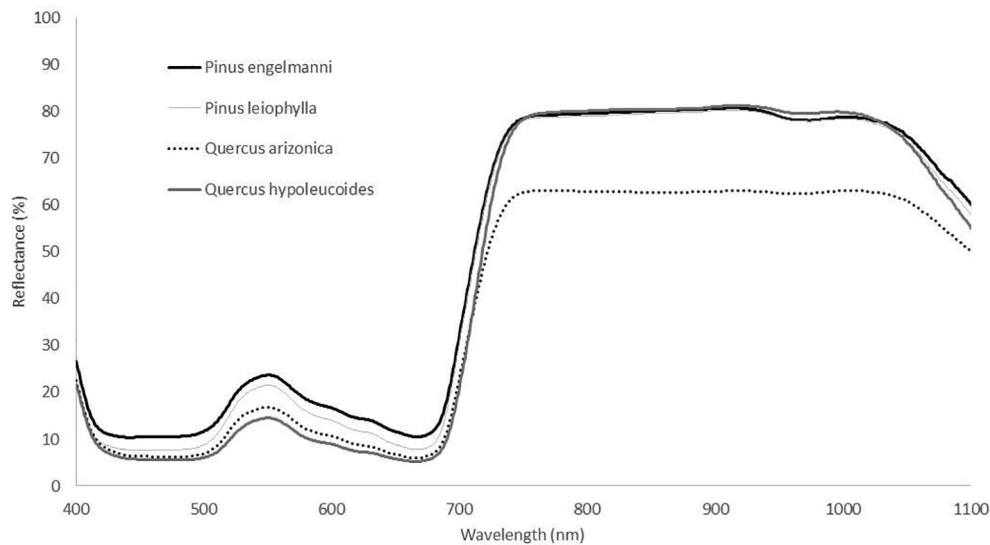
Fig. 4. Mean leaf spectral reflectance of the four study species: *Pinus engelmannii*, *P. leiophylla*, *Quercus arizonica*, and *Q. hypoleucoides* for 5-year old post-fire recruits in the Chiricahua Mountains, Arizona.

Fig. 5. Boxplots of spectral reflectance indices by species for leaves of the four study species: *Pinus engelmannii*, *P. leiophylla*, *Quercus arizonica*, and *Q. hypoleucoides* for 5-year old post-fire recruits in the Chiricahua Mountains, Arizona.
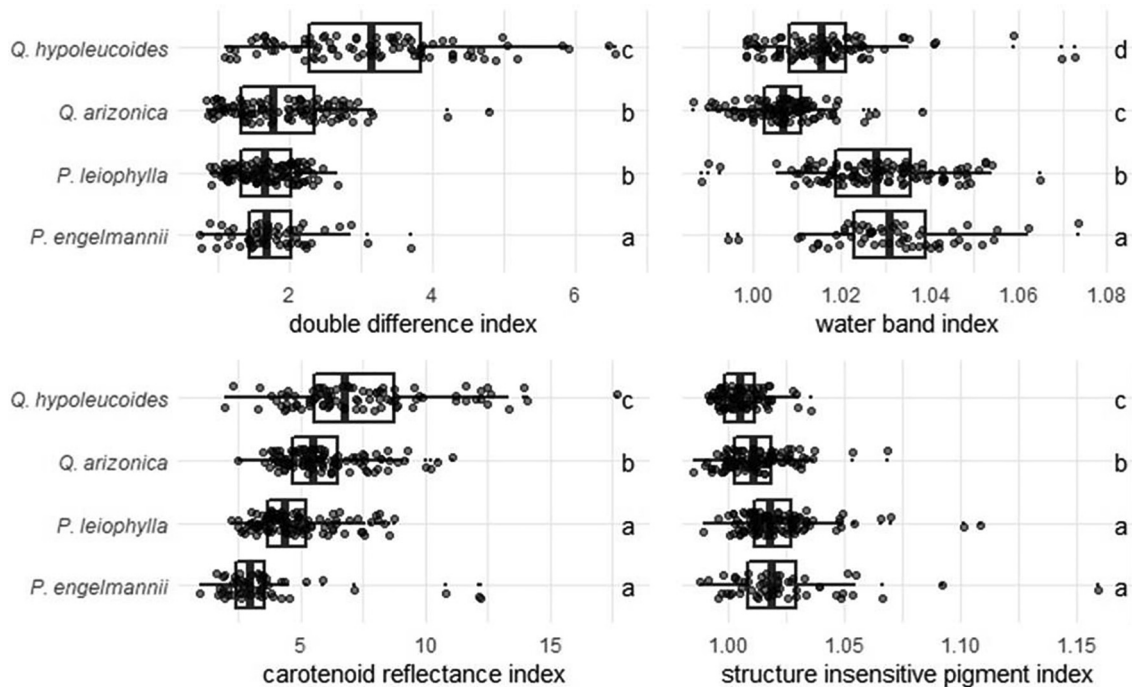
($P < 0.05$, SI Tables 1–3, Fig. 5).

