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RESEARCH ARTICLE

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Cavitation-resistant junipers cease transpiration earlier than cavitation-vulnerable oaks under summer dry conditions

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Abstract

Ashe juniper (*Juniperus ashei* Buchholz) and escarpment live oak (*Quercus fusiformis* Small) are two of the most common woody species of the Edwards Plateau, an arid-to-semi-arid region of nearly 100,000 km^2 in central Texas. They have very different hydraulic strategies, yet they experienced similar mortality rates during an extreme drought in 2011. We measured *J. ashei* and *Q. fusiformis* sap flow velocities during summer dry periods of 2016 and 2017 at six micro-sites. Although these were years with more-or-less average summer conditions, both included significant dry periods. To estimate the relative rate of decrease in sap velocity for each species during the dry periods, we fit a Bayesian exponential decay model to the sap velocity time series for each tree. We found that *Q. fusiformis* trees were better able to maintain transpiration than *J. ashei* during dry periods at five micro-sites and were comparable at the sixth micro-site. We conclude that it is likely that *Q. fusiformis* can better maintain transpiration during dry periods than *J. ashei*, on average, and that in the case of these two species, greater cavitation resistance may not translate to greater drought resistance.

KEYWORDS
Bayesian, drought resistance, Juniperus, Quercus, sap flow, transpiration, trees

1 | INTRODUCTION

Tree species vary in their ability to acquire water and in their physiological responses to water stress, and species with very different hydraulic strategies frequently coexist (van der Molen et al., 2011). Strategies for drought-resistance include “drought-tolerance,” or the ability to survive despite low water potentials, and “drought-avoidance,” or the ability to avoid low water potentials by maximizing water uptake and/or minimizing water loss (Polle et al., 2019; Touchette et al., 2007). Tactics conducive to drought-tolerance include osmotic adjustment to maintain turgor pressure and increased cell-wall thickness, while drought-avoidance might be achieved by growing deep roots, closing stomata, or dropping leaves during times of drought. The specific hydraulic strategies that a tree employs may increase or decrease vulnerability to the perils of drought, which include reduced carbon fixation (potentially leading to overtopping or carbon starvation) and the formation of air embolisms in the xylem (also called “cavitation”; potentially leading to temporary or permanent hydraulic failure) (Adams et al., 2017; McDowell et al., 2008).

The Edwards Plateau in Central Texas is expected become hotter and drier under climate change (Gutzler & Robbins, 2011; Venkataraman et al., 2016), which will likely affect species ranges and survival, yet the relative vulnerability of regional tree species to drought stress remains unresolved. Here, we consider the hydraulic strategies of two of the most common woody species of the Edwards Plateau ecoregion, *Juniperus ashei* J. Buchholz (“Ashe juniper”) and *Quercus fusiformis* Small (“escarpment live oak”), which coexist in many landscapes of the Edwards Plateau. Each of them is the dominant canopy species in some landscapes, and they can also be codominant (Elliott et al., 2009-2014). The native ranges of both populations are concentrated on the Edwards Plateau in the United States (Kartesz, 2015) and also extend southward into Mexico.

J. ashei and *Q. fusiformis* have different strategies for coping with water stress. Gymnosperms, such as *J. ashei*, are thought to be generally less vulnerable to cavitation than angiosperms, owing to their lack of large vessels combined with the presence of specialized pit membranes that prevent embolism spread (Delzon et al., 2010). Accordingly, the xylem in stems and roots of *J. ashei* have been found to be much more resistant to cavitation than that of *Q. fusiformis* (Johnson, Domec, et al., 2018; McElrone et al., 2004). The water potential associated with 50% loss of hydraulic conductivity (ψ_{50}) for branches of *J. ashei* has been estimated at a very low −13.1 MPa (Willson et al., 2008) while that of *Q. fusiformis* has been estimated at −1.8 MPa (Johnson, Domec, et al., 2018). Access to water via deep roots may also affect survival. The roots of both *J. ashei* and *Q. fusiformis* have been found to penetrate the epikarst (Heilman et al., 2014), but root samples from caves indicated that *Q. fusiformis* trees have much deeper root systems, consistently reaching to 18 m below the land surface; in contrast, *J. ashei* roots were found to reach to only 8 m below the land surface, and not consistently (Jackson et al., 1999). This implies that *Q. fusiformis* individuals may have access to water sources that *J. ashei* individuals do not, potentially allowing *Q. fusiformis* to avoid low xylem water potentials and drought-induced cavitation.

Evidence for a difference in the susceptibility of these two species to drought is mixed. Following the extreme drought of 2011, one study examined tree mortality in 30 plots on 16 properties spread across the southeastern Edwards Plateau, all of which contained *J. ashei* and 25 of which contained "live oak." This study found roughly equivalent mortality among individuals greater than 1 m high, with 18% of 3486 *J. ashei* stems versus 15% of 352 live oak stems dead (calculated as percent of stems with crown mortality less percent resprouting; Crouchet et al., 2019). Based on species ranges, the vast majority of the live oaks surveyed in this study should be *Q. fusiformis*, rather than *Q. virginiana* (Cavender-Bares et al., 2015; Elliott et al., 2009-2014). Another study, which looked at a large plot on the southeastern edge of the Edwards Plateau, found significantly greater mortality among *Q. fusiformis* than among *J. ashei*, with 34% of the 167 *Q. fusiformis* versus 6% of the 153 *J. ashei* succumbing to the 2011 drought (Kukowski et al., 2013). A third study that measured percent canopy cover loss along linear transects at four sites across the Edwards Plateau found 27% canopy cover loss in *J. ashei* versus 4% canopy cover loss in *Q. fusiformis* (Johnson, Domec, et al., 2018). The contrasting results of these studies support the ideas that the relative drought mortality between these two species is highly dependent on location and that in at least some locations, *Q. fusiformis* are less susceptible to drought than *J. ashei*.

Reports of differences in water use among these species during periods of water stress have also yielded mixed conclusions. Studies of leaf-level gas exchange during periods of water stress suggest that both *J. ashei* and *Q. fusiformis* regulate water loss by decreasing stomatal conductance by similar percentages (Owens & Schreiber, 1992; Bendevis et al., 2010; our interpretation of the charts showing their original results). However, Kukowski et al. (2013) found that during the exceptional drought summer of 2009, *Q. fusiformis* ceased transpiration in early June while *J. ashei* continued transpiring throughout the summer. The authors of that study suspected that the immediate area was constraining to root development, with no roots found in a cave beneath the site except at the entrance, implying that roots were limited to 5 m depth in the soil and bedrock. Their later survey at the same location during the 2011 drought found catastrophic *Q. fusiformis* mortality (34% for *Q. fusiformis* versus 6% for *J. ashei*), suggesting that *Q. fusiformis* may have trouble surviving drought when access to below-ground water is limited.

In order to deepen understanding of the hydraulic strategies of these two important species, we designed a study to compare relative rates of decline in their sap velocities during summer dry periods. Recognizing that the epikarst of the Edwards Plateau is nonuniform and that site-to-site differences may lead to differential success among the two species, we chose a variety of "micro-sites," each with two *J. ashei* and two *Q. fusiformis* growing in close proximity. This design allowed us to test the sap flow responses of the two species to changes in water availability throughout the summer while assuming their water access was similar at each micro-site, subject only to differences in their root architecture and root depth.

We hypothesize that on average, during normal summer dry periods, *Q. fusiformis* trees maintain higher levels of transpiration than *J. ashei*, relative to their non-stressed states. If this is indeed the case, it would support the argument that *Q. fusiformis* frequently have greater access to water than *J. ashei* in the same settings. In turn, this greater water access could explain its sometimes-lower drought mortality (Crouchet et al., 2019; Johnson, Domec, et al., 2018) despite its less-conservative hydraulic safety margins (Johnson, Domec, et al., 2018).

