

Wood anatomy constrains stomatal responses to atmospheric vapor pressure deficit in irrigated, urban trees

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Abstract Plant transpiration is strongly constrained by hydraulic architecture, which determines the critical threshold for cavitation. Because species vary greatly in vulnerability to cavitation, hydraulic limits to transpiration and stomatal conductance have not generally been incorporated into ecological and climate models. We measured sap flow, leaf transpiration, and vulnerability to cavitation of a variety of tree species in a well-irrigated but semi-arid urban environment in order to evaluate the generality of stomatal responses to high atmospheric vapor pressure deficit (D). We found evidence of broad patterns of stomatal responses to humidity based on systematic differences in vulnerability to cavitation. Ring-porous taxa consistently had vulnerable xylem and showed strong regulation of transpiration in response to D , while diffuse-porous taxa were less vulnerable and transpiration increased nearly linearly with D . These results correspond well to patterns in the distribution of the taxa, such as the prevalence of diffuse-porous species in riparian ecosystems, and also provide a means of representing

maximum transpiration rates at varying D in broad categories of trees.

Keywords Stomatal conductance · Transpiration · Ring-porous · Diffuse-porous · Urban ecology

Introduction

Transpiration rates of whole trees are a major component of the water cycle at the ecosystem, regional, and global scales. At the leaf level, transpiration is controlled by stomata in part to prevent excessive cavitation of xylem. This regulation occurs at the cost of reduced CO_2 supply and consequently has a large influence on photosynthesis and primary productivity. The degree of stomatal opening is strongly constrained by the hydraulic architecture of plants that determines the critical water potential threshold for cavitation (Sperry 2000). While there are many examples of species differences in vulnerability to cavitation, hydraulic constraints on gas exchange have not been evaluated in a large number of species. Yet broad classes of responses across functional types are needed to incorporate hydraulic mechanisms into larger scale models linking biological processes and the water cycle.

Within temperate angiosperm trees, xylem anatomy is broadly divided into plants with ring-porous versus diffuse-porous vessel elements. A major difference in these contrasting xylem anatomies is the diameter distribution of vessel elements. Ring-porous taxa have a bimodal distribution of vessel diameter associated with large, early season vessels and small late-season vessels, while diffuse-porous taxa show very little distinction between the diameter of vessel elements in early versus late wood (Tyree and Zimmerman 2002). Theoretically, we would

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expect these anatomical differences to result in different hydraulic capacities and transpiration rates (Tyree and Zimmerman 2002). However, previous attempts to quantify whole tree transpiration rate differences among trees with contrasting anatomies have yielded mixed results, with no clear systematic differences (Oren and Pataki 2001; Pataki and Oren 2003).

In this study we exploited a relatively new ecological environment to determine whether diffuse-porous trees systematically have different stomatal sensitivity to vapor pressure deficit (D) than ring-porous trees based on categorically different hydraulic constraints. Cities in arid and semi-arid regions are commonly associated with afforestation that replaces the native desert and grassland vegetation with irrigated forests (Nowak et al. 1996). In these ecosystems, non-native species experience D environments that greatly exceed the upper limits associated with their native habitats today, and in all likelihood at any time during their evolutionary histories. Urban forests in the western United States are unusual in that they comprise almost entirely non-native deciduous tree species from mesic environments, and their continued presence relies primarily on irrigation water to sustain soil moisture. From a management perspective, transpiration rates of urban trees are of great interest in the selection of water-conserving species. From an ecological perspective, we utilized this environment to test the hypothesis that differences in angiosperm xylem anatomy were a constraint on transpiration rates in moist soils in the high D environment of the Salt Lake Valley, Utah, where both ring-porous and diffuse-porous trees are routinely cultivated.

Materials and methods

Study site

The Salt Lake Valley (latitude 40.66; longitude 111.55; elevation 1,275–1,550 m) is a metropolitan area located in northern Utah, USA. The climate is semi-arid, with a mean annual temperature and precipitation of 11.1°C and

411 mm, respectively (Alder et al. 1998). Mean daytime D may exceed 5 kPa during the growing season in the Salt Lake Valley, whereas mean daytime D in mesic environments rarely exceeds 2 kPa. Sap flux measurements were made at three different locations in the Salt Lake Valley during the 2003 and 2004 growing seasons.

