

Leaf hydraulic parameters are more plastic in species that experience a wider range of leaf water potentials

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Abstract

1. Many plant species experience large differences in soil moisture availability within a season, potentially leading to a wide range of leaf water potentials (Ψ_{LEAF}). In order to decrease the risk of leaf dehydration, among species, there is a continuum ranging from strict control (isohdry) to little control (anisohdry) of minimum Ψ_{LEAF} .
2. In central Texas USA, species are exposed to a range of soil moisture from wet springs to hot, dry summers. There are diverging water management strategies among the four dominant woody species in this system; two of these species are more isohydric (*Prosopis glandulosa*, *Quercus fusiformis*) while two others are more anisohydric (*Diospyros texana*, *Juniperus ashei*).
3. To maintain leaf turgor and photosynthesis during periods of limited soil moisture, anisohydric species may adjust leaf hydraulic parameters more than isohydric species. To test this hypothesis, we quantified iso/anisohdry from 3 years of Ψ_{LEAF} predawn and midday measurements, and we measured the changes in turgor loss points (Ψ_{TLP}), osmotic potential at full hydration ($\Psi_{\pi 100}$), and resistance to leaf hydraulic dysfunction (leaf P_{50}) throughout the spring and summer of 2016.
4. *Diospyros* and *Juniperus* experienced more negative Ψ_{LEAF} and adjusted Ψ_{TLP} and $\Psi_{\pi 100}$ in response to both drying soils during the summer also in response to rainfall events during September. In contrast, the more isohydric species (*Quercus* and *Prosopis*) did not appear to adjust Ψ_{TLP} or $\Psi_{\pi 100}$ in response to soil moisture. The more anisohydric species also adjusted leaf P_{50} during periods of reduced soil moisture.
5. Our results suggest that species that experience wider ranges of Ψ_{LEAF} have a greater ability to alter leaf hydraulic properties. This provides insight on how species with different strategies for water potential regulation may modify properties to mitigate drought effects in the future.

KEYWORDS

drought, embolism, isohdry, pressure–volume curves, semi-arid, Texas, transpiration, turgor

1 | INTRODUCTION

To sustain carbon capture via photosynthesis and cell growth, plants must maintain adequate leaf hydraulic function (leaf hydraulic conductance, K_{LEAF}) and leaf cell turgor. If K_{LEAF} is reduced then the whole-plant hydraulic conductance is impaired (Johnson et al., 2016) and stomata must constrict to prevent plant hydraulic failure and leaf desiccation (e.g. Brodribb & Holbrook, 2003; Johnson, McCulloh, Woodruff, & Meinzer, 2009). Decline in K_{LEAF} under drought may at least partially be a consequence of the mesophyll cells losing turgor and shrinking, thus mechanically increasing resistance to water flow (Brodribb & Holbrook, 2004; Scoffoni, Vuong, Diep, Cochard, & Sack, 2014). If turgor is lost, stomata can close, plant cell metabolic processes can decline, and, if water potentials are severe enough, cell walls can collapse and cells can undergo plasmolysis and become metabolically inactive (Taiz, Zeiger, Møller, & Murphy, 2015). Although stomata are the primary regulators of leaf water status, the ability to adjust cell turgor and leaf hydraulic parameters could also ensure that leaves continue to photosynthesize under progressively drier conditions.

While some studies have shown that K_{LEAF} changes in response to water availability (Brodribb & Holbrook, 2003; Johnson et al., 2009), few studies have addressed how changes in the vulnerability of K_{LEAF} to hydraulic dysfunction may co-occur with shifts in leaf osmotic/turgor parameters during decreasing soil water availability. Martorell et al. (2015) found leaf resistance to hydraulic dysfunction increased and that leaf turgor loss point (Ψ_{TLP} , leaf water potential at turgor loss) and osmotic potentials became more negative in cultivars of *Vitis vinifera* throughout the summer as water potentials became more negative. Another recent study found strong relationships between Ψ_{TLP} , osmotic potential at full turgor, and degree of iso/anisohydry across multiple species (Meinzer et al., 2016), demonstrating the potential influence that these synchronous changes may have during drought periods. A few studies have individually shown changes to leaf osmotic/turgor parameters in response to soil drying. For example, Maréchaux, Bartlett, Iribar, Sack, and Chave (2017) observed seasonal adjustment in Ψ_{TLP} between wet and dry seasons in tropical lianas and Binks et al. (2016) observed leaf-level osmotic adjustments in response to long-term drought treatments. Meinzer, Woodruff, Marias, McCulloh, and Sevanto (2014) observed that an anisohydric species (a species that allows leaf water potential [Ψ_{LEAF}] to decline with declining soil water potential) adjusted its Ψ_{TLP} and osmotic potential with seasonal drying but that a co-occurring isohydric species (a species that regulates minimum leaf water potential much more strictly through stomatal closure) did not adjust these parameters. Meinzer et al. (2014) hypothesized that anisohydric species, in general, have to be able to adjust Ψ_{TLP} and osmotic potentials to compensate for their relatively limited stomatal control of Ψ_{LEAF} .

Shifts in leaf hydraulic function may be particularly important or adaptive in areas that experience extreme variation in soil moisture conditions. Vegetation in semi-arid regions, such as our study sites in central Texas, USA, is predicted to be severely impacted by major drought events relative to other community types (Ma, Huete, Moran, Ponce-Campos, & Eamus, 2015). Plants in semi-arid and

arid habitats typically experience large fluctuations in the amount of available moisture over spring and summer (e.g. Bailey, 1979). Relatively anisohydric species that inhabit these areas are therefore likely to experience Ψ_{LEAF} values that range from near zero to highly negative in the same season, while more isohydric species will avoid highly negative Ψ_{LEAF} due to stomatal closure during drier periods. One strategy for more anisohydric plants to maintain turgor under drying soils would be to have highly negative osmotic potentials and turgor loss points, but this would require investment in high concentrations of compatible solutes. Similarly, making K_{LEAF} resistant to hydraulic dysfunction would require investment in xylem with thick cell walls and/or small diameter lumens (Blackman, Brodribb, & Jordan, 2010; Domec, Palmroth, & Oren, 2016), where thicker cell walls require greater carbon investment and smaller diameter lumens are less conductive than wider ones (Sperry, Hacke, & Pittermann, 2006). Additionally, making K_{LEAF} resistant to hydraulic dysfunction would require changes in the water pathway outside the vein xylem (Scoffoni et al., 2014, 2017) and may include changes in membrane properties and/or aquaporin activity.

