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Research paper

Transpiration sensitivity of urban trees in a semi-arid climate is constrained by xylem vulnerability to cavitation

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Establishing quantitative links between plant hydraulic properties and the response of transpiration to environmental factors such as atmospheric vapor pressure deficit (*D*) is essential for improving our ability to understand plant water relations across a wide range of species and environmental conditions. We studied stomatal responses to *D* in irrigated trees in the urban landscape of Los Angeles, California. We found a strong linear relationship between the sensitivity of tree-level transpiration estimated from sap flux (m_T; slope of the relationship between tree transpiration and ln *D*) and transpiration at $D = 1$ kPa (E_{Tref}) that was similar to previous surveys of stomatal behavior in natural environments. In addition, m_T was significantly related to vulnerability to cavitation of branches (P_{50}). While m_T did not appear to differ between ring- and diffuse-porous species, the relationship between m_T and P_{50} was distinct by wood anatomy. Therefore, our study confirms systematic differences in water relations in ring- versus diffuse-porous species, but these differences appear to be more strongly related to the relationship between stomatal sensitivity to *D* and vulnerability to cavitation rather than to stomatal sensitivity per se.

Keywords: **stomatal control, xylem embolism.**

Introduction

Plant gas exchange and water transport are known to be linked through stomatal regulation (Sperry 2000, Meinzer 2002, Brodribb 2009). With leaf stomata open, plant transpiration (*E*) is driven by physical tension created by leaf water evaporation. Under tension, continuous water columns move through xylem tissue from roots to leaves. Microscopic air bubbles may penetrate into xylem water that is under tension and disable xylem conduits, phenomena known as xylem cavitation and air embolism (Sperry and Tyree 1988, Tyree and Sperry 1989, Tyree and Zimmermann 2002). While stomatal closure prevents the failure of water transport in plants (Sperry and Pockman 1993, Sperry et al. 1998, Sperry 2000), it also reduces photosynthetic rates—a trade-off that has important implications for plant function and growth (Kramer and Boyer 1995, Meinzer et al. 2001, Hubbard et al. 2001, Brodribb 2009), particularly under drought stress (Sperry 2000).

Vulnerability to cavitation varies greatly among species and vegetation types (Maherali et al. 2004). In particular, vascular species with diffuse-porous wood, bearing relatively uniform xylem vessels, generally exhibit greater resistance to cavitation than ring-porous species that develop longer and wider vessels in the beginning of the growing season (Hacke et al. 2006, Li et al. 2008, Taneda and Sperry 2008). Different hydraulic architectures and vulnerabilities to cavitation place different safety limits on *E* (Tyree and Zimmermann 2002) and therefore imply different stomatal strategies. Consistent with this premise, Bovard et al. (2005) (in a northern mixed forest in Michigan) and Bush et al. (2008) (in riparian and irrigated trees in Utah) found systematically stronger stomatal sensitivity to atmospheric vapor pressure deficit (*D*) in ring-porous trees that were also more vulnerable to xylem cavitation, compared with diffuse-porous trees that were less vulnerable to xylem cavitation.

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Stomatal responses to *D* also vary greatly within and between species (Oren et al. 1999, Pataki and Oren 2003). Oren et al. (1999) showed that species with greater stomatal sensitivity (i.e., whose stomatal conductance rapidly decreases in response to increasing *D*) exhibit systematically higher stomatal conductance at low *D*. They established a linear relationship between stomatal conductance at $D = 1$ (referred to as reference conductance) and stomatal sensitivity of a variety of species, therefore systematizing a wide range of stomatal behaviors. However, predicting stomatal sensitivity based on hydraulic properties of a plant remains a major challenge (Sperry 2000, Oren and Pataki 2001, Pataki and Oren 2003, Maherali et al. 2006). There is a great demand for quantitative links between plant hydraulic properties and stomatal sensitivities that would improve our understanding and predictive ability of the patterns of plant transpiration. For example, Novick et al. (2009) found that the product of sapwood-to-leaf area and the inverse of canopy height can be a good predictor of reference canopy conductance on a large spatial scale across many species and biomes. Currently, quantifying plant transpiration and stomatal sensitivity requires long-term field campaigns involving sap flux measurements (Granier et al. 1996, Köstner et al. 1998, Lu et al. 2004) or eddy covariance (Baldocchi et al. 1988, Greco and Baldocchi 1996, Wilson et al. 2001). Both methods can be logistically challenging (Burba and Anderson 2005, Pataki et al. 2011). On the other hand, determining stem hydraulic properties involves relatively brief field surveys and laboratory measurements (Sperry et al. 1988, Alder et al. 1997).

In this paper, we build on previous efforts to establish quantitative relationships between hydraulic properties and stomatal behavior across species. A major challenge to finding such relationships is the natural exposure of different groups of species to different environmental conditions, especially different ranges of *D* that do not allow for direct comparison. Bush et al. (2008) overcame this limitation by utilizing an urban forest in Salt Lake City, Utah as a 'common garden,' where species originating from different habitats were grown in the same well-irrigated setting. We used a similar approach by studying the biologically diverse, irrigated urban forest in the Los Angeles metropolitan area, California, where many tree species originating from a variety of habitats are exposed to similar (and relatively large) ranges of *D*.

To quantify stomatal responses to atmospheric evaporative demand, we evaluated transpiration sensitivity, i.e., the change in transpiration in response to increasing *D*. We asked the following questions: (i) In irrigated urban trees, is transpiration sensitivity linearly related to transpiration at low *D*, similar to the relationship reported for natural forests by Oren et al. (1999)? (ii) For species in the Los Angeles metropolitan area, is transpiration sensitivity systematically different between ring-porous and diffuse-porous trees, as reported in previous studies of urban forests (Bush et al. 2008, Peters et al. 2010)? (iii) Can transpiration sensitivity be predicted based on hydraulic properties such as wood anatomy and vulnerability to cavitation? Based on the generality and strong theoretical foundation of the relationship suggested by Oren et al. (1999), we expected transpiration sensitivity of irrigated urban trees to be proportional to tree transpiration at $D = 1$ kPa. After Bush et al. (2008), we hypothesized that transpiration sensitivity of diffuse-porous trees is generally larger than ring-porous trees. Finally, we hypothesized that within each wood anatomy type, species with more vulnerable xylem would have more stomatal control that would help prevent excessive cavitation (Sparks and Black 1999, Martinez-Vilalta et al. 2004, Poyatos et al. 2008). To test these hypotheses, we coupled sap flux measurements of five ring-porous and five diffuse-porous tree species with records of atmospheric *D* within the canopy and laboratory estimates of hydraulic conductivity and vulnerability to cavitation of branches.

This work has implications both for better understanding plant water relations, and for planning and management of urban forests in semi-arid environments. The ability to assess *E* and its responses to *D* across a wide range of species can inform decisions about appropriate landscape species based on potential water needs.

Methods

Study sites

This study was conducted in the Los Angeles Basin, which is a coastal plain in southern California surrounded by mountain ranges. The climate is classified as Mediterranean with annual temperatures of 17.0–18.3 °C and annual precipitation of 32.6–37.7 cm, which mostly occurs in winter and spring (Western Regional Climate Center, http://www.wrcc.dri.edu).

For quantifying sap flux and transpiration, we chose mature trees commonly planted in southern California and growing in groups that allowed for sufficient replication. The study trees were located at eight well-irrigated sites and one riparian site. Previous studies have shown that soil moisture remained high at these sites and trees did not experience significant water stress (McCarthy and Pataki 2010, Litvak et al. 2011). Trees were originally planted at low density and were open grown, without canopy closure.

In 2007, we measured sap flux at the following four locations: campus of the University of California, Irvine (33°38′N, 117°50′W), Los Angeles Zoo and Botanical Gardens (34°08′N, 118°17′W), residential street in the city of Los Angeles (34°04′N, 118°20′W) and Audubon Starr Ranch Sanctuary (33°37′N, 117°33′W). We will refer to the first site as 'Campus-07.' This site was called 'Irrigated' in McCarthy and

Pataki (2010) and 'Campus' in Pataki et al. (2011). It contained *Pinus canariensis* C. Sm. (Canary Island pine) and *Platanus racemosa* Nutt. (California sycamore), with groundcover comprised of turfgrass, ivy (*Hedera helix* L.) and ice plant (*Carpobrotus chilensis* (Molina) N. E. Br.). The site received regular irrigation from automated sprinklers. The second site was located at the Los Angeles zoo ('Los Angeles zoo' in Pataki et al. 2011). The plot contained *Jacaranda mimosifolia* D. Don. (blue jacaranda) with herbaceous understory. At the third, Street trees site ('Street trees' in McCarthy and Pataki (2010) and Pataki et al. (2011)), *P. racemosa* and *Platanus hybrida* Brot. (London plane) were growing in sidewalk insets along a residential city street. Although these trees were not irrigated, they apparently received indirect water inputs with the lateral flow from residential lawns and backyards, as they showed continually high transpiration (McCarthy et al. 2011). The fourth study site is 'Starr Ranch' ('Natural' site in McCarthy and Pataki 2010), located near a creek in Starr Ranch Sanctuary and contained naturally growing riparian *P. racemosa* and *Quercus agrifolia* Nee. (coast live oak). Both tree species are native to southern California. The site was neither irrigated nor fertilized, as it is preserved as a wildlife sanctuary. However, nearby urbanized areas may have provided additional water inputs through lateral flow of urban runoff (Bijoor et al. 2012).