Leaf mass per unit area (LMA) did not differ significantly between pines and oaks, likely demonstrating the high level of sclerophylly of the oak leaves ($P > 0.05$, SI Fig. 4). The independently-measured CHL and ANTH content data were similar to the spectral reflectance results: both pigments were significantly higher (and more variable) in the oaks than the pines and especially for *Q. hypoleucoides* relative to the three other species ($P < 0.05$; Fig. 3).

The isotope values for $\delta^{13}C$, $\delta^{18}O$, and ${}_iWUE$ differed significantly by species and for the interaction term of species and year for all analyses (Fig. 6; SI Tables 2–3), but pines did not differ significantly from oak in the genus-level comparisons (SI Fig. 6). *P. engelmannii* and *Q. hypoleucoides* both maintained significantly higher $\delta^{13}C$ and $\delta^{18}O$ discrimination and ${}_iWUE$ than *P. leiophylla* and *Q. arizonica* ($P < 0.05$)

over the time-series.

4. Discussion

Our results highlight the potential role of leaf gas exchange, pigment concentrations, and water balance in vegetation recovery following moderate- to high-severity wildfires in the Sky Islands of southwestern North America. While Barton and Poulos (2018) argued that the divergent post-fire success of oaks compared to pines stems largely from differences in resprouting capacity, the present study reveals that leaf-level attributes associated with desiccation tolerance may also influence post-fire vegetation dynamics in Madrean evergreen pine-oak woodlands. Five years after wildfire, the ecophysiological performance of two oaks and two pines diverged in leaf desiccation
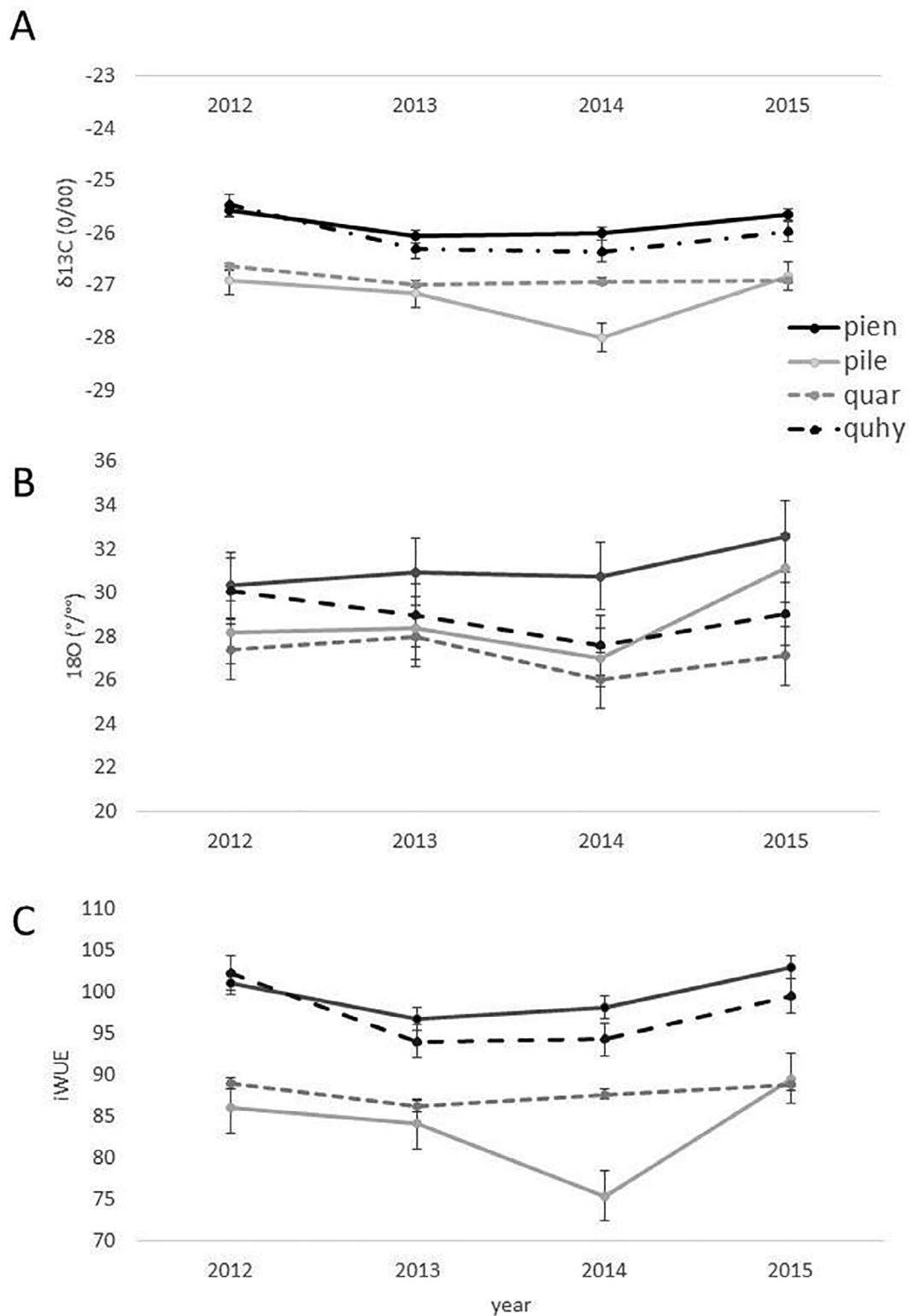
Fig. 6. Mean ± 1S.E. of A) δ^{13}C, B) δ^{18}O, and C) integrated water use efficiency (iWUE) of xylem tissue for each year of juvenile growth of *P. engelmannii* (pien), *P. leiophylla* (pile), *Quercus arizonica* (quar), and *Q. hypoleucoides* (quhy).