This study examined how K_{LEAF} and leaf osmotic and turgor loss parameters varied throughout the spring and summer in a semi-arid woodlands ecosystem of central Texas, USA. Four species were selected that comprise c. 94% of the vegetation cover (Johnson, Domec, et al., 2018; Moore et al., 2016; Schwantes et al. 2017) and are known to have contrasting stomatal strategies along the anisohydric/isohydric spectrum. For example, different predawn minimum water potentials have been observed in several of the common species of this region during dry parts of the summer (Kukowski, Schwinning, & Schwartz, 2013). We used the hydroscape framework of Meinzer et al. (2016) for determination of a species' degree of iso/anisohydry. We hypothesized that as soils dry over the course of the summer (1) species with larger hydroscape areas (i.e. more anisohydric) would exhibit large shifts in leaf turgor loss and osmotic potentials relative to species with smaller hydroscape areas (i.e. more isohydric); and (2) species with larger hydroscape areas would adjust their resistance to leaf hydraulic dysfunction.

2 | MATERIALS AND METHODS

The study site was located in the Edwards Plateau region (west-central Texas) in Colorado Bend State Park near Bend, TX (31.0451°N, 98.4762°W). This site has karst topography with shallow soils (typically less than 20 cm) with underlying fractured limestone (see Auken, Ford, Stein, & Stein, 1980; Brown, Stafford, Shaw-Faulkner, & Grubbs, 2011 for more detailed site descriptions). The area is considered semi-arid (based on the methods of Zomer et al., 2007; Zomer, Trabucco, Bossio, van Straaten, & Verchot, 2008) and has a mean annual temperature of 19.5°C and a mean annual precipitation of 702 mm, which is unevenly distributed in many years with the majority occurring in the spring, fall, and winter months (see Johnson, Sherrard, Domec, & Jackson, 2014 for example). The ecosystem is characterized by open savanna-like woodlands, and the dominant woody species are

Diospyros texana Scheele, *Juniperus ashei* J. Buchholz, *Prosopis glandulosa* Torr. and *Quercus fusiformis* Small.

This study was conducted from April through September of 2016. Ten individuals of *D. texana*, *J. ashei*, *P. glandulosa*, and *Q. fusiformis* were identified and tagged. These individuals were used for all physiological measurements with each set of measurements (e.g. water potential measurements) being performed on randomly selected individuals within the ten selected trees. All measurements were made on fully expanded leaves. Meteorological data were obtained from an NOAA National Climatic Data Center station in Lampasas TX (31.106°N, 98.196°W; Figure S1).

2.1 | Water potential measurements

Leaf water potential measurements were performed at predawn (5.00–6.00 local time) and mid-afternoon (c. 15.00 local time) on fully sun-exposed south-facing shoots on May 13, May 14, June 18, June 19, July 23, July 24 and September 24, 2016. Leaf water potential (Ψ_{LEAF}) was measured using a pressure chamber (PMS Instruments, Albany, OR, USA) on three to four individuals per species. Additionally, we had previously measured predawn and mid-day water potentials in the same species as part of field campaigns in 2013 and 2015, and those measurements were included in the hydroscape area calculations. About half of the water potential measurements from 2013 came from a nearby field site (Powell's cave site near Menard, TX, 30.918°N, 99.787°W, see Jackson, Moore, Hoffmann, Pockman, & Linder, 1999; McElrone, Pockman, Martinez-Vilalta, & Jackson, 2004). The other 2013 measurements and all 2015 measurements came from the same field site as used in 2016 (Colorado Bend site). Water potentials were averaged within month and site.

2.2 | K_{LEAF} and pressure–volume curves

For constructing K_{LEAF} and pressure–volume (P–V) curves, six branch samples (one per tree from six trees) were collected prior to dawn for each species on monthly sampling dates (May 14, June 19, July 24, and September 24, 2016). Branch samples of c. 30 cm were clipped and immediately placed in plastic bags with wet paper towels and put into a cooler. P–V curves and leaf hydraulic conductance were measured on these samples either the same day or shipped overnight to the laboratory where measurements began the following day. K_{LEAF} ($\text{mmol m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$) was determined, using a timed rehydration method described in Brodribb and Holbrook (2003), which is based on an analogy between rehydrating a leaf and discharging a capacitor:

$$K_{\text{LEAF}} = C_{\text{leaf}} \ln(\psi_0/\psi_f)/t, \quad (1)$$

where C_{leaf} = capacitance ($\text{mmol m}^{-2} \text{MPa}^{-1}$), Ψ_0 = leaf water potential prior to partial rehydration (MPa), Ψ_f = leaf water potential after partial rehydration, and t = duration of rehydration (s). For measurement of K_{LEAF} , sampled branches were rehydrated with distilled water until Ψ_{LEAF} was close to -0.5 MPa (c. 1 hr) and/or placed on the lab bench to dry for different amounts of time to reach a range of leaf water potentials. Branches were then bagged, placed in the

dark and allowed to equilibrate for at least 2 hr. Leaves (*Prosopis* and *Quercus*) or shoot tips (c. 3 cm in length; *Diospyros* and *Juniperus*) were then excised for determination of Ψ_0 . Leaves or shoot tips from the same branch were rehydrated for a period of t (ranging from 10 to 60 s), and Ψ_f was measured. Leaf water potential was measured using a pressure chamber. Leaf P_{50} was determined as the water potential corresponding to 50% of maximum leaf hydraulic conductance (see Section 2.3). K_{LEAF} curves were constructed using 25–98 leaves per species for each month (see Figure S3) and maximum K_{LEAF} was determined by calculating a mean of the five largest K_{LEAF} values for each month and species.