In 2008, we collected sap flux data from five additional study sites. These were located at the Fullerton Arboretum (33°53′N, 117°53′W), Los Angeles Police Academy (34°04′N, 118°14′W), campus of University of California, Irvine (33°38′N, 117°50′W) and Los Angeles Arboretum and Botanic Garden, Arcadia (34°08′N, 118°03′W). The first of these sites, located at the California State University Fullerton Arboretum ('Fullerton' in Litvak et al. 2011), contained a grove of irrigated *Sequoia sempervirens* D. Don. (coast redwood) grown as a single species stand with no understory along an artificial creek. The second site was located in an irrigated, hillside recreational rock garden at the Los Angeles Police Revolver and Athletic Club ('LA Police Academy' in Pataki et al. (2011) and 'Los Angeles' in Litvak et al. (2011)) and contained *P. canariensis*, *S. sempervirens*, and *Ulmus parvifolia* Jacq. (Chinese elm) with an understory of herbaceous plants and shrubs. The third site is 'Campus-08'; 'Irvine' in Litvak et al. (2011). This site was located across the street from Campus-07, on both sides of a drainage channel, and contained irrigated *Eucalyptus grandis* W. Hill ex Maiden (grand eucalyptus) and *S. sempervirens*, along with a tall herbaceous and shrubby understory. Two additional sites were located at the Los Angeles Arboretum (site A and site SA in Pataki et al. (2011) and site A and site B in McCarthy et al. (2011)). Site A contained tree species from Australia: *Brachychiton discolor* F. J. Muell (lacebark), *Brachychiton populneus* Schot & Endl. (kurrajong) and *E. grandis*. Site SA contained *Jacaranda chelonia* Griseb., native to South America, along with *Lagerstroemia indica* L. (crape myrtle), *Koelreuteria paniculata* Laxm. (goldenrain), *Ficus microcarpa* L. (laurel fig) and *Gleditsia triacanthos* L. (honey locust). Both sites at the Los Angeles Arboretum were irrigated, had little or no understory and contained some other isolated tree species without sufficient replication for sap flow measurements.

We divided studied tree species into functional groups based on their wood anatomy. In addition to angiosperm trees with ring-porous and diffuse-porous wood, we studied one species with semi-ring-porous wood (*F. microcarpa*) that is characterized by few wide vessels declining to narrower ones in every growth ring (Coder 1999). We also considered *Brachychiton* species as a separate group because these Australian species develop spongy sapwood comprised of wide vessels (Choat et al. 2005). Trees with coniferous wood were represented by *P. canariensis* and *S. sempervirens*. The characteristics of studied trees are summarized in Table 1.

Sap flux and D measurements

Sapflux was measured in the outer 2 cm of sapwood in 3–12 mature trees of each species (Table 1) in spring through winter of 2007 and 2008, using thermal dissipation probes (Granier 1987). For most trees, we installed sap flux sensors at a height of 1.35 m (breast height), but higher (up to 5 m) for street trees and some trees in public parks to avoid vandalism. At the end of the measurement period, we cored those trees at both breast and sensor heights, and multiplied measured sap flux by the ratio of sapwood area at sensor height to sapwood area at breast height to convert to breast height sap flux. Along with sap flux, we measured temperature and relative humidity at 1/3 to 1/2 of the canopy height (HMP45C, Vaisala Inc., Helsinki, Finland) to determine vapor pressure deficit in the canopy (D_T, or tree level, light-day averaged *D*). Measurements were taken by dataloggers (CR10X, CR1000 and CR3000, Campbell Scientific Inc., Logan, UT, USA) every 30 s, and the average values recorded every 30 min. We calculated the sap flux density in the outer 2 cm of sapwood (J_O, g cm^{-2} s^{-1}) using an empirical relationship after Granier (1987):

$$J_O = 119\left(\frac{\Delta T_{max} - \Delta T}{\Delta T}\right)^{1.231}, \quad (1)$$

where ΔT is the measured temperature difference between heated and reference sensors, and ΔT_{max} was measured at night when there was no sap flux. We assumed that only ΔT_{max} measured at $D_T \leq 0.2$ kPa corresponded to zero sap flow. To account for possible non-zero flow at nights with $D_T > 0.2$ kPa, we applied ΔT_{max} from the previous night with zero sap flux.

Tree transpiration

We followed Pataki et al. (2011) to calculate whole tree transpiration. First, the depth of sap wood was visually determined from tree cores (except at the Los Angeles zoo, where we were not

Table 1. Characteristics of studied trees, including sample size (n); basal area at 1.35 m (A_B); sapwood area at 1.35 m (A_S); intercept and slope of the function $E_T = E_{Tref} + m_T \ln D_T$ as described in the text; intercept and slope of the function $E_L = E_{Lref} + m_L \ln D_L$ as described in the text; and xylem pressure at 50% of loss of branch hydraulic conductivity (P_{50}). See Appendix for the list of abbreviations.

Species	Notation	Study site	n	A_B (m^2)	A_S (m^2)	E_{Tref} (kg day^{-1})	m_T (kg day^{-1}(ln(kPa))$^{-1}$)	E_{Lref} (mmol m^{-2} s^{-1})	m_L (mmol m^{-2} s^{-1}(ln(kPa))$^{-1}$)	P_{50} (MPa)
Ring-porous										
Gleditsia triacanthos	GLTR	LA Arboretum site SA	3	0.15 ± 0.04	0.07 ± 0.02	86.2 ± 1.7	25.7 ± 2.7	3.64 ± 0.47	1.08 ± 0.15	–0.41 ± 0.02
Koelreuteria paniculata	KOPA	LA Arboretum site SA	4	0.06 ± 0.01	0.05 ± 0.01	63.0 ± 1.2	25.6 ± 1.9	0.98 ± 0.14	1.03 ± 0.10	–0.42 ± 0.11
Lagerstroemia indica	LAIN	LA Arboretum site SA	6	0.02 ± 0.00	0.02 ± 0.00	41.0 ± 0.4	14.8 ± 0.7	1.59 ± 0.14	0.48 ± 0.09	–0.58 ± 0.10
Quercus agrifolia	QUAG	Starr Ranch	7	0.11 ± 0.04	0.03 ± 0.01	8.2 ± 0.2	3.9 ± 0.3	—	—	–0.58 ± 0.06
Ulmus parvifolia	ULPA	Police Academy	5	0.06 ± 0.01	0.06 ± 0.01	49.3 ± 0.6	19.8 ± 0.9	—	—	–0.31 ± 0.11
Diffuse-porous										
Eucalyptus grandis	EUGR-1	Campus-08	6	0.38 ± 0.11	0.06 ± 0.01	9.3 ± 0.1	3.9 ± 0.2	—	—	—
	EUGR-2	LA Arboretum site A	4	0.33 ± 0.06	0.07 ± 0.01	44.5 ± 1.0	17.0 ± 1.3	1.64 ± 0.24	—	—
Jacaranda chelonia	JACH	LA Arboretum site SA	3	0.07 ± 0.01	0.07 ± 0.01	63.2 ± 1.2	44.2 ± 1.7	4.01 ± 0.25	–1.03 ± 0.19	–1.17 ± 0.26
Jacaranda mimosifolia	JAMI	Los Angeles zoo	6	0.02 ± 0.00	0.02 ± 0.00	10.1 ± 0.2	2.8 ± 0.2	—	—	–2.10 ± 0.64
Platanus hybrida	PLHY	Street trees	4	0.21 ± 0.06	0.09 ± 0.02	119.3 ± 1.8	71.7 ± 3.6	—	—	–1.09 ± 0.15
Platanus racemosa	PLRA-1	Starr Ranch	8	0.14 ± 0.03	0.06 ± 0.01	22.1 ± 0.7	14.2 ± 1.0	—	—	–2.00 ± 0.18
	PLRA-2	Campus-07	5	0.13 ± 0.02	0.08 ± 0.01	48.9 ± 0.8	30.7 ± 1.6	—	—	–1.48 ± 0.30
	PLRA-3	Street trees	3	0.11 ± 0.01	0.08 ± 0.01	85.7 ± 0.8	46.6 ± 1.7	—	—	–1.79 ± 0.17
Semi-ring-porous										
Ficus microcarpa	FIMI	LA Arboretum site SA	4	0.08 ± 0.01	0.08 ± 0.01	91.1 ± 1.2	27.2 ± 1.8	1.38 ± 0.09	0.30 ± 0.07	–0.74 ± 0.15
Brachychiton spp.										
Brachychiton discolor	BRDI	LA Arboretum site A	12	0.23 ± 0.05	0.05 ± 0.01	18.3 ± 0.2	11.2 ± 0.3	0.62 ± 0.08	0.77 ± 0.08	–0.27 ± 0.04
Brachychiton populneus	BRPO	LA Arboretum site A	9	0.11 ± 0.02	0.03 ± 0.00	9.8 ± 0.1	6.8 ± 0.2	—	—	–0.74 ± 0.24