The “Campus” and “Red Butte” sites were measured in 2003. These sites were landscaped and regularly irrigated. The “Riparian” site was measured in 2004 and was a riparian forest along a major river corridor that runs from south to north across the middle of the valley. The Campus site was located at the University of Utah and consisted of diffuse-porous *Platanus acerifolia* (Ait.) Willd. and ring-porous *Gleditsia triacanthos* L. planted within a turfgrass lawn. The Red Butte site was located at the University of Utah Research Park at the mouth of Red Butte Canyon and consisted of diffuse-porous *Acer platanoides* L. and ring-porous *Quercus rubra* L. planted in turfgrass and interspersed with small groves of irrigated *Quercus gambelii* Nutt. The Riparian site was located in a riparian forest of *Populus fremontii* Wats. growing along the Jordan River in Sandy, Utah. Of these species, both *P. fremontii* and *Q. gambelii* were native to the study region. The mean diameter of study trees is given in Table 1.

Sap flux measurements

At each site, 20-mm-long thermal dissipation probes according to Granier (1987) were used to measure sap flux density (J_s) for ten individuals of each species. Sensor pairs were inserted radially at breast height (1.4 m), with a vertical separation of 15 cm. The axial direction of insertion was selected at random. The temperature difference associated with each sensor pair was measured every 30 s and averaged every 30 min with a datalogger (CR23X; Campbell Scientific, Logan, Utah) during June and up to and including September. J_s ($\text{g m}^{-2} \text{s}^{-1}$) was calculated according to the empirically derived equation (Granier 1987):

Table 1 Site location, xylem anatomy, water source, mean diameter at breast height (\pm SE), and mean sapwood depth at breast height (\pm SE) of each species

Species	Xylem anatomy	Site	Water source	Mean diameter (cm)	Mean sapwood depth (cm)
<i>Platanus acerifolia</i>	Diffuse	Campus	Irrigated	25.0 \pm 1.8	8.7 \pm 0.9
<i>Acer platanoides</i>	Diffuse	Red Butte	Irrigated	26.5 \pm 0.7	8.8 \pm 0.6
<i>Populus fremontii</i>	Diffuse	Riparian	Riparian	30.3 \pm 3.2	5.5 \pm 0.6
<i>Gleditsia triacanthos</i>	Ring	Campus	Irrigated	20.8 \pm 1.1	3.2 \pm 0.2
<i>Quercus gambelii</i>	Ring	Red Butte	Irrigated	13.5 \pm 0.5	2.8 \pm 0.2
<i>Quercus rubra</i>	Ring	Red Butte	Irrigated	21.4 \pm 1.1	3.1 \pm 0.2

$$J_s = 119(\Delta T_m / \Delta T - 1)^{1.231} \quad (1)$$

where ΔT is the temperature difference between the sensor probes and ΔT_m is the temperature difference between the sensor probes under zero-flow conditions. Trees were cored using an increment borer at the conclusion of the experiment to estimate sapwood depth visually at the sensor location. In all cases, the sensor depth did not exceed sapwood depth (Table 1).

Atmospheric and soil moisture measurements

Temperature and relative humidity were measured continuously at all three study locations (HMP35C, HMP45A; Vaisala, Helsinki). Measurement frequency and output was the same as for sap flux measurements. Time domain reflectometry probes (CS616; Campbell Scientific) integrating the top 30 cm of soil were used to monitor the seasonal course of soil moisture at the Campus and Red Butte sites. Eight probes, five at the Campus site and three at the Red Butte site, were distributed at different locations across each site. Measurements were made every 10 min and averaged every 30 min. In addition, irrigation water was collected in graduated cylinders at the Campus and Red Butte sites from the last week of August up to and including the third week of September. A small amount of oil was placed in the cylinders to minimize evaporation. Three cylinders were placed at each site. Soil water availability was monitored at the Riparian site with depth to the water table measurements using an onsite piezometer.

Water potential measurements

Predawn and midday water potential were measured on a monthly basis throughout the growing season for each species. Single leaves from five individual trees per species were cut using a sharp razor blade and measured immediately following excision using a Scholander-type pressure chamber (PMS, Corvallis, Ore.). In situ hydraulic conductance was estimated from sap flow measurements and the water potential gradient as measured by predawn and midday water potential according to Pataki et al. (2000).

