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Transpiration of urban forests in the Los Angeles metropolitan area

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Abstract. Despite its importance for urban planning, landscape management, and water management, there are very few in situ estimates of urban-forest transpiration. Because urban forests contain an unusual and diverse mix of species from many regions worldwide, we hypothesized that species composition would be a more important driver of spatial variability in urban-forest transpiration than meteorological variables in the Los Angeles (California, USA) region. We used constant-heat sap-flow sensors to monitor urban tree water use for 15 species at six locations throughout the Los Angeles metropolitan area. For many of these species no previous data on sap flux, water use, or water relations were available in the literature. To scale sap-flux measurements to whole trees we conducted a literature survey of radial trends in sap flux across multiple species and found consistent relationships for angiosperms vs. gymnosperms. We applied this relationship to our measurements and estimated whole-tree and plot-level transpiration at our sites. The results supported very large species differences in transpiration, with estimates ranging from 3.2 ± 2.3 $\mathrm{kg \cdot tree^{-1} \cdot d^{-1}}$ in unirrigated *Pinus canariensis* (Canary Island pine) to 176.9 ± 75.2 $\mathrm{kg \cdot tree^{-1} \cdot d^{-1}}$ in *Platanus hybrida* (London planetree) in the month of August. Other species with high daily transpiration rates included *Ficus microcarpa* (laurel fig), *Gleditsia triacanthos* (honeylocust), and *Platanus racemosa* (California sycamore). Despite irrigation and relatively large tree size, *Brachychiton populneas* (kurrajong), *B. discolor* (lacebark), *Sequoia sempervirens* (redwood), and *Eucalyptus grandis* (grand Eucalyptus) showed relatively low rates of transpiration, with values $< 45\ \mathrm{kg \cdot tree^{-1} \cdot d^{-1}}$. When scaled to the plot level, transpiration rates were as high as 2 mm/d for sites that contained both species with high transpiration rates and high densities of planted trees. Because plot-level transpiration is highly dependent on tree density, we modeled transpiration as a function of both species and density to evaluate a likely range of values in irrigated urban forests. The results show that urban forests in irrigated, semi-arid regions can constitute a significant use of water, but water use can be mitigated by appropriate selection of site, management method, and species.

Key words: ecohydrology; Jacaranda *spp.;* Koelreuteria paniculata; Lagerstroemia indica; Malosma laurina; *sap flow; transpiration;* Ulmus parvifolia; *urban forests; urban water use.*

INTRODUCTION

Transpiration of natural and urban forests is highly likely to differ due to the influence of management, disturbance, species composition, and many other aspects of decision making in urban forests as compared to their natural counterparts. Yet, despite its importance for ecology, hydrology, meteorology, and forest management, transpiration rates of urban forests are highly unconstrained. In particular, many cities in semi-arid regions do not naturally contain forests, and have been "afforested" with planted trees that are maintained by irrigation. The species composition of these forests may be quite unique and may contain species and cultivars from many regions around the world. The result is a unique set of biotic and abiotic conditions that make it difficult to predict urban-forest transpiration a priori. This is a critical limitation for urban forest management, water management, and urban planning where water resources are limited.

There has long been interest in the water use of urban trees for horticultural and urban forestry applications, and, more recently, in the ecohydrology of cities from the perspective of urban ecology and coupled human–ecological interactions. However, there are few datasets of transpiration rates of mature urban trees and forests in the field. Studies of urban landscape water use have generally focused on total evapotranspiration rates from meteorological measurements (Kalanda et al. 1980, Grimmond and Oke 1999, Christen and Vogt 2004) or models (Grimmond and Oke 1991, Berthier et al. 2006, Mitchell et al. 2008). These estimates are very important for studies of total landscape water and energy balance but provide little information about direct plant water use (excluding soil and surface evaporation) or differences among species. Measurements of urban leaf-level

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Table 1. Abbreviations used in the text.

A_B	basal area (cm^2)
A_S	sapwood area (cm^2)
A_i	sapwood area at depth i (cm^2)
D	vapor-pressure deficit (kPa)
E_C	canopy transpiration (mm/d)
E_T	tree transpiration (kg/d)
J_i	sap-flux density at depth i (g·cm^{-2}·d^{-1})
J_O	sap-flux density in the outer 2 cm of sapwood (g·cm^{-2}·d^{-1})
J_S	sap-flux density across the active sapwood (g·cm^{-2}·d^{-1})
I_O	incident overstory photosynthetically active radiation (mol·m^{-2}·d^{-1})
s_i	error estimate at depth i
s_O	error estimate in the outer 2 cm of sapwood
s_R	error estimate of the J_i/J_O ratio

gas exchange have been used to scale leaf transpiration to the tree level (Kjelgren and Clark 1993) and to parameterize models of transpiration of containerized trees (Kjelgren and Montague 1998; Montague and Kjelgren 2004), for which transpiration may be estimated by measurements of mass (Hagishima et al. 2007). In mature trees with large canopies, thermally based measurements of sap flow in stems have become common in natural forests (Granier et al. 2000, Pataki et al. 2000, Meinzer et al. 2001, Oren and Pataki 2001, Ewers et al. 2002, Pataki and Oren 2003, Cĕrmáket al. 2004, Barbour et al. 2005, Bovard et al. 2005, Wullschleger and Hanson 2006), agricultural ecosystems (Green and Clothier 1988, Steinberg et al. 1990, Cohen et al. 1997, Allen et al. 1999, Lu et al. 2000, Cohen and Naor 2002, Alarcon et al. 2003, Fernandez et al. 2006, Tognetti et al. 2009), and potted horticultural plants (Devitt et al. 1993, Blaikie and Chacko 1998, Bauerle et al. 2002, Lu et al. 2002, Ortuno et al. 2004). However, there have been relatively few measurements in mature urban trees. Barradas (2000) used sap-flux measurements of a hedgerow of *Fraxinus uhdei* in Mexico City to estimate latent heat fluxes, which varied seasonally. Cĕrmák et al. (2000) measured sap flux of urban *Acer campestre* and attributed variability among trees to differences in root area. Bush et al. (2008) measured sap-flux rates in mature trees of several species in Salt Lake City, Utah, USA, and found differences in stomatal responses to vapor pressure deficit (D; a list of all abbreviations is given in Table 1) in species of varying wood anatomy. However, these measurements were not scaled up to estimate plot-level urban-forest transpiration, which remains highly uncertain.

In a previous study we evaluated the physiological mechanisms underlying spatial and temporal variability in sap flux of two common species in the Los Angeles urban forest: *Platanus racemosa* and *Pinus canariensis* (McCarthy and Pataki 2010). We found that variations in D and overstory photosynthetically active radiation (I_O) explained a great deal of temporal variability, similar to natural ecosystems, and that spatial variability was attributable to differences in irrigation, soil nutrient status, and possibly tree allometry, which is difficult to measure in urban ecosystems. In this study we report sap-flux rates for a wide array of urban forest species grown in typical street and garden settings in the Los Angeles metropolitan area, and scale these measurements to the plot level. We posed the questions: (1) What is the magnitude of urban forest transpiration rates in these settings? Are transpiration rates similar to mesic, forested natural ecosystems? and (2) What is the role of species composition in influencing transpiration of these irrigated urban forests? Given that there is a wide range of species planted in these forests, from native trees to tropical, temperate, and xeric species from several habitats and continents, we hypothesized that species composition would be a larger determinant of plot-level transpiration rates than meteorological factors such as D.

Because measurements in urban ecosystems present a number of technical and practical challenges, such as limitations to intensive and destructive measurements in densely populated areas, we discuss the application of common scaling issues such as radial trends in sap flux with sapwood depth, and the propagation of error terms for uncertainty estimates. We then express plot-level transpiration rates as a function of tree-planting density, which varies greatly in urban ecosystems and often differs from natural forests. As far as we are aware, these are the first estimates of plot-level, canopy transpiration rates in irrigated urban forests. Such estimates have many practical and management applications for selecting species to plant and allocating water to urban landscapes, as well as ecological and hydrologic applications for the study of ecology, hydrology, meteorology, and land–atmosphere interactions in cities.

Materials and Methods

Sap-flux measurements in populated urban environments are challenging, as they require the study of trees of sufficient size, spatial distributions, and species replication, as well as sites suitable for placing monitoring equipment in the field, and landowners willing to grant permission for tree cores and other invasive measurements. This, in part, is why field data are lacking in these settings. Our goal in this study was to characterize sap flux and transpiration rates of mature urban trees in common types of urban land cover and management in the Los Angeles metropolitan area (California, USA). The study region is specifically the Los Angeles Basin, a coastal plain surrounded by the peninsular and transverse mountain ranges. The climate is Mediterranean with an average annual temperature of 18.3°C and precipitation of 38 cm (downtown Los Angeles, Morris 2009). Precipitation occurs primarily in winter. The basin is heavily urbanized; the U.S. census reported that the total population of the Los Angeles–Riverside–Orange County consolidated metropolitan statistical area was over 16 000 000 persons in 2000.