2 | METHODS

2.1 | Site descriptions

The Hill Country area of Central Texas, located at the eastern and southern edges of the Edwards Plateau, has a harsh summer dry season with long periods of little-to-no precipitation during the hottest part of the year, July–August. The soils in the area are very rocky, with the soil-rock matrix referred to as "regolith" (Woodruff & Wilding, 2008). The loose soil above the rocky layer tends to be shallow, just 10–30 cm, but the soil-rock matrix extends deeper, especially in sloped areas. Partially fractured limestone and dolomite bedrock lie beneath the regolith.

We conducted our study at two locations in Travis County, TX, at the eastern edge of the Edwards Plateau. Both locations were on private property west of Austin, with the 2016 location on Glen Rose limestone (at approximately 30.26° N, 97.94° W) and the 2017 location 15.0 km away on Edwards Limestone near Lady Bird Lake (at approximately 30.30° N, 97.79° W) (Bureau of Economic Geology, 2002 for the underlying geology). Lady Bird Lake is an artificial lake that was created by damming the Colorado River.

J. ashei and *Q. fusiformis* are the most abundant tree species at these locations. We aimed to study small groups of *J. ashei* and

Q. fusiformis growing so closely together that we could assume all trees had access to the same water resources, subject only to differences in their root architecture and root depth. At each location, we found three such sites, and at each site, we chose two *J. ashei* and two *Q. fusiformis* with adjacent or mingling canopies. We refer to these sites as "micro-sites" since they each consist of just four trees and to help differentiate them from the two "locations" of the study. All of the trees were at canopy level except for the 11.6-cm-diameter *J. ashei* at micro-site B. The locations of the micro-sites varied topographically, which may correspond to variation in water resources, although, due to the complexities of the epikarst, actual water availability at each micro-site was unknown. See Figure 1a for the relative locations of the sites. Table 1 contains descriptions of each micro-site. Soil depth above the rocky layer was measured by inserting a metal rod into the ground until it could not be pushed any further, and the average of 10 soil depth measurements at each micro-site is given. All soil depth measurements were taken by the same person.

Our study took place during the summers of 2016 and 2017. On the driest days of 2016 and 2017 that were included in the study, the U.S. Drought Monitor (National Drought Mitigation Center, 2009-2017) assigned drought levels "none" and "D1: moderate drought," respectively. Note that this is in contrast to the drought level D4 "exceptional drought" during the summers of 2009 (when the Kukowski et al., 2013, sap flow study took place) and 2011 (during and after which the Kukowski et al., 2013, Johnson, Domec, et al., 2018, and Crouchet et al., 2019, mortality studies took place).

2.2 | Tree species

J. ashei is an evergreen gymnosperm with scale-like leaves and small, berry-like female cones. Since European settlement, its density has increased greatly in Central Texas, to the extent that it sometimes crowds out other native species (Fowler & Simmons, 2009; Van Auken, 1993). This population increase was likely aided by fire suppression and its unpalatability to cattle and ungulates. There has been concern that *J. ashei* might use an outsized portion of rainwater, impairing recharge of the local aquifers which are important drinking water sources (Afinowicz et al., 2005; Hamilton & Ueckert, 2004). Because of this concern, and because of its tendency to crowd pastures, ranchers often spend significant amounts of money to remove *J. ashei* from their properties, often by digging it up by the roots. The female cones ("juniper berries") are palatable to birds, which aid its dispersal (Adams et al., 2020).

Q. fusiformis, formerly *Q. virginiana* var. *fusiformis* (Small) Sarg, is an angiosperm that is semi-evergreen, meaning that it drops all or most of its leaves for a short period every spring. Its xylem has been classified variously as diffuse-porous (Williams, 1942), semidiffuse-porous (Appel, 1995), or ring-porous (Johnson et al., 2014). *Q. fusiformis* spreads asexually via root sprouts, sending up multiple trunks within a small area, with the resulting cluster of stems called a genet. The ground under a *Q. fusiformis* genet is typically carpeted with short root sprouts that maintain a few leaves each, but which presumably do not grow into mature trees unless the canopy above dies (Appel, 1995; Russell & Fowler, 1999). *Q. fusiformis* also form root grafts with genetically distinct individuals, connecting them via underground vessels (Appel, 1995). This web of underground connections makes *Q. fusiformis* highly susceptible to oak wilt, a fungal disease that spreads easily from stem to stem via the root system and which kills most trees within 3–6 months of infection. The acorns are frequently consumed by weevils and often bear small holes from the weevil attacks (Stockton & Morgan, 2012). Young *Q. fusiformis* are heavily consumed by deer when other food options are scarce, which may lead to a lack of recruitment to adult size classes (Russell & Fowler, 1999).

Because of the likelihood that neighbouring *Q. fusiformis* are connected underground by their roots, we were concerned that the data from the two *Q. fusiformis* stems at each micro-site might be too highly correlated to be considered separate individuals. However, correlation matrices show that the sap velocities of *J. ashei* are much more strongly correlated than those of *Q. fusiformis* at each micro-site, with correlations between pairs of *J. ashei* at the same micro-site

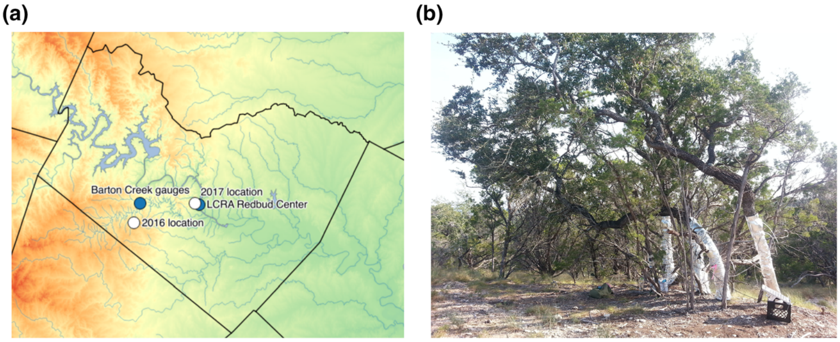

FIGURE 1 (a) Map of Travis County, TX. The two study locations are labelled, along with the Barton Creek stream discharge and rain gauges and the LRCA Redbud Center, which provided temperature and humidity data. (b) Sap flow monitoring at micro-site A. We studied sap flow in adjacent stems of *J. ashei* and *Q. fusiformis* so that it was reasonable to assume they had access to the same water resources, up to differences in root architecture. The two trees in the foreground are *Q. fusiformis*, with the two *J. ashei* behind. The sap flow probes were insulated on each side with quarter-spheres of polystyrene foam and then wrapped in reflective bubble insulation. The stems below the sap flow probes were wrapped in tinfoil to prevent thermal artefacts

TABLE 1 Descriptions of the six micro-sites and their relative locations

Year	Micro-site	Elevation (m)	Soil depth (cm)	Relative location (horizontal distance and heading)	Description
2016	A	304	8.7		Open canopy scrubland on hillslope
2016	B	289	9.7	81 m from micro-site A, at heading of 49°	Open canopy scrubland, just above limestone outcrop on hillslope
2016	C	284	15.7	105 m from micro-site A, at heading of 40°	Closed canopy woodland, adjacent to ephemeral stream
2017	D	199	10.8		Closed canopy woodland
2017	E	172	13.1	250 m from micro-site D, at heading of 27°	Closed canopy woodland, on bluff above inlet of Lady Bird Lake
2017	F	159	11.7	245 m from micro-site D, at heading of 41°	Closed canopy woodland, among hardwoods, on slope just above inlet of Lady Bird Lake

