

# Post-fire resprouting oaks (genus: *Quercus*) exhibit plasticity in xylem vulnerability to drought

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**Abstract** Resprouting is a key functional trait for species in disturbance prone environments. In many semi-arid environments, woody plants face both fire and drought as recurring disturbances. Past work has demonstrated that oaks inhabiting sky-island forests of the northern Sierra Madre Oriental have differing microhabitat preferences and heavy stem dieback occurred during the historic 2011 drought indicating potential xylem failure. These oak species, representing two sections within the genus, are all post-fire resprouters: they can resprout from underground storage organs when fire kills above ground tissue. Resprouts provide an opportunity to examine how functional traits may change as plastic responses to changing environmental conditions. Post-fire resprouts have increased root:shoot ratios relative to adults and therefore have access to more water relative to leaf demand. We expected that if resprouts exhibit plasticity in xylem function, they should favor water transport efficiency over safety: they should have higher maximum xylem conductivity, but greater susceptibility to drought-induced cavitation. We

examined four oak species common in the Davis Mountains in west Texas and compared adult physiology with that of resprouts following wildfire. We found that species differed in degree of desiccation avoidance (isohdry) consistent with microhabitat preferences and that the species that were most desiccation tolerant as adults had resprouts significantly more susceptible to xylem cavitation. We found no evidence for a trade-off between efficiency and safety, however.

**Keywords** Fire · Resprouting · Drought · Xylem cavitation · Plasticity · Desiccation

Plants living in wildfire prone ecosystems have traits that allow them to persist in the face of recurring disturbance. Woody plants may have fire-defense traits that enable survival or, instead, plants may depend upon post-fire seedling recruitment following fire and adult mortality. Among species that depend upon adult survival, two nonexclusive fire survival strategies are available: trees can invest in protecting above ground tissue by means of height and insulating bark (Schwilk and Ackerly 2001), or they may invest in carbon storage (often below ground), the buds necessary for resprouting following above ground tissue loss, and the protection/insulation of that bud bank (Clarke et al. 2013; Charles-Dominique et al. 2015). Different life history stages may be susceptible to different

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environmental stressors (Ackerly 2004). Post-fire resprouts, especially basal resprouts, face a different light and soil moisture environment than do the pre-fire mature adults and have radically altered root:shoot ratios. Resprouts, therefore, provide an opportunity to examine how functional traits may change throughout a plant's life as a plastic response to changing environmental conditions. Intra-specific variation in hydraulic traits, including plastic variation, has received less attention than has inter-specific variation, however (Anderegg 2015). Recent work has suggested that post-fire resprouts exhibit plastic shifts in xylem vulnerability to desiccation (Ramirez et al. 2012; Pratt et al. 2014). Disturbance regimes are likely to shift in the future with some areas experiencing drier or longer fire seasons (Hessl 2011; Moritz et al. 2012). More frequent fire may favor fire adapted species and increase the importance of the resprouting life history (Bond and van Wilgen 1996). Predicting potential range shifts under a changing climate requires understanding stress effects on different plant regeneration stages (Pausas et al. 2015; Zeppel et al. 2015).

Desert mountain ranges provide striking examples of plant species turnover over short distances often controlled by water availability (Whittaker and Niering 1965; Poulos et al. 2007; Poulos and Camp 2010). Woody plants have a range of responses to drought, and variation in hydraulic strategy is a major axis of niche differentiation (Davis et al. 1999; Cavender-Bares and Holbrook 2001; Cavender-Bares et al. 2004; Willson and Jackson 2006; Jacobsen et al. 2008; Pratt et al. 2010) and may promote species coexistence (Savage and Cavender-Bares 2011). Specifically, vulnerability to drought-induced xylem cavitation is an important trait predicting partial dieback and plant mortality during drought (Pockman and Sperry 2000; Anderegg et al. 2015). Drought-induced tree mortality generally occurs through some combination of two dominant mechanisms: carbon starvation or hydraulic failure (Mencuccini et al. 2015). When evaporative demand exceeds water supply, xylem cavitation can result in catastrophic hydraulic failure (Tyree and Zimmermann 2002). Carbon starvation occurs when stomatal closure to prevent hydraulic failure causes photosynthesis to drop so low that the plant starves from its inability to produce photosynthate. Delaying desiccation can help a plant prevent catastrophic hydraulic failure, but involves a high opportunity cost in the form of lost photosynthesis.

Species that tolerate drought may employ two possible strategies: desiccation delay or desiccation tolerance (Tyree et al. 2003). These strategies fall on continuous axis of trait variation from "isohydric" species which maintain midday water potential during drought by closing their stomata, to "anisohydric" species that experience lower water potentials but continue to photosynthesize under moisture stress (Tardieu and Simonneau 1998; McDowell et al. 2008; Meinzer et al. 2014). Anisohydric species should be tolerant of desiccation and continue to photosynthesize under drought stress. More isohydric species may avoid tissue desiccation at the cost of lost photosynthetic opportunity during drought and increased risk of carbon starvation.

Given the positive relationship between conduit diameters and vulnerability to cavitation, a trade-off between desiccation tolerance and efficiency of water transport is generally expected (Tyree and Sperry 1989; Tyree et al. 1994; Hacke et al. 2000; Pittermann et al. 2006; Sperry et al. 2008). Across species, however, this relationship is often weak (Pockman and Sperry 2000; Maherali et al. 2006; Gleason et al. 2015) and one might expect that the trade-off should be most apparent in plastic shifts within an individual given the strong relationship between conductivity and vulnerability across organs within an individual (Sperry and Saliendra 1994). Within an individual, hydraulic properties can vary across xylem produced in different seasons (Jacobsen et al. 2007, 2014), in different years (Melcher et al. 2003; Corcuera et al. 2004), or in response to environmental conditions (Corcuera et al. 2011; Plavcová and Hacke 2012). Despite such evidence, plastic shifts in xylem vulnerability in response to the environment have been studied less than have across species and across organ variation in vulnerability (e.g., Mencuccini and Comstock 1997).