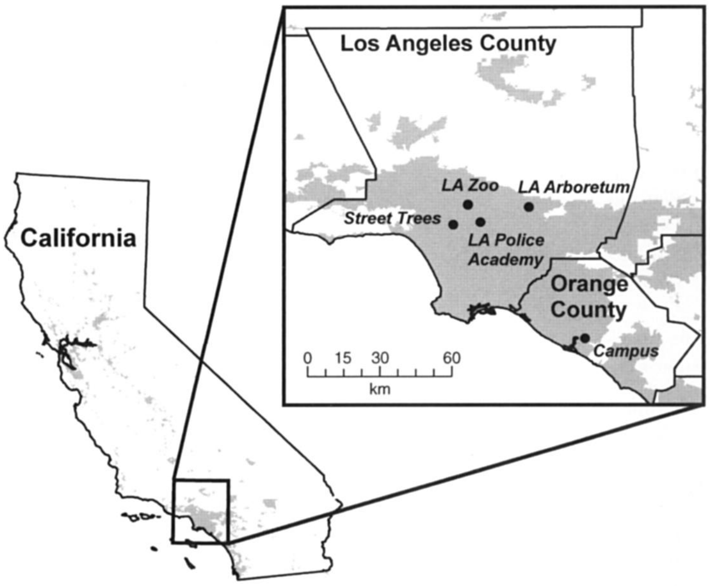

FIG. 1. Map of study sites in the metropolitan Los Angeles (LA) area (California, USA). Lines show county boundaries, and the shaded area shows Urban Areas as defined by the 2000 U.S. Census.

Study sites.—A map of all study sites is shown in Fig. 1. In 2007, we instrumented three sites that met the criteria for sap-flux measurements: the sites contained mature trees with adequate replication of individuals within species, and monitoring equipment could be placed at each site for several months. In all sites but one we were permitted to core the trees at the conclusion of sap-flux monitoring to determine sapwood depth. Where that was not possible (the Los Angeles Zoo site described below) we determined the relationship between tree diameter and sapwood area for the study species off site and applied that relationship to our study trees. The tree species we measured are either commonly found in the area or recommended for planting in southern California (Miller and Winer 1984, Lesser 1996, Mahoney et al. 1999; E. Ben-Horin, *unpublished data*; L. Weller and G. D. Jenerette, *unpublished manuscript*). Some of the study species are not commonly grown in urban areas outside of coastal California and other Mediterranean or subtropical climates due to their sensitivity to frost. However, several are common horticultural species in many cities in a range of climates, particularly *Platanus hybrida*, *Ulmus parvifolia*, *Gleditsia triacanthos*, and *Koelreuteria paniculata* (McPherson and Rowntree 1989, Raupp et al. 2006).

As is common in urban studies, we began the study by instrumenting our own University of California campus in Irvine (California, USA), which is landscaped with a variety of horticultural trees common to southern California. We chose a site that contained five individuals of *Platanus racemosa* Nutt. (California sycamore) and five *Pinus canariensis* C. Sm. (Canary Island pine). The trees were located in a typical irrigated garden setting planted with turfgrass, ice plant (*Carpobrotus chilensis*) and ivy (*Hedera helix*) groundcover. There were no trees in the plot other than the individuals we measured. This site is referred to as the "Irrigated" site in McCarthy and Pataki (2010). Plot and tree characteristics of all sites are given in Table 2. A second site focused on street trees growing in a narrow strip along the sidewalk of a Los Angeles residential street. The site, referred to as the "Street Trees" site in McCarthy and Pataki (2010) contained three individuals of *Platanus racemosa* Brot. and four *Platanus hybrida* (London planetree). These species are closely related and may hybridize (Rhymer and Simberloff 1996); however, their sap-flux rates were significantly different ($P < 0.05$) and therefore they will be treated separately in this study. The third site measured in 2007 was located at the Los Angeles Zoo and Botanical Garden. As part of its mission of habitat conservation, the Zoo was accredited as a Botanical Garden in 2003. It is managed with a variety of landscape plants, browse plants for the animal collection, as well as botanical collection specimens. We focused on landscape trees that are commonly planted through the Los Angeles Basin: we measured seven individuals of *Pinus canariensis*, five *Malosma laurina* (laurel sumac), and six *Jacaranda mimosifolia* D. Don. (blue Jacaranda). The *P. canariensis* and *M. laurina* trees were located in an unirrigated area, while the *J. mimosifolia*, although located directly adjacent, were irrigated. The irrigated area contained an herbaceous understory that we did not account for in our calculations of plot transpiration.

In 2008 we measured a different set of sites in order to collect data for additional species. One site was located at the Los Angeles Police Department's Revolver and Athletic Club, which we hereafter refer to as the LA Police Academy, or "LAPD" for brevity. The LA Police Academy is surrounded by a mature urban forest established as a rock garden and artificial waterfall in

Table 2. Plot and tree characteristics for all study sites in the metropolitan Los Angeles area (California, USA), including tree sample size (n), tree diameter at breast height (dbh), sapwood depth, the basal area (A_B):ground area (A_G) ratio, and the sapwood area (A_S):ground area ratio.

Site (area) and tree species	n	Mean dbh (cm) Mean ± SE	Sapwood depth (cm) Mean ± SE	A_B:A_G (cm^2/m^2)	A_S:A_G (cm^2/m^2)
Street trees (637 m^2)					
Platanus hybrida	4	56.8 ± 6.3	6.7 ± 0.1	13.4	5.7
P. racemosa	3	36.8 ± 1.4	10.6 ± 1.1	5.1	3.9
UC Irvine campus (1166 m^2)					
Platanus racemosa	5	47.5 ± 5.5	8.0 ± 0.8	8.0	4.2
Pinus canariensis	5	54.9 ± 2.1	15.2 ± 0.3	10.2	7.2
Los Angeles Zoo (1198 m^2)					
Jacaranda mimosifolia	6	14.5 ± 1.6	7.1 ± 0.8	0.9	0.8
Pinus canariensis (unirrigated)	7	43.7 ± 2.8	14.9 ± 0.3	9.0	6.9
Malosma laurina (unirrigated)	5	12.1 ± 1.2	5.9 ± 0.6	0.5	0.5
Los Angeles Police Academy (675 m^2)					
Ulmus parvifolia	6	28.9 ± 2.5	13.9 ± 1.2	6.0	5.6
Pinus canariensis	5	61.6 ± 4.6	18.0 ± 2.3	22.5	14.7
Sequoia sempervirens	5	39.4 ± 6.8	3.6 ± 0.6	10.1	3.0
Los Angeles Arboretum site A (2378 m^2)					
Brachychiton discolor	12	52.0 ± 5.7	2.9 ± 0.2	12.1	2.3
B. populneus	9	38.0 ± 3.2	2.8 ± 0.1	4.5	1.1
Eucalyptus grandis	4	67.0 ± 5.4	3.4 ± 0.3	6.0	1.1
Los Angeles Arboretum site SA (2007 m^2)					
Jacaranda chelonia	3	31.0 ± 3.4	14.2 ± 1.6	1.2	1.0
Lagerstroemia indica	11	17.7 ± 1.1	8.6 ± 0.5	1.4	1.3
Gleditsia tricanthos	3	45.2 ± 5.5	5.5 ± 0.7	2.5	1.0
Koelreuteria paniculata	6	29.6 ± 2.9	6.6 ± 1.2	2.2	1.4
Ficus microcarpa	4	32.2 ± 2.1	15.5 ± 1.0	1.6	1.5

Note: Los Angeles Arboretum: site A has trees native to Australia, and site SA has trees native to South America.

1935. The site is currently designated as a Cultural Heritage Monument and is managed as a public garden. Our measurements were conducted on five *Pinus canariensis*, six *Ulmus parvifolia* Jacq. (Chinese elm), and five *Sequoia sempervirens* D. Don (redwood). The site contained an understory of shrubs and herbaceous plants that we did not account for in our calculations of plot transpiration. Two additional sites were located at the Los Angeles County Arboretum and Botanic Garden in Arcadia, California, which is jointly managed by the Los Angeles Arboretum Foundation and the Los Angeles County Department of Parks and Recreation, and is therefore managed both as a Botanic garden and an urban park. The Arboretum is segregated into sections containing species from distinct geographical regions. Site A was located in the section dedicated to species from Australia, and contained 12 *Brachychiton discolor* F. J. Muell (lacebark), nine *Brachychiton populneus* Schott and Endl. (kurrajong), and four *Eucalyptus grandis* W. Hill (grand Eucalyptus). Site SA was located in the South American section (although it contained some species with native distributions outside of South America). At that site we measured 11 *Lagerstroemia indica* L. (crape myrtle), six *Koelreuteria paniculata* Laxm. (goldenrain tree), four *Ficus microcarpa* L. (laurel fig), three *Jacaranda chelonia* Griseb. (Jacaranda), and three *Gleditsia triacanthos* L. (honeylocust). These sites did not contain an understory, but there were isolated individual trees of other species present in the plots. There were insufficient replicates of these species available for characterizing transpiration. Therefore, we did not include these individuals in calculations of plot transpiration; from this perspective our estimates are underestimates in that understory vegetation and species that were not measured were not included in the final estimate.