TABLE 2 Study trees, with diameter at breast height (DBH) and canopy area

Year	Micro-site	Species	DBH (cm)	Canopy area (m^2)
2016	A	*J. ashei*	18.6	8.3
		J. ashei	17.3	10.5
		Q. fusiformis	18.1	23.7
		Q. fusiformis	18.9	15.0
2016	B	*J. ashei*	11.6	3.0
		J. ashei	17.9	11.7
		Q. fusiformis	13.9	5.9
		Q. fusiformis[a]	15.4	6.5
2016	C	*J. ashei*	31.5	17.9
		J. ashei	25.3	22.8
		Q. fusiformis	21.9	8.5
		Q. fusiformis	19.9	6.9
2017	D	*J. ashei*	22.8	11.2
		J. ashei	20.1	3.6
		Q. fusiformis	27.5	16.9
		Q. fusiformis	25.9	16.7
2017	E	*J. ashei*	19.7	6.7[b]
		Q. fusiformis	18.2	14.2
		Q. fusiformis	11.4	4.9
2017	F	*J. ashei*	21.7	11.0
		J. ashei	29.7	15.7
		Q. fusiformis	29.4	46.5
		Q. fusiformis	25.2	17.8

[a] Used in the sap flow study, but not for PWP measurements because the canopy was not reachable. Instead, an adjacent, similarly-sized *Q. fusiformis* was used for PWP.

[b] Canopy measurements were made later than the others, during February 2019.

ranging from 0.91 to 0.97 and correlations between paired *Q. fusiformis* at the same micro-site ranging from 0.28 to 0.88 (Supporting Information S1). We suspect that connected stems of *Q. fusiformis* do not completely share water resources. In any case, we judge that they were acting sufficiently independently to treat them as independent stems in our model.

2.3 | Diameter and canopy measurements

The sizes of the trees varied by micro-site, but at each micro-site, we selected trees of as similar size as possible for the study. Diameters at breast height ("DBH") ranged between 11.4 and 31.5 cm, while canopy areas ranged between 3.0 and 46.5 m^2 (see Table 2 for measurements of each study tree). Canopy area was estimated as an oval with the longest diameter of the crown as the major axis and the minor axis perpendicular to it. We used a clinometer to verify that we were directly below the edge of the crown when measuring.

2.4 | Sap flow velocity

The sap flow velocities of each of the *J. ashei* and *Q. fusiformis* were measured at 15-min intervals using the Granier method (Granier, 1985), also known as the thermal dissipation method. This method requires inserting a pair of vertically aligned probes into the xylem. The upper probe produces constant heat and also contains a copper-constantan thermocouple to measure temperature. The lower probe contains a second thermocouple that measures a reference temperature. The difference in temperature between the two probes is used to estimate the velocity of sap flow within the xylem. Transpiration data are collected in terms of the difference in voltage (mV) between the two copper-constantan thermocouples and converted to temperature differential ΔT (°C) by multiplying by a conversion factor of 25. The daily maximum temperature differential, ΔT_M (°C), representing the daily low point in sap flow, is assumed to correspond to a sap velocity of zero and is used to scale that day's sap velocity. That is a standard assumption even though it would not hold if there is significant night-time flow (Taneda & Sperry, 2008; see Bleby et al., 2010). Temperature differentials were converted to sap velocity using the Granier equation (Granier, 1985):

$$u = .0119\left[\frac{T_M - T}{T - T_\infty}\right]^{1.231},$$

where u is the sap velocity (cm/s), T is the temperature of heated thermocouple (°C), T_∞ is the temperature of unheated thermocouple (°C), and T_M is the temperature of heated thermocouple when sap is not flowing (°C).

The Granier equation is an empirical equation, meaning that it is not derived from physical principles. Rather, it is a model that was fitted to data from three tree species, and as such is not a perfect fit for every species. In particular, there is evidence that the equation underestimates sap flow rates for ring-porous tree species, which may include *Q. fusiformis* (see "Tree species" above). A study that included ring-porous *Quercus prinus* found that the Granier equation underestimated sap flow rates by 30%–80% (Renninger & Schäfer, 2012). We sidestepped this issue by restricting our analysis to each tree's relative rate of change in sap flow velocity, r, defined as

$$r = \frac{1}{u}\frac{\mathrm{du}}{\mathrm{dt}}$$

This approach implicitly assumes that the relationship between the Granier sap velocities and the actual velocities can be expressed as a constant multiplicative factor. Indeed, Renninger and Schäfer (2012) found that the relationship between the Granier-derived measurements and those derived from the tissue heat balance method (which is more accurate but was not feasible for the current study) was linear for three *Q. prinus* individuals with y-intercepts that averaged near zero, supporting our assumption. However, a single *Q. velutinus* individual did have a non-linear relationship.

Before installing the sap flow sensors on each tree, a small area of bark was scraped away until living tissues (cork cambium and phloem layers) were visible. They were left intact as much as possible to minimize harm to the tree. Each tree was fitted with one sensor consisting of two probes spaced 40 mm apart (TDP-30 model, Dynamax Inc., Houston, TX). The sensors were inserted into the south-facing side of each trunk at breast height. The probes were 30 mm long, with thermocouples located at the midpoints. A portion of the probes approximately 2 mm in length was left outside of the trunk to prevent the probes from breaking as the trees grew. Considering both the incomplete insertion and the likely width of the intact phloem layer, the thermocouples are thought to have been located at a depth of 8–11 mm within the xylem. Once installed, each sensor was insulated using Styrofoam and reflective bubble insulation (Figure 1b). The trunk of each tree was wrapped in aluminium foil to minimize the effect of direct sunlight on the temperatures measured by the probes. Data from one *J. ashei* tree at site E were lost due to the probe being accidentally applied to a dead portion of the trunk. Thus, the final dataset includes 11 *J. ashei* and 12 *Q. fusiformis*.

The sap flow data contained some erroneous measurements, many of which indicated sudden, implausible increases in sap flow velocity. We removed the erroneous data points from the data set after identifying them using an algorithm that was consistent across all trees (Supporting Information S2). We also removed 12 days of data for one *J. ashei* at micro-site C in August 2016 because it degenerated into nonsense data following a heavy rainfall, probably due to electrical shorts caused by water infiltration into the equipment. For the purpose of calculating average daily sap flow, we replaced the erroneous data with linearly interpolated values, but to be conservative, for a given tree, we threw out any day of data that had more than 10% of its data points deemed erroneous. In all, we removed 1.97% of the individual measurements from 2016 and 0.70% of the measurements from 2017. We do not believe that the presence of erroneous data points affected the results of our analysis, since the dataset is dense in time (96 data points per tree per day), our analysis uses daily averages, and none of the days that were removed because of many erroneous values occurred during the four dry periods that we used in our analysis.

2.5 | Predawn water potential

Predawn water potential was measured on three dates during the summer of 2016 using a Scholander-type pressure chamber (1000 model, PMS Instruments, Corvallis, OR). Each tree in the 2016 sap flow study was measured, with the exception of one *Q. fusiformis* at micro-site B whose canopy was not accessible. A similarly sized, adjacent *Q. fusiformis* was substituted for the water potential measurements only. Because neither the scale-like leaves of *J. ashei* nor the petioles *Q. fusiformis* were long enough to be held securely in the top of the chamber, we measured the water potentials of small twigs with attached leaves. On each measurement date, two twigs were cut from each tree and the average of the two measurements is presented. For comparison, mean ψ_{50} estimates were obtained from the literature for both species (Johnson, Domec, et al., 2018; Willson et al., 2008).

2.6 | Delineation of dry periods

Since we are interested in trees' transpiration changes during very dry conditions, it is necessary to objectively delineate the starting and ending points of the driest periods. These are not necessarily the longest periods without rain, since the quantity of rain, the level of dryness preceding the rainfall, and ambient temperature all affect dryness.