Five to six leaves of each species were used to construct P–V curves. P–V curve measurements were conducted on individual leaves or shoot tips, as above. To prevent artefacts, samples were not rehydrated (see Meinzer, Sharifi, Nilsen, & Rundel, 1988; Meinzer et al., 2014). The curves were created by plotting the inverse of Ψ_{LEAF} against relative water content (RWC, %), obtained from repeated determinations of fresh mass and Ψ_{LEAF} during slow dehydration of the shoot tip or leaf on the laboratory bench until values of Ψ_{LEAF} neared -4.0 MPa. For normalizing C on a leaf area basis, leaf areas for all species except *Juniperus* were obtained by scanning and measuring one-sided leaf area in ImageJ (Schindelin, Rueden, Hiner, & Eliceiri, 2015). For *Juniperus*, leaf area was calculated as the surface area of a network composed of cylindrical segments, which was obtained by multiplying the silhouette area (also from ImageJ) by π .

Leaf capacitance ($\text{mmol m}^{-2} \text{MPa}^{-1}$), osmotic potential at full turgor ($\Psi_{\pi 100}$, MPa), and water potential at leaf turgor loss point (Ψ_{TLP} , MPa) were estimated from P–V curves (Scholander, Hammel, Bradstreet, & Hemmington, 1965; Tyree & Hammel, 1972). The Ψ_{LEAF} corresponding to turgor loss was estimated as the point where the plot of $1/\Psi_{\text{LEAF}}$ vs RWC becomes linear. The slope of the quasilinear relationship prior to, and following turgor-loss provided C_{leaf} in terms of RWC (C_{RWC}) for pre-turgor loss and post-turgor loss respectively. The osmotic potential at full turgor was taken as the y-intercept of a line fitted to the post-turgor loss data for a plot of $1/\Psi_{\text{LEAF}}$ vs. $100 - \text{RWC}$. The bulk tissue modulus of elasticity (ϵ , MPa) was estimated as the slope of the relationship between turgor pressure (the difference between the osmotic potential line fitted to the post-turgor loss data as above and the water potential curve) and RWC (as in Meinzer et al., 2014). Leaf mass per unit area (LMA, g/m^2) was calculated as:

$$\text{LMA} = \text{DM}/\text{LA}, \quad (2)$$

where DM is the leaf dry mass and LA is the leaf area.

Hydroscape areas capture the predawn to midday $\Delta\Psi_{\text{LEAF}}$ integrated across the range of soil moisture favourable for photosynthesis. Hydroscape areas were determined in a similar fashion to Meinzer et al. (2016) with the exception that we defined the lower boundary as the convex hull containing observed mean water potentials rather than as the linear regression through these water potentials (see Figure 1). Furthermore, the boundaries of the hydroscape were not extrapolated to predawn water potentials of zero nor to water potentials where predawn Ψ_{LEAF} equals midday Ψ_{LEAF} (i.e. intersection with the 1:1 line).

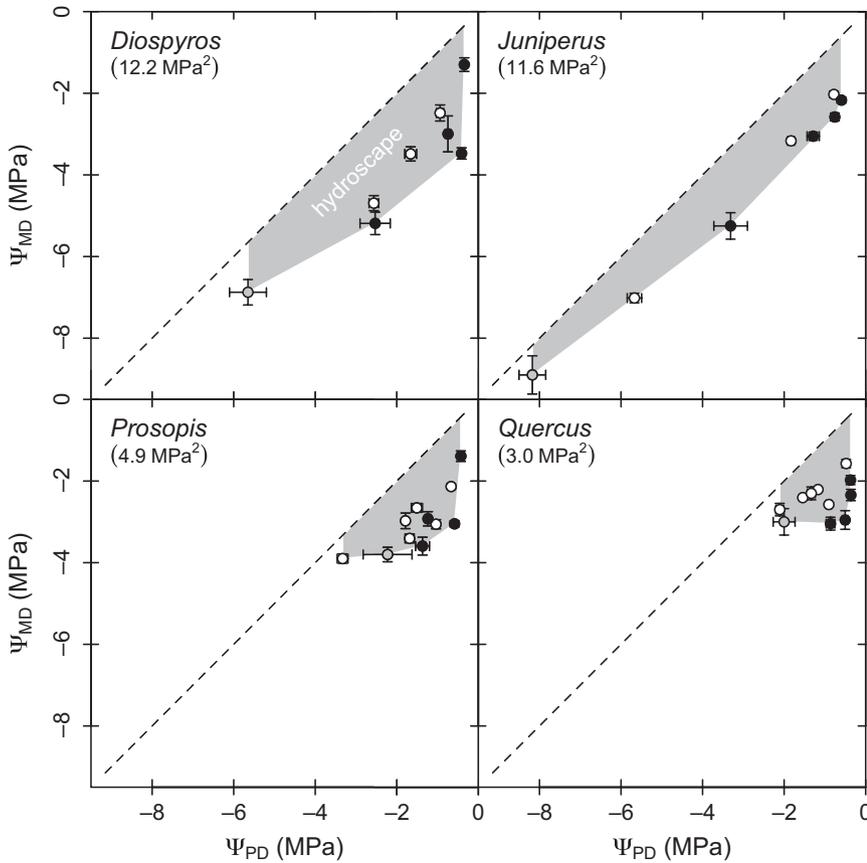


FIGURE 1 Mean mid-day (MD) vs. predawn (PD) leaf water potentials (from 2013 [open symbols], 2015 [grey symbols], and 2016 [black symbols]; see Section 2 for details) and fitted hydroscapic boundaries for four dominant woody species of the Texas Edwards Plateau: *Diospyros texana*, *Juniperus ashei*, *Prosopis glandulosa* and *Quercus fusiformis*. Numbers in parentheses are calculated hydroscapic areas. Error bars are SEs

These differences were because we were not able to observe this study species at predawn $\Psi_{\text{LEAF}} = \text{zero}$ or at predawn $\Psi_{\text{LEAF}} = \text{midday } \Psi_{\text{LEAF}}$. We considered this a conservative estimate of the hydroscapic area.

2.3 | Statistical analyses

For between-species and between-sampling date comparisons of physiological parameters, ANOVAs with post hoc Holm-Sidak comparisons were performed. ANOVA and post hoc tests were performed, using Sigmaplot 12.5 (Systat Software Inc., San Jose, CA, USA). Sigmoid models of the form: $y = y_0 + (a/(1 + e^{-[x-x_0/b]}))$ were fit to the K_{LEAF} data, and maximum K_{LEAF} was determined by averaging the five highest K_{LEAF} values per time period and species. Leaf resistance to leaf hydraulic dysfunction values (P_{50}) were considered significantly different if their 95% confidence intervals (confidence intervals from sigmoidal curve fits) did not overlap.