Sap-flux measurements.—Each study tree was instrumented with 2-cm-long, Granier-type constant-heat sap-flux sensors (Granier 1987, Oren et al. 1998, Pataki et al. 2000, Pataki and Oren 2003) on the north side of the bole (see Plate 1). Sensors were placed at breast height (1.35 m from the ground), with the exception of the Street Tree and Campus sites, where sensors were placed up to 5 m from the ground to deter vandalism. Measured sap-flux density in the outer 2 cm of sapwood (J_O) was converted to breast-height values by multiplying measured values by the ratio of breast height to measurement height sapwood area. The study trees generally exhibited upright, symmetrical boles, and values of J_O fell within the range of the linear calibration by Granier (1987). To account for nighttime transpiration, we assumed zero flux only when D was close to 0 kPa at night (which is common in this ecosystem due to the prevalence of coastal fog). When D was greater than ~0.3 kPa, we assumed that nighttime transpiration was possible and applied the baseline temperature difference from the last period of $D < 0.3$ kPa. Generally, high nighttime D only occurs during short periods of offshore ("Santa Ana") winds in fall and winter in this area.

Temperature and relative humidity were measured at each site within the canopy. Overstory photosynthetically active radiation (I_O) was measured at the Los Angeles Zoo, which was the only site where access to full sun conditions was possible. For the other sites, I_O values were taken from the nearest (<15 km) California Irrigation Management Information System (CIMIS) station (*available online*).[5] Sap flux and meteorological measurements were recorded on a datalogger (CR10X, CR1000, or CR3000, Campbell Scientific, Logan, Utah, USA) and averaged every 30 minutes. At the conclusion of sap-flux monitoring, the trees were cored at both the sensor height and at 1.35 m from the ground if the sensors were placed at a different height. Sapwood depth was determined visually at all sites except the Los Angeles Zoo. Because we could not core trees at this site, we determined the relationship between tree diameter and sapwood area for the study species at a comparable urban location and applied that relationship to our study trees.

Scaling to whole-tree and plot-level transpiration.— Our measurements were conducted in the outer 2 cm of sapwood depth due to restrictions on invasive measurements at these sites. Yet most studies that have evaluated radial trends in sap flux have found significant differences in flux rates with depth. Flux rates tend to decrease with depth, or sometimes show a parabolic relationship with peak values at sapwood depths other than the outermost (Nadezhdina et al. 2007, Cohen et al. 2008, Saveyn et al. 2008). These radial variations must be taken into account when estimating whole-tree transpiration rates in trees with deep sapwood.

Many authors have reported species differences in radial trends, as well as temporal trends that depend on environmental conditions such as D (Nadezhdina et al. 2002, Ford et al. 2004*b*, Saveyn et al. 2008), light (Nadezhdina et al. 2002, Fiora and Cescatti 2006, Saveyn et al. 2008), or soil moisture (Lu et al. 2000, Nadezhdina et al. 2002, Ford et al. 2004*a*), or on time of day (Poyatos et al. 2007) and tree size (Delzon et al. 2004). However, it has been somewhat difficult to directly compare results across studies as methods and units of measurement have varied with different types of sap-flux sensors and different combinations of absolute, relative, area-based, and depth-based units of measurement. Most previous studies have concluded that generalizations about radial trends across species and environmental conditions are not possible, and that direct measurements at multiple depths are required in every study (Ford et al. 2004*b*, Gebauer et al. 2008, Saveyn et al. 2008). Since this was not feasible in our study, we conducted a literature survey of all radial trends reported to date for which we could determine the ratio of sap flux in the outermost depth to the measurement depth, and the relative sapwood depth. In most studies, the outermost measurement depth was 1–2 cm; in cases where the depth was <1 cm we averaged the first 1 cm of measurements for consistency. This may cause a bias in the results for species with strong radial trends within the first centimeter of sapwood; however, there are insufficient measurements at a finer spatial resolution than 1 cm to evaluate this. All methods of measuring sap flux including heat-pulse velocity, constant heat, and heat-field deformation were combined. We extracted published data for 34 species including 17 diffuse-porous species, 8 ring-porous species, and 9 gymnosperms. Where measurements in multiple treatments or environmental conditions were available, we averaged the results for that species.

We utilized the resulting algorithms to estimate whole tree transpiration according to

$$E_T = \sum_{i=1}^{n} \frac{J_i A_i}{1000} \tag{1}$$

where E_T is the total daily tree transpiration (kg/d), n is the number of 2-cm increments in sapwood depth, and J_i and A_i are the sap-flux density ($g \cdot cm^{-2} \cdot d^{-1}$) and sapwood area ($cm^2$), respectively, at depth i.

Plot-level canopy transpiration (EC; mm/d), was estimated by summing E_T for all measurement trees and dividing by the plot area. The error of each estimate was generated by propagating the variance in sap-flux rates among individuals of each species with the error of the algorithm used to specify radial trends. To estimate the error at each each 2-cm-sapwood increment (σ_i), we used the following equation:

$$\sigma_i = J_i \sqrt{\left(\frac{\sigma_O}{J_O}\right)^2 + \left(\frac{\sigma_R}{J_i : J_O}\right)} \tag{2}$$

where J_O is sap flux in the outer 2 cm of xylem, σ_O is the standard deviation in J_O, and σ_R is the error of the radial trends regression estimate. The error in each sapwood increment was then propagated to obtain the total error in estimating whole-tree transpiration.

Because our goal was to estimate transpiration of typical street, park, and garden settings, we attempted to define plot areas according to the intended boundaries of each park or garden—generally the continuous

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[5] ⟨http://www.cimis.water.ca.gov⟩

Table 3. Meteorological variables recorded during the study, including temperature, vapor-pressure deficit (D), and overstory photosynthetically active radiation (I_O), by year and site.

	Daytime temp. (°C)			Daytime D (kPa)			Daily sum I_O ($\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$)		
Site	May–June	July–August	September–October	May–June	July–August	September–October	May–June	July–August	September–October
2007									
Street trees	20.0 (2.7)	24.2 (1.7)	22.0 (3.4)	1.0 (0.6)	1.3 (0.4)	1.4 (0.7)	49.1 (10.2)	47.7 (6.0)	36.6 (7.9)
Campus		23.3 (1.5)	21.3 (3.1)		0.9 (0.3)	1.1 (0.7)		48.9 (6.0)	36.4 (10.2)
Zoo		27.0 (2.4)	23.3 (4.7)		2.0 (0.7)	1.8 (1.0)		44.6 (7.0)	32.4 (8.7)
2008									
LAPD	20.2 (4.4)	23.4 (1.4)	23.4 (3.4)	1.2 (0.7)	1.2 (0.2)	1.7 (0.9)	48.0 (14.0)	47.4 (5.2)	33.9 (5.1)
Arb. A	22.0 (5.3)	26.3 (1.5)	25.4 (3.6)	1.6 (1.0)	1.9 (0.4)	2.2 (0.9)	43.3 (14.9)	48.0 (3.7)	36.3 (6.8)
Arb. SA	21.8 (5.0)	26.0 (1.4)	24.9 (3.4)	1.5 (0.9)	1.7 (0.3)	2.0 (0.9)			

Note: Data are means with SD in parentheses; see Table 2 for full names of the sites.

pervious soil area that encompassed the measurement species. For the Street Tree site, where the projected canopy area was unusually large relative to the pervious soil area (because the trees were grown in narrow planting strips), we defined the plot boundaries as the center of the street and the center of the sidewalk. Admittedly, this is a relatively arbitrary method of estimating plot areas to determine ground-area-based transpiration, as different landowners may make a wide range of decisions about tree-planting density, garden area, and pervious soil area. For example, if the pervious-only area at the Street Tree site were designated as the plot boundaries, the plot area would only be 151 m^2, resulting in four-fold higher tree densities and unusually high rates of E_C (relative to natural ecosystems) as discussed in *Results*, below. Therefore, we also conducted a sensitivity analysis of the effects of tree density on E_C to evaluate the effects of varying plot sizes and densities on total ground-area-based transpiration.