We use stream discharge as a proxy for environmental water availability, reasoning that trees likely get their water from the epikarst during dry periods and interpreting stream discharge as an integration of the soil and epikarst moisture at the ecosystem level. During and immediately following significant rainfall events, surface flow causes the discharge rate to become very high and very variable, but within a matter of hours, surface flow reduces, and stream discharge begins a gradual decrease until the next rainfall. A caveat of this method is that streamflow is fed by an entire watershed and may or may not coincide with local moisture conditions. We mitigate this potential issue by defining the start and end dates of the dry periods as occurring between local rainfall events and use the stream discharge data only to rank the periods in order of water stress severity. Figure 2 compares the rainfall, stream discharge, temperature, and vapour pressure data for 2016 and 2017.

We use Barton Creek stream discharge data (m^3/s) from the United States Geological Survey gauge at 30.2961°N, 97.9253°W (United States Geological Survey, 2016-2017), which is 4.7 km from the 2016 study location and 12.8 km from the 2017 location, selecting the days in the 2-year period 2016–2017 when the average discharge rate was in the lowest tenth percentile. We define "significant rainfall events" as rainfall totalling at least 0.5 cm during a single day (see "Rainfall data") and define a "dry period" as a period between two significant rainfall events that includes at least 1 day in the lowest decile of daily average streamflow. This leads to the delineation of four dry periods—one in 2016 and three in 2017. A fifth, less-significant, low-streamflow event occurred in November 2017, but at that point, no sap flow data were being collected, so it is not included in this study.

Generally speaking, average daily transpiration rates for each tree decreased gradually as the days progressed during the dry periods. However, at the beginning of the third and fourth dry periods, most of the trees increased transpiration rates before starting a gradual decrease, possibly representing a period of time needed to repair damaged tissues or residual cloud cover from recent rain events. In order to decrease error in model fit, the start dates of the third and fourth dry periods are adjusted forward by 1 and 3 days, respectively, so that the dry periods align with the time period during which the greatest number of trees experienced decreasing transpiration. Table 3 shows the start and end days for the unadjusted and adjusted dry periods and their length in days. The adjusted dry periods will be subsequently referred to as the "dry periods."

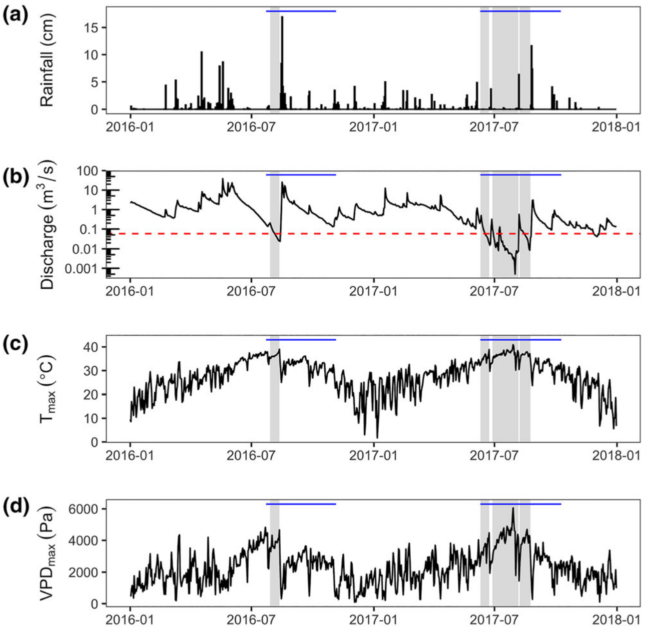

FIGURE 2 (a) Daily rainfall (cm) from the LCRA rain gauge on Barton Creek (1 January 2016 through 8 May 2017) and our own rain gauge (9 May 2017 through 31 December 2017). The local summer rainfall pattern—long periods of little-to-no precipitation punctuated by significant rainfall events—is apparent during the summers of 2016 and 2017. (b) Daily average stream discharge (m^3/s) from the USGS gauge on Barton Creek. The dashed red line shows the cut-off point for the lowest decile of streamflow over the 2-year period, located at 0.0575 m^3/s. (c) Daily maximum temperature and (d) daily maximum VPD from the LCRA Redbud Centre. In all charts, areas shaded in grey represent the four unadjusted dry periods, (1)–(4), considered in the study. The dry periods are the periods between rainfall events of at least 0.5 cm which contain stream discharge rates in the lowest tenth percentile, calculated over the 2-year period. Horizontal blue bars show the range of dates during which sap flow data were collected. A fifth, less significant dry period in November 2017 was not included because we did not collect sap data during that time

2.7 | Rainfall data

We use two different sources of rainfall data. For the dates 1 January 2016 to 8 May 2017, we use daily rainfall amounts from the Lower Colorado River Authority ("LRCA") Barton Creek rain gauge at 30.2961°N, 97.9253°W (Lower Colorado River Authority, site #4519, 2016-2017a). This location is 4.8 km from the 2016 study location. Starting on 9 May 2017 (before any sap flow data were collected in 2017), we began collecting rainfall data at the 2017 study location using a data-logging rain gauge (RG3-M model, Onset Computer Corporation, Bourne, MA).

TABLE 3 The four dry periods observed in the study, each of which contain at least 1 day with the Barton Creek rain gauge in its lowest decile for the two-year period 2016–2017

Dry period	Year	Unadjusted dates	No. days	Adjusted dates	No. days
1	2016	29 Jul–12 Aug	15	29 Jul–12 Aug	15
2	2017	10 Jun–23 Jun	4–14[a]	10 Jun–23 Jun	4–14[a]
3	2017	28 Jun–6 Aug	40	29 Jun–6 Aug	39
4	2017	8 Aug–24 Aug	17	11 Aug–24 Aug	14

Note: The unadjusted dates represent the full dry period between two rainfall events. The adjusted dates represent the days during which the average tree experienced decreasing average daily transpiration, as described in *delineation of dry periods*.

[a] Dry period (2) had already started when equipment was set up in 2017, and between 4 and 14 days' worth of sap flow data were collected during the remaining part of this dry period, depending on the micro-site.

2.8 | Temperature and vapour pressure deficit

Vapour pressure deficit (VPD), defined as the difference between saturation vapour pressure and actual vapour pressure, affects the rate of water evaporation from stomata. We calculate vapour pressure deficit from temperature and relative humidity data from LRCA's Redbud Center at 30.2921°N, 97.7838°W (Lower Colorado River Authority, site #4500, 2016-2017b). This site is approximately 15.6 km from the 2016 study location and 0.9 km from the 2017 location. Data from LCRA's Dripping Springs site, which is was slightly closer to the 2016 study location, were highly similar (correlation coefficient = 0.961).

2.9 | Bayesian model of sap velocity—overview

During the dry periods, the trees reduced their sap flow as water became more limited (Figure 3a,b), with the reduction happening at a greater rate at the beginning of the period and slowing down as time went on, suggesting exponential decay in sap flow rate. We tested our hypothesis that *Q. fusiformis* are better able to maintain transpiration rates during dry periods than *J. ashei* by using a Bayesian approach to fit an exponential model in the form $V = ae^{rt}$ to the average daily sap flow data (V) for each tree and each dry period, where t represents time in days and a and r are fitted parameters. The parameter r is of interest because it represents the relative rate of change in sap velocity for each tree, as described above (see *Sap flow velocity*). Since sap flow decreases over time, r takes on negative values in our model, with a more negative value of r meaning the sap flow is decreasing more rapidly. Our hypothesis, that *Q. fusiformis* is better able to maintain sap flow than *J. ashei* on average during summer dry periods, can be stated in terms of the model as the average value of r for *Q. fusiformis*, r_Q, is greater than the average value of r for *J. ashei*, r_J. That is,

$$r_{\text{diff}} = r_Q - r_J > 0.$$

The multiplicative coefficient, a, is needed to fit the curves, but is not interpretable given the uncertainty in the absolute values of the Granier-type sap flow measurements, which may understate the rates of *Q. fusiformis* sap flow, also described above. We defined the exponential model without an additive constant to force an asymptote at zero, which is reasonable since we would expect trees to eventually stop transpiring completely (and presumably die) once many days have passed since the last rainfall.