Post-fire resprouts have high root:shoot ratios and, therefore, relatively favorable water supply to demand relationships compared to adults. Additionally, rapid post-fire growth may be favored over safety in resprouting species (Falster and Westoby 2005; Pausas et al. 2015). This suggests that the optimum position on a xylem efficiency vs safety axis should also shift and resprouts may increase efficiency at the expense of safety by increasing xylem conduit diameter or by increasing the size and/or number of xylem pits. What little data exist on post-fire plastic shifts in xylem vulnerability, however, is contradictory and

previous studies of within species plastic variation have generally focused on a single species. For California chaparral shrubs, it appears that post-fire resprouts may have tissue more vulnerable to xylem embolism than do adults (Ramirez et al. 2012; Pratt et al. 2014). On the other hand, Utsumi et al. (2010) found that post-fire resprouts of California walnut (*Juglans californica* S. Watson) were less susceptible to cavitation than were adults, but this may be an artifact of cavitation fatigue in the adult trees (nonfunctional fatigued vessels showing artificially high vulnerability, Hacke et al. 2001).

Drought tolerance and fire survival strategies are especially important in the desert sky-islands forests of the southwestern United States. These isolated forest patches at the highest elevations of desert mountain ranges comprise one of the most diverse temperate forest ecosystems in the world (Whittaker and Niering 1965; Warshall 1994; Poulos and Camp 2010). Trees are surviving at the resource-limited edge of their physiological tolerances atop these sky-islands, making them potentially more vulnerable to the effects of drought and wildfire. Furthermore, projected climate change may include more frequent droughts as well as lengthening fire seasons (IPCC 2014). Shifts in tree distributions have already been documented in some locations (Allen and Breshears 1998; Koepke et al. 2010; Rigling et al. 2013) and recent droughts have resulted in widespread plant dieback and mortality in this region (Waring and Schwilk 2014; Poulos 2014).

Oaks (*Quercus*) are the prominent upland trees across a wide elevational range in the mountain ranges of west Texas and the northern Sierra Madre Oriental. Past work has demonstrated variable investment in fire-defense traits across species that is associated with microhabitat (Schwilk et al. 2013). There is rapid species turnover within *Quercus* over small spatial scales (Poulos and Camp 2010) and such turnover appears to be associated with local soil moisture and with fire regime (Schwilk et al. 2013). Most oaks are ring-porous species generally assumed to be vulnerable to xylem cavitation and dependent upon an isohydric stomatal control strategy. In the west Texas mountain ranges, however, oaks occupy the full range of soil moisture habitats at which trees are found—from the wettest canyons to the driest grass- and juniper-dominated slopes. We therefore expect to see differences in hydraulic strategy within the group. We

studied a suite of coexisting oak species, all post-fire resprouters but with presumed differences in drought tolerance, to examine potential plastic shifts in desiccation tolerance. If resprouts can exhibit plasticity in xylem function, we would expect decreased safety and increased efficiency (greater maximum rates of conductivity), in resprouts than in conspecific adults.

We examined leaf water potentials and xylem vulnerability to drought during extreme drought in five *Quercus* species in the Davis Mountains of west Texas. We examined hydraulic traits and water potentials in the four most common oak species in this range (*Quercus emoryi* Torr., *Q. gambelii* Nutt., *Q. grisea* Liebm., and *Q. hypoleucoides* A. Camus). We followed leaf water potentials during and following the historic 2011 drought, the most-extreme one-year drought on record (Nielsen-Gammon 2012). To examine xylem susceptibility to drought, we created xylem vulnerability curves: percent loss of hydraulic conductivity (PLC) as a function of xylem water potential. Such curves are often summarized by the P50 value: the water potential at which 50 % of the xylem's conductivity has been lost relative to the maximum conductivity of a fully hydrated stem. Based on observed habitat preferences (Poulos and Camp 2010; Schwilk et al. 2013), we expected that these species should differ in desiccation tolerance, from greatest tolerance (lowest P50) to least tolerance (highest P50): *Q. grisea*, *Q. emoryi*, *Q. gambelii*, and *Q. hypoleucoides*. Wildfires that burned an ongoing study site provided an opportunity to compare xylem vulnerability to cavitation across two life history stages (adult and resprout) in each species. We compared adults and post-fire resprouts to test for a plastic shift in desiccation tolerance. We predicted that, within a species, resprouts should exhibit reduced safety (higher P50 values) and increased efficiency (greater maximum conductivity,  $K_h$ ).

## Materials and methods

The study took place within the Nature Conservancy's Davis Mountains Preserve, Jeff Davis County, Texas. The Davis Mountains comprise a desert sky-island surrounded by Chihuahuan desert grasslands. In addition to the four species included in this study (Table 1), *Quercus gravesii* Sudw. is the next most common oak species, but is restricted to the most

**Table 1** Average tree sizes and study sample sizes by elevation, aspect, and study component

Species	Adult tree size		Sample sizes by elevation and aspect			
	DBH (cm)	Individual basal area (cm <sup>2</sup> )	1900 m		2200 m	
			North	South	North	South
<i>Q. grisea</i>	20.3 (7.44)	360 (192)	5, 1, 4	5, 5, 0		5, 3, 5
<i>Q. emoryi</i>	24.8 (11.2)	734 (505)	5, 2, 7	5, 6, 1		
<i>Q. hypoleucoides</i>	18.3 (6.90)	403 (473)	5, 6, 8		5, 3, 6	
<i>Q. gambelii</i>	14.9 (3.58)	185 (92.7)			8, 6, 5	