Statistics.—Gaussian functions were fitted to radial trends data after Ford et al. (2004*b*). For curve fitting, we used nonlinear regression functions in Sigma Plot version 10.0 (SYSTAT Software 2006). Differences in radial trend relationships among functional groups (gymnosperms, diffuse-porous, and ring-porous) were evaluated through full vs. reduced model F tests using Proc NLIN in SAS version 9.2 (SAS Institute 2008).

Results

Environmental conditions during the study periods are shown in Table 3. The inland sites, particularly the Los Angeles Zoo and the Los Angeles Arboretum (California, USA), were generally warmer, with higher D (vapor-pressure deficit) and lower I_O (photosynthetically active radiation) than the sites located closer to the coast (Fig. 1, Table 3). The Street Tree site experienced relatively mild temperatures and low D (Table 3), yet in 2007, the highest daily J_O was measured in *Platanus* species at the Street Tree site, while the lowest rates were found in unirrigated *Pinus canariensis* and *Malosma laurina* at the Zoo (Fig. 2). Since a complete set of data for all species and sites was available during the month of August in both 2007 and 2008, we conducted species comparisons during this period. During the month of August, J_O averaged 298.6 ± 91.6 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ for *Platanus hybrida* and 184.0 ± 23.5 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ for *Platanus racemosa* (means ± SE). In contrast, values in the unirrigated portion of the Zoo were 4.2 ± 2.8 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ for *Pinus canariensis* and 9.4 ± 8.1 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ for *Malosma laurina*. During some periods, J_O for the unirrigated trees was actually below the detection limit of the sensors; we treated these periods as missing values rather than assuming zero flow. This likely resulted in a slight overestimate of the actual mean values.

There was somewhat less site-specific and interspecific variation in sap-flux measured in 2008, in part because measurements included only irrigated trees during this period. Nevertheless, there were large differences even among irrigated trees (Figs. 3 and 4). For example, *Pinus canariensis* and *Sequoia sempervirens* at the Police Academy showed relatively low J_O: during the month of August the average fluxes were 37.9 ± 15.6 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ and 52.0 ± 9.9 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$, respectively. *Ulmus parvifolia* at the Police Academy showed higher fluxes, with average values of 137.0 ± 24.8 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ in August. In contrast, *Lagerstroemia indica* and *Jacaranda chelonia* at the Arboretum SA site showed much higher flux rates, with average values of 240.5 ± 26.2 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ and 185.3 ± 52.3 $\text{g}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$, respectively, in August.

These results highlight the importance of species differences in transpiration rates for understanding urban water fluxes; however, they cannot be directly applied to comparisons of whole-tree water use without considering the influence of tree size, sapwood depth, and radial trends in sap flux across the xylem. In order to scale measured sap flux in the outermost xylem to the whole tree, we evaluated a broad range of previously reported radial trends across 34 different species. We

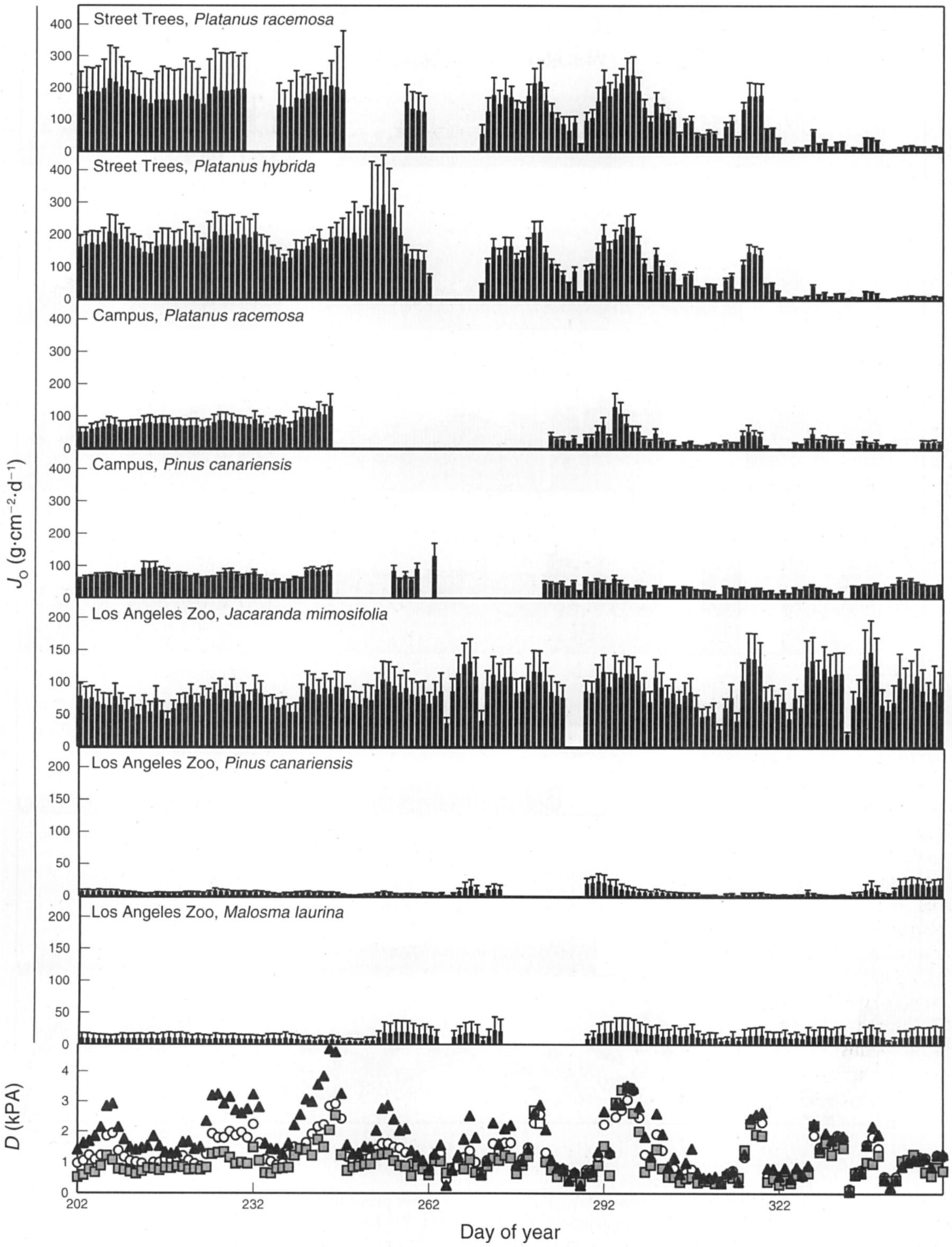

FIG. 2. Sap flux in the outer 2 cm of sapwood (J_O) and mean daily vapor-pressure deficit (D) at the Street Trees (circles), Campus (UC Irvine; squares), and Los Angeles Zoo (triangles) sites. There are missing values due to equipment failure. Error bars show the standard error.