3 | RESULTS

Juniperus and *Diospyros* had much greater hydroscapic areas (12.2 and 11.6 MPa^2 , respectively) than either *Prosopis* or *Quercus* (4.9 and 3.0 MPa^2 , respectively; Figure 1). *Juniperus* and *Diospyros* experienced predawn and midday Ψ_{LEAF} that were 1–2.5 MPa more negative than *Quercus* and *Prosopis* (Figures 1 and S2; $p < .001$). Turgor loss points were more negative in July in *Diospyros* and *Juniperus* than in *Quercus*

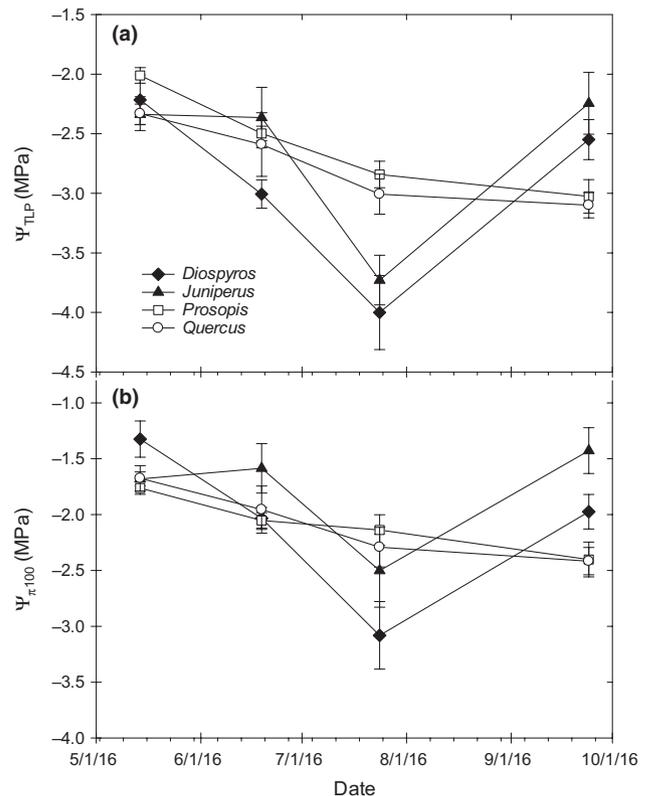


FIGURE 2 Pressure–volume curve parameters in *Diospyros texana*, *Juniperus ashei*, *Prosopis glandulosa* and *Quercus fusiformis*: (a) water potential at turgor loss (turgor loss point, Ψ_{TLP}) and (b) osmotic potential at full turgor ($\Psi_{\pi,100}$). Error bars are SEs

and *Prosopis* (Figure 2a, all p values < .05). Turgor loss points in *Diospyros* and *Juniperus* increased by 1.4–1.5 MPa between July and September ($p < .001$ for both comparisons). In July, osmotic potentials at full turgor were significantly more negative in *Diospyros* than in either *Prosopis* (Figure 2b; $p < .001$) or *Quercus* ($p = .007$). Osmotic potential at full turgor increased by 1.1 MPa in both *Diospyros* and *Juniperus* between July and September ($p < .001$ for both comparisons). In contrast to the patterns observed in *Diospyros* and *Juniperus*, Ψ_{TLP} and $\Psi_{\pi 100}$ decreased linearly in *Prosopis* and *Quercus* between May and September. However, this decrease in $\Psi_{\pi 100}$ was only significant for *Quercus* (May vs. September comparison $p = .023$) but the decrease in Ψ_{TLP} was significant in both *Prosopis* and *Quercus* ($p = .005$ and $.028$, respectively). There were no significant changes in ϵ over the measurement period for *Quercus* and *Juniperus* ($p = .945$ and $.944$, respectively), but ϵ significantly decreased in *Prosopis* ($p = .018$) and increased in *Diospyros* ($p = .004$) between May and September (Figure 3a). There were no differences in LMA between species in May but by July LMA was 1.6–1.9 \times greater in *Diospyros* than the other species ($p < .001$ for all comparisons; Figure 3b). At the end of the study (September), there were no significant differences in LMA between species.

Maximum K_{LEAF} was highly variable in *Quercus*, ranging from $35.5 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ in May to $11.3 \text{ mmol m}^{-2} \text{ s}^{-1} \text{ MPa}^{-1}$ in September (Figure 4, $p < .001$). The variation in maximum K_{LEAF} across the measurement period was less pronounced in the other

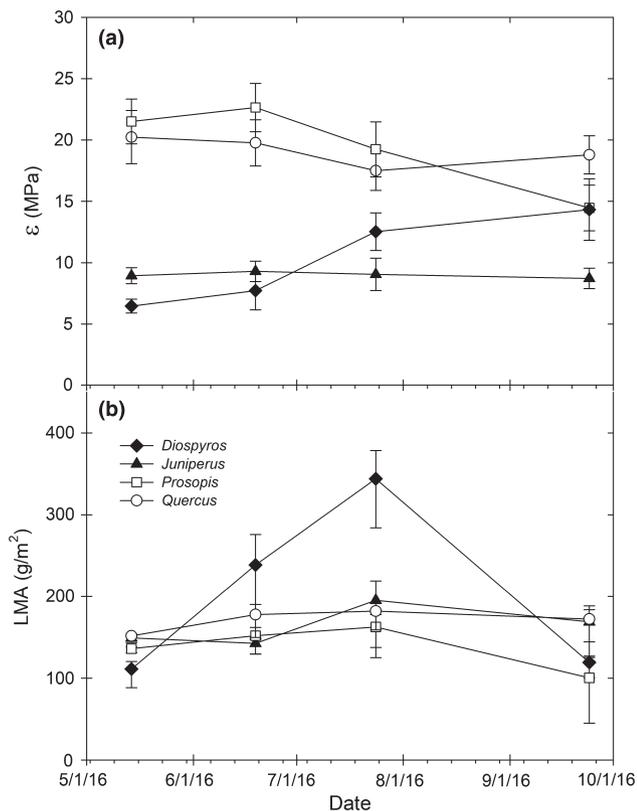


FIGURE 3 Pressure–volume curve parameters in *Diospyros texana*, *Juniperus ashei*, *Prosopis glandulosa* and *Quercus fusiformis*: (a) bulk tissue modulus of elasticity (ϵ) and (b) leaf mass per unit area (LMA). Error bars are SEs