tolerance. At one extreme, *Pinus engelmannii*, an obligate seeder, was highly desiccation avoidant and exhibited signs of drought-associated damage to its photosynthetic capacity. At the other end of the continuum, *Quercus hypoleucoides* and *Q. arizonica*, prolific resprouters after fire-caused topkill, tolerated leaf desiccation and drought stress. *P. leiophylla*, with a lower capacity to resprout than the oaks, fell in between these two extremes in terms of water conservation and water-

stress related damage.

Instantaneous gas exchange, wood isotopes, and leaf pigment concentrations provide key reinforcing evidence of leaf ecophysiological divergence among the four species. *P. engelmannii* displayed invariably low A_{max}, low g_s and E, and high relative leaf water content during the peak of the May-June drought in 5-year-old recruits (sensu Tardieu, 1993; Tardieu and Simonneau, 1998). These responses are strongly

indicative of a desiccation-avoidant leaf that prioritizes water conservation over carbon fixation in arid conditions. In contrast, both oaks displayed clear signs of leaf desiccation tolerance, with high levels of g_s and E, and low relative leaf water content. Gas exchange in *P. leiophylla* was similar to the oaks, except that its relative water content was similar to that of *P. engelmannii*, as was its low g on topographically exposed, high-severity fire sites. Wood isotope data from the first four years of post-fire growth are consistent with these gas exchange results. Compared to the other two species, *P. engelmannii* and *Q. hypoleucoides* exhibited significantly higher $\delta^{13}C$, $\delta^{18}O$ and $_iWUE$ values—a pattern that appears to have arisen from different mechanisms in the two species. In desiccation-avoidant *P. engelmannii*, low instantaneous g_s and high $\delta^{18}O$ suggest that low stomatal conductance rather than high photosynthetic rates led to high water use efficiency, whereas lower $\delta^{18}O$ and very high pigment concentrations in *Q. hypoleucoides* suggest a more important role for *A*.