Gas exchange measurements

Leaf-level gas exchange was measured with a steady state porometer (LI-1600; LI-COR Biosciences) from mid June up to and including early July 2006 between 1000 and 1600 hours for two of the six species in this study. Because

of the logistical difficulty of characterizing whole-canopy stomatal conductance with leaf-level measurements on many replicate trees, *P. acerifolia* and *Q. rubra* were selected as representative species having diffuse-porous and ring-porous wood anatomy, respectively. Average species-level responses to ambient D conditions for these two species were evaluated from consecutive measurements of three trees per species, where four independent, south-facing, leaf measurements were made per tree for a given measurement period. Porometry measurements were made relatively early in the growing season to avoid potentially confounding effects of significant changes in leaf-level transpiration rates over time, but late enough in the season to capture high ambient D conditions.

Vulnerability curve measurements

Vulnerability to cavitation was measured according to the centrifuge method described in Alder et al. (1997). Six stem segments from independent trees for each species were collected before dawn and placed in large plastic bags where they remained until analyzed within a 3-day period. In order to reduce water loss from the stems during storage, a wet paper towel was placed inside the bags, and bags were stored in a walk-in refrigerator. Where possible, only stems representing current year growth were collected. In addition, stem cross-sectional areas were combined with vulnerability curve measurements to assess differences in stem area specific conductivity among species.

Results

Temperature, humidity, and D were very similar at the Campus and Red Butte sites, which were measured simultaneously in 2003 (Fig. 1). Although the Riparian site was measured in 2004, the seasonal pattern was similar. Mean daytime D reached a maximum of 5 kPa in July (Fig. 1). Volumetric water content measurements showed intra- and inter-site specific variation at the Campus and Red Butte sites (Fig. 2), with mean values generally ranging between 20 and 30%. No clear pattern of seasonal decline in volumetric water content was observed, with the exception of a brief drier period at the Red Butte site in September (Fig. 2, days 254–264). The average amount of irrigation recorded at each site from the last week of August up to and including the third week of September was 300 and 310 mm, respectively. However, the amount of irrigation was probably underestimated, as on several occasions the cylinders were filled to capacity and the maximum cylinder height was recorded. At the riparian site, the depth to the water table was ~ 1 m throughout the

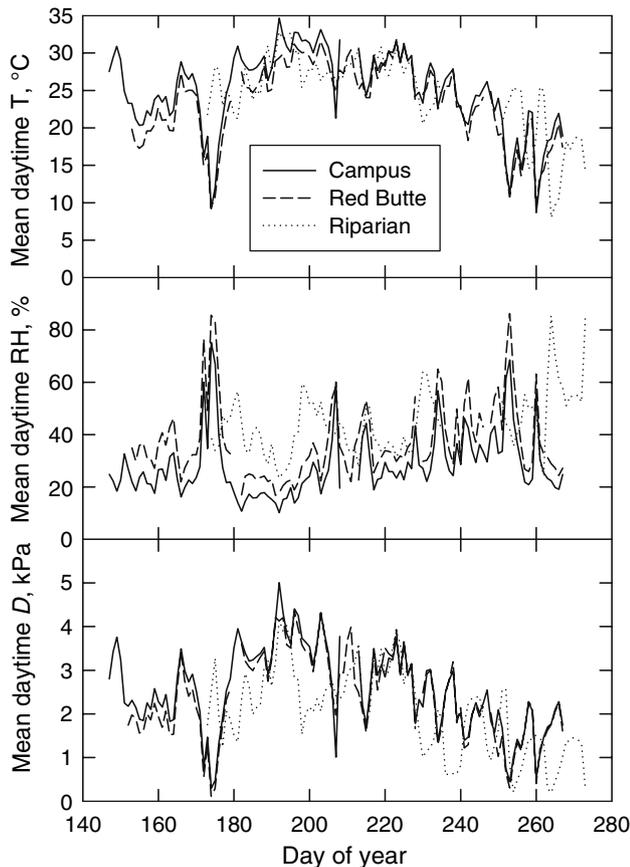


Fig. 1 Daytime average temperature (T), relative humidity (RH), and vapor pressure deficit (D) at each site during the study period. The Campus and Red Butte sites were measured in 2003 and the Riparian site was measured in 2004