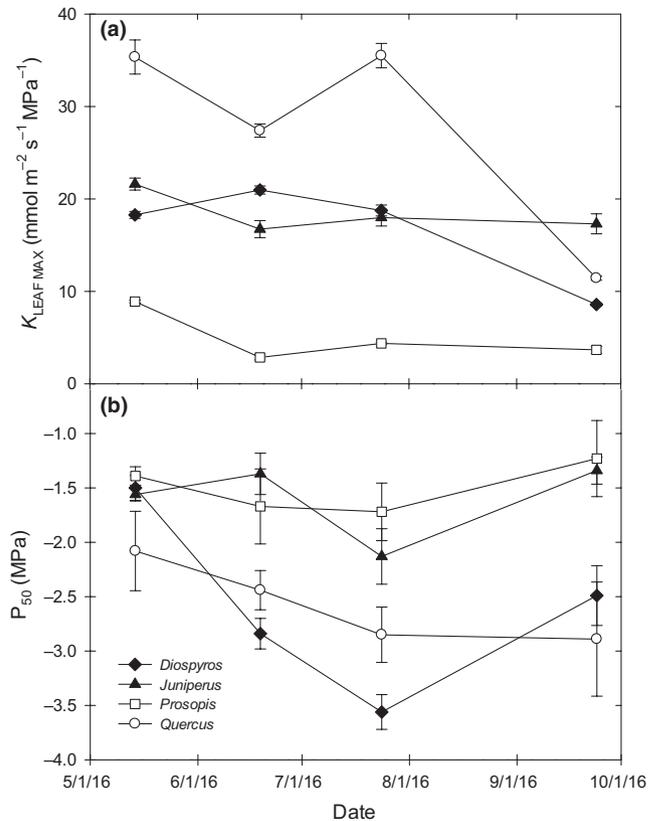


FIGURE 4 Maximum leaf hydraulic conductance (a, K_{LEAF}) and the water potential at which K_{LEAF} declined by 50% (b, leaf P_{50}) in *Diospyros texana*, *Juniperus ashei*, *Prosopis glandulosa* and *Quercus fusiformis*. Error bars in panel a are SEs and error bars in panel b are 95% confidence intervals

species; however, there were still differences across the measurement periods. In both *Juniperus* and *Prosopis*, K_{LEAF} was greater in May than in any other months (p from < .001 to .007); and in *Diospyros*, K_{LEAF} was lowest in September compared to other months ($p < .001$). Different species also had different trends in leaf P_{50} values measured across the season. In both *Juniperus* and *Quercus*, P_{50} was more negative in July than in the other months (except in *Quercus*, September was not significantly different from July). *Diospyros*' P_{50} declined from -1.5 MPa in May to -2.8 MPa in June, to -3.6 MPa in July and then increased to -2.5 MPa in September. In *Prosopis*, there were no significant changes in P_{50} across the measurement period. All species were predicted to lose near 100% of K_{LEAF} in the driest part of the season except *Quercus* which was predicted to lose 57%.

All species had predawn leaf water potentials that were less negative than their Ψ_{TLP} (Figure 5; except *Juniperus* in July). However, only *Quercus* maintained midday Ψ_{LEAF} less negative or the same as leaf Ψ_{TLP} . All other species experienced midday Ψ_{LEAF} that was more negative than Ψ_{TLP} , especially in July. *Diospyros* had the greatest seasonal range in Ψ_{TLP} (1.8 MPa), $\Psi_{\pi 100}$ (1.8 MPa), and leaf P_{50} (2.1 MPa; Figure 7). *Juniperus* also had large seasonal ranges in Ψ_{TLP} (1.5 MPa) and $\Psi_{\pi 100}$ (1.1 MPa), but less range in leaf P_{50} (0.75 MPa). *Quercus* and *Prosopis* had less variability in leaf hydraulic properties than the