Coniferous										
Pinus canariensis	PICA-1	Police Academy	5	0.24 ± 0.04	0.20 ± 0.03	41.0 ± 0.6	5.2 ± 0.9	—	—	−5.74 ± 0.18
	PICA-2	Campus-07	5	0.20 ± 0.02	0.17 ± 0.01	52.5 ± 0.8	16.1 ± 1.4	—	—	−5.26 ± 0.46
Sequoia sempervirens	SESE-1	Police Academy	5	0.11 ± 0.04	0.04 ± 0.01	9.9 ± 0.1	3.5 ± 0.2	—	—	−4.11 ± 0.59
	SESE-2	Campus-08	8	0.12 ± 0.02	0.04 ± 0.01	37.1 ± 0.3	8.5 ± 0.4	—	—	−5.93 ± 0.63
	SESE-3	Fullerton Arboretum	9	0.15 ± 0.04	0.05 ± 0.01	24.5 ± 0.2	10.8 ± 0.3	—	—	−5.75 ± 0.48

allowed to core trees, so we instead estimated their sapwood depth from empirical relationships obtained from similar trees in a different location). Then, to account for radial trends in sap flux, we considered sapwood depth as a set of 2 cm increments (with the last increment usually accounting for a remainder smaller than 2 cm), and applied generalized Gaussian functions (Pataki et al. 2011) to estimate the sap flux density in each increase for angiosperms as

$$J_i = 1.033 J_O \exp\left(-0.5\left(\frac{x - 0.09963}{0.4263}\right)^2\right), \quad (2)$$

and for gymnosperms as

$$J_i = 1.257 J_O \exp\left(-0.5\left(\frac{x + 0.3724}{0.6620}\right)^2\right). \quad (3)$$

Here x is the normalized depth of each sapwood increment ($0 \leq x < 1$), J_O is determined using Eq. (1) and J_i is the corresponding sapflux density. We calculated whole tree transpiration (E_T, kg day^{-1}) by summing sapflux densities in all depth increases:

$$E_T = 10^{-3} \sum_{i=0}^{n} A_i J_i, \quad (4)$$

where A_i are sapwood areas of each depth increase in cm^2.

We modeled tree transpiration as a linear function of the logarithm of D_T, with the slope m_T (kg day^{-1}(ln(kPa))$^{-1}$) representing sensitivity of E_T to D_T and the intercept E_{Tref} representing transpiration at $D_T = 1$ kPa:

$$E_T = E_{Tref} + m_T \ln(D_T). \quad (5a)$$

We tested whether the model parameters E_{Tref} and m_T are linearly correlated, in agreement with Oren et al. (1999). Unlike the previous study, we considered E_T instead of canopy conductance to avoid autocorrelation between the modeled parameters (Monteith 1995, Oren et al. 1999, Novick et al. 2009).

Leaf gas exchange

We measured leaf gas exchange in July 2008 in the Los Angeles Arboretum at site A on *B. discolor* and *E. grandis*, and at site SA on *J. chelonia*, *L. indica*, *K. paniculata*, *F. microcarpa* and *G. triacanthos*. We obtained VPD-response curves using a portable gas exchange system (LI6400, LI-COR Inc., Lincoln, NE, USA) on one sun-exposed leaf from each of three representative mature individuals of each species. We evaluated the responses of leaf-level transpiration (E_L, mmol m^{-2} s^{-1}) to D near leaf surfaces (D_L, kPa) by gradually increasing D_L from

1.6 ± 0.2 to 4.0 ± 0.4 kPa (value ± SD). Each measurement of E_L was taken under stable leaf temperatures (25–30 °C) and saturating intensities of photosynthetically active radiation (1180–1500 μmol m^{-2} s^{-1}). We then modeled E_L as a function of D_L, similarly to tree-level transpiration:

$$E_L = E_{Lref} + m_L \ln(D_L), \quad (5b)$$

where the slope m_L (mmol m^{-2} s^{-1}(ln(kPa))$^{-1}$) is the sensitivity of E_L to D_L and intercept E_{Lref} is the transpiration at $D_L = 1$ kPa.

Vulnerability to cavitation

We collected straight ~20 cm branch segments within 6 m of the ground from six individuals of each tree species for which sap flux was measured (one sample per tree, with the exception of *E. grandis*, which had no branches at or below 6 m height). When the branches of fewer than six trees were accessible, we collected samples from similar trees growing nearby under similar conditions. In addition, in 2010–11 we collected branches from trees within the LA Arboretum that did not participate in sap flux measurements (Table 2). We only collected three branches per species (one branch per tree) because only three individuals were available.

The samples were brought to the laboratory in sealed plastic bags with wet paper towels and stored in the refrigerator for 1–6 days. Before measurements, samples were cut to the length of 14 cm, and the bark was shaved off at both ends. To assess vulnerability to cavitation, we first removed any potentially present emboli by running ultrapure water (Epure, Barnstead, Dubuque, IA, USA) at 14 psi through the samples for 1 h. The only species for which we omitted this step was *S. sempervirens* because its hydraulic conductivity declined in response to pushing water through its stems. Therefore, following Burgess et al. (2006), we collected the samples of this species after rainfall to minimize the degree of native embolism.

Table 2. Vulnerability to cavitation (P_{50}, xylem pressure at 50% loss of hydraulic conductivity) of tree branches from the Los Angeles Arboretum measured in 2010–11.

Species	Notation	P_{50} (MPa)
Ring-porous		
Albizia julibrissin Durazz.	ALJU	−0.89 ± 0.10
Citrus aurantium L.	CIAU	−1.41 ± 0.05
Citrus limon (L.) Burm.f.	CILI	−0.42 ± 0.01
Citrus sinensis (L.) Osbeck	CISI	−0.25 ± 0.08
Diffuse-porous		
Betula pendula Roth	BEPE	−2.09 ± 0.23
Casuarina obesa Miq.	CAOB	−1.39 ± 0.46
Cocculus laurifolius (Roxb.) DC.	COLA	−0.64 ± 0.06
Ficus burkei Miq. (Miq.)	FIBU	−1.12 ± 0.09
Liquidambar styraciflua L.	LIST	−2.80 ± 0.62
Magnolia grandiflora L	MAGR	−2.02 ± 0.46
Pittosporum undulatum Vent.	PIUN	−1.19 ± 0.29
P. racemosa	PLRA	−1.56 ± 0.02
Tabebuia chrysotricha (Mart. ex DC.) Standl.	TACH	−0.19 ± 0.02
Thevetia peruviana (Pers.) K. Schum.	THPE	−0.71 ± 0.18

We measured hydraulic conductivity after Sperry et al. (1988) by letting ultrapure water flow from an elevated reservoir through the samples to a container weighed by a precise balance (accuSeries, Fisher Scientific Inc., Waltham, MA, USA). The balance readings were logged to a computer every 5 s and used to calculate hydraulic conductivity of each sample. The stem area specific hydraulic conductivity (K, mg s^{-1} MPa^{-1} mm^{-2}) was obtained from the rate of water flow through the samples following Sperry et al. (1988). We then iteratively decreased K of each sample by applying centrifugal force to induce xylem cavitation (Alder et al. 1997), and assessed percent loss of K after each run in the centrifuge (Sorvall RC 5C Plus, Thermo Fisher Scientific Inc., Waltham, MA, USA). We stopped the process when percent loss of K reached ~100% or ceased increasing and determined the negative pressure at which 50% of K was lost (P_{50}) from vulnerability curves (Tyree and Sperry 1989).

Functional hydraulic conductivity

We measured functional K of 4–6 samples (one stem per tree) from *L. indica*, *J. chelonia*, *B. discolor* and *B. populneus* once a month from August to October 2008, and from *U. parvifolia* in August 2008. We collected the stems from 1:15 PM to 3:45 PM, transported them to the laboratory as described above and immediately measured functional K. For this, we placed samples (cut to the length of 14 cm with the bark shaved off at the ends) directly in the Sperry apparatus (Sperry et al. 1988). After measuring functional K, we flushed samples with ultrapure water for 1 h to remove the present emboli, and then measured K once again to estimate maximum conductivity.

Statistical methods

We fitted linear relationships between E_T and ln(D_T) (Eq. (5a)) for each tree at $\alpha = 0.05$ using R (version 2.10.1, R foundation for Statistical Computing, http://www.r-project.org). We determined whether the parameters varied by study site and wood type using analysis of variance (ANOVA) followed by Tukey's honest significance test (R version 2.10.1). We calculated P_{50} from the parameters of sigmoidal vulnerability curves for individual trees obtained with SigmaPlot (Version 10, Systat Software Inc., Chicago, IL, USA). To evaluate the effects of time, species and wood type on functional K and corresponding maximum K, we used repeated measures ANOVA followed by Tukey's honest significance test (R version 2.10.1). To test for homogeneity of slopes of the relationships $m_T(E_{Tref})$ and $m_T(P_{50})$ for ring-porous versus diffuse-porous trees, we applied two-level

ANCOVA (R version 2.10.1). Linear functions for $E_L(\ln D_L)$ (Eq. (5b)) and $m_L(P_{50})$ were fitted using SigmaPlot (Version 10, Systat Software Inc.).