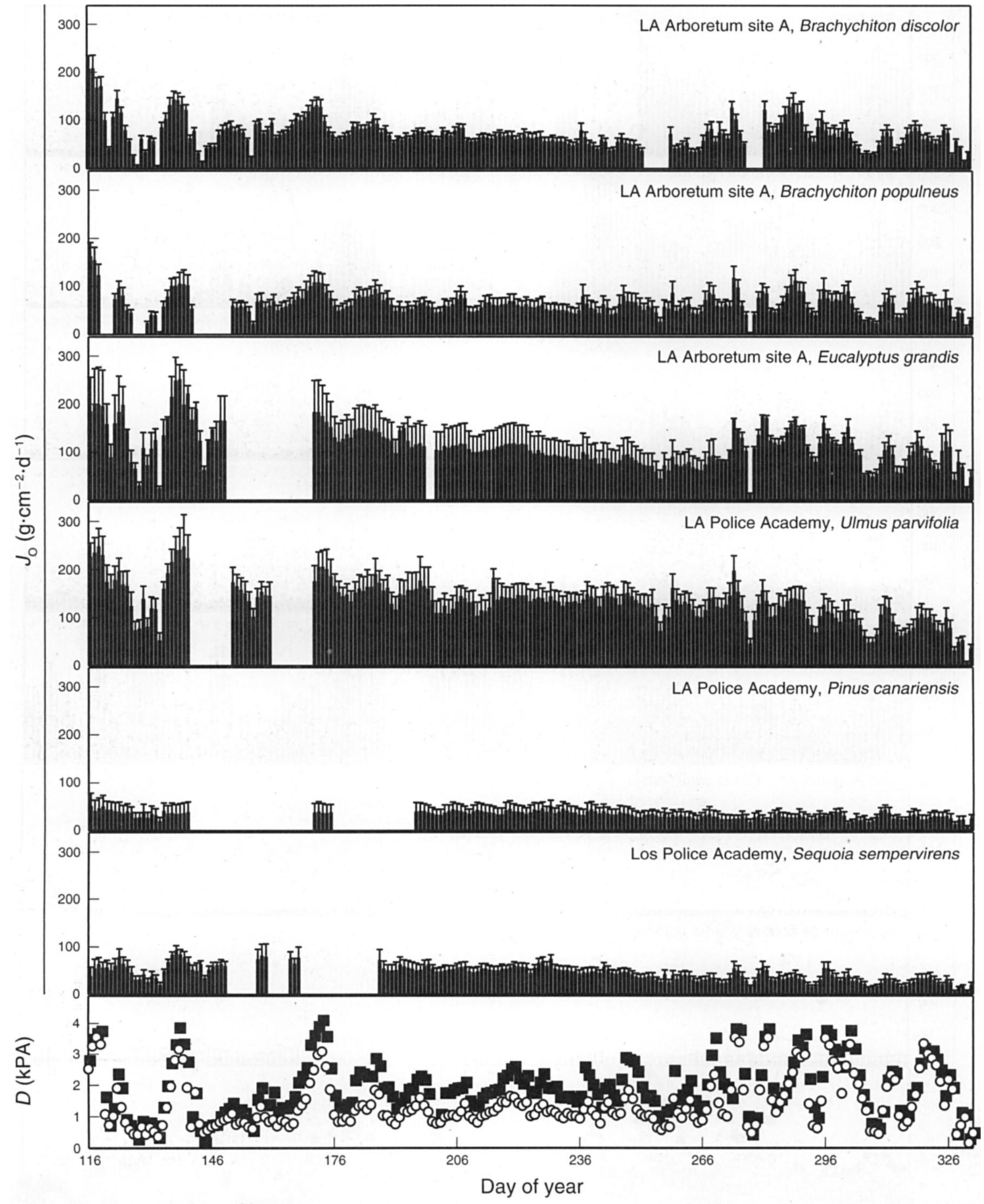

FIG. 3. Sap flux in the outer 2 cm of sapwood (J_O) and mean daily vapor pressure deficit (D) at the Los Angeles Arboretum site A (squares) and Los Angeles Police Academy (circles). There are missing values due to equipment failure. Error bars show the standard error.

found that there was, in fact, a fairly consistent pattern of J_i/J_O, (Fig. 5). In angiosperms, there was no significant difference in the relationship between diffuse-porous and ring-porous species ($P > 0.05$), but gymnosperms showed a significantly different relationship ($P < 0.05$). We therefore fitted two different Gaussian functions (Ford et al. 2004*b*) to angiosperms vs. gymnosperms to derive the equations

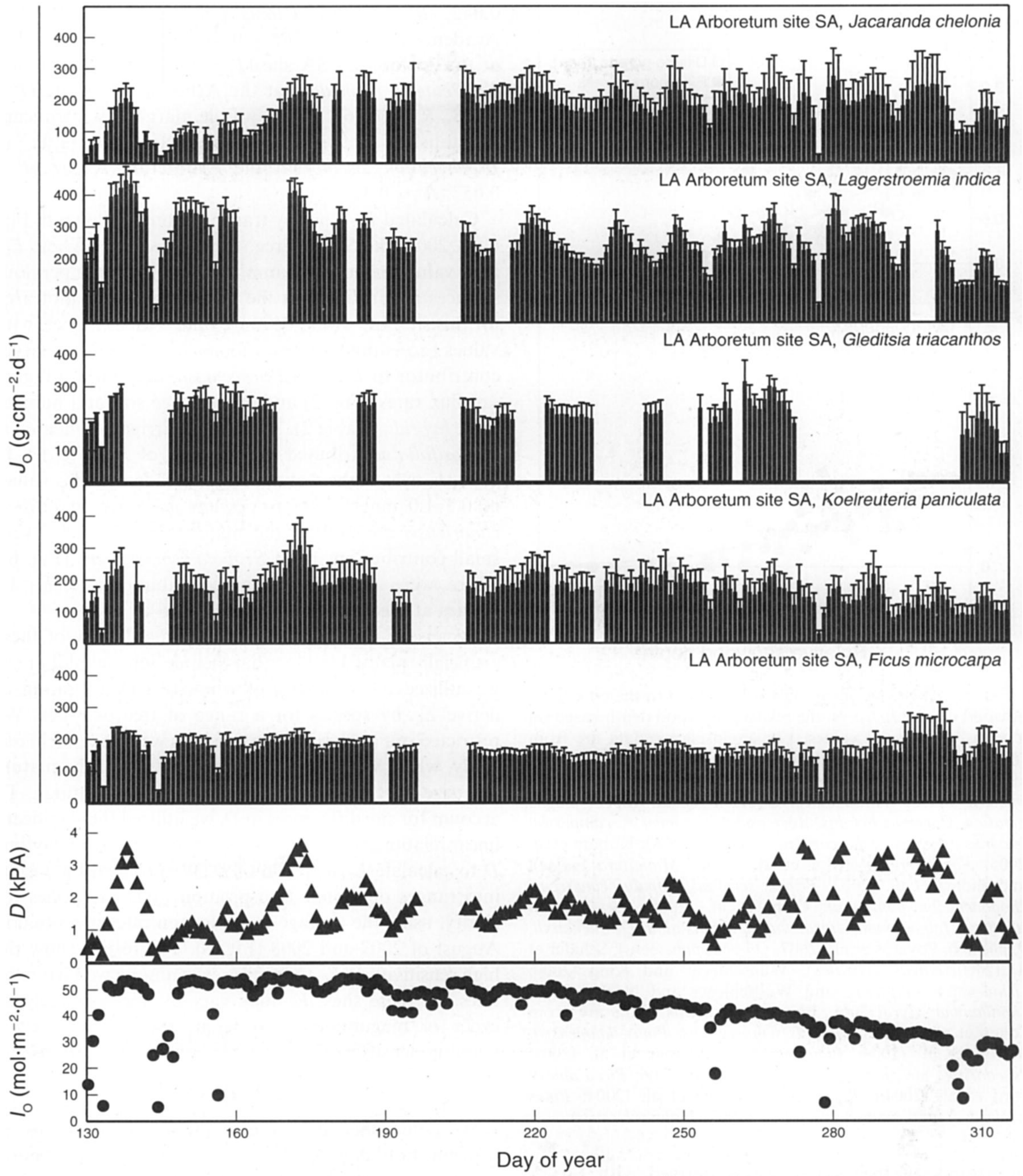

FIG. 4. Sap flux in the outer 2 cm of sapwood (J_O), mean daily vapor pressure deficit (D), and daily overstory incident radiation (I_O) at the Los Arboretum SA site. There are missing values due to equipment failure. Error bars show the standard error.

$$\text{angiosperm} \quad J_i/J_O = 1.033 \times \exp\left[-0.5\left(\frac{x - 0.09963}{0.4263}\right)^2\right] \tag{3}$$

$$\text{gymnosperm} \quad J_i/J_O = 1.257 \times \exp\left[-0.5\left(\frac{x + 0.3724}{0.6620}\right)^2\right]. \tag{4}$$

For angiosperms, $R^2 = 0.63$ and for gymnosperms $R^2 = 0.76$. While there is still unexplained variability in the data shown in Fig. 5, the relationships are surprisingly robust given the variety of methods, species, and environmental conditions inherent in each study. We applied these relationships to our measured sap-flux rates to determine whole-tree transpiration by dividing measured sapwood depths into discrete, 2-cm intervals, and applying Eqs. 3 or 4 to each interval (Table 4). The