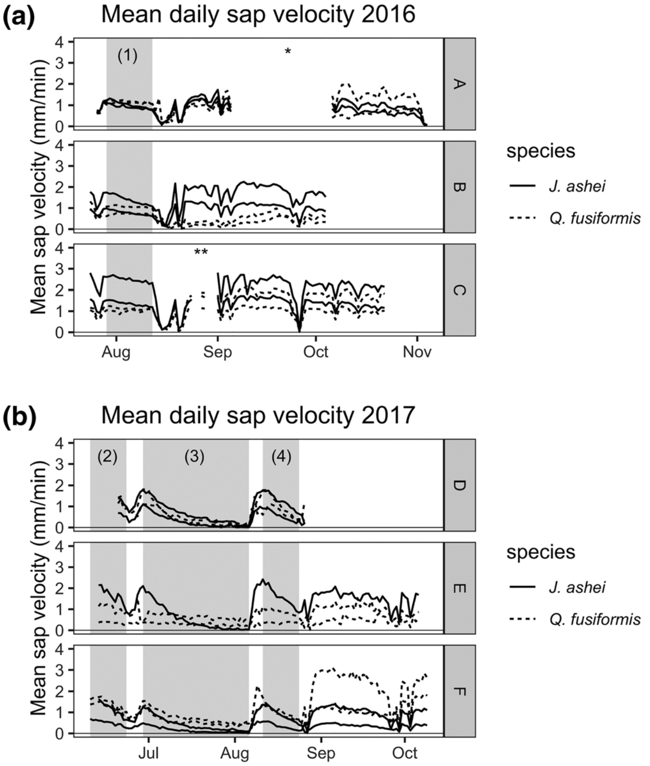

FIGURE 3 Average daily sap velocity (mm/min) for each tree at each of micro-sites (a) A–C in 2016 and (b) D–F in 2017. See Table 1 for descriptions of the micro-sites. Note that since the Granier equation can understate sap velocity for ring-porous species (Renninger & Schäfer, 2012), and some *Q. fusiformis* have been described as ring-porous (Johnson et al., 2014), the values for *Q. fusiformis* are possibly understated. The four dry periods are shaded in grey and labelled (1)–(4). The overall trend is that transpiration decreases for both species during dry periods. *At micro-site A, battery failure led to loss of data in September and October 2016. **At micro-site C, an equipment malfunction after heavy rain, likely caused by shorts in the system, caused widespread data loss in August 2016

Adopting a Bayesian framework provides several advantages. While our dataset has a complex hierarchy—2 years with four dry periods and 23 trees of two species divided across six different micro-sites—we are able to specify a single hierarchical model rather than fitting many individual models. This structure takes advantage of the conditional independence of parameters to allow reliable estimation of the higher level aggregate parameters, such as r_{diff}, which are of greatest interest. The Bayesian approach also provides estimates of the fully integrated posterior parameter distributions, rather than focusing on single values that maximize likelihood for each parameter, which may poorly characterize both the expectation and uncertainty of the estimate.

We wanted a model that fulfils the following criteria: (1) it mirrors the hierarchy of the data (that is, includes species-, micro-site-, and tree-level aggregation) and is relevant to testing our hypothesis, (2) the parameters are identifiable and multicollinearity between the parameters is minimized, and (3) it provides a good fit to the data. We tested multiple different model parameterizations, and our chosen model, described below, is the only one that met all of these criteria. Furthermore, for our chosen model, none of the 95% posterior credible intervals for the parameters associated with species and micro-site contain the value zero, supporting the inclusion of these parameters in the model. As a second check, we used the widely applicable information criterion ("WAIC"; Watanabe, 2010) to compare our chosen model with three alternate versions of the model in which we removed first the species parameter, then the micro-site parameters, and lastly both the species and micro-site parameters, respectively. Of these models, our chosen model is the top-ranked model based on WAIC, further supporting the inclusion of both the species and micro-site hierarchical levels in the model.

TABLE 4 Details of the Bayesian model specification

Model

$V \sim N(\mu, \sigma)$
$\mu = ae^{rt}$
$a = a_{tree,P}$
$r = r_{J_{site}} + r_{\text{diff}} \cdot D_{\text{species}} + r_{tree}$
where:
t is the time in days since the centre date of the dry period,
$D_{species}$ is defined as 0 for *J. ashei* and 1 for *Q. fusiformis*,
The subscript J_{site} indicates the average parameter value for *J. ashei* at a given micro-site, A-F,
The subscript "diff" indicates the difference between average parameter values for *J. ashei* and *Q. fusiformis*,
The index *tree* represents the individual trees, numbered 1–23,
And the index *P* represents the dry period, (1)–(4).

Prior distributions

$a_{tree,P} \sim N(\mu_a, \sigma_a)$
$r_{J_{site}} \sim N(\mu_J, \sigma_J)$
$r_{\text{diff}} \sim N(0, 0.1)$
$r_{\text{tree}} \sim N(0, \sigma_{r_{tree}})$
$\sigma \sim HC(0, 1)$

Hyperprior distributions

$\mu_a \sim N(0, 1)$
$\sigma_a \sim HC(0, 1)$
$\mu_J \sim N(0, 0.1)$
$\sigma_J \sim HC(0, 0.1)$
$\sigma_{r_{tree}} \sim HC(0, 0.1)$

Note: The notation $HC\ (\mu, \gamma)$ refers to the half-Cauchy distribution, the positive-value restriction of the Cauchy distribution centered at μ with scale-parameter γ.

2.10 | Model implementation

The parameter r is defined as the sum of an average value for *J. ashei* at each micro-site plus an adjustment for the species *Q. fusiformis* and an adjustment for each tree. We do not allow the parameter r to vary by dry period because we want to maximize the power of inference by fitting a single r value for each tree. The parameter a is fitted separately for each combination of tree and dry period. Table 4 presents the full model definition. This model formulation contains each of the levels of data structure inherent in the study's design, that is, micro-site, species, and tree.

To enhance model convergence, we centre the data for both the independent and dependent variables. The values of the independent variable, t, are centred around zero for each dry period by numbering the days for each dry period, starting with 1, then subtracting 1/2 of the number of days in the dry period rounded down to the nearest day. The average daily sap flow data are centred geometrically around 1 for each dry period by dividing each data point by the geometric mean of the points at $t = 0$.

We use regularizing priors, rather than flat priors, in order to reduce overfitting (McElreath, 2018). Our chosen priors and hyperpriors are either normal with mean zero, or, in the case of parameters that are restricted to positive numbers, positive half-Cauchy distributions centred at 0. Centring the priors and hyperpriors at 0 is a conservative choice. For the parameter r_{diff}, which relates to our hypothesis, setting the mean of the prior distribution to zero represents a scenario where the relative rates of change in sap velocity of *J. ashei* and *Q. fusiformis* transpiration are equal; thus, the prior could be considered a null hypothesis.

We programmed the model in R (R Core Team, 2018) using the *rethinking* package (McElreath, 2016) and ran it in four cores, each with 20,000 steps. The first 10,000 steps of each core are used to calibrate the Monte Carlo sampler, and the last 10,000 steps provide posterior probabilities for each of the model parameters. This leads to a total of 40,000 post-calibration model steps. The *rethinking* package uses *RStan* (Stan Development Team, 2018), which is the R interface to Stan, for the Monte Carlo sampling. The output of each of the 40,000 post-calibration steps is one possible set of model parameters, so the entire output is essentially 40,000 different model fits. For visualizing the model results, we use the mean value of each parameter, referred to hereafter as the "mean model." We also use a number of the Tidyverse packages for data manipulation and visualization (Wickham et al., 2019).