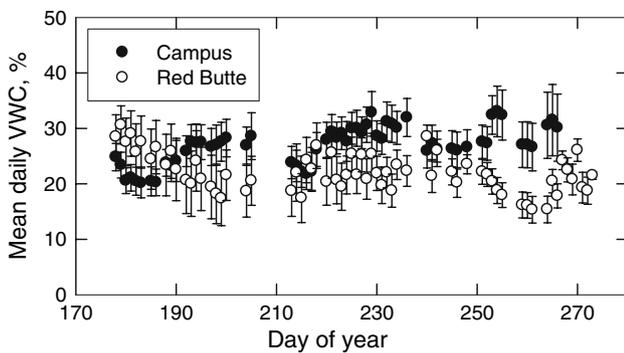


Fig. 2 The seasonal course of volumetric water content (VWC) from 0–30 cm for the two irrigated sites. Data are shown \pm SE

measurement period based on measurements from an onsite piezometer.

Measured predawn water potential showed some variation over the course of the measurement period (Fig. 3), with all species showing some decline by September. However, the absolute values remained relatively positive and ranged between -0.3 and -0.8 MPa (Fig. 3). There

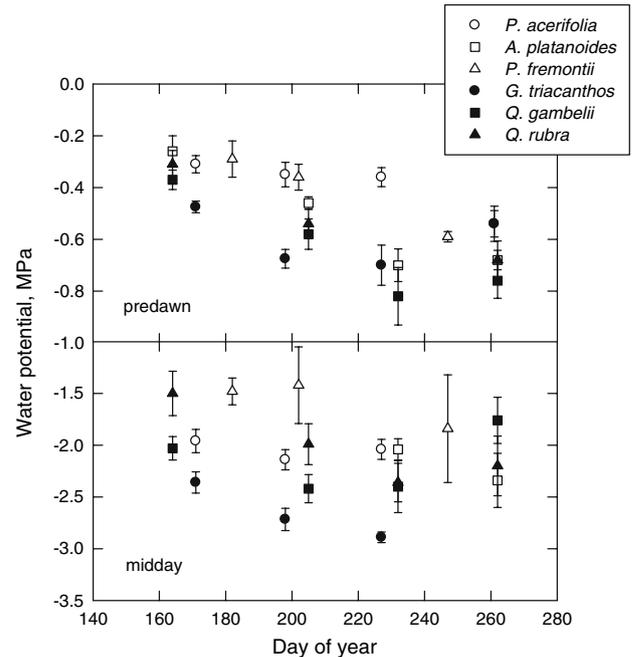


Fig. 3 The seasonal course of predawn and midday water potential measurements. All species were measured in 2003 except *Populus fremontii*, which was measured in 2004. Ring-porous species are shown with closed symbols and diffuse-porous species are shown with open symbols. Error bars represent the SE

were no differences between June and July measurement periods for all species (ANOVA, $P > 0.05$) except *G. triacanthos*, which showed a small mean difference of 0.2 MPa (ANOVA, $P < 0.05$). The largest mean difference observed for any species over the entire measurement period was 0.45 MPa for *Q. gambelii* between June and August. Midday leaf water potentials did not show a clear seasonal pattern and ranged from -1.5 to -3 MPa (Fig. 3). Both predawn and midday water potential were more negative in ring-porous than diffuse-porous species (predawn, -0.63 ± 0.03 and -0.45 ± 0.02 MPa; midday, -2.2 ± 0.08 and -1.6 ± 0.08 MPa; $P < 0.05$). There were no significant differences among species within wood anatomy groups (ANOVA, $P > 0.05$).

Species differed in both the magnitude and the seasonal variation of J_s . The diffuse-porous species showed high J_s in the outer 20 mm of sapwood, but also showed large declines during the growing season for *P. acerifolia* and *A. platanoides* (Fig. 4). In contrast, J_s of *G. triacanthos*, *Q. gambelii*, and *Q. rubra* was relatively low and constant throughout the season (Fig. 4). These species differences appeared to be related to two distinct patterns of responses of daily J_s to average daytime D . In diffuse-porous species, seasonal declines in J_s were related to the seasonal decline in D , in that J_s of diffuse-porous species was closely correlated with D (Fig. 5). Surprisingly, even at the highest D , the diffuse-porous trees showed very little stomatal control