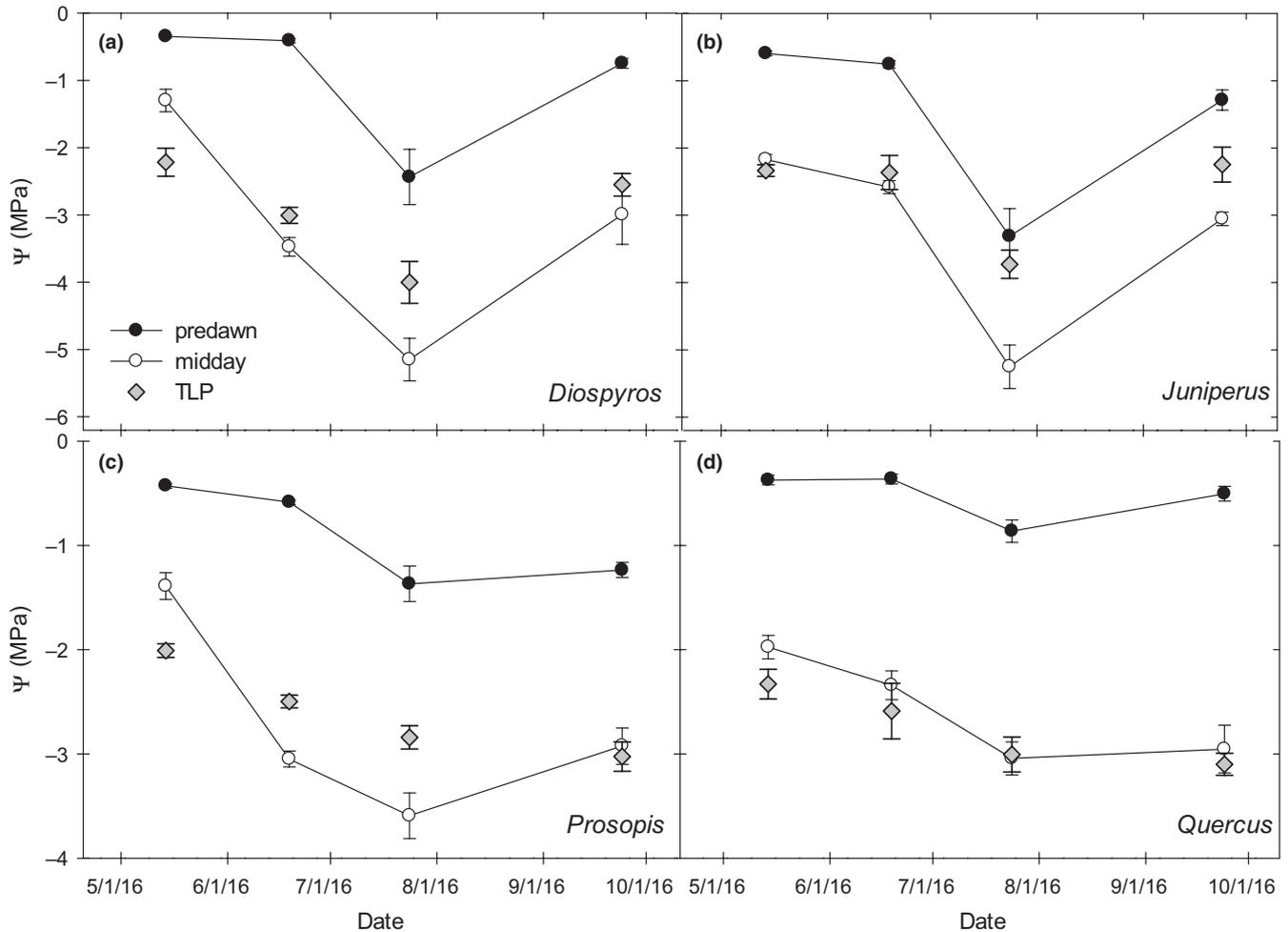


FIGURE 5 Mean predawn (Ψ_{PD}) and midday (Ψ_{MD}) leaf water potentials and leaf turgor loss points (TLP) in *Diospyros* (a), *Juniperus* (b), *Prosopis* (c), and *Quercus* (d). Error bars are SEs

other two species; seasonal range in Ψ_{TLP} , $\Psi_{\pi 100}$, and leaf P_{50} varied by 0.5–1.0 MPa across the season in *Quercus* and *Prosopis* (Figure 6).

There were strong correlations between leaf hydraulic parameters when all data were combined (Figure 7). The positive relationship between Ψ_{TLP} and $\Psi_{\pi 100}$ was particularly strong ($r^2 = .85$), as was the negative relationship between P_{50} and LMA ($r^2 = .58$). Somewhat less strong, but still significant were correlations between LMA and $\Psi_{\pi 100}$ ($r^2 = .39$), LMA and Ψ_{TLP} ($r^2 = .50$), P_{50} and $\Psi_{\pi 100}$ ($r^2 = .45$), and P_{50} and Ψ_{TLP} ($r^2 = .46$).

4 | DISCUSSION

This study tested whether strategies for regulating water balance (anisohydric/isohydric) were related to seasonal shifts of leaf P–V parameters and leaf vulnerability to hydraulic dysfunction within a semi-arid central Texas ecosystem. To our knowledge, this is the first study demonstrating unique shifts in leaf biophysical and hydraulic parameters across a summer and across the dominant woody species of an ecosystem. The observed patterns in Ψ_{LEAF} , Ψ_{TLP} , and $\Psi_{\pi 100}$ supported our first hypothesis. Species that were more anisohydric (larger

hydroscape areas) had the most plasticity in leaf P–V parameters. We also found evidence that supported our second hypothesis because the species that experienced the widest range of Ψ_{LEAF} altered significantly their resistance to leaf hydraulic dysfunction during the driest part of the summer.

Due to extreme variability in rainfall in arid and semi-arid habitats, these species must produce tissue that can respond to wide ranges of Ψ_{LEAF} . New leaf tissue is typically produced in spring when moisture is abundant. But in many semi-arid habitats, such as the one in this study, hot, dry summers resulting in depletion of soil moisture often occur even during years not considered “drought years” (e.g. Kukowski et al., 2013). Plants have evolved different strategies for dealing with this range of soil moistures. For example, plants exist along a continuum of stomatal regulation of leaf water status: some plants close stomata at set Ψ_{LEAF} values, while others allow their Ψ_{LEAF} to decrease with declining soil moisture (Martínez-Vilalta, Poyatos, Aguadé, Retana, & Mencuccini, 2014; Meinzer et al., 2014, 2016; Tardieu & Simonneau, 1998). In central Texas, *Juniperus* and *Prosopis* have more anisohydric characteristics and thus, larger hydroscales, while *Diospyros* and *Quercus* are more isohydric (Figure 1). During dry periods, more isohydric plants risk carbon imbalances due to lack of photosynthesis,