Adult tree sizes are summarized as mean diameter at 1.37 m height of largest stem (DBH, cm) and mean total individual basal area at 1.37 m height (cm<sup>2</sup>). Mean values shown with standard deviations in parentheses. For sample sizes, the first number is the sample size of oaks tagged for water potentials (numbers for summer 2011 after we lost some adults to fire). The second number is the sample size for adult vulnerability curves, and the third number is the sample size for resprout vulnerability curves

mesic parts of the landscape and few individuals burned so we could not obtain replicated resprout vulnerability curves for this species. Although these species do have specific microsite affinities, turnover occurs over very short distances and it is possible to find sites at which three of the four coexist (for example, our low-elevation north-facing site included *Q. grisea*, *Q. emoryi*, and *Q. hypoleucoides*, Table 1). Trees were identified using Powell (1998) and Muller (1940). *Q. grisea* and *Q. gambelii* are in section *Quercus*; *Q. emoryi* and *Q. hypoleucoides* are in section *Lobatae* (Muller 1940; Manos et al. 1999; Hipp et al. 2014) and all are ring-porous (confirmed with cross sections). *Q. hypoleucoides* is the only truly evergreen species in the group, although *Q. grisea* and *Q. emoryi* can have leaves at nearly any time of year and are more drought-deciduous than winter-deciduous.

#### Water potential measurements

Naturally occurring trees were sampled at two sites 3.6 km apart: one low-elevation site (1900 m) and one high elevation site (2200 m). At each site, a pair of 100-m-diameter plots was established, with one plot in each pair on a generally north facing aspect and one on a south aspect. The plots in each pair were less than 0.5 km apart from one another and the two sites were approximately 3 km apart. Within each plot, we randomly selected 5 individuals of each oak species for long-term study (Table 1). These trees were permanently tagged. We used a pressure chamber (PMS instruments, Albany, Oregon) to measure

predawn and midday water potentials on each individual tree on five occasions between April 2011 and June 2013 (April 2011, October 2011, June 2012, August 2012, June 2013). Not every tree was measured during the first sampling in 2011 and some sites were only measured once in summer 2012. For tagged trees that burned and resprouted basally, we continued to measure water potentials following resprouting.

#### Xylem conductivity and vulnerability measurements

For stem xylem conductivity measurements, a subset of the tagged adult trees was sampled at each plot during the growing season, June–July 2011. We aimed for 5–10 individuals per species. A portion of the low site burned in the Tejano Canyon fire in June 2011 and the higher elevation site and some low-elevation trees burned in the Livermore Ranch Complex fire in April 2012 (<http://inciweb.nwcg.gov/>). Resprouts that were burned in 2011 began resprouting in late summer and fall of 2011; trees burned in the Livermore Complex Fire resprouted immediately after the April 2012 fire. Resprouts were sampled within the burned area at each site in June–July 2013. Because the Tejano Canyon fire and others nearby interrupted measurements of adult stem conductivity in 2011, additional adult trees were added to increase sample sizes in 2013 (Table 1). We selected unburned adults in or adjacent to the original 100-m-diameter plots when possible, but in some cases, we collected from trees found outside the originally delineated plots up to a maximum distance

of 0.5 km away from the initial collection plots but at similar elevation and aspect. Not all adults that we initially measured burned and resprouted, so we did not create a paired design, but chose resprouting individuals that were distinct from the adult individuals sampled. Table 2 reports sample sizes by site, aspect, and species. For each tagged tree, we selected a stem that included a straight 14-cm-long segment that was 6–12 mm in diameter. We then cut the branch containing this target segment under water. The branch was kept bagged and on ice with the cut end in water and brought to the lab within 48 h of cutting.

We determined hydraulic conductivity ( $K_h$ ) by measuring net increase in fluid flow through a stem segment after applying a pressure head. We recut the field-collected stems to the 14 cm desired length under water. To measure flow, stems were connected to a tubing apparatus with the basal stem end fed by the elevated pressure reservoir (an IV bag) and the distal end connected to a reservoir on an analytical balance. Stems were kept submerged in water during and between measurements and a fresh razor blade was used to shave a small amount from the proximal end before each measurement. The pressure head was kept between 3 and 6 kPa. Mass flow was recorded by serial output from the balance to a computer and flow rates calculated using custom open-source Python software we wrote (<https://github.com/schwilklab/hydro-balance>). The perfusing solution was 20 mM KCl that was vacuum degassed for 30 min (Melcher et al. 2012) and then filtered to 0.1  $\mu\text{m}$  (inline filter; GE Water and Process Technologies, Trevose, PA, USA). Before and after each flow measurement, we measured background flow with no pressure head. We calculated  $K_h$  as the pressure-driven flow corrected for

background flows divided by the pressure gradient and standardized to unit stem length. To calculate stem area specific conductivity ( $K_s$ ),  $K_h$  was divided by stem sapwood cross-sectional area at the distal end, which was calculated from caliper measurements of xylem and pith diameters measured on two orthogonal axes. We used these cross sections to confirm that all species were ring-porous. To calculate leaf-specific conductivity,  $K_{\text{leaf}}$ , we divided  $K_h$  by the total area of all leaves distal to the stem segment.