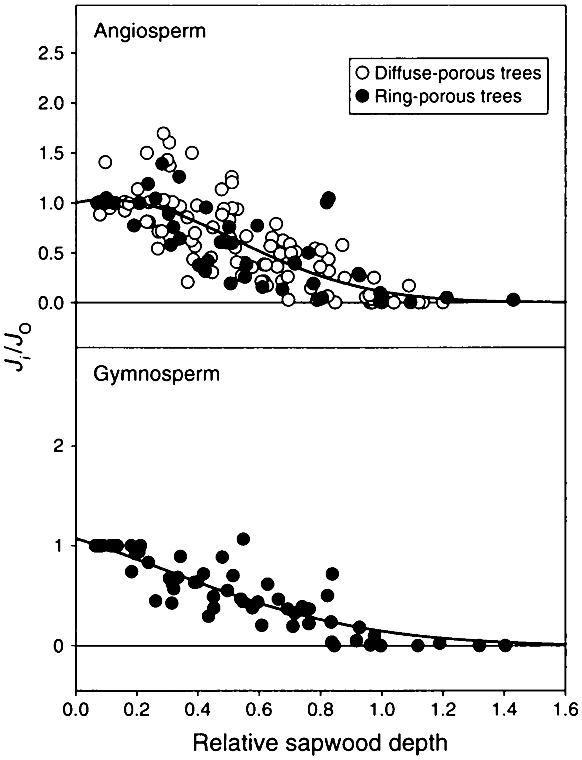

FIG. 5. The ratio of sap flux at the actual to the outermost sapwood depth (J_i/J_O) vs. the relative sapwood depth based on previously published values. For angiosperms, data are from Cohen et al. (2008; *Eucalyptus camaldulensis*, *Quercus calliprinos*, *Q. ithaburensis*, *Q. rotundifolia*, *Malus domestica*, *Citrus sinensis*, *Persea americana*); Gebauer et al. (2008; *Fagus sylvatica*, *Carpinus betulus*, *Acer psuedoplatanus*, *A. campestre*, *Fraxinus excelsior*, *Tilia cordata*, *T. platyphyllos*); Kubota et al. (2005; *Fagus crenata*); Lu et al. (2000, *Mangifera indica*); Nadezhdina et al. (2002, *Prunus serotina*, *Populus canescens*, *Rhododendron ponticum*); Oishi et al. (2008; *Liriodendron tulipifera*, *Liquidambar styraciflua*, *Quercus alba*, *Q. michauxii*, *Q. phellos*); Poyatos et al. (2007, *Quercus pubescens*); Schäfer et al. (2000, *Fagus sylvatica*); Wullschleger and King (2000; *Liriodendron tulipfera*); and Wullschleger and Norby (2001; *Liquidambar styraciflua*). For gymnosperms, data are from Cohen et al. (2008; *Cupressus sempervirens*, *Pinus halapensis*); Delzon et al. (2004; *Pinus pinaster*); Domec et al. (2005; *Psuedotsuga menziesii*); Fiora and Cescatti (2006; *Picea abies*); Ford et al. (2004*a*; *Pinus taeda*); Irvine et al. (2004; *Pinus ponderosa*); and Nadezhdina et al. (2002, *Pinus sylvestris*).

uncertainty of the estimates was derived with Eq. 2, where σ_R was 0.2583 for angiosperms and 0.1714 for gymnosperms.

J_S (sap-flux density across the active sapwood) and E_T (tree transpiration) estimated with this method are shown in Table 4. Error estimates were relatively large as a proportion of J_S and E_T for species with low fluxes; in fact, values for *Malosma laurina* were not distinguishable from zero. The highest J_S was found in *Lagerstroemia indica* while the highest E_T was found in *Platanus hybrida*. Within species the tree size explained some of the variability in sap flux only in some species and sites: *Platanus racemosa* at the Campus site (P = 0.042, R^2 = 0.80), *Ulmus parvifolia* at the Police Academy (P = 0.010, R^2 = 0.84), *Lagerstroemia indica* at the Arboretum SA site (P = 0.043, R^2 = 0.38), and *Koelreuteria paniculata* at the Arboretum SA site (P = 0.008, R^2 = 0.86). There was a marginally significant relationship between tree size and sap flux in *Brachychiton discolor* at the Arboretum A site (P = 0.057, R^2 = 0.32).

Calculated E_C (canopy transpiration) is shown in Fig. 6. In 2007, the Street Tree site showed the highest E_C, with values exceeding 2 mm/d (Fig. 6). If only pervious surfaces are included in the determination of plot area for this site, EC would be more than 4 times higher, with values exceeding 9 mm/d. *Platanus hybrida* was a larger contributor to E_C than *P. racemosa*, due both to higher sap-flux rates (Fig. 2) and greater tree size and number in *P. hybrida* (Table 2). At the Zoo, irrigated *Jacaranda mimosifolia* contributed the majority of E_C (Fig. 6). In 2008, E_C was highest at the Police Academy, with values of 0.5–1.0 mm/d (Fig. 6). *Ulmus parvifolia* and *Pinus canariensis* constituted the majority of E_C, with very small contributions from *Sequoia sempervirens* (Fig. 6). There were relatively equal contributions to E_C by species at the Arboretum sites (Fig. 6).

Because E_C is highly affected by the density of these artificially planted trees within their designated plot areas, we utilized our estimates of whole-tree transpiration to derive E_C by species for a range of tree densities. We restricted our analysis to the tree sizes we measured in our study, which were generally representative of the mature tree size of these species in horticultural settings. To account for site differences in D, we utilized the significant linear relationships (Fig. 7) between E_C and mean daytime D to calculate E_C at 1 kPa of D. We grouped the results into ranges of similar transpiration rates by species for clarity, using the average transpiration rates measured in August of 2007 and 2008 (Fig. 8). The results show the high sensitivity of E_C to species, even among well-irrigated trees. At these sites, E_C may vary by approximately an order of magnitude for different species for a given planting density and set of environmental conditions.

DISCUSSION

We determined both the magnitude of urban-forest transpiration as well as the role of species composition for this set of six study sites in the Los Angeles metropolitan area (California, USA). While there is clearly a high degree of geographic, management, socioeconomic, and biotic spatial heterogeneity in urban ecosystems, and these results cannot therefore be directly scaled to the whole region, they are informative for providing initial estimates of urban-forest canopy transpiration (E_C) and for determining the major factors underlying the estimated variability.

Species differences in sap flux.—We found large species differences in measured sap-flux density in the outer 2 cm of sapwood (J_O; Figs. 2–4). Some of this variability was related to environmental variables,

TABLE 4. Sap flow in the outer 2 cm of sapwood (J_O) and whole-tree water use across total sapwood depth, expressed both as total sap flux per unit sapwood area (J_S) and as water use per tree (E_T).

Tree species	J_O (g·cm^{-2}·d^{-1})	J_S (g·cm^{-2}·d^{-1})	E_T (kg·tree^{-1}·d^{-1})
Malosma laurina, unirrigated	9.4 ± 8.1	7.5 ± 10.9	0.8 ± 1.2
Pinus canariensis, unirrigated	4.2 ± 2.8	2.8 ± 2.0	3.2 ± 2.3
Jacaranda mimosifolia	70.3 ± 17.4	56.5 ± 24.7	8.8 ± 3.9
Brachychiton populneus	56.3 ± 16.0	42.3 ± 34.8	12.7 ± 10.4
Sequoia sempervirens	52.0 ± 9.9	35.5 ± 13.8	12.7 ± 4.9
Brachychiton discolor	59.2 ± 10.1	43.2 ± 23.0	18.9 ± 10.1
Eucalyptus grandis	97.2 ± 37.4	65.9 ± 46.6	42.9 ± 30.3
Lagerstroemia indica	240.5 ± 26.2	192.7 ± 48.6	45.3 ± 11.4
Platanus racemosa, campus	77.4 ± 24.9	50.0 ± 22.0	47.4 ± 20.8
Pinus canariensis, LAPD	37.9 ± 15.6	24.1 ± 13.3	49.1 ± 27.0
Koelreuteria paniculata	187.6 ± 49.7	115.5 ± 30.3	50.8 ± 13.3
Ulmus parvifolia	137.0 ± 24.8	110.7 ± 25.8	67.7 ± 15.8
Pinus canariensis, campus	70.3 ± 8.6	44.0 ± 6.5	73.7 ± 10.8
Ficus microcarpa	146.9 ± 20.6	119.1 ± 20.4	89.9 ± 15.4
Gleditsia triacanthos	209.1 ± 33.8	136.6 ± 35.8	89.9 ± 23.6
Jacaranda chelonia	185.3 ± 52.3	156.6 ± 27.2	99.2 ± 17.2
Platanus racemosa, street	184.0 ± 23.5	118.5 ± 36.3	102.6 ± 31.4
Platanus hybrida, street	298.6 ± 91.6	168.4 ± 71.6	176.9 ± 75.2

Notes: Values are ordered by the magnitude of E_T. Values ± SE are given for J_O, while table entries for J_S and E_T are values ± the error term derived from Eq. 2 in the text, accounting for both uncertainty in J_S and in the radial trend of sap flux.

particularly soil moisture, as *Pinus canariensis* and *Malosma laurina* at the Los Angeles Zoo were unirrigated. McCarthy and Pataki (2010) described the mechanisms underlying spatial and temporal variability in sap flux rates within species at the Zoo, Campus, and Street Tree sites. Differences in soil moisture between irrigated and unirrigated trees were very important in explaining spatial variability in that study, although among irrigated sites, soils remained near saturation for most periods and did not strongly influence transpiration rates. In addition, temporal variability in sap flux was largely related to fluctuations in daily vapor-pressure deficit (D) and photosynthetically acrive radiation (I_O) over time.