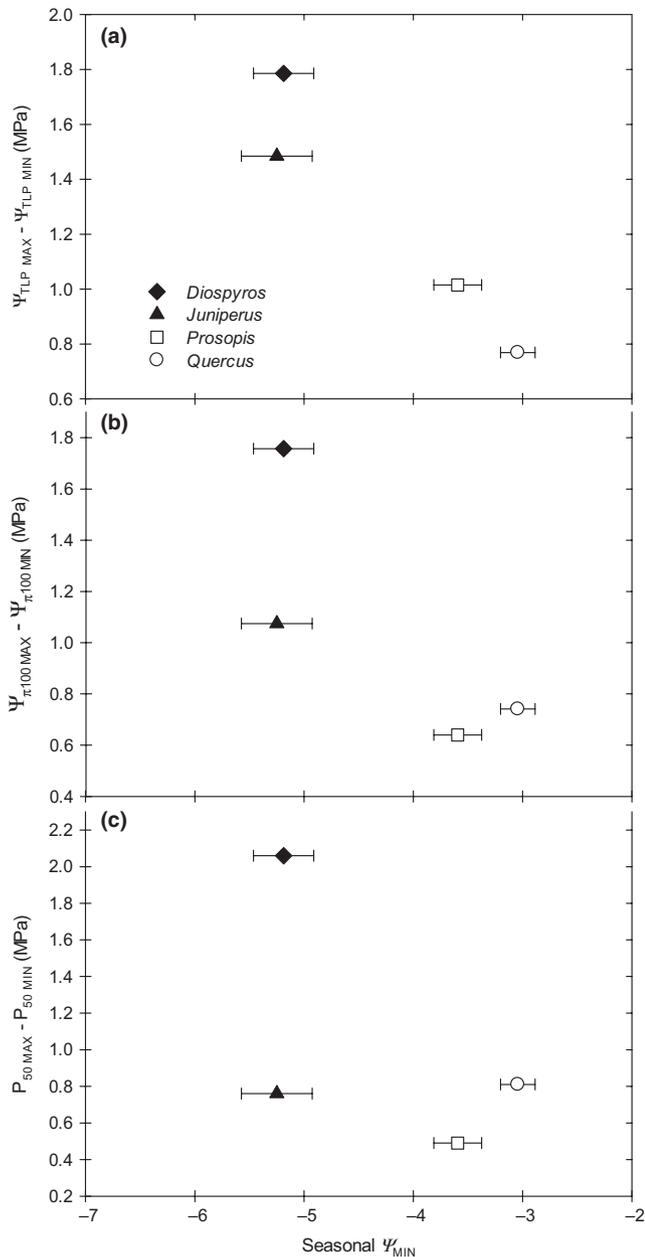


FIGURE 6 Variation in leaf hydraulic parameters in each species: maximum observed turgor loss points (TLP)–minimum observed TLP (a), maximum observed π_{100} –minimum observed TLP π_{100} (b), and maximum observed P_{50} –minimum observed P_{50} (c). All y-axis data were plotted against the seasonal minimum water potential for each species. Error bars are SEs

while anisohydric plants risk hydraulic dysfunction (McDowell, 2011; Sevanto, McDowell, Dickman, Pangle, & Pockman, 2014).

Although stomatal closure to maintain leaf water potentials has large and obvious impacts on leaf physiological processes, changes in leaf biophysical properties can also allow for maintenance of physiological functioning during soil moisture depletion. In particular, more negative Ψ_{TLP} and $\Psi_{\pi100}$ and greater ϵ can maintain leaf physiology by maintaining protoplast volume and turgor as Ψ_{LEAF} become more negative (Kaiser, 1982; Marshall &

Dumbroff, 1999; Saito & Terashima, 2004), thus extending photosynthesis with drying soils. We hypothesized that species with larger hydroscares would be able to be more plastic and adjust leaf biophysical properties more readily than species with smaller hydroscares. The data presented here support observations in the *Pinus edulis/J. monosperma* woodlands of New Mexico USA. There, the more anisohydric *J. monosperma* had more negative Ψ_{TLP} with decreasing water availability, but Ψ_{TLP} in the more isohydric *P. edulis* did not change (Meinzer et al., 2014). Additionally, in *Larrea tridentata*, a strongly anisohydric desert shrub, Ψ_{TLP} was observed to change by as much as 2 MPa over short time periods (Meinzer et al., 1988). Another recent study found that a more anisohydric species (*Acacia aptaneura*) adjusted Ψ_{TLP} during drought cycles but a more isohydric species (*Eucalyptus camaldulensis*) did not (Nolan et al., 2017). In this study, the more anisohydric *Diospyros* and *Juniperus* experienced the most negative Ψ_{LEAF} (and the widest range of Ψ_{LEAF}) and had more negative Ψ_{TLP} and $\Psi_{\pi100}$ values than *Quercus* and *Prosopis*, which experienced much smaller ranges and less negative Ψ_{LEAF} . Additionally, LMA in *Diospyros* increased nearly three-fold from May to July and then decreased by the same amount by September. This threefold increase and decrease in LMA is typically observed between leaf-out in the spring, mid-summer and fall senescence (Reich, Walters, & Ellsworth, 1991) but in this study all leaves were fully hardened in May and were not senescent in September. Meinzer et al. (2014) hypothesized that anisohydric species, in general, may have a greater capacity to alter leaf biophysical properties than more isohydric species, and our data support this hypothesis. In the anisohydric species in this study, we observed decreases in Ψ_{TLP} and $\Psi_{\pi100}$ during the driest parts of the summer and increases after soil moisture increased due to rainfall. Further, Meinzer et al. (2016) also demonstrated that Ψ_{TLP} and $\Psi_{\pi100}$ were strongly correlated with a species' degree of isohydry and suggested that these parameters could be used as proxies for a species' location along the isohydry/anisohydry continuum. Our results support this idea, as *Juniperus* and *Diospyros* had both the most negative Ψ_{LEAF} and the greatest adjustment in Ψ_{TLP} with drying soils. Although, our results also highlight the importance of comparing species' relative degree of isohydry during periods of seasonal minimum soil water status.

Surprisingly, all species in this study except *Quercus* experienced afternoon Ψ_{LEAF} values that were more negative than their Ψ_{TLP} . In fact, recent studies have suggested that Ψ_{LEAF} less negative than those associated with turgor loss should result in stomatal closure and loss of leaf hydraulic conductance, thus preventing the loss of turgor (Bartlett, Klein, Jansen, Choat, & Sack, 2016; Scoffoni & Sack, 2017). One likely effect of turgor loss would be for mesophyll cells to shrink and become photosynthetically inactive or inhibited in the afternoon. Reductions in turgor are also likely to be at least partially responsible for the observed decline in photosynthesis with Ψ_{LEAF} that occurs independent of stomatal closure (Lawlor & Tezara, 2009; Tezara, Mitchell, Driscoll, & Lawlor, 1999). Overall, evidence that plants may often surpass Ψ_{TLP} suggests that a re-evaluation of the physiological significance of this parameter is needed.