The centrifuge method was used to induce xylem tension and cavitation (Holbrook et al. 1995; Alder et al. 1997). We followed the methods as outlined in Tobin et al. (2013). We mounted stems in a custom rotor (Alder et al. 1997) that enabled them to be spun in a centrifuge (Sorvall RC-5C; Thermo Fisher Scientific, Waltham, MA, USA) with stem ends submerged in solution contained in L-shaped reservoirs. The solution level in the reservoirs was kept even at both ends of the stem, so no flow was induced during centrifugation. We added foam pads (Covergirl brand make-up application pads, Procter & Gamble) to the vertical section of reservoirs to keep the solution in contact with stem ends when the rotor was not spinning as described in Tobin et al. (2013). Stems were spun at the desired RPM for 5–6 min. Maximum  $K_h$  was measured on stems flushed with the same solution used for  $K_h$  measurements at 75 kPa for 45 min to refill embolized vessels. For each tension applied, we calculated the percent loss of conductivity (PLC) as  $100 \times K_h/K_{\text{max}}$ . To correct for possible cavitation fatigue (Hacke et al. 2001), we spun each stem to  $-0.25$  MPa after flushing and used the subsequently measured conductivity as the maximum value ( $K_{\text{max}}$ ).

**Table 2** Oak ecophysiological traits. Minimum seasonal water potentials during 2011 drought (June–July 2011), estimated  $\psi_{\text{crit}}$ , and estimated P50 values

Species	Adult $\psi_{\text{min}}$ (MPa)	Adult $\psi_{\text{crit}}$ (MPa)	Adult P50 (MPa)	Resprout P50 (MPa)
<i>Q. grisea</i>	$-3.41 \pm 0.14$	$-3.63$ ( $-4.47, -2.80$ )	$-2.28 \pm 0.08$	$-1.09 \pm 0.10$
<i>Q. emoryi</i>	$-2.36 \pm 0.43$	$-2.75$ ( $-3.60, -1.90$ )	$-1.87 \pm 0.13$	$-0.93 \pm 0.14$
<i>Q. hypoleucoides</i>	$-2.39 \pm 0.19$	$-2.09$ ( $-2.96, -1.21$ )	$-1.05 \pm 0.11$	$-0.80 \pm 0.04$
<i>Q. gambelii</i>	$-2.16 \pm 0.10$	$-1.95$ ( $-2.85, -1.05$ )	$-0.65 \pm 0.10$	$-0.76 \pm 0.10$

$\psi_{\text{min}}$  shown as means  $\pm$  standard errors.  $\psi_{\text{crit}}$  values are shown with the lower and upper 95 % confidence intervals in parentheses. Adult and resprout P50 values are coefficient estimates from the individual species 1-factor Weibull model fits and are shown  $\pm$  coefficient standard errors

## Analyses

In addition to calculating minimum seasonal water potentials ( $\Psi_{\min}$ ) during the 2011 drought for each individual (Bhaskar and Ackerly 2006), we characterized each species's position on an isohydry–aniso-hydry axis by calculating a proportional drop in water potential ( $\Psi_{\text{drop}}$ ) for each predawn–midday water potential measurement pair as

$$\frac{\Psi_{\text{md}} - \Psi_{\text{pd}}}{\Psi_{\text{md}}},$$

where  $\Psi_{\text{pd}}$  is predawn water potential and  $\Psi_{\text{md}}$  is midday water potential that same day. We then modeled  $\Psi_{\text{pd}}$  as a linear function of this new variable and compared the resulting y-intercepts across species. We termed this intercept value a theoretical  $\Psi_{\text{crit}}$ : it is the value of predawn water potential below which there is no further drop in midday water potential. This is similar to the minimum seasonal water potential,  $\Psi_{\min}$ , but is estimated based on all of the available water potential values rather than on a single observation. Although we do not have continuous measures of stomatal conductance, both  $\Psi_{\min}$  and  $\Psi_{\text{crit}}$  are measures of iso vs. anisohydry with higher values indicating more isohydric species and lower values indicating more anisohydric species. To calculate  $\Psi_{\text{crit}}$  and compare species, we fit mixed linear models using the `lme()` function of the `nlme` package in R (Pinheiro et al. 2015). Because we had repeated measurements on individuals, we included individual as a random effect when fitting the models. Only leaf water potential from adult trees was used in these analyses.

To compare adult xylem vulnerabilities across species, we fit a re-parameterized Weibull curve model to the data (Ogle et al. 2009) using the `n1me()` function of the `nlme` package in R (Pinheiro et al. 2015). We parameterized the Weibull function so that one of the two estimated parameters was the P50 value in MPa and the other was the slope at 50 % loss conductivity ( $s_{50}$ ). We used applied water potential as the independent variable, fatigue-corrected PLC as the dependent variable, species as a factor, and individual stem (tree) as a random nesting effect on both estimated Weibull parameters. To test for significant effect of species on P50, we used a conditional  $F$ -test as recommended by Pinheiro and Bates (2000) using the model comparison `anova()` function in R.

To test for differences in P50 by life stage (adult versus resprout), we fit nested nonlinear models as described above, but separately for each species with life stage as a fixed effect and individual stem as a random effect. We tested for a significant effect of life stage on P50 using conditional  $F$ -tests.

We tested for effect of species and life stage on maximum stem- and leaf-specific conductivities and on Huber values (leaf area/sapwood area) with 2-factor linear models (ANOVA) and  $F$ -tests using the `lm()` and `anova()` functions in R.