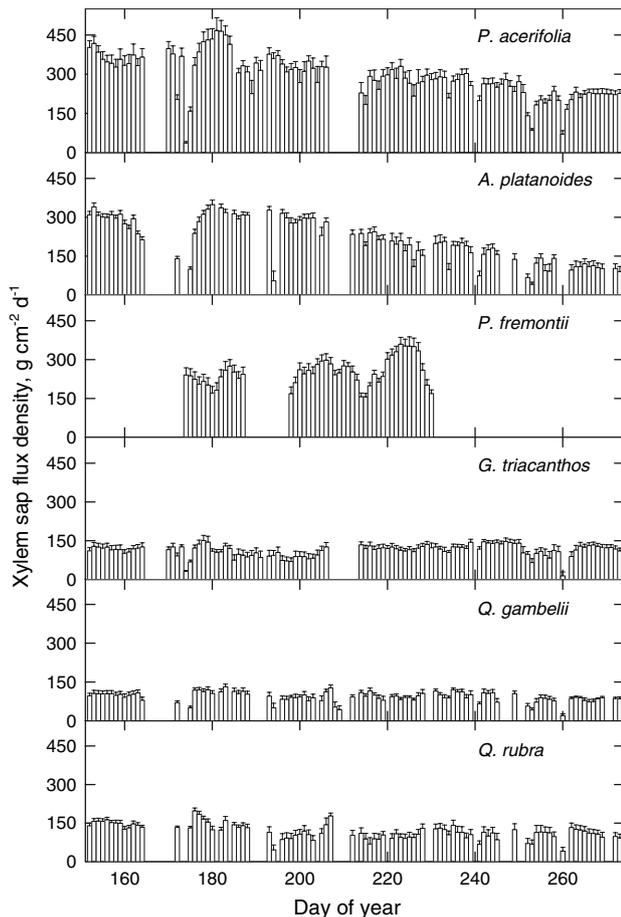


Fig. 4 Average daily sap flux density during the growing season for each species. All species were measured during the 2003 growing season except *P. fremontii*, which was measured in 2004. Error bars represent the SE. *d* Day

of transpiration as evidenced by the linearity of the J_s response to D . However, a reduction in J_s was observed for diffuse-porous species as the growing season progressed (Fig. 5). In contrast, ring-porous species showed a saturating response to increasing D , reaching maximum J_s near D values that are commonly associated with the maximum D in mesic ecosystems, around 2 kPa. Additionally, maximum J_s of ring-porous trees did not show any appreciable decline over the course of the growing season (Fig. 5). There was a significant decline in calculated in situ hydraulic conductance of *P. acerifolia* between June and July and *A. platanooides* between August and September (paired t -test, $P < 0.05$; Table 2). The other species did not show significant declines in hydraulic conductance between sampling periods.

There has been some discussion about the appropriate methodology for applying sap flux measurements to ring-porous trees (Clearwater et al. 1999; Granier et al. 1994). The basis for methodological concerns is twofold. First, large radial differences in the J_s along the sensor length

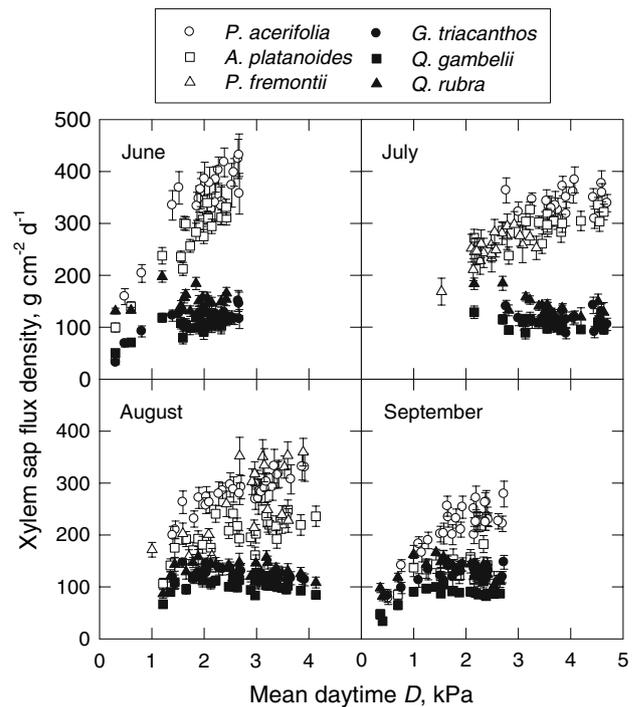


Fig. 5 Average daily sap flux density for diffuse-porous (open symbols) and ring-porous (closed symbols) species in response to average daytime D for June, July, August, and September