Results

Tree and leaf transpiration

In both 2007 and 2008 D_T varied from ~0.1–0.2 to ~3.5–4.5 kPa. The maximum D_T in our record was 4.8 kPa in Los Angeles zoo in early September of 2007 (see Litvak et al. (2011), McCarthy and Pataki (2010) and Pataki et al. (2011) for detailed weather and soil moisture data). Daily E_T from the studied trees generally increased in response to increasing D_T. E_T varied from maxima of ~70 kg day^{-1} in *Brachychiton* species, ~100 kg day^{-1} in conifers, ~150 kg day^{-1} in ring-porous species, ~175 kg day^{-1} in semi-ring-porous *F. microcarpa* and ~260 kg day^{-1} in diffuse-porous species (Figure 1).

Leaf transpiration (E_L) generally increased in response to increasing D_L up to ~ 2.5 kPa. As D_L further increased, E_L either reached saturation or declined (Figure 2). E_L of *J. chelonia* were higher than *K. paniculata* and *L. indica* and E_L of *G. triacanthos* were higher than and *E. grandis*, *F. microcarpa* and *B. discolor* ($P < 0.05$).

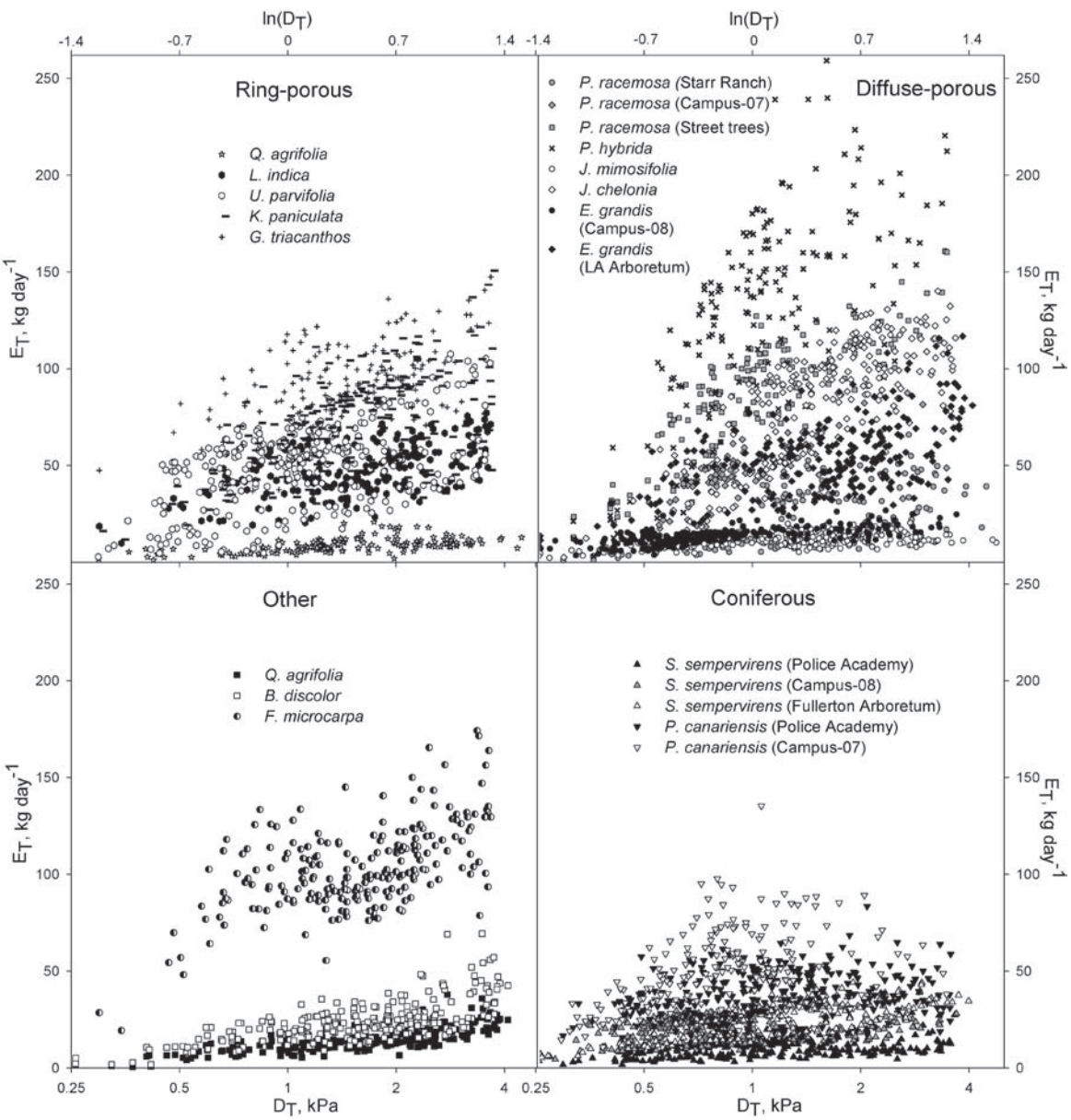

Figure 1. Daily tree transpiration upscaled from sap flux measurements (E_T) plotted against daily averaged vapor pressure deficit within the tree canopy (D_T). Note that D_T axes are logarithmic.

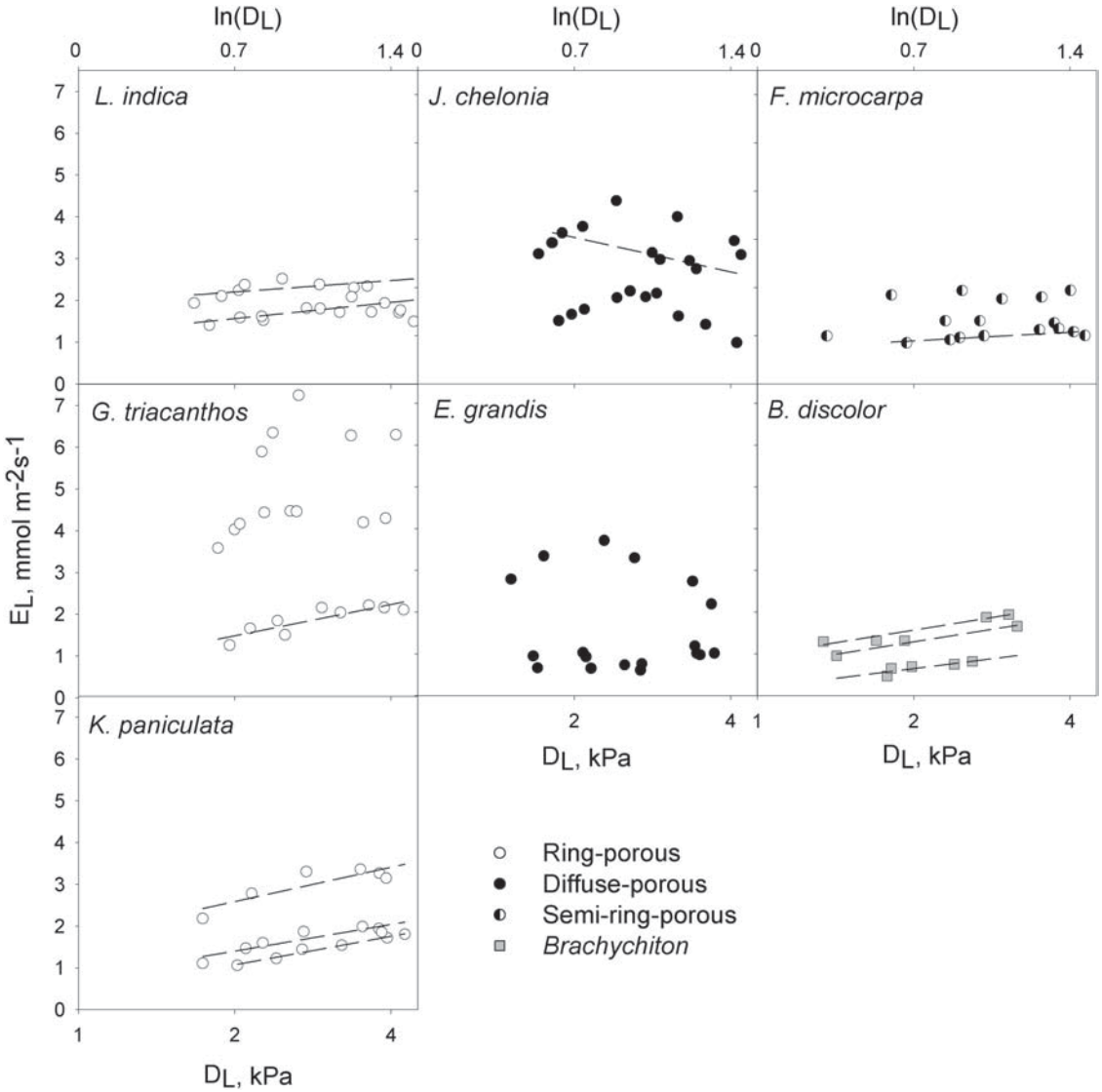

Figure 2. Response of leaf transpiration (E_L) to increasing vapor pressure deficit at the leaf surface (D_L). D_L is shown on a logarithmic scale; regression lines are significant at $\alpha = 0.05$.