3 | RESULTS

3.1 | Sap velocity

Sap velocity generally fluctuates due to water availability and weather, but during the dry periods of this study, the trees experienced gradual decreases in average daily sap velocity (Figure 3a,b). Both *J. ashei* and *Q. fusiformis* continued to transpire throughout dry periods (1), (2), and (4), but at the end of the longest dry period, period (3) in 2017, transpiration was impacted greatly. On the last day of dry period (3), all six *Q. fusiformis* continued to transpire at a fraction of their typical levels, while only one *J. ashei* continued faintly with its normal pattern of transpiration, three had essentially stopped transpiration, and the remaining *J. ashei* showed slight movement of sap that did not match timing-wise to a typical transpiration pattern (Figure 4).

The *Q. fusiformis* individuals at micro-site B had dropped most of their leaves by 11 September 2016, which appears to have caused a decrease in their transpiration rates even though rainfall had occurred recently. However, the *Q. fusiformis* trees at micro-site E in 2017 experienced similar low transpiration in July following rainfall without a noticeable loss of leaves. We did not observe any significant loss of leaves or branchlets in *J. ashei*.

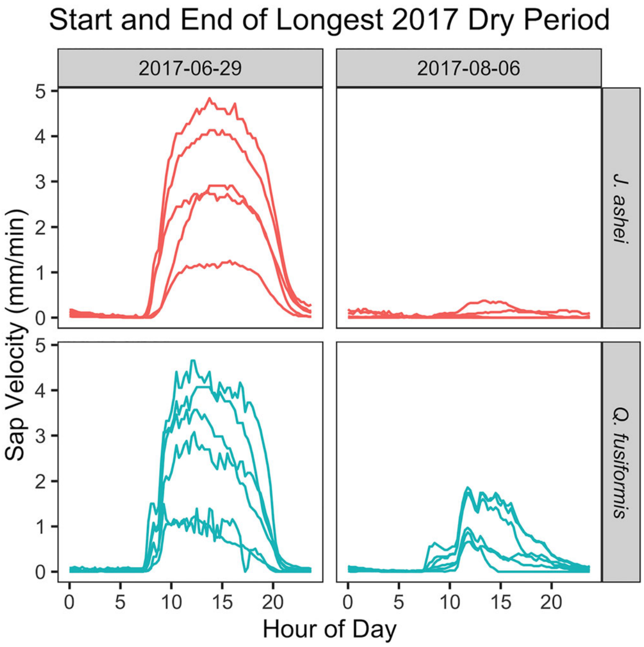

FIGURE 4 The sap velocity of each tree, measured at 15-min intervals on two different dates: the first and last days of dry period (3), which lasted 39 days and is by far the longest we considered. Each line corresponds to one tree. Note that the Granier equation typically understates sap velocity for ring-porous species, and some *Q. fusiformis* have been described as ring-porous. On the first day, following a rainfall event, sap velocity is similar for *J. ashei* and *Q. fusiformis*, both in shape and in absolute values, although *Q. fusiformis* exhibits more micro-variations in sap velocity and has greater flow rates in the morning, while *J. ashei* sap velocity peaks in the afternoon. On the last day, the trees of both species have experienced material decreases in sap velocity, but *J. ashei* has been affected more markedly. Only one *J. ashei* individual (the 29.7-cm DBH trunk at micro-site F) had any semblance of the normal pattern

3.2 | Bayesian model results

We confirmed that the mean model, determined by setting the value of each parameter equal to its mean across the 40,000 model steps, provides a good fit to the measured data (Figure 5). We then examined the posterior distributions of key parameters. Comparing the 95% equal-tailed credible intervals of the r parameters for the various trees, one can see that *J. ashei* generally lose sap velocity at greater rates than *Q. fusiformis* within a given micro-site (Figure 6). We tested this finding statistically by examining the posterior distribution of r_{diff}, the difference between the average relative rates of change in sap flow for *J. ashei* and *Q. fusiformis*. Of the 40,000 post-calibration steps of the Bayesian model, only 107 estimated a value for r_{diff} that is less than or equal to zero, allowing us to estimate a 99.73% probability that *Q. fusiformis* were able to maintain transpiration better than *J. ashei* at the locations we studied (Figure 7). The difference between the two species was material, with the mean relative rate of change for *J. ashei*, r_{J}, being -0.0506, while the mean for *Q. fusiformis*, r_{Q}, was -0.0238, a difference of 53.0%. Refer to Supporting Information S3 for the posterior distributions of other key model parameters.

3.3 | Predawn water potential

We measured PWPs on three dates in 2016: 29 July, 12 August, and 6 September. The Barton Creek average discharge, our proxy for environmental dryness, on those three dates was 0.207 m^3/s, 0.025 m^3/s, and 1.741 m^3/s, respectively, making the second measurement date the driest and the third date the least dry. *J. ashei*'s PWPs were lower than those of *Q. fusiformis* on the first two dates (Figure 8), but the two species were about equal on the third, when both species were probably under less water stress. Measured PWPs for both species stayed above their respective ψ_{50} values, although the PWPs of *Q. fusiformis* got much closer to the estimated ψ_{50} of -1.8 MPa, while *J. ashei*'s PWPs were always far above the estimated ψ_{50} of -13.1 MPa (ψ_{50} estimates from Johnson, Domec, et al., 2018, and Willson et al., 2008).

4 | DISCUSSION

Our sap velocity data indicate that transpiration decreased at a faster relative rate for *J. ashei* than for *Q. fusiformis* during summer dry periods. In 2016, *J. ashei*'s sap velocity declined at all three micro-sites while *Q. fusiformis*'s sap velocity held relatively steady. In 2017, both species had declines in sap velocity, with *J. ashei*'s declining more rapidly than *Q. fusiformis*'s at two micro-sites, and trees of both species experiencing similar declines at the third micro-site. Our fitted model provides strong support (probability 99.73%) for our hypothesis that *J. ashei*'s sap velocity decreases at a faster relative rate than

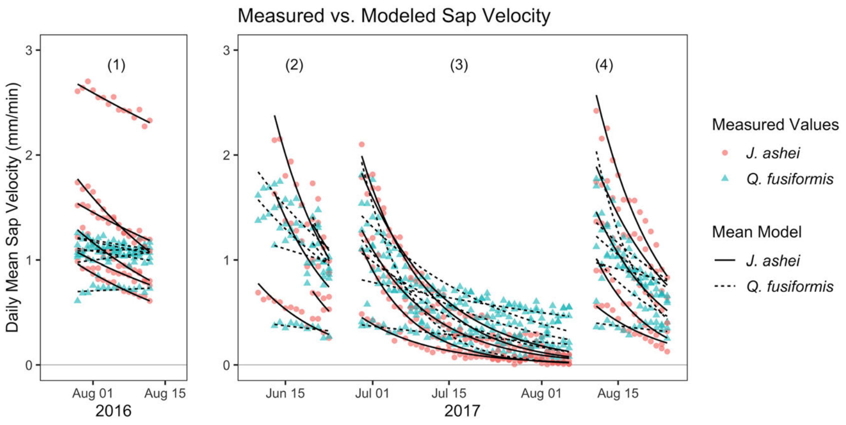

FIGURE 5 Fit of the "mean model," which uses average parameter values from the 40,000 post-calibration model steps, to the recorded sap velocity data during dry periods (1)–(4). One should avoid making direct comparisons of sap flow magnitude between the two species since *Q. fusiformis* sap flow is possibly understated (Renninger & Schäfer, 2012)