## Results

### Water potentials

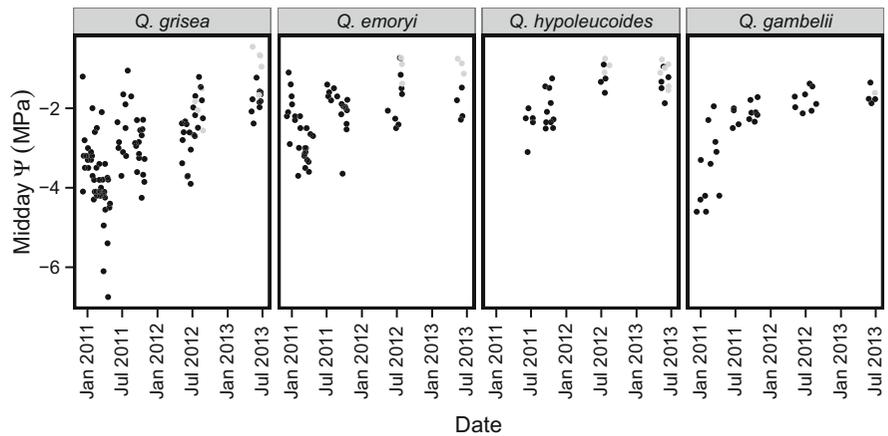
These four species exhibited substantial variation in water potential during and after the 2011 drought (Fig. 1). Adult minimum seasonal water potentials during summer 2011 ranged from  $-3.4$  MPa in *Q. grisea* to  $-2.16$  MPa in *Q. gambelii* (Table 2). Although we measured lower water potentials on *Q. grisea* and *Q. emoryi* in April 2011 (Fig. 1, which includes all data), these are not included in this calculation for Table 3 because not all individuals had leaves at this time and because we did not measure all species. Those individuals measured had few leaves and the very low water potentials measured in some individuals in April 2011 may indicate branches that died before the summer 2011 measurements. We only have water potentials of post-fire resprouts after the period of extreme drought, but resprout water potentials are generally higher than those of conspecific adults at the same time when available in 2012 and 2013 (Fig. 1).

The relationship between predawn water potential and the diurnal proportional drop in water potential differed across species (Fig. 2; Table 3). Theoretical  $\Psi_{\text{crit}}$  values were generally quite similar to the empirical minimum seasonal water potentials and ranged from  $-3.63$  MPa in *Q. grisea* to  $-1.95$  MPa in *Q. gambelii* (Fig. 2; Table 3).

### Hydraulic conductivity and xylem vulnerability

Adult xylem vulnerability curves differed among the four species (Fig. 3; conditional  $F$ -test on P50  $F_{4,180} = 291.0$ ,  $p < 0.001$ ) and estimated P50 values

**Fig. 1** Midday water potentials ( $\psi$ ) over time among four species of *Quercus*. Black circles indicate adults and gray circles indicate post-fire resprouts



**Table 3** Conditional  $F$ -Test parameters for  $\psi_{crit}$  model

	$F$ degrees of freedom	$F$	$P$
Intercept	1, 88	1721	< 0.001
$\psi_{drop}$	1, 88	694.7	< 0.001
Species	3, 88	25.7	< 0.001
$\psi_{drop}$ : species	3, 88	15.2	< 0.001

Number of observations = 170, number of groups = 75. Repeated measures model with  $\psi_{min}$  as response, species and  $\psi_{drop}$  as fixed effects, and individual within species as a random effect

were associated with  $\Psi_{crit}$  across these four species (Table 2). Ordered from least to most vulnerable to desiccation, these were *Q. grisea*, *Q. emoryi*, *Q. hypoleucoides*, and *Q. gambelii*.

The three species with the lowest P50 values as adults had significantly more vulnerable xylem as resprouts (Fig. 3, *Q. grisea*  $F_{2,78} = 840.9$ ,  $p < 0.001$ ; *Q. emoryi*  $F_{2,105} = 234.4$ ,  $p < 0.001$ ; and *Q. hypoleucoides*  $F_{2,125} = 336.1$ ,  $p < 0.001$ ). In the case of *Q. hypoleucoides*, however, the magnitude of the shift was quite small (Fig. 3). For *Q. gambelii*, resprouts were slightly less vulnerable than adults (Fig. 3,  $F_{1,49} = 363.6$ ,  $p < 0.001$ ), which was in the direction opposite of that predicted.

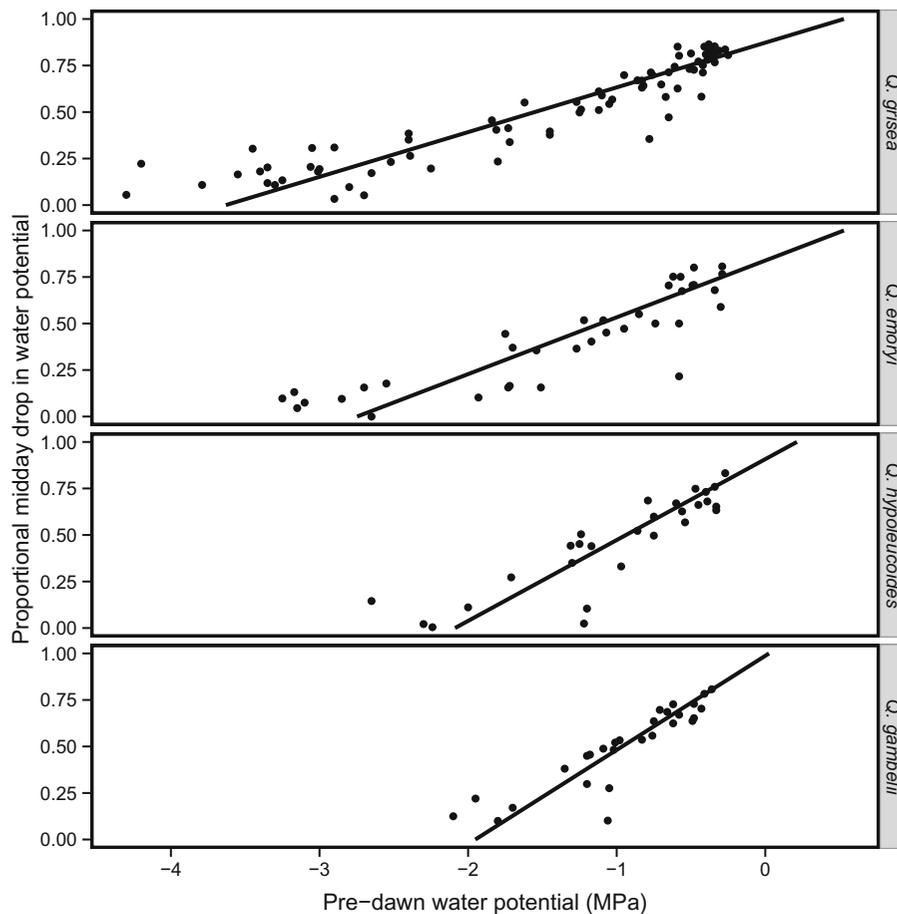
Maximum stem- and leaf-specific conductivities showed little pattern across species and life stage (Figs. 4, 6) and there was no significant effects of either factor or interactions (all  $p > 0.05$ ). There were no consistent difference in Huber values with species, but resprouts tended to have higher Huber values than did adults ( $F_{1,20} = 21.7$ ,  $p < 0.001$ , Fig. 5). Despite