Transpiration sensitivity to D

For the majority of studied trees the model parameters m_T and E_{Tref} (Eq. (5a)) were statistically significant ($P < 0.05$). However, the coefficients were not significant for two *Q. agrifolia*, one *P. racemosa* (at Campus-07), one *P. canariensis* (at Police Academy) and one *S. sempervirens* (at Campus-08). Therefore, we did not include the coefficients for these trees when calculating averages (shown in Table 1). Overall, m_T varied from 2.8 ± 0.2 kg day^{-1}(ln(kPa))$^{-1}$ (*J. mimosifolia*) to 71.7 ± 3.6 kg day^{-1}(ln(kPa))$^{-1}$ (*P. hybrida*). Unlike the previous study (Bush et al. 2008), m_T ranges of ring-porous (from 3.9 ± 0.3 to 25.7 ± 2.7 kg day^{-1}(ln(kPa))$^{-1}$) and diffuse-porous species (from 2.8 ± 0.2 and 71.7 ± 3.6 kg day^{-1}(ln(kPa))$^{-1}$) largely overlapped (Figure 3).

Two diffuse-porous species (*E. grandis* and *P. racemosa*) and two coniferous species (*S. sempervirens* and *P. canariensis*) were present at more than one study site (Table 1). We compared m_T of the same species at different study sites using ANOVA. m_T of *E. grandis* was significantly lower at Campus-08 compared with LA Arboretum ($P = 0.01$) and m_T of *P. racemosa* was significantly lower at Starr Ranch compared with Street trees site; m_T of *S. sempervirens* was significantly lower at Police Academy compared with Fullerton ($P = 0.01$), while m_T of *P. canariensis* was not significantly different among study sites ($P = 0.004$, Table 1).

Similar to Oren et al. (1999), we considered m_T as a function of E_{Tref} (Figure 4). There was a significant linear relationship for both ring-porous and diffuse-porous species. The slope of the fitted line was significantly steeper ($P = 0.007$)

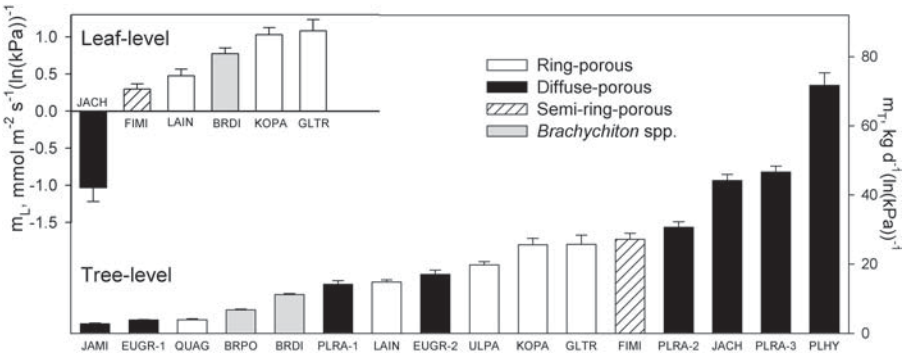

Figure 3. Leaf-level and tree-level sensitivity of transpiration to vapor pressure deficit ($m = dE/d\ln D$). Leaf-level sensitivity (m_L) is derived from instantaneous leaf transpiration and vapor pressure deficit at the leaf surface; tree-level sensitivity (m_T) is based on daily tree transpiration obtained from sap flux measurements and vapor pressure deficit in the canopy. Error bars show model error. Species notations—ring-porous: GLTR—*G. triacanthos*, KOPA—*K. paniculata*, LAIN—*L. indica*, QUAG—*Q. agrifolia*, ULPA—*U. parvifolia*; diffuse-porous: EUGR—*E. grandis* (1—Campus-07, 2—LA Arboretum), JACH—*J. chelonia*, JAMI—*J. mimosifolia*, PLHY—*P. hybrida*, PLRA—*P. racemosa* (1—Starr Ranch, 2—Campus-07, 3—Street trees); semi-ring-porous: FIMI—*F. microcarpa*; *Brachychiton* spp.: BRDI—*B. discolor*, BRPO—*B. populneus*.

for diffuse-porous species (slope = 0.61) compared with ring-porous (slope = 0.30).

Leaf-level transpiration was significantly related to D for only about half of studied leaves. Exclusion of insignificant model parameters removed *E. grandis* from consideration and reduced our sample size of leaf transpiration to one replicate for *G. triacanthos*, *J. chelonia* and *F. microcarpa*, two for *L. indica*, *B. discolor* and three for *K. paniculata.* Values of m_L ranged from -1.03 ± 0.19 mmol m^{-2} s^{-1} (ln(kPa))$^{-1}$ for *J. chelonia* to 1.08 ± 0.15 mmol m^{-2} s^{-1} (ln(kPa))$^{-1}$ for *G. triacanthos* (Table 1 and Figure 3).

Vulnerability to cavitation

P_{50} of ring-porous, diffuse-porous and coniferous trees formed three distinct ranges that did not overlap (Table 1 and Figure 5). P_{50} varied from -0.31 ± 0.11 MPa (*U. parvifolia*) to -0.58 ± 0.10 MPa (*L. indica* and *Q. agrifolia*) in ring-porous trees, from -1.09 ± 0.15 MPa (*P. hybrida*) to -2.10 ± 0.64 MPa (*J. mimosifolia*) in diffuse-porous trees and from -4.11 ± 0.59 MPa (*S. sempervirens* at Police Academy) to -5.93 ± 0.63 MPa (*S. sempervirens* at Campus-08) in coniferous trees (Table 2 and Figure 5). However, there was an overlap of the ranges of P_{50} of ring-porous and diffuse-porous trees when we considered additional P_{50} data collected in 2010–11. P_{50} of ring-porous trees varied from -0.25 ± 0.08 MPa (*Citrus sinensis* L.) to -1.41 ± 0.05 MPa (*Citrus aurantium* L.), and P_{50} of diffuse-porous trees varied from -0.19 ± 0.02 MPa (*Tabebuia chrysotricha* Mart. ex DC.) to -2.80 ± 0.62 MPa (*Liquidambar styraciflua* L.) (Table 2 and Figure 5).

Functional hydraulic conductivity

All measured stem segments exhibited some degree of native embolism (Figure 6). Overall, maximum K did not significantly change from month to month ($P = 0.35$) and was the largest in ring-porous trees, followed by diffuse-porous *J. chelonia* and *Brachychiton* species ($P < 0.05$). Functional K increased in September in all species ($P = 0.049$), and then declined by October ($P = 0.027$). While maximum K in diffuse-porous *J. chelonia* was significantly smaller than in ring-porous ($P = 0.035$ for *L. indica* and $P < 0.0001$ for *U. parvifolia*), its functional K was larger than *L. indica* ($P = 0.029$) and not significantly different from *U. parvifolia* ($P = 0.57$ for August). This was caused by significantly lower % loss of K in *J. chelonia* compared with ring-porous species (Figure 6, $P < 0.001$ for both *L. indica* and *U. parvifolia*).

Coordination between transpiration sensitivity and vulnerability to cavitation

Transpiration sensitivity (m_T) of both ring-porous and diffuse-porous trees increased with increasing vulnerability to cavitation (Figure 7). There was a strong linear correlation between m_T and P_{50} for these two functional groups, with ring-porous and diffuse-porous groups having similar slopes ($P > 0.05$, Figure 7). *Brachychiton populneus* and *B. discolor* appeared to fall in the same range as the ring-porous species, while values for *F. microcarpa* fell between those of ring-porous and diffuse-porous species. Due to their distinctly lower P_{50} values, coniferous trees were analyzed separately (Figure 7). However, their range of m_T (from 3.5 ± 0.2 kg day^{-1}(ln(kPa))$^{-1}$ in *S. sempervirens* at Police Academy to 16.1 ± 1.4 kg day^{-1}(ln(kPa))$^{-1}$ in *P. canariensis* at Campus-07) was not large enough to reveal a correlation with P_{50}.

Leaf transpiration showed a different pattern with P_{50}. Transpiration sensitivity (m_L) increased linearly with vulnerability to cavitation across all wood types (Figure 8). However, similar to tree-level transpiration (Figure 7), *B. discolor* appeared to be in the same range as the ring-porous species, and *F. microcarpa* fell somewhat in between ring-porous and diffuse-porous species, preserving the same order of m_L (Figure 3).