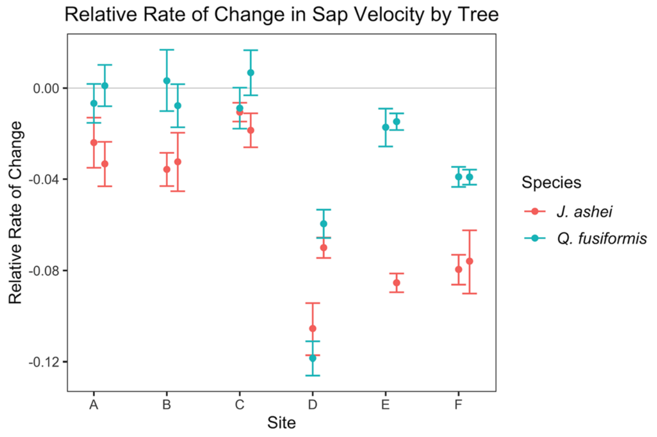

FIGURE 6 Mean values and 95% equal-tailed credible intervals of the relative rate of change in sap velocity during the dry periods, *r*, for each tree in the study, based on the 40,000 post-calibration model steps. During the 2016 dry period (sites A–C), *J. ashei* sap velocity decreased while *Q. fusiformis* sap velocity held relatively steady. During the 2017 dry periods (sites D–E), all trees studied experienced decreasing sap flow, with the two species showing similar decreases at micro-site D, and with *J. ashei* sap flow decreasing more rapidly than *Q. fusiformis* at micro-sites E and F

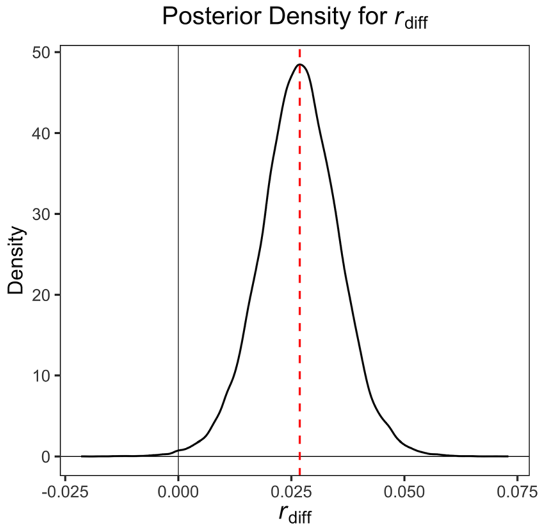

FIGURE 7 Shows the posterior density of r_{diff} from the 40,000 post-calibration model steps, where $r_{\text{diff}} = r_Q - r_J$ represents the difference between the average daily relative rates of change in transpiration for *J. ashei* and *Q. fusiformis* across all micro-sites; 39,893 (99.73%) of the model steps had $r_{\text{diff}} > 0$, and only 107 (0.27%) had $r_{\text{diff}} \leq 0$, meaning that it very likely that the transpiration rates of *J. ashei* were decreasing faster on average than those of *Q. fusiformis* at the two locations. The mean value of r_{diff} (shown as a dashed red line) is 0.0268, supporting our hypothesis that $r_{\text{diff}} > 0$

Q. fusiformis's on average during summer dry periods, at least at our two study locations. Additionally, by the end of the longest dry period studied (39 days in 2017), at least three of the five *J. ashei* trees had stopped transpiration while all of the *Q. fusiformis* continued transpiring. These results support the idea that, on average, *J. ashei*'s transpiration is impacted more quickly by water shortage than *Q. fusiformis*'s, likely because *J. ashei* lack access to deeper water resources in the epikarst that sustain *Q. fusiformis* during dry periods.

We selected trees growing very closely together within each micro-site so as to minimize differences in abiotic conditions between the trees. We therefore assume that the differences in sap flow responses among trees within a micro-site are caused mostly by differences in biotic factors, such as physiological properties, root architecture and depth, canopy structure, stomatal behaviour and leaf phenology, which together can be interpreted as the "hydraulic strategy" of the trees. In contrast, we consider the differences in sap flow responses between micro-sites to be largely due to differences in abiotic factors, such as underlying geology, water availability, properties of the soil, and year-to-year variation in climate. Because of concern that the Granier equation may materially understate the sap velocity of *Q. fusiformis*, we considered only relative rates of change in our analysis, making our findings independent of starting sap velocity. While oak wilt has been identified in Travis County, TX, we do not believe that any of our *Q. fusiformis* trees were afflicted with oak wilt at the time of the study because all of them were still alive when last observed—6 months or more after sap flow data collection had stopped.

The idea that *Q. fusiformis* have greater water access than *J. ashei* during dry periods is also consistent with our measurements of predawn water potential (PWP) for these species. We measured PWP for four *J. ashei* and six *Q. fusiformis* on three dates. We found that

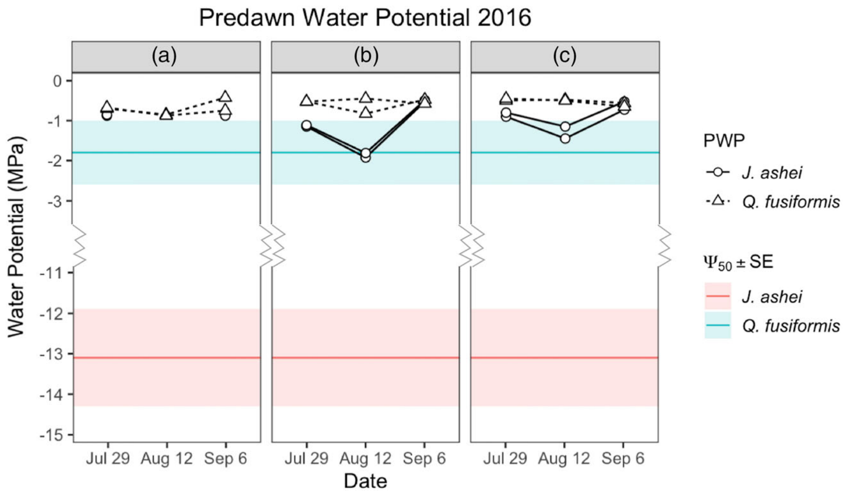

FIGURE 8 Predawn twig water potentials ("PWP") at three dates during the summer of 2016 for micro-sites A–C. Each point in this chart is the average of two measurements from the same tree. Note that there were two *J. ashei* and two *Q. fusiformis* at each of micro-sites A, B, and C. No measurements were taken for *J. ashei* at micro-site A in August. The mean stem Ψ_{50} values (solid horizontal lines) and ranges of one standard error above and below (shaded regions) are given for both species (Willson et al., 2008 for *J. ashei*; Johnson, Domec, et al., 2018, for *Q. fusiformis*)

Q. fusiformis PWPs were less sensitive to dryness than those of *J. ashei*, in that they changed little among the three dates, whereas *J. ashei* PWPs dropped significantly on the driest date of measurement. This is consistent with findings of prior studies (Dammeyer et al., 2016; Kukowski et al., 2013; Schwinning, 2008), and we interpret it to mean that the *J. ashei* trees we studied had less total water access than the *Q. fusiformis* trees, which could be explained by *Q. fusiformis*'s having significantly deeper root systems than *J. ashei* (Jackson et al., 1999). Another possible interpretation for *Q. fusiformis*' higher PWP is that *Q. fusiformis* trees are better at conserving their water supply to protect against hydraulic failure. We find this explanation unlikely because our sap flow data show that *Q. fusiformis* continued to transpire at a rate that was greater than that of *J. ashei* relative to each tree's sap flow at the start of the dry period. The fact that the trees were in such close proximity, with adjacent or mingling canopies, also supports the hypothesis of a deeper root system for *Q. fusiformis*. If both species were rooted to the same depth, it seems unlikely that they would be able to conserve water resources since they likely have overlapping root systems, and one would expect them to have more similar PWPs.