may lead to errors in interpreting and scaling measurements to whole trees, and to comparing species with contrasting wood anatomy. Radial trends have been reported for ring-porous species, although results have not always been consistent (Clearwater et al. 1999; Lu et al. 2004; Phillips et al. 1996). A related issue is whether J_s is underestimated in ring-porous trees if transpiration is concentrated largely in the current year vessels, which is difficult to measure. While more information is needed to resolve these issues, several studies have shown good agreement between sap flux measurements in ring-porous trees and independent measurements of transpiration including ventilated chambers and stem water absorption (Goulden and Field 1994; Granier et al. 1994). Regardless of this, systematic underestimation of sap flux in the ring porous species in this study would not explain the saturating response at high D if errors in estimating sap flux of ring-porous trees are independent of D . Differences in stomatal responses to humidity were also observed with independent leaf-level gas exchange measurements (Fig. 6). There was a linear increase in transpiration in response to increasing D for diffuse-porous *P. acerifolia* ($P < 0.001$; Fig. 6), but no response to increasing D for ring-porous *Q. rubra* ($P > 0.1$; Fig. 5).

Vulnerability to cavitation measurements also showed two categories of responses to decreasing water potential. In ring-porous species, lower relative hydraulic

Table 2 Hydraulic conductance (means \pm SE) estimated from midday sap flux and the difference between predawn and midday water potential

Species	Day of year	Hydraulic conductance ($\text{g m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$)
<i>P. acerifolia</i> ^a	171	84.1 \pm 15.0
	198	28.1 \pm 7.0
	227	31.3 \pm 5.4
	261	47.5 \pm 11.0
<i>A. platanoides</i> ^a	232	50.8 \pm 8.2
	262	28.2 \pm 5.6
<i>P. fremontii</i> ^a	182	22.7 \pm 7.5
	202	50.3 \pm 3.0
<i>G. triacanthos</i> ^b	171	19.1 \pm 2.5
	198	11.4 \pm 2.5
	227	15.1 \pm 2.9
<i>Q. gambelii</i> ^b	164	13.0 \pm 0.9
	205	18.8 \pm 1.8
	232	19.6 \pm 3.9
	262	39.8 \pm 12.2
<i>Q. rubra</i> ^b	164	21.4 \pm 0.8
	205	20.1 \pm 0.3
	232	25.0 \pm 2.7
	262	28.2 \pm 5.8

^a Diffuse-porous species

^b Ring-porous species

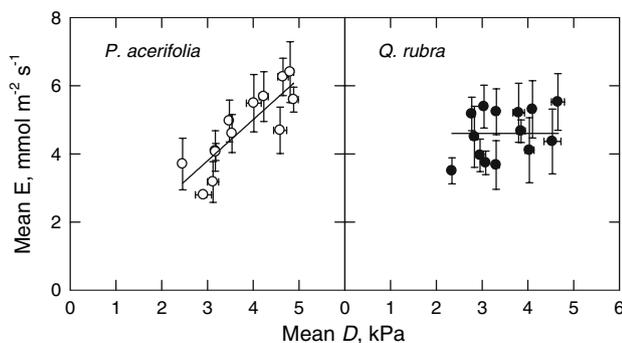


Fig. 6 Leaf-level transpiration (E) for diffuse-porous (*Platanus acerifolia*; left panel) and ring-porous (*Quercus rubra*; right panel) trees in response to ambient D conditions. The slope of the relationship between transpiration and D was significant for *P. acerifolia* ($P < 0.001$), but not for *Q. rubra* ($P = 0.168$)

conductance was sustained at negative stem water potentials than in diffuse-porous species (Fig. 7, upper panel). In addition, stem area-specific conductivity for ring-porous species showed higher potential conducting efficiency at the cost of increased vulnerability to cavitation, whereas diffuse-porous species showed less vulnerability to cavitation at the cost of lower potential conducting efficiency