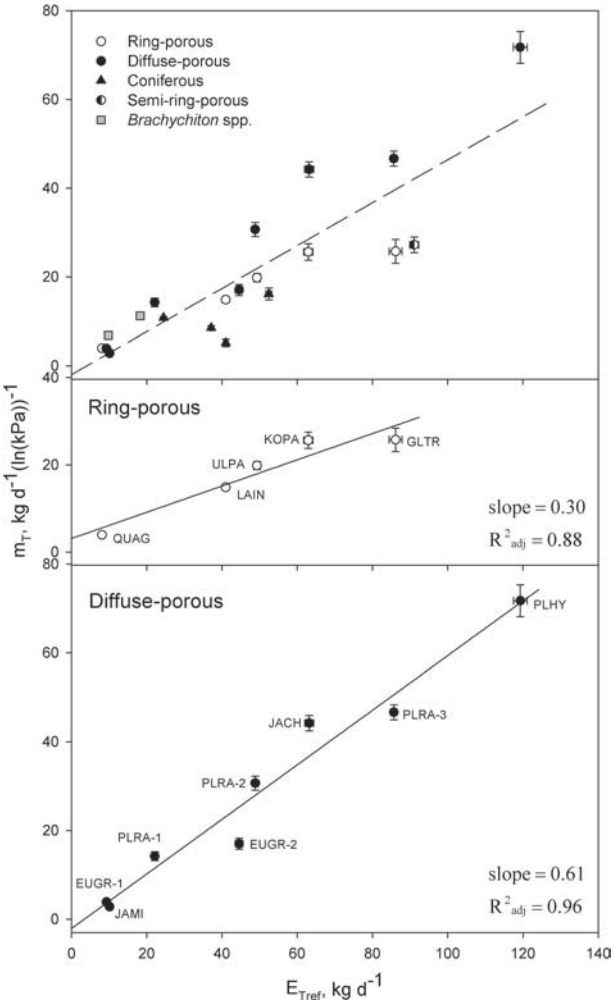

Figure 4. Sensitivity of tree-level transpiration to vapor pressure deficit (D_T) in the canopy ($m_T = dE_T/d\ln D_T$) as a function of tree transpiration at $D_T = 1$ kPa (E_{Tref}). E_{Tref} is the intercept of the function $E_T = E_{Tref} + m_T \ln D_T$, and m_T is the slope. Error bars show the model error. Species notations—ring-porous: GLTR—*G. triacanthos*, KOPA—*K. paniculata*, LAIN—*L. indica*, QUAG—*Q. agrifolia*, ULPA—*U. parvifolia*; diffuse-porous: EUGR—*E. grandis* (1—Campus-07, 2—LA Arboretum), JACH—*J. chelonia*, JAMI—*J. mimosifolia*, PLHY—*P. hybrida*, PLRA—*P. racemosa* (1—Starr Ranch, 2—Campus-07, 3—Street trees).

Discussion

We found a strong linear relationship between m_T and E_{Tref} of the studied urban trees (Figure 4). In contrast to our initial hypothesis, the ranges of m_T of ring-porous and diffuse-porous trees largely overlapped (Figure 3). Both m_T and m_L linearly increased with increasing vulnerability to cavitation. However, m_T of ring-porous and diffuse-porous trees formed two parallel linear relationships with P_{50}, while m_L of both functional groups formed a single linear relationship with P_{50} (Figures 7 and 8).

The relationship between tree-level transpiration sensitivity and E_{Tref}

Similar to Oren et al. (1999), we found a strong linear relationship between tree-level transpiration sensitivity m_T and E_{Tref} (Figure 4). We chose E instead of stomatal conductance as the variable for analysis (Eq. (5a)) due to concerns about autocorrelation when D is used to calculate conductance (Monteith 1995, Oren et al. 1999). E may be considered equivalently because within a wide range of stomatal conductance values, the decline of conductance with increasing D corresponds to a nearly linear increase in E with increasing ln(D) (Monteith 1995, Oren et al. 1999). Moreover, because the leaf area of urban trees is extremely difficult to quantify (most trees are open grown and street trees may also be pruned) we could not provide estimates of canopy conductance comparable to literature values. This does not affect the relationship between m_T and E_{Tref} (Figure 4). Therefore, our empirical model (Eqs. (5a) and (5b)) should allow for adequate consideration of stomatal function.

To obtain an accurate representation of stomatal responses to D, it is essential to exclude stressful environmental conditions, particularly soil drought, from the analysis (Oren et al. 1999). For example, Bovard et al. (2005) reported pronounced stomatal closure at $D > 1$ kPa during soil drought episodes in three diffuse-porous species from a mixed hardwood forest, which was not observed when soil moisture was high. However, previous studies have shown that our urban, irrigated trees do not experience significant soil water limitations, as frequent irrigation maintains high values of soil moisture throughout the season (McCarthy and Pataki 2010, Litvak et al. 2011). Therefore, the observed linear correlation between m_T and E_{Tref} (Figure 4) reveals the patterns of stomatal responses by these urban trees to D.

The vast experimental evidence of the proportionality of stomatal sensitivity to stomatal conductance at $D = 1$ ('reference conductance') is strongly supported by the model expressing leaf conductance as a function of leaf–soil water potential gradient, D, and hydraulic conductance (Oren et al. 1999). This proportionality reflects the tendency of species with stronger stomatal control to have higher conductance at low D values. Therefore, species with more sensitive stomata also tend to maintain more efficient photosynthetic activity at low, 'safe' range of D represented by reference conductance. In addition, a higher slope in the relationship between stomatal sensitivity versus reference stomatal conductance (σ; *slope* in Oren et al. 1999) corresponds to more stable leaf water potentials maintained by stomatal adjustment to changing D, and lower σ values correspond to weaker or no regulation of leaf water potential at high D. Stomatal behavior allowing water potentials to decline may be explained by sustained hydraulic conductance at high D, and was previously reported in some desert

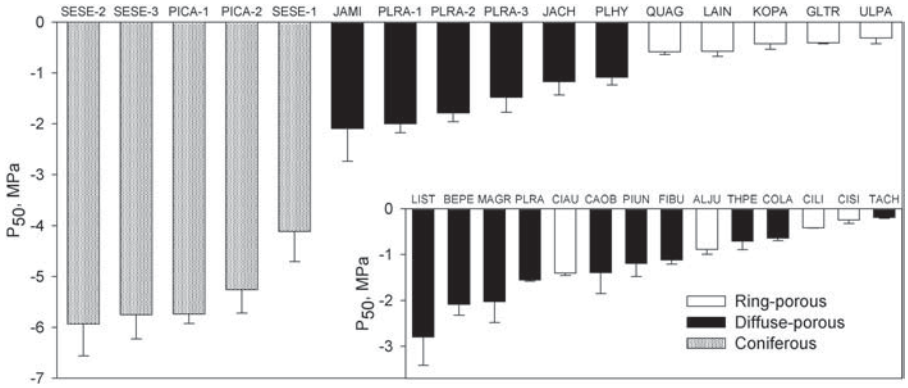

Figure 5. Xylem pressure at 50% loss of hydraulic conductivity (P_{50}) in branches of conifers, diffuse-porous and ring-porous trees. Additional P_{50} measured in 2010–11 are shown in the inset. Error bars represent one standard error. Species notations—ring-porous: ALJU—*A. julibrissin*, CIAU—*C. aurantium*, CILI—*C. limon*, CISI—*C. sinensis*, GLTR—*G. triacanthos*, KOPA—*K. paniculata*, LAIN—*L. indica*, QUAG—*Q. agrifolia*, ULPA—*U. parvifolia*; diffuse-porous: BEPE—*B. pendula*, CAOB—*C. obesa*, COLA—*C. laurifolius*, FIBU—*F. burkei*, JACH—*J. chelonia*, JAMI—*J. mimosifolia*, MAGR—*M. grandiflora*, LIST—*L. styraciflua*, PIUN—*P. undulatum*, PLHY—*P. hybrida*, PLRA—*P. racemosa* (1—Starr Ranch, 2—Campus-07, 3—Street trees, not numbered—LA Arboretum), TACH—*T. chrysotricha*, THPE—*T. peruviana*; coniferous: PICA—*P. canariensis* (1—Police Academy, 2—Campus-07), SESE—*S. sempervirens* (1—Police Academy, 2—Campus-08, 3—Fullerton Arboretum).

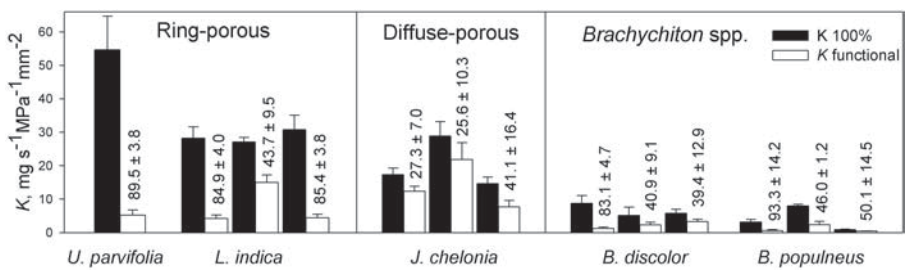

Figure 6. Maximum and functional hydraulic conductivity (K) of stems collected in August, September and October 2008 (from left to right; *U. parvifolia* was measured only in August). Corresponding % loss of functional hydraulic conductivity with respect to the maximum is shown for each functional K. Error bars represent one standard error.

species (Oren et al. 1999). Summarizing, there are two overall patterns in stomatal regulation suggested by theory: (i) stronger stomatal sensitivities generally correspond to higher reference conductances, and (ii) higher σ are characteristic of species with more pronounced reduction of stomatal conductance at high D, for a given reference conductance.

In this study, we found m_T to be proportional to E_{Tref}, which is in agreement with (i) above (Figure 4). In addition, we found the ratios of m_T to E_{Tref} for ring-porous and diffuse-porous trees to be significantly different ($P < 0.05$, the slopes in Figure 4), with smaller m_T corresponding to the same range of E_{Tref} in ring-porous trees. Smaller m_T values indicate greater reduction of stomatal conductance with D for a given reference conductance, which is equivalent to higher σ (statement ii above). Higher σ in ring-porous trees compared with diffuse-porous was also identified by Oren et al. (1999). It can be attributed to a greater loss of hydraulic conductivity with increasing D in ring-porous trees (discussed below) that, in accordance with the theory, causes stomatal sensitivity to increase. In turn, lower σ of diffuse-porous trees corresponds to weaker reduction of stomatal conductance with D.