Across all irrigated species, there was no relationship between dbh and sap flux ($P = 0.589$), which is contrary to Meinzer et al. (2001, 2005). Meinzer et al. (2001) found that tree size explained most of the variation in sap flux of tropical trees in Panama. Meinzer et al. (2005) extended this work to species in temperate ecosystems and found that some scaling rules still applied, but that species fell into distinct categories, particularly for angiosperms vs. gymnosperms. We found a marginally significant relationship between dbh and sap flux in angiosperms in our study ($P = 0.10$). The trees measured in our study were considerably smaller than those measured in Meinzer et al. (2005), which included trees with diameters >1 m. Relationships between tree size and sap flux are difficult to discern without a very large range of tree sizes, which are somewhat unusual in urban settings.

We suggest that species differences in this study, which remain after accounting for variability in environmental conditions and tree size, may be related to their origin, as we measured a wide variety of tropical and temperate species from many regions. Essentially, these species were grown in a "common garden" setting with fairly similar environmental conditions. Among the irrigated trees, the highest tree transpiration (E_T) was generally found in riparian and tropical species, while the lowest was found in Australian species (*Eucalyptus* and *Brachychiton*), as well as *Sequoia sempervirens*, and *Jacaranda mimosifolia* (Table 4). Because trees differed in size and sapwood allocation, species differences in sap-flux density across the active sapwood (J_S) were not well correlated with E_T. While *Lagerstroemia indica* showed the highest J_S, it is a small tree at maturity and therefore was not associated with the highest E_T. *Platanus hybrida* street trees showed the highest E_T due to a combination of high J_S, large size, and deep sapwood, albeit with a relatively high degree of error that was associated with interspecific variability in J_O (Table 4).

In general, there are still insufficient data for common horticultural species to determine whether there are systematic differences between water relations of urban and natural forests. Whole-tree water use of *Eucalyptus grandis* has been measured previously, but generally in very young plantation trees (Dye 1996, Kalma et al. 1998). *Sequoia sempervirens* has been reported to have very low rates of sap flux in its natural habitat, which is very foggy, necessitating the use of alternative measurement methods suitable for low flow rates (Burgess and Dawson 2004). In the higher D environment of the Los Angeles Basin, we were able to successfully use constant-heat sap-flux sensors, although the measured rates of J_S were among the lowest of all sampled species (Table 4). Given the relatively large error in measuring J_S in species with low flow rates (Table 4), alternative measurement methods such as the heat-ratio method

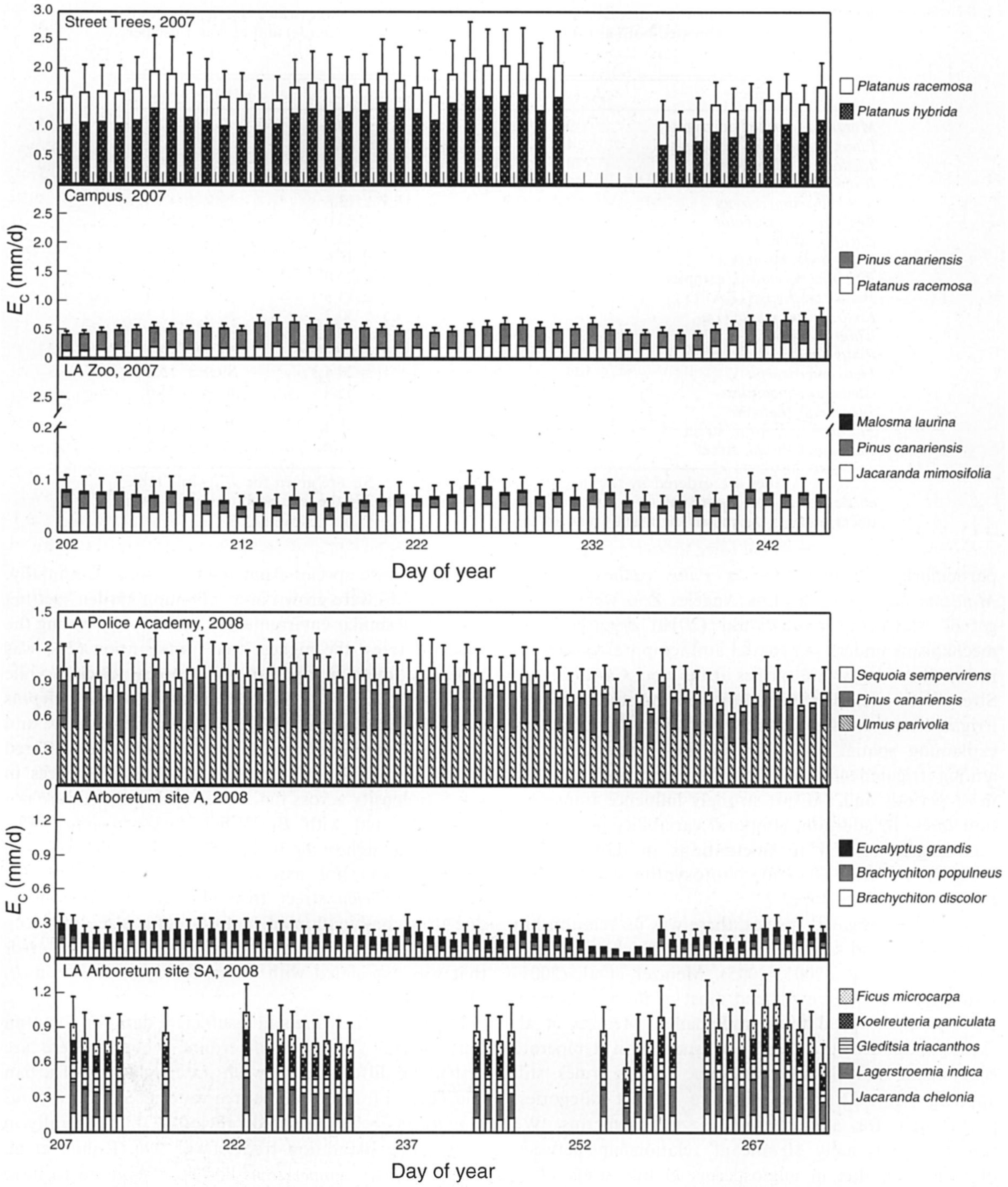

FIG. 6. Plot-level canopy transpiration (E_C) for all sites. Some missing data are shown for the Street Tree site. Error bars show the standard deviation using the error propogration calcuation shown in the text (see Eq. 2 and following). Note the difference in scale between the sites measured in 2007 vs. 2008.

would be advisable for these species. Bush et al. (2008) measured J_O in *Gleditsia triacanthos* in an urban setting in Salt Lake City (Utah, USA) and reported mean rates of about 150 $g \cdot cm^{-2} \cdot d^{-1}$. Our measured rates for *G. triacanthos* had a range of 84–312 $g \cdot cm^{-2} \cdot d^{-1}$. Our study trees were much larger, with a mean dbh of 45.2 cm compared to 21.4 cm. McCarthy and Pataki (2010) compared sap flux of *Platanus racemosa* at the Street Tree and Campus sites to measurements in a natural riparian forest, and found that the two urban sites

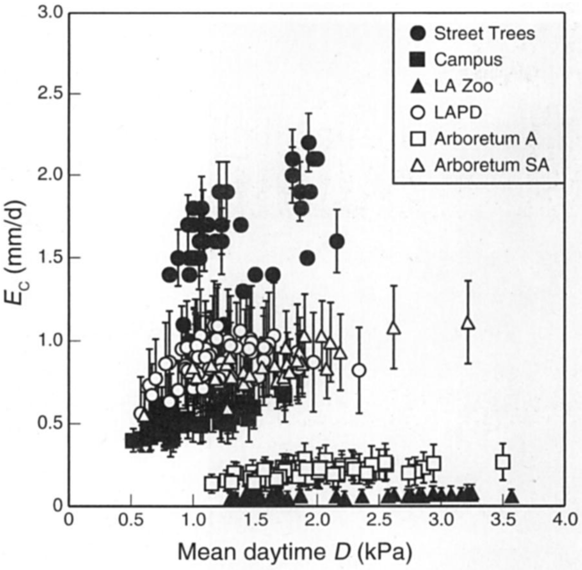

FIG. 7. Plot-level canopy transpiration (E_C) as a function of mean daytime vapor pressure deficit (D) at six study sites. Error bars show the standard deviation using the error propogation calcuation shown in the text (see Eq. 2 and following).

showed higher sap-flux rates than the natural site. They speculated that the lower flux rates in the natural settings were due to water stress, and the very high flux rates of the street trees were due to high nutrient availability in the Street Tree soil.