If, as our data and model support, *Q. fusiformis* frequently maintain transpiration at higher rates than *J. ashei* during dry periods, a consistent picture emerges. Even though *Q. fusiformis* have more vulnerable xylem than *J. ashei* (Johnson, Domec, et al., 2018; McElrone et al., 2004), their frequently much-deeper root systems (Jackson et al., 1999) protect their xylem by providing greater water resources, as evidenced by PWP data (Schwinning, 2008; Kukowski et al., 2013; Dammeyer et al., 2016; Johnson, Domec, et al., 2018; current study), and sap flow data (current study), allowing them to maintain relatively high rates of transpiration. However, as water resources dwindle, *Q. fusiformis* may reduce gas exchange (Bendevis et al., 2010; Owens & Schreiber, 1992) or drop leaves (Owens & Schreiber, 1992; Schwinning, 2008; Kukowski et al., 2013; present study) to maintain high water potentials. In contrast, *J. ashei*'s cavitation-resistant xylem allows them to continue transpiration under water stress until their water resources dwindle and water potentials drop, at which time *J. ashei* will begin to reduce gas exchange to protect against hydraulic failure. While *J. ashei* can endure much lower stem water potentials than most other tree species (Willson et al., 2008), our sap flow data and model, as well as gas exchange data from prior studies (Owens & Schreiber, 1992; Bendevis et al., 2010; our interpretation of the charts showing their original results), show that *J. ashei* also regulate transpiration to avoid catastrophic loss of hydraulic conductivity.

During conditions of water stress, trees can close their stomata to slow water loss, but they are subject to a trade-off between water loss and carbon starvation. Continuing transpiration and photosynthesis will decrease water potential and put the xylem at risk of hydraulic failure (Tyree & Sperry, 1988), but closing stomata to protect the xylem will reduce photosynthesis and carbon stores (McDowell et al., 2008) while also exposing leaves to photo-oxidative stress (Takahashi & Badger, 2011). Species at opposite ends of this trade-off are frequently classified as *isohydric* or *anisohydric*, where isohydric species adjust stomata pore size during periods of water stress in order to maintain a near-constant midday (minimum) leaf water potential, and anisohydric species risk cavitation by maintaining normal levels of transpiration and photosynthesis even under water stress (Tardieu & Simonneau, 1998).

J. ashei's predawn water potential varies significantly throughout the year, while that of *Q. fusiformis* changes much less, and the pattern also holds for midday water potentials (Johnson, Berry, et al., 2018). This seems to imply that *J. ashei* are more anisohydric and *Q. fusiformis* more isohydric, as Johnson, Berry, et al. (2018) found. However, data on differences in stomatal conductance from prior studies do not support the distinction. Both species reportedly reduced their stomatal conductance g (mol m^{-2} s^{-1}) by similar percentages during the dry periods of June 1988, July 1989 and July 2005, with each dry month having about 1/3 or less of the conductance of the preceding month for both species (Owens & Schreiber, 1992; Bendevis et al., 2010; our interpretation of the charts showing their original results). Johnson, Domec, et al. (2018) found similar confusion when applying different methods of determining of isohydry and anisohydry for *J. ashei* and *Q. fusiformis*, getting opposite results depending on the method used.

The hydraulic strategies of *J. ashei* and *Q. fusiformis* may be better-described by the ideas of "drought tolerance" and "drought avoidance," as defined in Touchette et al. (2007) and Polle et al. (2019). Under this framework, a drought-tolerant species can survive low xylemic water potentials using strategies such as maintaining cellular turgor pressure via osmotic adjustment or increasing cell-wall thickness, while a drought-avoidant species maintains high xylemic water potentials via strategies such as growing deep roots, closing stomata, or dropping leaves. This framework is similar to that of isohydry/anisohydry, but it does not specify stomatal regulation as the method for achieving drought avoidance, and does not assume drought-tolerant species regulate their stomata any less than drought-avoidant ones. Instead, it allows for a number of possible strategies that could lead to drought tolerance or avoidance.

We suggest that *Q. fusiformis* achieve a drought-avoidant strategy by maximizing potential uptake through their deep roots and minimizing water loss through drought-deciduousness (dropping leaves during times of water stress), a pair of strategies that have been suggested in the past as alternatives to highly cavitation-resistant xylem in arid regions (Choat et al., 2018). Indeed, the dropping of leaves during water stress has been observed in *Q. fusiformis* (Owens & Schreiber, 1992; Schwinning, 2008; Kukowski et al., 2013; present study). In contrast, we suggest that *J. ashei* achieve a drought-tolerant strategy via xylem that continues to function at very low water potentials without experiencing catastrophic hydraulic failure. There is no evidence that *J. ashei* are drought-deciduous, but there is evidence that both species are about equally drought-resistant, meaning that both species survive drought conditions at about the same rate, based on the Crouchet et al. (2019) mortality study following the 2011 drought, although canopy mortality data may imply that *Q. fusiformis* is more drought-resistant than *J. ashei* (Johnson, Domec, et al., 2018) and there is great site-to-site variation (Kukowski et al., 2013).

Acknowledging the different routes of these species to roughly similar drought-resistance suggests other questions for research. Which strategy will do best under different types of drought conditions, such as short, very-hot droughts, or long, very-hot droughts? *Q. fusiformis*' deep root moisture access is likely dependent on local conditions; what types of future rainfall regimes might cause a lack of replenishment of those deep-water sources, making *Q. fusiformis* more drought-vulnerable? *J. ashei* has highly cavitation-resistant xylem, allowing the xylem to withstand low water potentials with little cavitation. However, do those low water potentials negatively affect the living cells of *J. ashei*? What other adaptations might those cells have that keep them from losing turgor pressure under water stress and low xylem water potential? Generally speaking, it remains a challenge to connect hydraulics to mortality rates, and while drought is associated with increased tree mortality, it is not yet clear whether desiccation or carbon starvation is the main contributing factor in any given instance (McDowell et al., 2019). It would be interesting to understand whether the differences in hydraulic strategies between the two species affect the relative likelihoods of death by desiccation versus carbon starvation.

By showing that *Q. fusiformis* can often maintain higher levels of transpiration than *J. ashei* during summer dry periods, this work fills a void in understanding the hydraulic strategies of the two species. Our results suggest that when deep underground water resources are available, *Q. fusiformis*'s deeper root systems can offset the risk posed by its cavitation-vulnerable xylem during times of drought. This understanding is important for predicting how the plant communities of Central Texas might change in the future, under the possibility of a hotter and drier climate (Gutzler & Robbins, 2011; Venkataraman et al., 2016) which could alter the dominance of these trees, and for predicting changes in the regional carbon cycle. It may also provide clues to understanding the coexistence of hydraulic strategies across other landscapes, being especially relevant to other regions where *Juniperus* and *Quercus* species are in competition in woodlands that are in a state of flux (e.g., DeSoto et al., 2010; Nunes Biral et al., 2019; Schott & Pieper, 1987; Torquato et al., 2020) as well as to other arid or semi-arid regions where some species have very deep roots.

5 | CONCLUSIONS

We have shown that *Q. fusiformis* trees at six micro-sites maintained their transpiration rates better than *J. ashei* on average during summer dry periods. This work fills a gap in understanding the hydraulic strategies of the two species, given that it is the opposite result of a previous study (Kukowski et al., 2013) and it may help explain why *Q. fusiformis* had significantly less canopy die-back (Johnson, Domec, et al., 2018) and roughly equivalent overall mortality (Crouchet et al., 2019) after the extreme 2011 drought. We discussed the hydraulic strategies of the two species in relation to one another and how they fit into a framework of drought tolerance versus drought avoidance. Our findings may have implications for future changes in regional community structure, and may provide clues to understanding the coexistence of hydraulic strategies in other regions.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available on GitHub at https://doi.org/10.5281/zenodo.5063998

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