The leaf spectral reflectance indices and chlorophyll and anthocyanin content of the oaks relative to the pines corroborate the gas exchange and wood isotope results. These results demonstrate the higher potential of C-sequestration in the oaks compared to the pines during the peak of the dry season. Leaf spectral reflectance is significantly correlated with pigment concentrations for chlorophyll and the suite of accessory pigments including anthocyanins, xanthophylls, and carotenoids (Richardson et al., 2002, Sims and Gamon, 2002). The higher spectral reflectance of the pines and the shift in the red edge position to shorter wavelengths is typical for less stress-tolerant plant taxa because both plant pigment concentrations and photosynthetic efficiency decline (as does absorption) under drought stress in southwestern tree species (Carter, 1993; Carter and Knapp, 2001; Poulos and Berlyn, 2007). In other words, it appears that the photosynthetic apparatus of the pines was compromised in the post-fire environment compared to the oaks.

Five years after the Horseshoe Two Fire, Barton and Poulos (2018) found vigorous resprouting of oaks, especially *Q. hypoleucoides*, little seedling establishment of either the seeder-obligate *P. engelmannii* or *P. leiophylla*, and low levels of resprouting of this latter species. We hypothesized that leaf ecophysiological differences between pines and oaks amplify differences in resprouting capacity between the two genera and play a role in these post-fire vegetation dynamics. Our results support the idea that differences in leaf desiccation tolerance might be important in post-fire success among these four dominant species in Madrean pine-oak forest. Post-fire regeneration in *P. engelmannii* may have been hampered by both dependence on seedling establishment and a lack of leaf desiccation tolerance, whereas in the oaks, intact root systems, resprouting capacity, and leaf desiccation tolerance might have provided a potent recipe for post-fire regeneration success for this tree genus. The results are less certain for *P. leiophylla*, which presents intermediate attributes for both resprouting capacity and leaf desiccation tolerance, but very low post-fire regeneration performance similar to that of *P. engelmannii*. Thus, although this study provides evidence for the potential role of leaf ecophysiology in post-fire dynamics, our results indicate the connection between the two is more complicated than simply pines vs. oaks. Patterns of leaf desiccation tolerance and the extent of surviving root systems could interact in complex ways in the post-fire environment. Separating the impacts of intrinsic root and leaf functional traits on leaf water relations is both challenging and crucial to fully understanding the mechanisms underlying tree physiological responses and regeneration after wildfire.

The importance of leaf desiccation tolerance vs. avoidance as an influence on plant performance and community dynamics is well-documented elsewhere. For example, extreme drought in the Southwest USA has led to widespread mortality in mature desiccation-avoidant piñon pines with low stomatal conductance, while sympatric desiccation-tolerant junipers survive and continue to photosynthesize (Allen and Breshears, 1998; Breshears et al., 2005; Breshears et al., 2009; McDowell et al., 2008). Our finding of higher desiccation tolerance in

oaks compared to pines has also been documented in other studies in North America (Cooper et al., 2018a,b) and Europe (Martínez-Vilalta and Garcia-Forner, 2017; Zang et al., 2012). Our results do not match up, however, with global generalizations showing that non-resprouters tend to exhibit higher levels of dehydration tolerance than do resprouting species (Pausas et al., 2016; Zeppel et al., 2015 present contrasting conclusions contested in Pausas et al., 2016). Pausas et al. (2016) provide a possible rationale for this discrepancy. Using a single trait descriptor such as resprouting may be simplistic, and resprouting vs. not resprouting may well be associated with different sets of traits in different ecosystems, depending on biogeographic history and environmental conditions. The Pausas et al. (2016) analysis includes many species from Mediterranean biomes, especially shrubs, for example, and the relationships of resprouting and ecophysiology might differ from those found in Madrean pine-oak forests. It's also important to acknowledge that Pausas et al. (2016) includes results for resistance to xylem cavitation (embolism), a crucial trait that we did not measure.