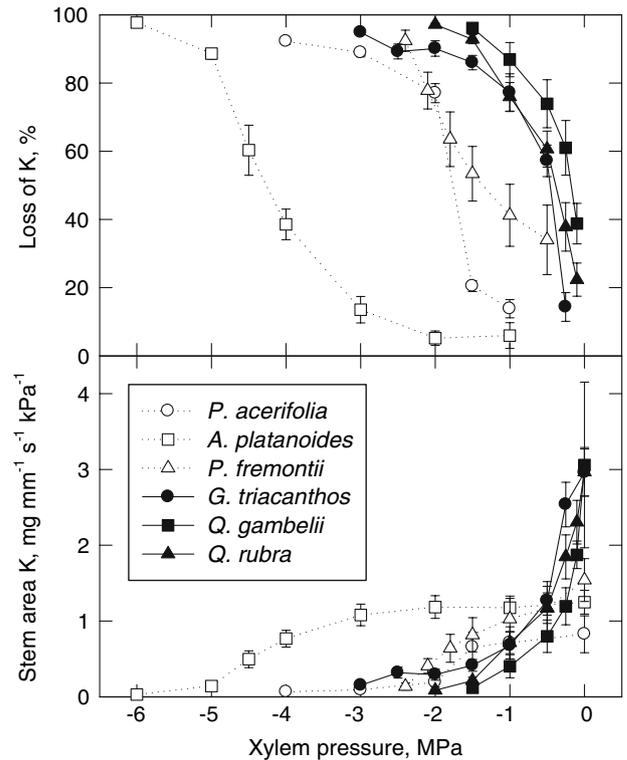


Fig. 7 The cavitation vulnerability of xylem (upper panel) and absolute stem area specific hydraulic conductance (lower panel) for diffuse-porous (open symbols) and ring-porous (closed symbols) species with increasing xylem tension

(Fig. 7, lower panel). Differences among species within a given wood type were also observed, particularly for diffuse-porous species. However, the categorically different responses observed between wood types were not driven by any single species, as all diffuse-porous species showed a more gradual change in % loss conductivity and stem area-specific conductivity with decreasing xylem pressure relative to ring-porous species, particularly between 0 and -0.5 MPa (Fig. 7).

Discussion

Our results show two categories of J_s responses to D across wood anatomy types that we attribute to differences in stomatal sensitivity to D , with the most pronounced differences occurring at D values that exceed those generally found in the native range of mesic trees (Fig. 5). In general, previous studies of the response of transpiration to D have been associated with a relatively small D range. Our measured J_s rates are comparable to previously measured values of J_s under conditions of low D (Hultine et al. 2007; Bovard et al. 2005; Catovsky et al. 2002; Oren and Pataki 2001; Oren et al. 1999; Pataki and Oren 2003; Phillips et al.

1996). However, the small range in D associated with most previous sap flow measurements as well as studies of stomatal responses of leaves to D (e.g., Franks and Farquhar 1999) has made it difficult to determine whether there are clear differences in the sensitivity of ring vs. diffuse-porous trees. While there is some indication of differences in stomatal sensitivity to D among diffuse vs. ring-porous species at low D (Oren and Pataki 2001; Oren et al. 1999), a survey of the available literature yields limited results because of the lack of data of stomatal responses of ring-porous species to very high D exceeding 3 kPa. Additional measurements in a broader range of taxa and biomes are needed to confirm the generality of these results; however, they are supported by observed patterns in the distribution of the species. In semi-arid environments, riparian trees currently overwhelmingly comprise diffuse-porous species. Our results suggest that this is a competitive advantage: diffuse-porous species can maintain high rates of stomatal conductance and therefore continue photosynthesis under highly desiccating atmospheric conditions.

Independent leaf-level transpiration measurements showed patterns of transpiration response to increasing D that were similar to those obtained with J_s measurements (Figs. 5, 6). While differences in the magnitude of transpiration were observed at the leaf scale relative to the whole plant scale (Figs. 5, 6), likely attributable to methodological or scaling factors (particularly variations in leaf–sapwood area ratios), the pattern of response to increasing D (linear for diffuse-porous and saturating for ring-porous) remained consistent. These results provide further evidence that the observed patterns of J_s in response to D result from differences in stomatal sensitivity to D between wood anatomy types. However, additional measurements of leaf-level transpiration will be needed to determine the extent of this response at smaller temporal and spatial scales.