Given weaker stomatal sensitivity of diffuse-porous trees, their m_T were not systematically higher compared with ring-porous trees, contrary to the initial hypothesis (Figure 3). In addition, inter-specific differences also contributed to the variability of m_T (Figure 3 and Table 1). Given the variability of m_T, the m_T versus E_{Tref} relationship is useful for discerning systematic differences between stomatal behaviors of ring-porous and diffuse-porous trees. The analysis of m_T versus E_{Tref} led us to the conclusion that ring-porous trees have stronger stomatal control compared with diffuse-porous. However, if ring-porous trees have stronger stomatal control, why did not they exhibit systematically higher E_{Tref} and m_T compared with diffuse-porous trees? In order to address this question, we need to consider the influence of hydraulic transport on tree-level transpiration sensitivity.

Stomatal–hydraulic coordination in ring-porous and diffuse-porous trees

Ring-porous trees in this study were more vulnerable to cavitation than diffuse-porous species (Figure 5 and Table 1). Given their vulnerable earlywood (McCulloh et al. 2010, Zanne et al.

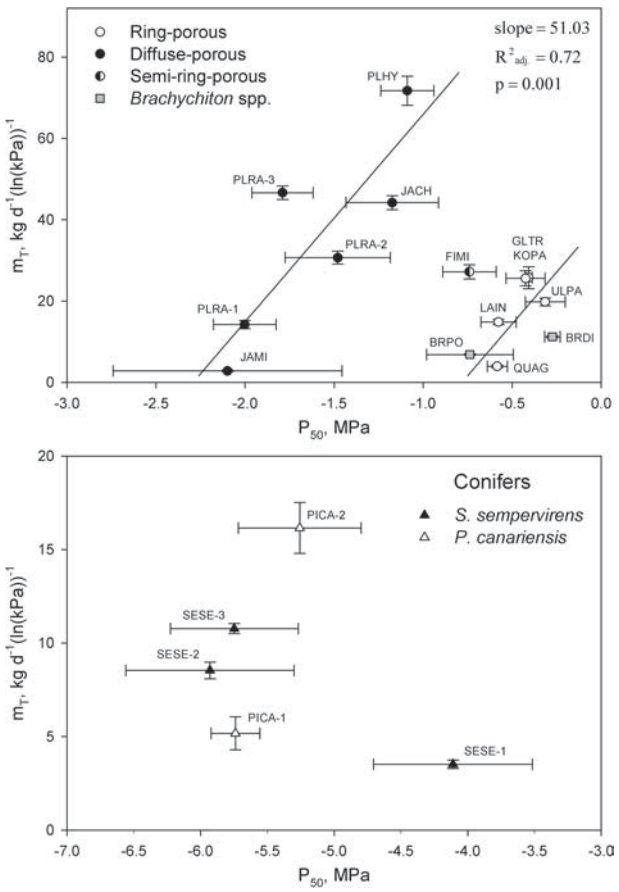

Figure 7. Sensitivity of tree-level transpiration to vapor pressure deficit in the canopy ($m_T = dE_T/d\ln D_T$) as a function of vulnerability to cavitation (P_{50}, xylem pressure at 50% loss of branch hydraulic conductivity). Linear relationships are shown only when significant at $\alpha = 0.05$, namely for ring-porous and diffuse-porous trees. Error bars represent one standard error for P_{50} and the model error for m_T. Note that the panels are shown with different scales. Species notations—ring-porous: GLTR—*G. triacanthos*, KOPA—*K. paniculata*, LAIN—*L. indica*, QUAG—*Q. agrifolia*, ULPA—*U. parvifolia*; diffuse-porous: JACH—*J. chelonia*, JAMI—*J. mimosifolia*, PLHY—*P. hybrida*, PLRA—*P. racemosa* (1—Starr Ranch, 2—Campus-07, 3—Street trees); semi-ring-porous: FIMI—*F. microcarpa*; *Brachychiton* spp.: BRDI—*B. discolor*, BRPO—*B. populneus*; coniferous: PICA—*P. canariensis* (1—Police Academy, 2—Campus-07), SESE—*S. sempervirens* (1—Police Academy, 2—Campus-08, 3—Fullerton Arboretum).

2010), xylem embolism in ring-porous trees occurs relatively quickly, so that stronger stomatal regulation is needed to prevent water potentials from dropping with increasing D_T. Ring-porous trees generally maintain fairly constant leaf water potentials to avoid excessive xylem cavitation at high D_T (*isohydry*, Hacke et al. 2006, Taneda and Sperry 2008). The diffuse-porous species that we studied were more resistant to xylem cavitation than ring-porous (Figure 5) and could, therefore, allow weaker stomatal control, and more negative leaf water potentials with increasing D_T. Such *anisohydric* behavior results from a smaller reduction of stomatal conductance (Figure 1) leading to more efficient functioning at high D_T (Oren et al. 1999, Hacke et al. 2006, Taneda and Sperry 2008).

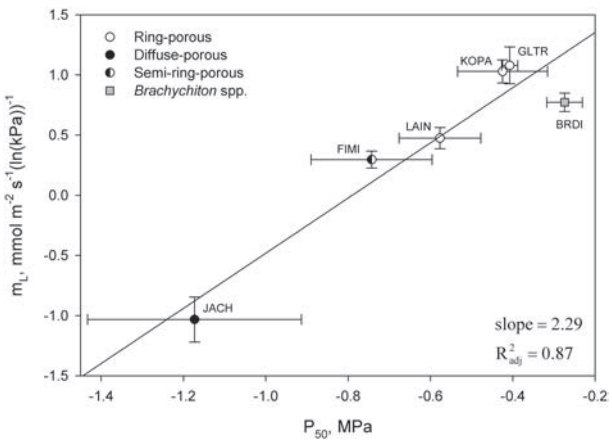

Figure 8. Sensitivity of leaf-level transpiration to vapor pressure deficit at the leaf surface ($m_L = dE_L/d\ln D_L$) as a function of vulnerability to cavitation (P_{50}, xylem pressure at 50% loss of branch hydraulic conductivity). A linear relationship is fitted to all functional groups. Error bars represent one standard error for P_{50} and the model error for m_L. Species notations—ring-porous: GLTR—*G. triacanthos*, KOPA—*K. paniculata*, LAIN—*L. indica*; diffuse-porous: JACH—*J. chelonia*; semi-ring-porous: FIMI—*F. microcarpa*; *Brachychiton* spp.: BRDI—*B. discolor*.

Previous studies have suggested that differences in stomatal sensitivity (both within and between species) are linked to different degrees of resistance to cavitation (Jones and Sutherland 1991, Wullschleger et al. 1998). Sparks and Black (1999) attributed intra-specific differences in stomatal sensitivity among populations of *Populus trichocarpa* Torr. & A.Gray growing along a gradient of environmental conditions to variations in cavitation resistance. Martinez-Vilalta et al. (2002) and Poyatos et al. (2008) found stronger stomatal control during dry summer months in tree species that were more vulnerable to cavitation. In addition, stronger stomatal regulation of some ring-porous trees compared with diffuse-porous was found to be consistent with their systematically lower resistance to cavitation in a hardwood forest in Michigan (Bovard et al. 2005) and in an irrigated urban forest in Utah (Bush et al. 2008).

In this study, we tested the hypothesis that trees that were more vulnerable to xylem cavitation would systematically exhibit more stomatal sensitivity to *D*. We found two relevant patterns in the relationship between stomatal sensitivity and resistance to cavitation. First, m_T increased with vulnerability to cavitation, and second, m_T of ring-porous and diffuse-porous trees formed two separate, linear relationships with P_{50} (Figure 7). The linear increase of m_T with increasing vulnerability to cavitation links stomatal function with a widely discussed trade-off between resistance to cavitation ('safety') and transport capacity ('efficiency'). On one hand, high transpiration rates associated with photosynthetic activity require adequate water transport capacity. On the other hand, efficient water transport requires the presence of wide pores in xylem membranes that are susceptible to cavitation. In turn, cavitation reduces water transport efficiency and may lead to run-away embolism and hydraulic system

failure (Sperry and Pockman 1993, Brodribb and Field 2000, Pockman and Sperry 2000, Meinzer 2002, Brodribb et al. 2003, Hacke et al. 2006, Maherali et al. 2006, Lens et al. 2011). Theoretically, because a more efficient water transport system is more vulnerable to cavitation, it requires more sensitive regulation of water potentials that drive transpiration. However, the safety and efficiency of the hydraulic pathway may rely not only on physical properties of xylem but also on other physiological and ecological strategies of coping with water stress, such as water storage and embolism refill (Goldstein et al. 1998, Vogt 2001, Meinzer et al. 2008, 2009, Sperry et al. 2008, Taneda and Sperry 2008, Holtta et al. 2009). Therefore, the trade-off between hydraulic safety and efficiency may occur at the whole-plant scale (Andrade et al. 1998, Meinzer et al. 2010, Lauri et al. 2011). In this study, the linear increase of m_T with xylem vulnerability to cavitation P_{50} (Figure 7) illustrates that stomatal function is explicitly adjusted to hydraulic safety limits of stems. Even though stem P_{50} represents vulnerability to cavitation on a segment level, trees whose branches were more vulnerable to cavitation exhibited higher transpiration sensitivity on a canopy level, and trees whose branches were more resistant to cavitation exhibited lower sensitivity.