Radial trends in sap flux.—We found a surprisingly consistent relationship between relative sapwood depth and the ratio of sap-flux density between the outer 2 cm of sapwood and all the active sapwood (J_O:J_i) across species (Fig. 5). It is particularly surprising that the trends were consistent between ring- and diffuse-porous species, as it has been commonly assumed that ring porous species in particular show a pronounced radial trend (Granier et al. 1994, Swanson 1994, Clearwater et al. 1999). However, our results do not support differences by wood anatomy (Fig. 5). It is possible that differences between ring- and diffuse-porous trees would be more apparent if many measurements were available at a finer spatial resolution than 1 cm; however, this is not the case. Two measurement points within the first centimeter of sapwood were reported only by Nadezhdina et al. (2002) and Wullschleger and Norby (2001). In both cases maximum sap flux did not occur in the outermost sapwood, and averaging the measurements to 1-cm increments appears reasonable to capture the radial trend.

Nevertheless, there is clearly still variability in the relationships shown in Fig. 5, which we attempted to account for by propagating the error of the model fit into our estimates. In addition, this should introduce a random error into our estimates, rather than the systematic overestimate that results from assuming constant sap-flux rates across the entire sapwood depth (Nadezhdina et al. 2002, Delzon et al. 2004, Ford et al. 2004*b*, Fiora and Cescatti 2006). Ideally, radial trends should be measured directly for each site and study species, either with multiple sensors or with a single point containing multiple measurement points (Nadezhdina et al. 2002, Nadezhdina et al. 2007). However, where measurements must be minimally invasive, the relationships shown in Fig. 5 and reported in Eqs. 3 and 4 may be useful for constraining estimates of whole-tree water use.

Plot-level transpiration.—Our estimates of E_C varied among sites due to differences in tree size and density as well as species composition (Fig. 6). For the same D, the highest E_C was found at the Street Tree site, while the LA Zoo and Arboretum A sites showed very low E_C (Fig. 7). The Police Academy site actually had the highest tree density (237 trees/ha) and basal area (Table 2), but this was offset by the fact that much of the basal area was attributable to *Sequoia sempervirens*, which

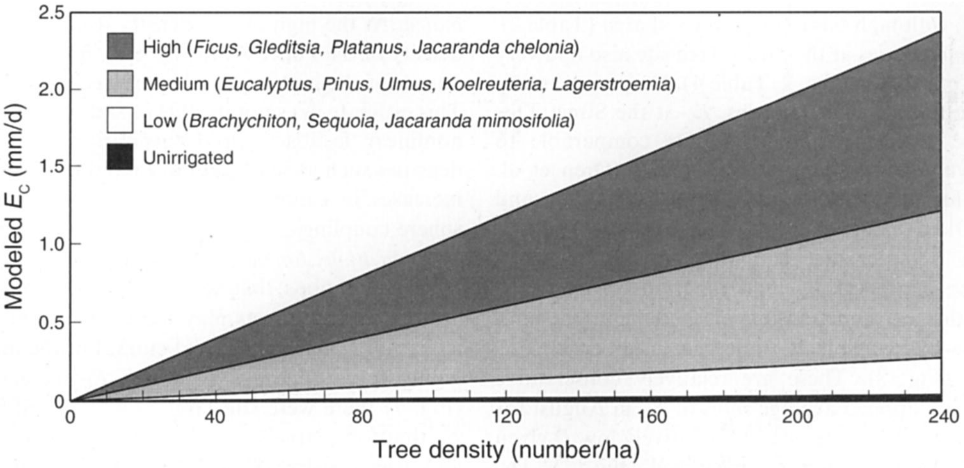

FIG. 8. Plot-level canopy transpiration (E_C) modeled as a function of tree density at a mean daytime vapor pressure deficit of 1 kPa.

PLATE 1. H. R. McCarthy installing sap flow sensors in street trees in Los Angeles, California, USA. Photo credit: D. E. Pataki.

had very low fluxes (Fig. 3, Table 4). The Street Tree site had a fairly low tree density (110 trees/ha) but the trees were large, with high basal and sapwood area (Table 2). The *Platanus* species at the Street Tree site also had very high rates of sap flux (Fig. 2, Table 4). Despite the semiarid environment in Los Angeles, E_C at the Street Tree and Police Academy sites was quite comparable to reported values for mesic natural forests (Oren et al. 1998, Granier et al. 2000, Pataki et al. 2000, Oren and Pataki 2001, Ewers et al. 2002, Barbour et al. 2005).

Because tree densities can vary greatly in urban settings, we expressed E_C as a function of density in scenarios that extrapolated our measurements to simulated single-species plots at a reference mean daytime D of 1 kPa (Fig. 8). These are relatively conservative estimates that applied average rates of E_T in August for groups of species by category at a relatively low D given the range of values that we measured (Fig. 7). The results consider tree density regardless of size; that is, basal area and total sapwood area vary for each species, as some trees are quite small at maturity in horticultural settings, such as *Malosma laurina* and *Lagerstroemia indica*. At the highest tree density scenario (equal to the density of the Police Academy site), modeled E_C was 2.4 mm/d for the highest category of tree water use (Fig. 8). This estimate does not include mixed-species canopies or nonlinear feedbacks to transpiration at high canopy densities such as self-shading, altered tree allometry, and increases in canopy D due to reduced canopy–atmosphere coupling.

Implications for management and policy.— The two main conclusions that we have drawn from this study are that urban forests may use a significant amount of irrigation water in semi-arid cities, but the magnitude is highly species specific. Although E_C increased with D (Fig. 7) there were still large plot-to-plot differences in E_C that were largely attributable to species composition and tree density (Figs. 7 and 8). Fortunately, both species composition and tree density are chosen by landowners and managers, and can be changed in response to water conservation and other criteria. To do this, direct measurements are critical. For many species, our measurements are the first data reported in any ecosystem. Even for species that have been measured previously, urban settings differ greatly within and across cities, and between urban and natural ecosystems. Hence it is difficult to ascertain species-specific transpiration rates without direct measurements under typical urban conditions. Our results do not necessarily support assumptions about tree water use based on anecdotal evidence or transpiration rates in natural ecosystems. For example, *Eucalyptus grandis* was previously a very commonly used landscape species in southern California, but its use has greatly declined, in part because of assumptions about its high water use. However, we found that despite their large size, *E. grandis* and the two species of *Brachychiton* actually showed relatively low whole-tree water use due to a combination of low sap-flux rates and shallow sapwood depths (Table 4). In contrast, the *Platanus* species, including the California native *P. racemosa*, which is currently very widely planted, showed high rates of water use and subsequently high E_C (Table 4, Figs. 6 and 8). Other species with low E_T had higher sap-flux rates but were relatively small trees, such as *Jacaranda mimosifolia* and *Lagerstroemia indica*. The latter species showed the highest J_S that we measured (Table 4). Not surprisingly, the unirrigated trees, which included the native California shrubland species *Malosma laurina*, showed very low J_S and E_T (Table 4), which translated to E_C that was an order of magnitude lower than the high transpiration species (Fig. 8).

Many cities are currently implementing large-scale tree-planting campaigns to improve aesthetics and mitigate environmental problems such as greenhouse gas emissions and pollution (Pataki et al. 2010, Pincetl 2010). In semi-arid cities, these programs may have a substantial water cost unless species and planting sites are chosen carefully. Consider the addition of one million new trees to the urban forest, which has been proposed as a target in Los Angeles, New York, and other American cities. Our results suggest that in Los Angeles (and cities with similar climates), selecting high water-use species such as *Platanus* spp., *Ficus microcarpa*, or *Gleditsia triacanthos* would utilize approximately 112 million L/d, or 30 million gallons of water per day during the month of August. This would constitute about 5% of the total daily municipal water use (according to the Los Angeles Department of Water and Power, per capita water use is 144 gallons per day for a population of 3.8 million persons). Therefore, it is possible that large-scale tree planting could further stress an urban water system that is already struggling to find effective methods for water conservation due to persistent water limitation, drought, and climate change. However, because urban-tree water sources are very poorly constrained, the amount of additional irrigation required to support additional trees is unknown: depending on their location, trees may be accessing groundwater, surplus irrigation runoff due to inefficient water application over large spatial scales, or even leaking water pipes. Detailed studies of the complete water budget of these landscapes are needed to assess tree water sources, the efficiency of current irrigation regimes, and the optimal combination of species composition, water application, and irrigation method. In general, it will be very difficult to make informed decisions about urban water management without an increased emphasis on measurement and modeling studies of urban ecohydrology that include explicit ecophysiological information for horticultural species in real urban settings. With a sufficient data set, it is feasible to make reasonable projections for urban forest E_T and E_C for future urban planning, landscape design, and urban water management.

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