this, maximum leaf-specific conductivity showed no pattern across species and life stage (Fig. 6).

## Discussion

Despite relatively close co-occurrence, these species demonstrate a range of water use strategies. *Q. grisea* and *Q. emoryi* are among the lowest elevation oaks in this mountain range, co-occurring with *Juniperus deppeana* Steud. and *Pinus cembroides* Zucc. As we predicted, these two species exhibited the lowest minimum seasonal water potentials (Table 3) and were the most desiccation-tolerant adult trees (Fig. 3). *Q. grisea* is found at the very driest sites but is an elevation generalist found even on south-facing slopes at the highest elevations. *Q. emoryi*, on the other hand, is generally found only at low to medium elevations, and at the lowest elevations is restricted to ravines, washes, and seasonal water courses. *Q. hypoleucoides* is restricted to canyons and north-facing slopes; therefore, its vulnerability to desiccation is not surprising given its habitat preferences (Poulos and Camp 2010) and the extensive dieback and mortality witnessed in this species during the 2011 drought (Schwilk, personal observation). The extreme xylem vulnerability we measured in *Q. gambelii* is consistent with other work on this ring-porous species (Taneda and Sperry 2008) and with its generally high elevation and canyon distribution in this region.

Past work has suggested a relationship between fire survival strategy and soil moisture habitat (Schwilk et al. 2013). Oaks that inhabit drier, grass fuel-



**Fig. 2** Degree of isohydry/anisohydry among four species of *Quercus*. Lines indicate linear models used to determine  $\psi_{crit}$  (the  $x$ -intercepts in these panels). Note that the  $y$ -axis

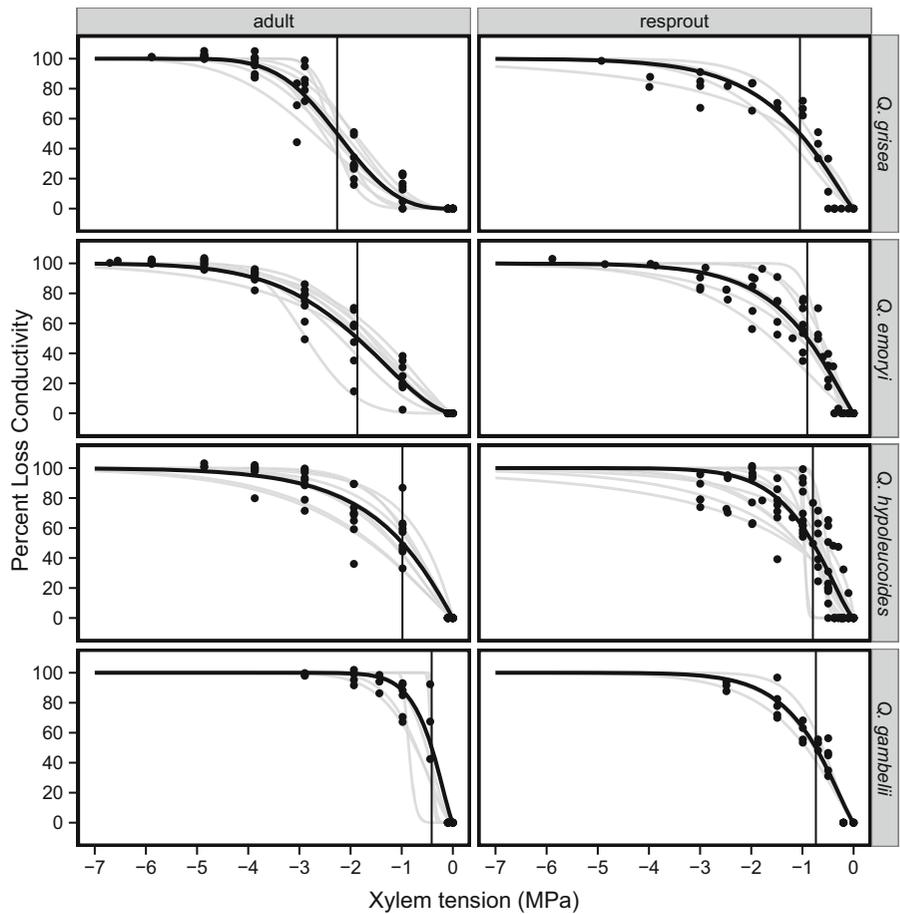
(proportional midday drop in water potential) is the independent variable in the linear model and the  $x$ -axis ( $\psi_{pd}$ ) is the dependent variable. The  $x$ -intercept values are  $\psi_{crit}$  as reported in Table 2

dominated sites may experienced more frequent fire and show early investment in bark as a fire defense, while oaks inhabiting mesic canyons may experience less frequent but more intense crown fire and delay bark investment, relying instead on resprouting as a fire survival strategy when young. *Q. grisea* and *Q. emoryi* are typical of the first strategy and *Q. hypoleucoides* typical of the second. In light of our current results, *Q. gambelii* is an exception to this pattern. It exhibits early investment to thick bark (Schwilk et al. 2013), but its hydraulic strategy demonstrated here is akin to that of *Q. hypoleucoides*.