Plant species can produce a broad range of phenotypes in response to variation in the abiotic environment (Callaway et al., 2003; Silvertown and Gordon, 1989; Sultan and Bazzaz, 1993). We have previously-documented species-level differences in pine and oak physiology in relation to elevational distribution and corresponding environmental conditions (Barton, 1993; Barton and Teeri, 1993; Poulos et al., 2007b; Schwilk et al., 2016; Schwilk et al., 2013), yet few studies in this region have examined plasticity in pine or oak plant functional traits within individual species across their distributional ranges (but see Poulos and Berlyn, 2007). The lack of significant differences in tree physiological responses across both fire severity and physiographic gradients in the species examined here was surprising, especially since areas of higher fire severity and more exposed topographic positions were likely hotter and drier than sites that burned at low-severity and maintained an intact forest canopy or less exposed topographic positions that were wetter and received lower incident solar radiation (Barton, 1993, 1994). Our results suggest that the four dominant species in this forest type display largely fixed plant functional traits, exhibiting little phenotypic plasticity in relation to environmental setting. This pattern was most prominent for *P. engelmannii*, the least successful species in terms of both post-fire regeneration and physiological response, and least prominent for *Q. hypoleucoides*, which was by far the most successful species in terms of post-fire regeneration and physiological performance. Our research focused on the most arid part of the year, during an extended drought, five years after a wildfire. Under such conditions, few sites might be suitable for high rates of plant gas exchange. At other times of the growing season (i.e., early Spring and the monsoon season) and in other years, environmental variation might allow more pronounced expression of ecophysiological variation within species. This association of low plasticity and pine recruitment especially warrants further investigation and concern as pines compete in a warmer, drier, more fire-prone climate.

4.1. Conclusions and management implications

Most projections call for increased aridity, intensification of moisture-deficits, and larger and more frequent wildfire in southwestern North America (Adams, 2013; Ault et al., 2016; Cook et al., 2015). Such conditions are likely to amplify the species differences in leaf ecophysiological responses reported here. This may accelerate the transition of these pine-oak forests to an alternative shrubland stable state in the Sky Islands (see Falk, 2013 for a discussion of this phenomenon). Resprouting capacity, desiccation tolerance, and phenotypic plasticity in plant functional traits are likely to play crucial roles under future environmental change (Gratani, 2014) in determining which plants will persist under both a hotter climate and in response to more frequent crown fire. As such, the traits and responses of *Q. hypoleucoides* documented here may further promote oak shrubland dominance and resilience well into the future.

Few studies have applied an ecophysiological approach for understanding tree recruitment patterns following wildfire (but see Clemente et al., 2005; Cooper et al., 2018a; Hodgkinson, 1992; Reich et al., 1990; Richards and Lamont, 1996; Schwilk et al., 2016,), and this study represents an important contribution to the fire science and adaptive management communities, both for understanding the mechanisms of post-wildfire type conversion and for guiding post-wildfire forest restoration activities under a continually warming climate. Sites that have experienced high-severity wildfire may require pine restoration through enrichment planting by managers to re-populate pines in severely burned areas if the management goal is to maintain the mixture of pines and oaks in fire-affected pine forests within the Sky Island systems of the American Southwest and beyond. Clearly, the soil moisture needs of pines in this region relative to oaks suggests that pine restoration activities will be most successful in refugial sites with higher moisture levels and lower probability of severe fire and in years with high precipitation. Regardless, continued biological monitoring is needed for understanding the changing nature of forest recovery over time in the wake of high-severity wildfire.

Author contributions

HMP and AMB procured funding for, conceived, and designed the project. HMP, AMB, DWS, CEF, and WCM performed the experiments. HMP analyzed the data. HMP and AMB wrote the manuscript, with HMP taking the lead. GPB and DWS provided editorial advice.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2019.117704.

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