Notably, higher m_T corresponded to higher E_T in each functional group (Figure 1). Even though higher E_T from trees with stronger stomatal control may seem counterintuitive, it is a direct consequence of more sensitive stomatal regulation. As implied by proportionality between E_{Tref} and m_T (Figure 4), stronger stomatal control is associated with greater stomatal conductance at $D = 1$ kPa (Oren et al. 1999). Hence, trees with stronger stomatal control reach larger values of E_T when exposed to low D, before a reduction in stomatal conductance at higher D (Figure 1).

We compared transpiration responses to D across species and functional types using a 'common garden' approach: all studied trees were exposed to relatively similar D ranges and experienced non-limiting soil moisture. This allowed us to investigate relationships between m_T and P_{50} (Figure 7), but at the cost of evaluating other important physiological mechanisms of coping with water stress. For instance, most ring-porous species in this study naturally avoid water stress by growing in mesic environments and/or being deciduous. In addition, many Australian tree species including *Brachychiton* are dry season deciduous, and have swollen stems capable of storing water during drought (Boland et al. 2006). Therefore, sensitive stomatal regulation in response to D may not always be of primary importance in native habitats. Thus, while the intrinsic stomatal–hydraulic coordination is fundamental to tree physiology, its ecological significance may vary depending on species and habitats.

Leaf-level versus tree-level transpiration

Transpiration sensitivity derived from leaf gas exchange showed a different relationship with P_{50} (m_L, Figure 8) than tree-level, sap flux-based estimates (m_T, Figure 7). A limitation of our leaf-level data is the limited range of D_L; we were unable to measure E_L at D_L lower than 1 kPa during the leaf-level measurements. This resulted in significant relationships between E_L and D_L for only one diffuse-porous species, *J. chelonia* (Figure 2). Nevertheless, unlike the tree-level pattern (Figure 7), on a leaf level, m_L of three ring-, one semi-ring- and one diffuse-porous species all appeared to show a similar relationship with P_{50} (Figure 8). This may imply a consistent difference between leaf-level and tree-level transpiration sensitivity by wood type.

The difference between leaf-level and tree-level relationships is likely due to the fact that while m_L of ring-porous trees was higher than diffuse-porous, their m_T range largely overlapped with diffuse-porous trees (Figure 3). Higher m_L of ring-porous trees are consistent with the conclusion of their stronger stomatal control. However, why was m_T of ring-porous trees not higher than diffuse-porous, resulting in a single linear relationship with P_{50}, similar to the leaf level (Figure 8)?

The discrepancy between leaf-level and tree-level transpiration sensitivities could have resulted from systematically lower sapwood areas or leaf-to-sapwood area ratios of ring-porous trees compared with diffuse-porous. For example, Wullschleger et al. (2001) found that ring-porous trees had 3–4 times smaller sapwood areas compared with similarly sized diffuse-porous trees in a deciduous forest in Tennessee. In addition, Bowden and Bauerle (2008) reported ~1.7–3.7 lower leaf-to-basal areas for semi-ring-porous *Prunus* spp. compared with diffuse-porous *Acer* spp. and *P. hybrida* in a deciduous stand in South Carolina. However, in a study of a northern hardwood forest, ring-porous *Quercus rubra* L. possessed leaf-to-sapwood areas up to 13.5 times higher than three co-occurring diffuse-porous tree species (Bovard et al. 2005). In addition, leaf-to-sapwood area may significantly vary within the same species due to climatic influences (Oren et al. 1986, Mencuccini and Grace 1994, Mencuccini and Bonosi 2001), differences in height and age (Ewers et al. 2005) and, in urban areas, pruning practices (Peters et al. 2010). Leaf area may also change seasonally and in response to environmental stresses (Hatton and Wu 1995), therefore being more variable than sapwood area on shorter time scales. We did not observe a systematic difference in sapwood-to-basal areas between ring- and diffuse-porous species in this study (Table 1). We could not quantify leaf area of studied urban trees, but their leaf-to-sapwood area seems unlikely to systematically differ between the wood types.

We suggest that the difference between leaf-level and tree-level relationships (Figures 7 and 8) may have arisen from different time scales of the leaf and tree measurements. Leaf-level sensitivity m_L was based on instantaneous changes in leaf transpiration E_L in response to increasing D_L, and therefore solely captured stomatal responses to D_L. On the other hand, tree-level sensitivity m_T derived from daily tree transpiration E_T (kg day^{-1})

was not only controlled by stomatal regulation, but also by xylem embolism. Earlywood of ring-porous species, which accounts for a major part of their maximum K (McCulloh et al. 2010, Zanne et al. 2010), may become severely embolized on a daily basis in semi-arid environments (Taneda and Sperry 2008). Taneda and Sperry (2008) reported that ring-porous *Quercus gambelii* Nutt. growing in a riparian forest in Utah had similar to larger stomatal conductance and E_L compared with diffuse-porous *Acer grandidentatum* Nutt., but much lower water use on a tree scale. In that study, *Q. gambelii* had 81–89% loss of K at midday, while *A. grandidentatum* had only 2–3% loss. In our study, ring-porous *L. indica* had 44–85% loss of K (August–October 2008) and *U. parvifolia* had 90% loss (August), while diffuse-porous *J. chelonia* had only 26–41% loss (August–October, Figure 6). This resulted in significantly smaller functional K of these ring-porous trees compared with diffuse-porous *J. chelonia* ($P < 0.05$).

Xylem embolism caused by diurnal D_T variations may have limited the water transport capacity of studied trees and reduced their canopy conductance. However, unlike stomatal regulation, we expect hydraulic limitation caused by embolism to reduce rather than enhance transpiration sensitivity. Having vulnerable xylem, ring-porous trees exhibit significant declines in K at small negative pressures (Figure 6). Therefore, the major reduction in transpiration caused by embolism may happen at relatively low D_T. Reducing tree-level transpiration at relatively low D_T would lower E_{Tref} and m_T of ring-porous trees, placing them in the same range with diffuse-porous trees (Figure 3). Without this hydraulic limitation, we could expect m_T values of ring-porous species to be generally larger than diffuse-porous (analogous to m_L, Figure 3) and both functional types to appear on a single linear relationship between m_T and P_{50} instead of relationships with different intercepts (Figure 7).

Tree-level transpiration sensitivity may also be influenced by changes in stem capacitance driven by D_T. Stem water storage may comprise 10–25% of daily tree transpiration (Wullschleger et al. 1998) and buffer hydraulic transport limitations to some extent. In this study, the role of water storage may be important for *Brachychiton* species whose wood structure is capable of high water storage (Choat et al. 2005, Boland et al. 2006). The dynamic of stored water utilization may be an important factor influencing tree transpiration sensitivity which requires further investigation.

Conclusions

We studied functional coordination between stomatal control of transpiration and hydraulic properties of irrigated trees in the semi-arid Los Angeles area. The study trees were not limited by soil moisture, yet were exposed to a large range of D (Figure 1). Even though most of the studied trees were planted and managed, their stomatal behavior was consistent with the general relationship between transpiration and stomatal sensitivity observed in natural environments (Figure 4, Oren et al. 1999). Hence, it is unlikely that the coordination between stomatal regulation and vulnerability to cavitation found in this study (Figures 7 and 8) is specific to urban trees.

This study revealed a systematic difference in transpiration responses to D between ring-porous and diffuse-porous trees, which manifested differently at leaf and whole tree scales. At the leaf level, transpiration sensitivities of ring-porous trees were significantly higher than diffuse-porous, with m_L of both wood types following a similar linear relationship with P_{50} (Figure 8). At the tree level, transpiration sensitivities of ring-porous trees were similar to diffuse-porous (Figure 3), and the relationship between m_T and P_{50} had similar slopes but different intercepts (Figure 7). We attribute this difference to the influence of xylem embolism on tree-level transpiration responses to D_T. Overall, we conclude that studied ring-porous trees have higher stomatal sensitivity compared with diffuse-porous trees. In addition, our measurements support large reductions in tree-level transpiration of ring-porous trees caused by xylem embolism.

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Appendix: List of abbreviations

A_S (m^2)	sapwood area at breast height
A_B (m^2)	basal area at breast height
D (kPa)	vapor pressure deficit of the air
D_L (kPa)	D at leaf surface
D_T (kPa)	D inside tree canopies
J_O (g cm^{-2} s^{-1})	density of sap flux in the outer 2 cm of sapwood
E_L (mmol m^{-2} s^{-1})	leaf transpiration
E_{Lref} (mmol m^{-2} s^{-1})	leaf transpiration at $D_L = 1$ kPa
E_T (kg day^{-1})	daily tree transpiration
E_{Tref} (kg day^{-1})	daily tree transpiration at average daytime $D_T = 1$ kPa
K (mg s^{-1} MPa^{-1} mm^{-2})	stem area specific hydraulic conductivity
m_L (mmol m^{-2} s^{-1} (ln(kPa))$^{-1}$)	leaf-level transpiration sensitivity, $m_L = dE_L/d\ln(D_L)$
m_T (kg day^{-1} (ln(kPa))$^{-1}$)	tree-level transpiration sensitivity, $m_T = dE_T/d\ln(D_T)$
P_{50} (MPa)	negative pressure causing 50% loss of K due to cavitation
σ	coefficient of proportionality between stomatal sensitivity and stomatal conductance at $D = 1$ kPa