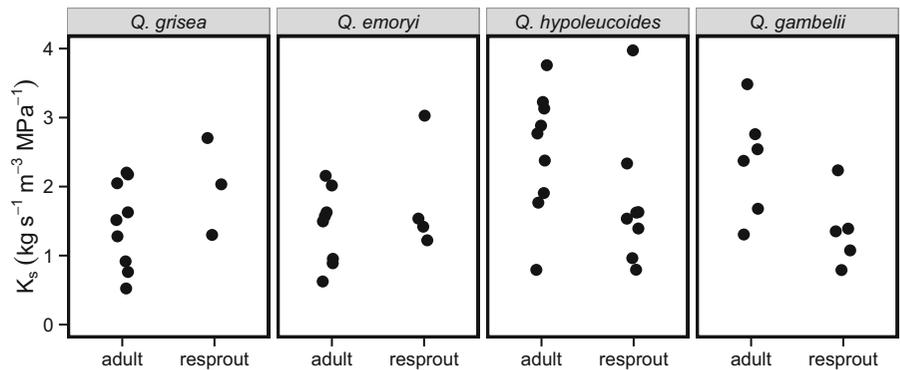
Although we find variation in vulnerability across species, even the most drought-tolerant oaks in our study appear to employ a generally “high vulnerability” strategy. Adult water potentials in 2011 were well

below the P50 values estimated (Table 3; Fig. 3). Even in the wetter years following 2011, water potentials during the growing season often dropped below the P50 values for both adults and resprouts (Fig. 1). Our work is consistent with studies of ring-porous oaks: ring-porous species are often highly vulnerable to desiccation (Li et al. 2008; Taneda and Sperry 2008; Christman et al. 2012; Urli et al. 2015) and dependent upon an isohydric hydraulic strategy (Hacke et al. 2006). Although there has been controversy over the use of the centrifuge method for long-vessel species such as oaks (Choat et al. 2010; Cochard et al. 2010), there is growing evidence that the method is suitable for even long-vessel species (Jacobsen and Pratt 2012; Sperry et al. 2012; Hacke et al. 2015) and that centrifuge vulnerability curves

**Fig. 3** Xylem vulnerability by species and life stage among four *Quercus* species. *Gray lines* show Weibull fits for individual stems, *black lines* show overall fits for species and life stage. *Vertical lines* indicate estimated P50 values by species (Table 2). Separate nonlinear mixed effect models were run for each species. Resprouts differed significantly from adults for each species (all  $p < 0.001$ ), although for *Q. gambelii* this was in the opposite direction from that predicted



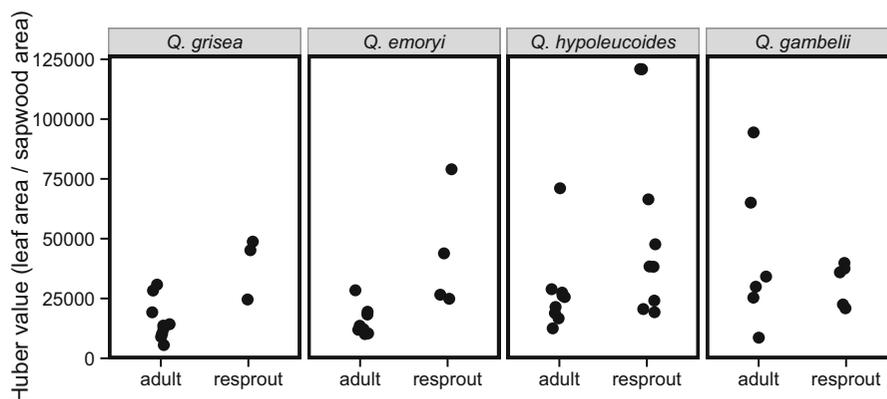
**Fig. 4** Maximum stem-specific conductivity by species and life stage for four *Quercus* species



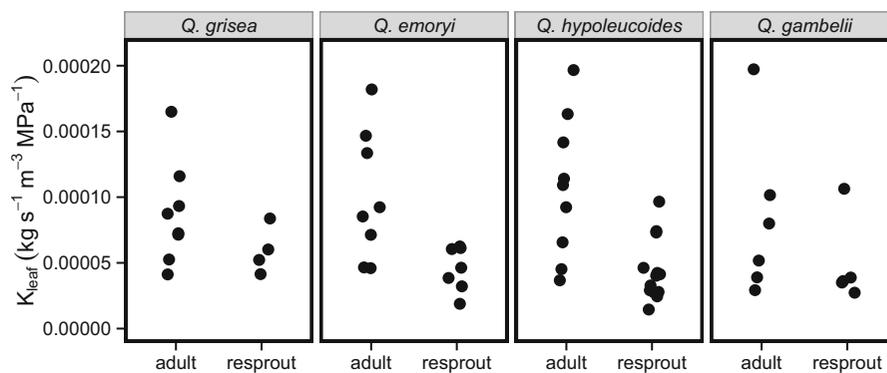
agree with dehydration curves (Tobin et al. 2013; Hacke et al. 2015). Xylem vulnerability has been reported for only one of our study species, *Q. gambelii*, which routinely operates at high levels of native embolism and is able to refill embolized vessels (Li et al. 2008; Taneda and Sperry 2008). The r-shaped

vulnerability curve and P50 values we calculate for *Q. gambelii* are consistent with findings by Christman et al. (2012) in which bench dry-downs and single-vessel air injections were compared to evaluate the importance of rare, leaky pits to overall xylem vulnerability to cavitation.