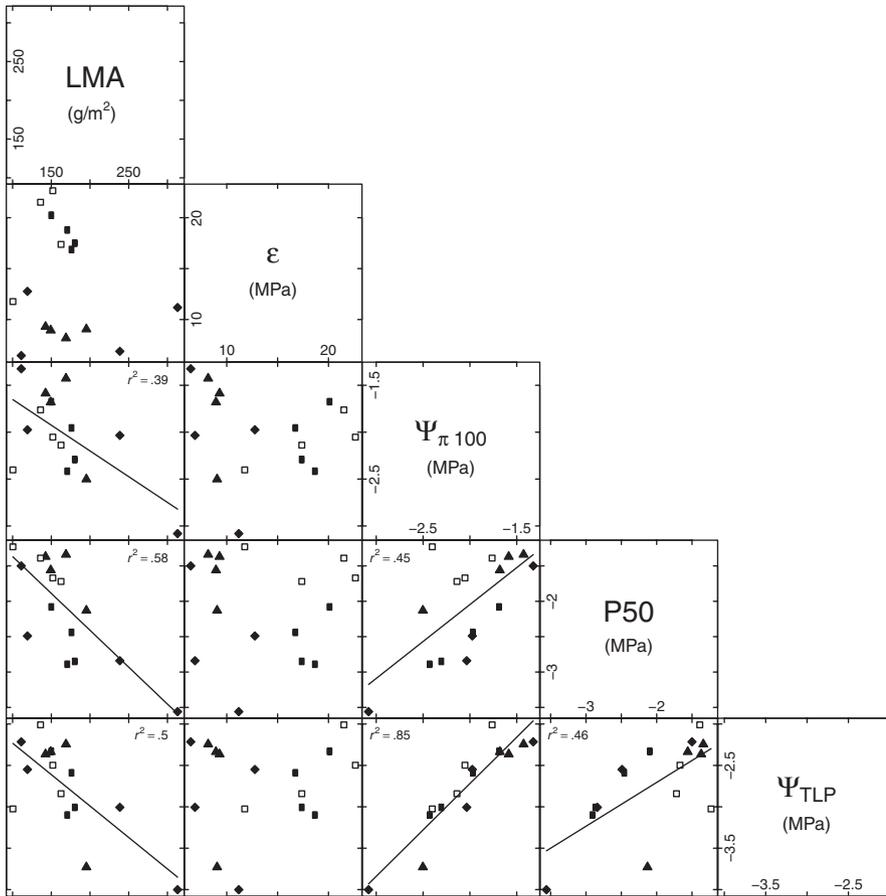


FIGURE 7 Correlation analysis of all leaf mass per unit area (LMA), bulk tissue modulus of elasticity (ϵ), osmotic potential at full turgor ($\Psi_{\pi 100}$), water potential at 50% loss of K_{LEAF} (P_{50}) and water potential at turgor loss (turgor loss point, Ψ_{TLP}) data. Symbols for each species are the same as in previous figures. Only significant ($p < .05$) relationships are shown with fitted lines

In addition to changes in leaf biophysical properties, we also hypothesized that more anisohydric species would exhibit changes in their resistance to hydraulic dysfunction. Although seasonal changes in maximum leaf hydraulic conductance have been observed (Brodribb & Holbrook, 2003; Lo Gullo, Nardini, Trifilò, & Salleo, 2005), measurements of seasonal changes in resistance to leaf hydraulic dysfunction are rare in the literature. In a recent study, Martorell et al. (2015) observed more negative leaf P_{50} (along with more negative Ψ_{TLP} and $\Psi_{\pi 100}$) in *Vitis* subjected to decreasing water potentials. In this study, *Diospyros* and *Juniperus* had more negative leaf P_{50} during July than either June or September. Leaf P_{50} in *Quercus* did decline seasonally, but it appeared to be a nearly linear decline and not a response to reduced soil moisture availability in July. Interestingly, seasonal changes in Ψ_{TLP} and $\Psi_{\pi 100}$ in *Quercus* (as well as *Prosopis*) were very similar in shape to their seasonal changes in leaf P_{50} . Due to leaf xylem development occurring early in the year, these changes in leaf P_{50} were likely due to changes in the water pathways outside the leaf xylem (Buckley, 2015; Scoffoni, 2015). The negative relationship between leaf P_{50} and LMA (Figure 7) supports this idea because increased LMA after leaves have hardened must come from additional chemical inputs to mesophyll tissue since veins have already formed. However, there could also be cellular changes in the mesophyll (e.g. alteration of cell walls) that could result in this relationship but were not accounted for here.

In this study, the more anisohydric species (larger hydroscape areas) altered leaf Ψ_{TLP} , $\Psi_{\pi 100}$, and resistance to leaf hydraulic

dysfunction with declining leaf water potentials, whereas the more isohydric species did not. One exception was in *Quercus* where July leaf P_{50} was significantly more negative than in May. Decline of K_{LEAF} with declining Ψ_{LEAF} may be the consequence of leaf vein xylem embolism (Brodribb et al., 2016; Johnson, McCulloh, Meinzer, & Woodruff, 2012; Nardini, Salleo, & Raimondo, 2003; Nardini, Tyree, & Salleo, 2001) but also bundle sheath and mesophyll cells losing turgor and shrinking, thus mechanically increasing resistance to water flow (Brodribb & Holbrook, 2004; Scoffoni et al., 2017). The concept of a turgor-limited passage through the bundle sheath and mesophyll is supported by the correlations between the point of turgor loss and K_{LEAF} (Brodribb & Holbrook, 2003; Domec et al., 2009, 2016; Woodruff, McCulloh, Warren, Meinzer, & Lachenbruch, 2007). These leaf-level adjustments have significant implications for ecosystems with increasing exposure to frequent and severe droughts. At present, it is unclear how common these leaf-level adjustments are in habitats with limited soil moisture or during droughts. As more severe droughts become an ever-present reality for many ecosystems, studies need to further consider species-specific abilities to modify physiology. Plant responses to soil drying are complex and require an integrated understanding of seasonal variation in hydraulic functioning. A better understanding of the plasticity of leaf hydraulic parameters during periods of limited soil moisture availability will lead to better predictions of tree physiological processes under scenarios of increasing drought severity and frequency.

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AUTHORS' CONTRIBUTIONS

D.M.J., Z.C.B., D.D.S., K.A.M. and J.-C.D. designed the study; D.M.J., Z.C.B., D.D.S., K.A.M., K.V.B. and J.-C.D. performed the data collection and analysis; D.M.J., Z.C.B., D.D.S., K.A.M., K.V.B. and J.-C.D. all participated in writing the manuscript.

DATA ACCESSIBILITY

All data from the study are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.vb188> (Johnson, Berry, et al., 2018).

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