The contrasting patterns of J_s with increasing D shown by ring and diffuse-porous trees are likely related to differences in the vulnerability of these species to xylem cavitation (Fig. 7). The notion that there may be a safety versus efficiency tradeoff in xylem transport that is related to the size of conducting xylem conduits has long been proposed (Tyree and Zimmerman 2002). Larger diameter conduits have the capacity for greater efficiency in sap transport, while smaller diameter conduits are generally more resistant to xylem cavitation events. While the exact mechanisms are still the focus of ongoing research, differences in vulnerability to cavitation between ring and diffuse-porous species were recently described by Hacke et al. (2006) and Li et al. (2007) and confirmed here (Fig. 7). Hence, diffuse-porous trees can tolerate the negative water potentials that develop in xylem when stomata remain open at high D . These differences may not be

manifested in bulk leaf midday water potential, which did not differ greatly among the taxa (Fig. 3). Our results also cannot be explained by age differences among species, as there were no systematic differences in age between ring and diffuse-porous species in this study.

The consequence of lack of stomatal regulation in diffuse-porous trees was that some cavitation was apparent by late summer, as evidenced by reduced rates of J_s (Figs. 4, 5) and a relatively constant predawn to midday water potential difference resulting in lower values of calculated, in situ hydraulic conductance (Table 2). There was little indication of progressive soil drought during the growing season that would have caused additional water stress. While there was a small decline in predawn water potential at both of the landscaped sites as the growing season progressed, this decline was unlikely to account for the reduced J_s rates, as the timing of the change in water potential and J_s did not coincide. Additionally, nighttime transpiration precludes the use of predawn water potential measurements as a proxy for soil water potential, which would also introduce errors into the calculation of hydraulic conductance. There was some evidence of nighttime sap flow during the study period (data not shown); during these periods, ΔT_m from Eq. (1) was prescribed from earlier periods when D approached zero, as in Daley and Phillips (2006). However, despite the difficulty in estimating effective plant soil water potential and hydraulic conductance in semi-arid environments, progressive cavitation resulting from lack of stomatal regulation of water loss seems to be the best explanation for the change in the relationship between J_s and D in diffuse-porous species late in the growing season.

Previous studies have suggested deeper rooting in ring-porous than in diffuse-porous trees (Abrams 1990; Burns and Honkala 1990; Pallardy and Rhoads 1993), although this has been difficult to quantify in mixed species stands. In our study, there was little evidence of deeper rooting in ring-porous species, as predawn water potential was more rather than less negative in ring-porous compared to diffuse-porous trees (Fig. 2). However, the absolute differences among taxa were small and water potentials remained relatively high due to irrigation. Here, we show that differences in J_s responses to D persist in the absence of large differences in access to water among the taxa. In addition, our results suggest that a tendency for ring-porous trees to be more deeply rooted would be advantageous given their more vulnerable transport system. The degree to which ring-porous species systematically have deeper rooting distributions relative to diffuse-porous species as a consequence of differences in cavitation vulnerability is not known and warrants further study. In addition, the diffuse-porous species measured in this study had consistently greater sapwood depths than the ring-porous species

(Table 1), which may be an additional mechanism for coping with water stress. In particular, root-to-sapwood area and leaf-to-sapwood area ratios are important aspects of allometry that may govern plant responses to water stress; however, they are very difficult to measure in mature trees. Additional data are needed across the taxa to determine if variations are consistent by wood type.

From a whole ecosystem perspective, our results suggest that changes in D due to altered temperature and/or humidity would have different effects on ring and diffuse-porous species. Provided that soil moisture is not limiting, an increase in D would correspond to increased water vapor fluxes from forested areas dominated by diffuse-porous trees, whereas transpiration of forests dominated by ring-porous trees would show little change. In the long-term, sustained shifts in average D may ultimately impact competition for water resources and affect the distribution of species.

In general, models of stomatal response to humidity have relied on empirical parameters to describe a phenomenon that is well understood mechanistically (Buckley 2005). It is well known that stomatal closure at decreasing humidity is a mechanism to regulate plant water status and avoid damaging effects of water stress such as excessive cavitation (Sperry 2000; Sperry et al. 1998). This mechanism has not been incorporated into most ecological and land surface models because vulnerability to cavitation has been described as highly species specific and difficult to generalize across broad functional classes. Here we provide evidence that stomatal response to humidity may indeed be predictable based on functional types of two broad classes of deciduous trees. While these results apply specifically to conditions of high soil moisture, they provide a basis for describing the maximum rate of transpiration under non-limiting soil moisture, but varying atmospheric conditions.

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