**Fig. 5** Huber values (leaf area/sapwood area) by species and life stage for four *Quercus* species. There were no consistent difference in Huber values with species, but resprouts tended to have higher Huber values than did adults ( $F_{1,20} = 21.7, p < 0.001$ )



**Fig. 6** Maximum leaf-specific conductivity by species and life stage for four *Quercus* species



If this vulnerable strategy is associated with high maximum conductivity rates, then for these oaks this strategy may allow rapid growth under favorable wet conditions (Pratt et al. 2015). But this vulnerability can result in significant tissue loss during drought. For example, the 2011 drought resulted in massive canopy dieback of oaks throughout west Texas (Waring and Schwilk 2014; Poulos 2014). Resprouts do not appear immune to this dieback: we did observe stem mortality in post-fire resprouts during 2012 and 2013, primarily in resprouting *Q. hypoleucoides* (Schwilk, personal observation). On a global scale, resprouting species appear to be more vulnerable to desiccation than are nonsprouters (Pausas et al. 2015). On the other hand, high tissue-specific vulnerability does not necessarily result in mortality during drought. Recent resampling of sites with extreme oak canopy dieback in the Chisos mountains of west Texas indicates that many individuals can recover relatively quickly through epicormic and basal post-drought resprouting (Schwilk, unpublished data).

We found some support for our prediction that resprouts would be more vulnerable to desiccation: The three species with the lowest adult P50 values had resprouts with significantly more vulnerable xylem (Fig. 3, life stage effect  $p < 0.001$  in all cases), although this shift was of very small magnitude for *Q. hypoleucoides* in which adults were already very vulnerable. The small but significant negative shift in P50 in *Q. gambelii* resprouts was a puzzle. One previous paper has found that post-fire resprouts in the California walnut (*Juglans californica*) were less vulnerable than were adults (Utsumi et al. 2010). In that study, the authors tentatively attributed the shift not to true plasticity but to fatigued vessels in the adults (Hacke et al. 2001). Our reported P50 values are based on a “maximum”  $K_h$  measured following a centrifuge spin to  $-0.25$  MPa, however, and therefore should account for cavitation fatigue. Post-fire resprouting provides a natural experiment in which to evaluate plasticity which might otherwise require common garden experiments. Experiments have revealed mixed

evidence for plasticity with studies finding significant plastic shifts in vulnerability (Wortemann et al. 2011; von Arx et al. 2012) or no such shifts (Lamy et al. 2014). Although we demonstrate that resprouts are more vulnerable on a tissue-specific basis in several cases, this does not necessarily imply greater susceptibility to climatic drought: greater root:shoot ratios and greater available soil water following fire as a result of decreased stand-level transpiration (Whitehead et al. 1984; Nolan et al. 2014) may compensate for increased vulnerability to desiccation.

Contrary to our prediction, we found no evidence for an efficiency-vulnerability trade-off across or within species. Stem and leaf-specific conductivity were not greater in the more vulnerable species nor were they greater in resprouts than in adults (Figs. 4; 6, species and life stage linear models,  $p > 0.05$  for both). Although Huber values (leaf area to sapwood area ratios) differed between adults and resprouts, these values may be influenced by some drought-deciduousness among these species during the 2011 drought. We therefore advise caution in interpreting these or leaf-specific conductivity (Figs. 5; 6). In their work on co-occurring *Quercus* species in temperate forest, Maherali et al. (2006) also found little correlation between safety and efficiency within the genus. The negative correlation between safety and efficiency found across plant organs within an individual has sometimes been difficult to detect in cross-species comparisons and may be driven by differences in xylem anatomy across major phylogenetic groups (Maherali et al. 2004). Studies of plastic shifts have also failed to find such a trade-off (Plavcová and Hacke 2012). The trade-off between efficiency and safety is based on pit-level traits, however (Wheeler et al. 2005; Sperry et al. 2006; Christman et al. 2012). If vessel diameter or density are more plastic than are pit traits such as pit membrane resistance, then there may be no trade-off in safety versus efficiency during development.

## Conclusion

Resprouting plants dominate many arid and semi-arid ecosystems (Bond and Midgley 2001; Clarke et al. 2013). The resprouting strategy allows recovery following drought-induced dieback, fire, or other disturbance. Recently, it has been suggested that resprouters are more resilient to drought than are nonsprouters

(Zeppel et al. 2015), although overall evidence points to greater tissue-specific desiccation tolerance in nonsprouters (lower P50 values, Pausas et al. 2015). The ability to recover through resprouting combined with generally deeper roots than co-occurring nonsprouters (Keeley 1991; Bell 2001) implies that resprouters with xylem very vulnerable to desiccation may still tolerate climatic drought. The potential for plastic shifts in vulnerability, however, suggests some caution in interpreting adult P50 values as indicative of desiccation tolerance across life stages as argued by Zeppel et al. (2015). During extreme droughts, despite dieback, resprouting oaks have exhibited lower mortality than have nonsprouting pines (Poulos 2014) and there is evidence that recent warming may have led to greater oak abundance in California (McIntyre et al. 2015). A better understanding of the costs and benefits of resprouting will be important for predicting vegetation shifts under changing climate.

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